THE DEVELOPMENT OF SPRUCE FOREST ON RAW HUMUS SITES IN NORTHERN FINLAND AND ITS ECOLOGY

BY

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Foreword

In the spring of 1949 the then acting Director-in-Chief of the Forest Service, Professor V. K. Lihtonen, today Professor of the Science of Forest Mensuration at Helsinki University, asked me whether I would be willing to undertake the study of certain silvicultural problems of North Finland, particularly an investigation of the thick-moss type, considered problematic for many years, and its treatment. In natural conditions, the annual increment on this forest site type has generally been found surprisingly small. On the other hand, artificial regeneration, e.g. as carried out by Professor Olli Heikinheimo, on sites formerly of thick-moss type seems to have led to surprisingly good results so far. Hence the standard conception of the real character of the thick-moss type has begun to be questioned. Just what the thick-moss type is and, as far as possible, what factors govern its formation and changes required study. With great misgivings I accepted the task, realizing it would assume proportions beyond the capacity of any one man.

As a result of an inquiry in summer 1949 I was able to tackle the study of mensurational problems the following year. The necessary material was collected in 1950—1952. After the pilot investigation of 1950 it was possible to formulate a programme for the separate studies of the ecological aspects of the problem. In the main this programme was carried out in the summer of 1951, supplemented to some extent in the following growing seasons.

Obviously, a comprehensive and difficult investigation can hardly be undertaken without considerable assistance.

I wish to extend my respectful thanks to Helsinki University, to the State Board of Natural Sciences, to the Swedish Scientific Central Council, to the Forest Service for the grants I have received, and above all to the Foundation for the Research of Natural Resources in Finland which in the last two years has alone borne the brunt of financing my research work. The chairman of the Foundation, Professor N. A. Osara, Director General of the Forest Service, has played a very prominent part in organizing the financing. To Professor Yrjö Ilvessalo, Member of the Academy of Finland, who has supported my applications for grants, I also wish to express my reverential gratitude.

Up to 1954, I worked during the winter as assistant at Helsinki University Institute for Silviculture and had the opportunity of using continuously the laboratory and equipment of the Institute. In many other ways, too, I have received support from my chief, Professor Erkki Laitakari, to whom I am greatly indebted.

My sincere thanks also go to Professor Erik Lönnroth, former Rector of Helsinki University, for all the help he has given me over the years.

Right from the outset the Forest Service has supplied both funds and auxiliary labour for different tasks. My especial thanks are due to Professor V. K. Lihtonen for his contribution in the early stages of my work, and above all for his patience and moral support as the work assumed drawn-out proportions. Director-in-Chief M. Lappi-Seppälä and V. K. Ahola, Supervisor of Silviculture have also adopted a favourable attitude to my work and contributed to it in many ways. I wish to express my deep gratitude to them.

The assistance provided me by the Forest Service District Office of Perä-Pohjola and by the foresters of the supervisory areas has been of special value. I attach very great importance to the support the former venerable Chief of the District, Mr Yrjö Pöyhönen, has given me in a most varied range of matters.

The Forest Research Institute has also given me valuable help. Professor V. T. Aaltonen kindly lent me some instruments difficult to obtain and permitted me to have soil analyses made at the Soil Research Department. When my work was in the manuscript stage Professor Aaltonen attracted my attention to many shortcomings, for which I am very grateful. The Departments for Silviculture and Experimental Areas have also afforded remarkable assistance in permitting me to establish a number of sample plots in the experimental areas of Kivalo and Kaihua. I owe an especial debt of gratitude to District Forester Väinö Sandström who has followed my work with interest.

I have had opportunities of discussing the methods of studying stand climate with Professors J. Keränen and M. Franssila. The latter made valuable comments after perusing the forest-meteorological sections of the manuscript. I wish to express my sincere thanks.

I am also very grateful to Professor Jouko Vuorinen, Chief of the Agricultural Research Centre Department for Soil Science, for the help he has given me.

In the finishing stages of my work, I have received ready advice from Professor Olli Heikinheimo, Professor Yrjö Ilvessalo, Member of the Academy of Finland, Dr Erkki K. Kalela and Dr Kullervo Kuusela. To them goes my deep gratitude for the valuable advice received.

Foresters Aaro Karjalainen, Leo Hellgren, Hanno Kantele, Lauri Kärki, Matti Valtonen, Jarl Länsinotko and Teuvo Hinttala have assisted me at different times in the collection of the material and partly in its treatment. Their work, carried out in difficult conditions, made it possible to realize the investigation programme as planned. I wish to thank them all for this help and for their cheerful co-operation.

In the treatment of the material I have been assisted also by agrologist A. V. Krogell and Miss Tellervo Pesonen. The chemical analyses were made by Mr:s. O. Halonen, H. Tulkki and U. Koivuniemi. The illustrations were touched up by Mr. P. Haataja, and the bibliography was checked by Mr. Eino Oinonen, Master of Agriculture and Forestry, and Mr. Aake Kaarnama, Forester. I wish to express my cordial thanks to all of them.

I am also greatly indebted to the hospitable and friendly inhabitants of the Lapland wilderness and to all the others who in one way or another have given their help.

The publication was translated into English by Mrs. Hilkka Kontiopää, M.A. (Helsinki) and Mr. L. A. Keyworth, M.A. (Cantab). I wish to thank them for good work.

I also wish to express my delight over the fact that the Society of Forestry in Finland has accepted my investigation for publication in their series.

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Gustaf Sirén

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I. THE DEVELOPMENT OF SPRUCE FOREST ON RAW HUMUS SITES

Introduction

The forest resources of North Finland, in recent years in particular, have been the subject of a lively exchange of opinions. The report of the Industrialization Committee (1951) gave the start proper to public discussion. The problem in its entirety was soon the subject of consideration by the various economic and political bodies whose interests were involved. However, the discussion was confined primarily to special questions of national economy and little attention was devoted to the primary fundamental prerequisite of the whole industrialization project, the forest resources of North Finland and, particularly, their continued sufficient availability. Problems of power supply and timber marketing displaced the raw material problem. In forestry circles only was the necessity of an undelayed realization of northern growing stock capital emphasized. This attitude has its special, weighty reasons.

From the National Forest Surveys effected under Ilvessalo it is known that the age class distribution of the forests of North Finland presupposes heavy cuttings in over-aged forests in order to correct in the near future, at least to some extent, the very perceptible shortage of young forests and to ensure the necessary continuity of forestry. However, the abundance of old forests is not in itself a serious disadvantage; the really decisive point is that considerable quantities of large-sized timber material dry up standing and fall down annually. This phenomenon, highly serious from the forestry view point, termed natural removal, is illustrated indicatively, though not absolutely accurately, by the national forest surveys: in 1937 the growing stock volume was smaller by approx. 30 million cu.m than that of 1922 (Ilvessalo 1942, p. 104), although the quantity of timber utilized in various ways in the 15-year period of 1922—1937 was smaller than the growth in the same period.

Provided no inaccuracy is involved in the survey method — the error would in any case be exceedingly small expressed percentually — the said wasted timber quantity can probably be referred to natural removal. It may be pointed out for the sake of comparison that Ilvessalo (1942, p. 117) assessed the quantity of dry standing timber in North Finland at approx. 40 million cu.m in 1936—38.

The above raw material losses are perhaps no great cause of worry to the layman; natural removal is believed to be replaced by natural regeneration. But this normal advantage of forestry over the exploiting trades is no self-evident phenomenon, realized everywhere without difficulty. As early as some 30 years ago Heikinheimo published an investigation showing that the natural regeneration of northern spruce forests was of no practical significance. Productive forest lands occupied by such old spruce forests probably still total nearly 1.0 million ha[1] in the northern part of Finland. Natural removal in them is high but no regeneration acceptable from the forestry point of view is observable. The result is the progressive low productiveness of extensive forest areas.

The old forests, expressly the spruce forests of North Finland, still of relatively great growing stock at the moment in view of the circumstances, thus suffer quite heavy removal of large-sized matured trees at present. Simultaneously, their natural regeneration, normally replacing the removal, seems totally inadequate. The economic loss resulting from these natural occurrences can be estimated at milliards of marks.

Due to the fact that the vast majority of northern forests is still controlled by the state, the Finnish Forest Service, on the eve, as it seems, of the implementation of the industrialization project, has shown far-sighted interest in the special problems of northern forests. On the initiative of the Forest Service steps were taken once again in 1949 to investigate the problems of regeneration in these forests. The first task to be tackled was the study of the numerous and, judging from the earlier attempts, exceedingly difficult problems offered by the spruce forests. Primary importance was attached to the study of the low productiveness of spruce stands weak in growing stock on fresh forest land with a cover of raw humus, the so-called thick-moss or *Hylocomium-Myrtillus* type (HMT).

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[1] ha = hectares.

North Finnish spruce forests in the literature

In spite of the interest long taken in North Finnish spruce forests, few forest science investigations have dealt with them. Among the publications printed before the establishment of the Forest Research Institute are only a few studies, confined primarily to botanical and general questions, concerned with these forests. A. G. Blomqvist is probably the first forest scientist to have devoted attention to the special features of the northern spruce forests in his attempt to work out growth tables (1872, 1879) for North Finland. In his book »Granen» (The Spruce), based to a certain extent on observations made during his 1868 trip into North Finland, he deals with the spruce forests there (1883). Wainio (1878), gives a description, surprisingly accurate considering the then investigation methods, of the vegetation of the northern and eastern spruce forests. The same subject is touched upon by Hult (1881) in his attempt to create an analytic basis for the study of the internal structure of plant associations (see also Hult 1886, 1898).

The next prominent study connected with these subjects did not appear until 1916, when A. K. Cajander published his supplemented forest site type system which covered the North Finnish spruce forests also. A striking feature is a slight indefiniteness regarding the so-called thick-moss type, HMT; the hesitation is reflected e.g. in a subsequent statement of the following wording (in translation): »Distinguishing thick-moss forests on firm land from *Myrtillus* type forests requires a very accurate eye» (Cajander 1917 b, p. 310). Later on, discussing the influence of tree species on the physiognomy of the forest site type, Cajander is more accurate in his definition of this forest site type, reminiscent of the *Myrtillus* type but of fairly low productiveness: »It seems quite probable that the North Finnish thick-moss type actually is a result of the deterioration of forest land caused by spruce forest in certain climatic conditions; many facts actually point in that direction» (1949, p. 55). It may be added that Cajander advanced similar ideas on this point at a very early stage (Cajander 1917 a, pp. 201—202, Cajander &

Ilvessalo 1921, pp. 16—17 and Rubner 1927, pp. 239—240). It is also possible that Cajander's critical attitude was inspired by the investigations of Airaksinen in 1914 and 1915 into the vegetation and development of the spruce forests of Kuolajärvi (Salla). These investigations distinctly show the close relationship between the vegetation and the tree stand, and Airaksinen suggests that forest site types can only be determined after the universal rules governing the vegetation changes are known (1919, p. 344). Tree stand and vegetation also interested Lakari (1920 a and b). His two investigations deal with the North Finnish forest site types and the growth conditions of spruce and pine. One of them describes e.g. the vegetation on HMT, the other shows that the growth of pine exceeds that of spruce on the thick-moss type.

Thanks to Heikinheimo's numerous investigations opinion on the northern spruce forests entered a new phase. Having first studied certain points connected with the development of spruce (1920 a), the occurrence of spruce forests (1920 b) and their susceptibility to snow damage (1920 c), and the forests of the forest limit (1921), he published an investigation into the birth, development and management of North Finnish spruce forests (1922).

In outlining the background to his investigation Heikinheimo concludes, both from his own observations and from special investigations carried out by others, that northern spruce forests result from the special characteristics of the climate in North Finland and from their indirect consequences which he considers to account expressly for the origination of HMT. On the other hand, it is emphasized that the data from meteorological observations in North Finland do not concur with the conditions typical of spruce forest areas which, for the most part, are situated in relatively high, wooded fell region and permit considerable local climatic variations. For instance, the maritime character of the fell climate is most typically seen on the northern slopes which, as a result, are generally occupied by thick-moss type spruce stands (cf. Lakari 1920a, p. 50). The growing season, in addition, both observed and according to local popular belief, is found to be longer in wooded fell regions than expected.

Heikinheimo devotes attention to the soil also. HMT spruce stands are generally found to occur on moraine gravel soils situated above the post-glacial marine line, though there are exceptions; e.g. sample plots from sandy and silty soils are reported. The soils generally found consist of strongly leached iron podzol in which pan formation in the B-horizon is sometimes distinctly observable. HMT soil is generally fresh, often even slightly paludified (this applies particularly to sub-type PHMT)[1]. From part investigations into the nutrient content of the soil it appears that almost all soil layers of HMT contain less lime and phosphorus than the corresponding soil layers on *Vaccinium* type (VT), a site quality class considered highly superior to HMT. On the other hand, the latter contains considerably more nitrogen than VT. However, Heikinheimo attaches no great value to this fact as he feels that the amount of total nitrogen does not give a correct picture of the quantity of assimilative nitrogen.

In his efforts to find other causes for the poor productiveness of HMT forests Heikinheimo presumes that the local climate cannot constitute the minimum factor accounting for the poor growth of spruce forests. Improvement in the growth of forests by thorough soil preparation (clearing and burning-over) and forest fires would not be possible if its causes were only climatic.

In his study of factors connected with the origin of spruce forests Heikinheimo also states that the regeneration of northern spruce forests is highly inadequate, above all due to lack of seed[2] and the poor germination bed that the moss layer makes. The few spruce seedlings, primarily on decomposed fallen trees and in the hollows left by uprooted trees, are not numerous enough to form a closed seedling stand. Seedlings of other species occur only scantily in sparse old spruce stands.

Heikinheimo points out that in contrast to the stunted and relatively sparse seedling stand of spruce forests, birch and pine seedling stands of good growth occur in forests that have experienced fires or controlled burning. However, he reports having encountered in many places spruce seedlings of luxuriant growth developed after the forest fire or controlled burning (op.c. pp. 51—52). In spite of this he persists in his doubt that spruce can thrive on newly burnt lands (cf. Heikinheimo 1915). This doubt looks like exaggerated caution in the face of both examples and certain facts published in tabular form (Heikinheimo 1922, table 10, p. 56). Another valuable result of the investigation is the table (op.c. p. 60) showing that of all the forest lands of North Finland the fresh forest lands on HMT, referred to a poor site quality class because

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[1] PHMT = *Polytrichum-Hylocomium-Myrtillus* type.

[2] Heikinheimo repeatedly confirms his observation of the insufficient availability of seed (cf. Heikinheimo 1932, 1937 and 1948).

of their tree growth, are the soils generally preferred for burning-over for crops. The reason for the extensive burning-over practised in early times is probably solely the production of a good cereal crop (cf. Heikinheimo 1915). It may also be added that he found the burning effecting a considerable increase in available nutrients (1917, p. 28).

The various regeneration cuttings involving spruce forests on HMT have not, according to Heikinheimo, produced the desired result. Following additional investigations he brings his idea to a head, as follows (in translation): »— — it is impossible to find a method of regeneration cutting that will ensure the regeneration of these forests without artificial measures.» (1939, p. 124). The same conclusion regarding the treatment of HMT spruce stands or similar forests has been arrived at by investigators in Sweden, Norway, Russia and Canada (cf. pp. 106—107).

The problem of the development of spruce forests was of quite special interest to Heikinheimo. Referring for example to Kujala's (1921) investigations into the formation of raw humus and its consequential phenomena, and to Auer's (1922) observations of the continuous deterioration of northern swamp types, Heikinheimo concludes that the transition of forest site types into new types, in typical spruce forest regions mostly presumably from *Myrtillus* type (MT) to a thick-moss type, must be considered the result of lengthy development over thousands of years and not, as is assumed by several scientists, especially Swedish, a change forward or backward during a few tens of years (Heikinheimo 1922, p. 68). The majority of forest site types (note the plural!) reached the thick-moss type stage centuries ago, even though forest fires and burning-over locally have temporarily interrupted the natural development. Some of Aaltonen's (1932) conclusions as to the influence of trees on soil properties support the idea of a very slow process of degeneration. It may however be remembered that spruce arrived in Lapland only some 3 000 years ago (Auer 1928).

In contrast to old HMT spruce stands that have already reached their state of equilibrium, Heikinheimo terms the plant associations on soils subjected to recent fires as young thick-moss types. To support his idea of the development of spruce stands Heikinheimo also refers to popular tradition, old control books and old place-names.

In the chapter dealing with the treatment of North Finnish forests Heikinheimo mentions the controversy over the biological properties of forests and the economic considerations affecting their treatment. He concludes that this is the principal reason for earlier failure to reach certainty as to the most advantageous silvicultural methods for these forests. Heikinheimo personally recommends the introduction of burning-over or controlled burning and artificial regeneration on HMT soils. The original proposal advanced by the forestry inspectors of North Finland in the early 1900's thus receives strong support for the first time from a representative of forest science (cf. also Herlin 1913, s. 23). Heikinheimo, however, evidently at the request of the then Forest Service, puts forward different alternatives based on the ability of small trees left on cutting to recover and the slight natural regeneration in spruce forests. He emphasizes that in spruce forests admixed with pine the significance of pine seed trees, especially on HMT, remains small unless the ground vegetation is throughly destroyed. As the most advantageous method of destruction he recommends burning, which should include scarifying the ground and especially the felt-like raw humus layer. This method ensures the most favourable result in both natural and artificial regeneration. It may be added that Heikinheimo was very successful in 1923—1932 in establishing a number of plantations by artificial regeneration methods after burning in Kivalo experimental area.

At the same time as Heikinheimo studied the silvicultural problems of spruce forests Kujala (1921) devoted attention to their vegetation; regionally the investigation was confined to the southern parts of North Finland. He finds from his material that the HMT present in Kuusamo differs from the South Finnish MT; he reports on the most prominent differences by plant species (op.c. p. 4). Great attention is focussed on vegetation developing after forest fires. The material collected reveals, although Kujala does not particularly emphasize this point, a surprising similarity to the vegetation on MT. Worthy of note in this connection is the conclusion that the forest site type returns to thick-moss type already during the first spruce generation after the fire (op.c. p. 8). In his special investigation into the effect of fires on the ground vegetation of North Finnish forests Kujala arrives at the conclusion, however, that even important fundamental characteristics of forest vegetation persist unchanged on burnt areas.

Both Heikinheimo and Kujala have found that the increased thickness of the moss layer and raw humus results in the advancing impoverishment of the composition of vegetation and in the disappearance especially of meso-eutrophic species. Kujala also shares Heikinheimo's opinion on the influence of tree species on ground vegetation

In an example (op.c. p. 9) he gives, the ground flora on thick-moss type is largely dependent on the tree species, i.e. spruce.

Furthermore, Kujala later on states clearly and unequivocally that HMT is but a northern parallel type to the South Finnish MT (1938, p. 4). This statement seems to be based upon parallel studies in both North and Central Finland (cf. Kujala 1936, pp. 32—34).

Ilvessalo's (1937) mensurational study of the development of the naturally normal forests of Peräpohjola (Far North) introduces many interesting facts connected with HMT. Above all it emerges that it was difficult to find suitable objects of study owing to the sparse nature of the northern spruce forests. Expressly young spruce stands were almost impossible to find. On this point Ilvessalo had the same experience as A. G. Blomqvist (1872) before him. Ilvessalo nevertheless managed to collect 23 sample plots in all, 15 from pure spruce stands and the balance from pure, fairly young birch stands. The only mention of the origin of the stands is that it varies. Ilvessalo considers his material limited.

The phytosociological similarity of HMT and MT has been stressed in several connections above. Nothing, however, evidences it so clearly as the plant lists made out by Ilvessalo. The minor differences in the coverage and frequency of species indicate rather that HMT is at least as fertile as MT. The only remarkable difference is in the frequency of mosses, and this may be accounted for by the great difference in the ages of the sample plot stands compared; the mean age of the HMT spruce stands studied is approx. 185 years, of the MT stands approx. 75 years only. As is known, the moss cover increases in thickness and density with the age of the forest (cf. e.g. Heikinheimo 1922, pp. 12—19, Kujala 1926a, and Hesselman 1937). Judged exclusively on the basis of differences in ground flora it seems difficult therefore to distinguish these forest site types, as has already been pointed out by Cajander when he defined this forest site type.

Ilvessalo's investigation (1937), however, concentrates on the mensurational characteristics of the northern forest site types. From a comparison of the growing stock volumes of the various forest site types Ilvessalo finds that spruce-growing HMT is one of the poorest. Only the barren and dry pine-growing ErClT, according to the curves presented, can be considered inferior to HMT in growth; this conclusion presupposes a cycle exceeding 200 years. However, the comparison, due to differing premises, must be considered somewhat inadequate since from Lakari's (1920b) investigations it may be assumed that HMT would give a higher yield growing pine than spruce. In his final survey Ilvessalo, in fact, suggests the replacement of spruce by pine. Birch stands on HMT are also studied; because of the limited material, however, most of the numerical data and conclusions are considered to be approximate. In this connection it may be emphasized that Ilvessalo's intention has been to establish growth tables of all kinds of natural and managed stands, but this large work has been retarded by national surveys and research work of greater importance.

Ilvessalo's special study of North Finnish forest site types is not the only one in which he discusses the problematic HMT forests. Many points illuminating the complex character of the northern spruce forests have also emerged in connection with the National Forest Surveys (Ilvessalo 1927, 1940, 1942).

The First National Forest Survey of 1922 puts the total area of HMT forest lands in North Finland at no less than 865 000 ha, i.e. approximately the same as in Heikinheimo's earlier calculations (1920 b). Fifteen years later no more than 718 000 ha of HMT forests were found. Where the rather great balance had disappeared cannot be seen from a glance at the tables, but some suspicion is inevitable on the score of the northern MT forests which show an increase in area in the same period of well over 0.5 million ha. The heads of the survey groups evidently have been unable to distinguish between the northern MT and HMT, very similar to one another especially in borderline cases.

All this does nothing to support the concept of HMT as a type of unambiguous character.

Among Ilvessalo's investigation results may be mentioned another interesting finding regarding the proportionate distribution of tree species in HMT forests. No other forest site type of fresh soils is occupied by a single species to the same extent as HMT: over 90 per cent of all HMT forests are either pure spruce stands or forests dominated by spruce (Ilvessalo 1933, p. 27, 1935, p. 199, and 1942, p. 281).

Pride of place as a special expert on North Finnish soils must go to Aaltonen. Among his numerous investigations reference is made in this connection only to those that in one way or another apply to the fresh site types of North Finland. Particularly the HMT soils and the strong podzolization occurring in this site type have been repeatedly treated by him (Aaltonen 1933, 1935, 1939, 1941c, 1948). He has also clarified the subject of the acidity of the fresh firm forest lands of North

Finland in connection with the other investigations. The properties and formation of humus have been illustrated in connection with nitrification and litter studies (1926, 1950). In addition, investigations into the biological competitiveness of spruce elicited certain new features of the ecological plasticity of this species (1920 a, b, 1936 a). The most important achievements of forest soil science up to 1940 and 1948 are collected in the extensive works of reference of those two years. Of special interest is his assumption that HMT is a result of the soil degeneration caused by spruce (cf. Aaltonen 1940, pp. 296, 474, 490) although he earlier supported the opinion of a very slow degeneration rate (cf. Aaltonen 1932, p. 54).

Sarvas suggests like Metsänheimo (1936 b) that the low soil temperature retards the decomposition of organic debris, with accumulation of raw humus and paludification as the result (1937, pp. 11—12). Later Sarvas (1938), discussing the vigour of artificially regenerated young stands on burned areas, emphasizes their poor growth compared with spontaneous seedling stands. In a literature study (1952) he pays attention to the ecology of the moss-lichen forests in North Finland and stresses the importance of the temperature as a limiting factor.

Teivainen (1952) concentrates his study of vegetation on fresh sites in North Finland to two limited areas outside the main HMT region. The vegetation at Pisavaara in southern Lapland has a lot of features common with the central part of Finland and the spruce stand vegetation at Pallastunturi is more boreal than the typical HMT. Like Cajander and Kujala he found only small differences between MT and HMT and consequently he suggests that the northern MT is to be considered only as a sub-form of HMT, mainly caused by climatic conditions (op.c. p. 133). Discussing the influence of the stand upon the vegetation and forest site type, Teivainen puts forth some examples of the similarities between EMT climax pine stands and HMT pine stands of different successional stages. But he proposes no way in which confusion might be avoided. Like Heikinheimo (1922), Kujala (1921, 1938) and the present author (1949, 1952) he emphasizes also the influence of spruce on the ground vegetation and the stand climate. A sub-type of HMT in the Kainuu district has been described by A. Kalela (1952).

North Finnish spruce forests have also been studied by Multamäki (1921) for statistics on forest site types, and Tikka (1932, 1934 1937, 1947) for investigations into injuries to trees occurring in spruce forests.

Saari (1923) has compiled statistics on forest fires in North Finland, subsequently supplemented by Ahola (1950). Lihtonen's (1951) publications on the forest resources of remote districts apply mainly to North Finnish forests and expressly to the spruce forests there.

The general nature of central North Finland has been comprehensively described in the investigations e.g. by Lakari (1920 a), Heikinheimo (1920 b) and Ilvessalo (1937). Supplementary to them in climatology are the special studies by Keränen (1920, 1943), Franssila (1945, 1949) and A. Sirén (1949), and in soil science those by Mikkola (1938, 1941) and Okko (1944) and, dealing with Lapland to some extent, by Aarnio (1938).

Many valuable indications of the effects of civilization on northern forests, e.g. of the first raids by the »lantalaiset», a term for the Finnish raiders from the South, of forest utilization by the Lapps and of the first Royal Decree on forest burning, are obtainable from Pohjankanervo's (1939) article on Lapland of bygone ages. The interesting, extensive compilation by Itkonen (1948) on Lapp civilization also supplies numerous hints on the forest utilization measures employed by the Lapps (see also Heikinheimo 1920 and Jutila 1925).

The treatment of HMT forests has naturally had a quite particular interest for practical forestry men. Discussion of the origin and properties of HMT spruce stands and of the silvicultural technique to be applied to them has in fact continued without interruption, especially since the 1930's. Contributions to this exchange of ideas have been published in periodicals e.g. by Kuosmanen (1915), Aaltonen (1917, 1936 b), Järvinen (1929, 1930), Metsänheimo (1929, 1936 a and b), Tikka (1932, 1937), Koponen (1934), Räsänen (1934, 1937), Heikinheimo (1935, 1947), Oksanen (1937, 1938), Kettunen (1937), Siitonen (1937, 1942), Sipi (1937, 1949), Ahola (1946, 1947, 1950), Paloheimo (1949), Sirén (1949, 1952), Lihtonen (1950, 1951), Eini (1951).

A great deal of literature connected in one way or another with HMT or similar plant associations has of course been published outside Finland. Particularly in northern Scandinavia and Russia, where this forest site type or its variants are abundant, the problems are indentical to ours. Among the investigations dealing with the same questions in these countries only some of the most recent will be mentioned.

In Sweden the literature on associations similar to HMT is tremendously large, as can easily be seen from some of the most recent works by Arnborg (1943), Malmström (1949) and Teikmanis (1954). The regeneration difficulties for instance have been thoroughly discussed by many authors (see p. 106). Of special interest to the present study are the ideas of forest dynamics put forward by Lundström. He suggests that forests must be classified into primary, secondary and degenerated stages (cf. Lundström 1902, pp. 205—206). In Norway Eide (1926 a) and Mork (1927) have paid great attention to similar problems of northern spruce forests. Also in Russia the thick-moss spruce forest is known as a problematic association. Particularly Regel (1935—1941) gives an extremely large review of the current literature, with many references from North Russia and Siberia. Like Regel, Seifriz (1934) also concentrates on the Kola Peninsula, where the *Picetum-Myrtillosum* proves to be an association similar to HMT. Noteworthy is also Sukatshev's assumption (1932, pp. 237—239) that the degeneration of spruce forests is caused by the heavy accumulation of raw humus which gives rise to a development ending in swamp stages. In the Canadian forest literature e.g. Raup (1946) and Moss (1953) deal with problems concerning associations of similar type (cf. also Ilvessalo 1929, Kujala 1945 and Hustich 1949). The circumpolar nature of the thick-moss covered and raw humus spruce forests is definitely stated by the fact that similar associations seem to occur in some climatic regions in Japan too that are favourable for humus accumulation (cf. Sakai 1931). The investigations in the countries mentioned will be referred to to some extent in connection with various part of this study.

Definition of the problem and object

The literature on North Finnish spruce forests and especially HMT spruce stands, briefly reviewed above, in many respects provides the foundation of the present study. Many earlier ideas and results, however, have become obsolete with changed conditions, and some others seem contradictory to the modern view. Several points of special interest are listed in the following.

The data on the extent (total area) of spruce forests vary within wide limits. As the recently completed Third National Line Survey of Forests will obviously supply in the near future a reliable idea of the present extent of the forests in question, this need hardly concern us here. Within the present-day frontiers the spruce forests probably occupy a total area of some 600 000 ha, the bulk of it apparently thick-moss type.

Many different views have been advanced regarding the value of HMT expressly as a spruce-growing habitat. The creator of the forest site type theory, A. K. Cajander, himself questioned the nature of HMT, and failed to define in detail whether it was the growing stock or the ground flora that he found abnormal for the habitat. Both Cajander and many others (cf. Heikinheimo 1922, Rubner 1927, Tertti 1939, etc.) consider the quality classification method based on forest site type theory poorly adaptable to this type.

Kujala, who has studied the Finnish forest site types most extensively and thoroughly, concludes (1938, p. 4), in brief, that HMT is the North Finnish parallel to the *Myrtillus* type (cf. also A. Kalela 1949, s. 71). The fairly divergent descriptions of ground flora given by different authors (cf. Wainio, Lakari, Heikinheimo, Ilvessalo, Kujala, Cajander) make it easy to understand Kujala's assertion. The similarity of the ground vegetation of HMT and MT in Ilvessalo's special study (1937) is obvious. The potential error involved in the quality classification method developed for practical purposes is therefore great in this special case. For instance, in classifying forest lands for taxation considerable errors may arise where MT is referred to Yield Class I and HMT to Class III. The physiognomic similarity of these forest site types has posed a still greater problem in the National Forest Surveys: the results for HMT and MT areas are highly contradictory.

From the foregoing, the general characteristics of the forest site types in question seem to be similar to such a degree that the basic principle of Cajander's theory, that of the importance of forest site types for mensurational purposes, is highly disputable for HMT and the northern MT as defined.

On the basis of Ilvessalo's growth and yield tables (1920 b) the forest soils of South Finland are known to assume the following order of site quality, from the poorest upwards: ClT, CT, VT, MT, OMT, etc.; dry sites on firm forest lands are succeeded by fresh sites. In North Finland the order is different. HMT, which must be classed among the fresh sites, has a poorer productivity than all the dry sites until the spruce stand reaches the age of approx. 200 years, a point at which the volume of standing stock of *Ericaceae-Cladina* type remains smaller than that of an HMT spruce stand.

In so far as the kind of parallelism suggested by Kujala really exists between the North Finnish and South Finnish forest site types, it must be said that the yield figures of HMT poorly fit in this picture of a coordination between South Finland and North Finland. On the other hand it is known that HMT, as far as its mineral soil is concerned, is neither so poor in nutrients nor so unfavourable structurally (cf. Heikinheimo 1922, Pesola 1928 and Aaltonen 1939) that these factors could account for the disproportion. There must be also other reasons, so far unknown, for the poor site quality.

HMT spruce stands, however, have a further characteristic, in addition to the small growing stock. Lakari (1920 b) and Heikinheimo (1922) and many others have found that the regeneration is quite inadequate. Bearing in mind that the fairly sparse seedling material, of exceedingly slow growth, in spruce forests is as a rule very old (the majority often over 100 years), it is easy to imagine what the total increment of a new stand amounts to.

On the other hand, it may be asked whether all the present HMT forests originated exactly as described above. The number of stems per hectare in many HMT spruce stands still exceeds considerably, even in the present stage of development (a better term would perhaps be stage of regression!), with a heavy natural removal, the figure presupposed by the reproduction values given by Heikinheimo (1922) for moss-dominated spruce forests. In addition, in contrast to the low number of spontaneous seedlings and slow growth referred to above, Heikinheimo quotes certain examples of spruce seedling stands that have developed among birch after fire. The density conditions of these spruce seedling stands admittedly vary a great deal, but in their growth particularly the spruce individuals evenaged with the birches are exceptionally good. A comparison, based on a limited material, between growing stock volumes of old HMT spruce stands and of mixed forests of spruce and birch formed after fire, justifies the assumption that the yield conditions of the latter stands are very different from those of the old HMT spruce stand (cf. Heikinheimo op.c. p. 56).

Ilvessalo (1937) has also devoted attention to the part played by birch in young HMT forests although he found time to study the mensurational characteristics of pure birch stands only. The national forest surveys indicate that HMT sites are covered approx. 35 per cent by pure spruce stands and approx. 35 per cent by spruce stands with birch as an admixed species and approx. 20 per cent by other stands dominated by spruce. Assuming that all the birches cannot be *Betula pubescens* reproduced mainly from sprouts (cf. Mikola 1942, p. 25), for expressly in the old spruce stands the large-sized birches present side by side with sprout birches are generally *Betula verrucosa*, it must be concluded that a number of these spruce stands has apparently originated immediately after a forest fire. If this is the case the part played by birch in the earlier stages has naturally been a much bigger one than at present (cf. e.g. Hult 1886, pp. 31—32, Heikinheimo 1922, Kalela 1946 and Arnborg 1949).

The natural development of HMT forests has not been studied in detail from this point of view, nor have growing stock volume tables been worked out.

In this connection it is also necessary to recapitulate the various conceptions of the development of spruce forests. Heikinheimo and, together with him, most Finnish forestry experts consider HMT a forest site type created by the spruce itself or an association (Tertti 1939) of which the primary factor is the macroclimate. Even the word »degeneration» is mentioned, but it is envisaged as the result of only a very prolonged development. On this point the Finnish view differs distinctly from the Swedish. According to the latter, regression becomes an accomplished fact in the course of a single tree generation. The Swedish view is supported to some extent by the names of HMT forest lands encountered in many places in North Finland and mentioned by Heikinheimo (1922) and Kujala (1921). In these names the second part of a compound word indicating birch forest often consists of the equivalents of grove (*lehto*), field burnt-over for crops (*halme* and *huhta*), hardwood thicket (*viita* and *vitikko*), etc. Different names indicative of the same trend, like Great Spruce Stand (*Isokuusikko*), are employed for forest lands now growing young mixed stands of birch and pine of rapid growth. Kujala's (1921) investigations support most markedly the assumption advanced by Lundström (1902) and other Swedish authors of the rapidity of the regression.

The study of the causes affecting the development of spruce forests seems to have been left to discussion and to references to the literature by most investigators, even those working in the field. Heikinheimo only has advanced his view of the indirect influence of climate and at the same time suggested the decisive importance of spruce in the origination of HMT. His material reveals certain tangible facts; for instance, it is found that raw humus and moss cover increase in thickness (1922) with the age of the stand. But he pays no appreciable attention to this, a point which affects the ecology of plants and, expressly, of trees. Like Kujala (1921) he believes that this phenomenon only has mainly an impoverishing influence on the composition of species and tends to inhibit regeneration. Apart from a study by Teivainen (1952) of certain part problems, no investigation has been made of the ecology of the North Finnish spruce forests.

It will be clear from the foregoing that different views exist of the development of spruce forests on fresh sites in North Finland. The yield figures of HMT, the commonest forest site type of these lands, are not in agreement with those of the dry sites in so far as the comparison is made with conditions in South Finland. According to the examples quoted by Heikinheimo, the yield figures of HMT forests after a fire justify the suspicion that the yield figures later quoted by Ilvessalo for HMT are too low in so far as they are comparable. As, in addition to all the above, the differences between the forest site types on fresh firm lands have proved to be fairly indefinite, it is evident that the problem of the development and biological properties of the northern spruce forests in its entirety requires a detailed re-investigation.

In view of all this, the object of the present investigation is to study:
(a) the natural development of spruce stands on fresh site types, and
(b) the ecological causes of this development.

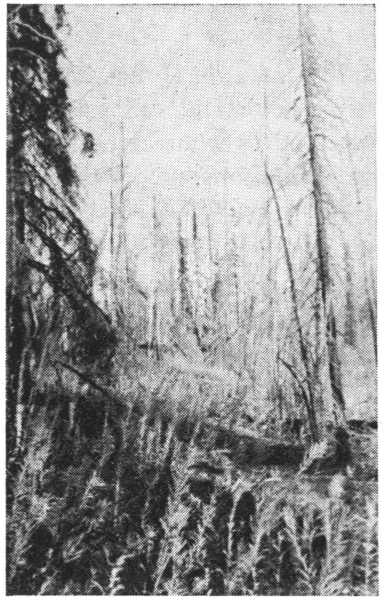
Limitations of the study

In approaching the problem of the development of spruce forests the first consideration might well be how a spruce stand can originate in general and how it usually starts in nature and to what cases the study can be limited without risk of misleading conclusions.

The thick-moss type, it was pointed out above, is the most spruce-dominated of the North Finnish forest site types; over 90 per cent of the HMT forests grow pure spruce stands or stands dominated by spruce. These forests have another special characteristic: they contain hardly any young spruce stands. Bearing in mind the present difficult regeneration conditions of spruce forests, a question presents itself: how could the regeneration occur 150—300 years ago? To answer this we must recall some biological properties of the spruce. The wide ecological range of this tree species, especially as regards its requirements of light, temperature and nutrients, and its unique power of recovery and regeneration in both crown and root system make the spruce the most competitive tree species on northern moraine soils.

On the habitats concerned the conditions attending the start of a new tree generation can vary within very wide limits from the primary stage, i.e. burnt open land (Fig. 1) to well past the climax stage found in old spruce forests with a thick moss cover. It seems impossible to analyze all the potential starting points of regeneration within this vast range. What is more, such an analysis would be inappropriate. The cases most frequently encountered in nature can be classified on the basis of some common characteristic without any risk of imposing too strict a formalism on the variety encountered in reality.

Hence, we may assume that spruce regenerates both on forest-covered and on open habitats. The fresh moraine soils of North Finland, as has been repeatedly pointed out before, generally grow spruce at present. Tree species other than pine and birch can be excluded from the study, although aspen, sallow and rowan occur in HMT forests almost without exception, as admixed species of little importance only. The question of the invasion by spruce of old forests as spontaneous young growth can, therefore, be confined to the following cases: a sparse or fairly dense spruce seedling stand, either evenaged or unevenaged, appears in (a) a spruce stand, (b) a birch stand, (c) a pine stand, or (d) different mixed stands. The most important prerequisite for regeneration, apart from



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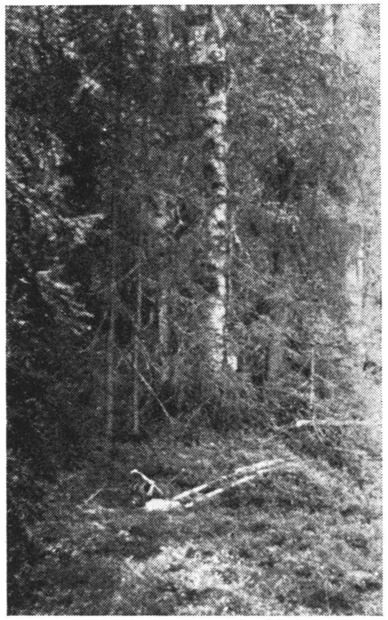

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Fig. 1. A burnt HMT spruce stand. Sample Plot 1. Keikkuma-aavansaari, Sodankylä.
Kuva 1. Palanutta HMT- kuusikkoa. Näyteala 1. Keikkuma-aavansaari, Sodankylä.

Fig. 2. Spruce invading a birch stand. Sample Plot 12. Roukuma, Kittilä.
Kuva 2. Kuusi tunkeutumassa koivun alle. Näyteala 12. Roukuma, Kittilä.

seed[1], is of course living space. Young growth in the closed spruce stands of North Finland appears only temporarily, just as in South Finland (cf. Hertz 1932 and Kalela 1948), and even where it survives such young growth is too sparse to form an economically acceptable new stand. In sparse spruce stands the regeneration is easier but even there the result is a more or less unevenaged, irregular seedling stand of unsatisfactory reforestation value. More or less evenaged spruce stands of at least satisfactory density conditions may, however, develop in certain special circumstances. This

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[1] Vegetative reproduction of spruce will be disregarded in the present investigation because this form of regeneration has been found of very little importance in the area under review. Heikinheimo's findings (1920 a) refer probably to conditions in the forest limit zone where vegetative reproduction is common (cf. also Hustich 1950, p. 42).

may occur e.g. when, in forests dominated by birch or pine, large scattered spruce trees happen to have good seed years at a time when the regeneration of birch or pine, for one reason or another, is not yet possible. It is a known fact that germination and stabilization conditions are particularly suitable for spruce seedlings in birch stands in which leaf litter has prevented the moss from forming a dense carpet inhibiting regeneration (Hult 1886, p. 32, Hertz 1932, p. 166 etc.). The biological strength of the spruce results before long in the formation of a pure spruce stand.

Where an adequately closed spruce seedling stand invades a birch or pine stand it almost completely inhibits the regeneration of the dominant species. This suggests that the birch and pine stands on HMT have been able to establish themselves only after great devastations. It is also apparent that a considerable part of the existing northern spruce forests have developed from previous spruce undergrowth present in birch and pine forests. The spruce may have entered the site undergoing a reforestation process either later than or at the same time as the main tree species (cf. Fig. 2, see also Tirén 1937, p. 158, and Arnborg 1949, p. 20).

Ilvessalo's investigations reveal that birch is a more common admixed species in HMT spruce forests than pine. This may perhaps be due to the superiority of birch as a pioneer species in the early stage of succession and especially to the capacity of white birch *Betula pubescens* for vegetative reproduction in old spruce stands. A natural question in this connection is why pine has been unable to occupy the burnt areas of HMT spruce stands to any great extent. The following factors may have contributed to this phenomenon.

Pines capable of seeding are often very few in old HMT spruce stands. Their effective seed yield is fairly low, due to the unfavourable climate of northern Scandinavia, (cf. Kujala 1927, p. 45—48 and Tirén 1937, p. 161). In addition, the burnt areas and other open sites capable of regeneration are more readily afforested by tree species that have lightweight seeds or a very marked sprouting ability. The principal species entering into question are birch, aspen and sallow. As a result of a somewhat slower initial development compared with deciduous trees the pine seedlings generally have a poor chance of survival in the thickets formed by these tree species. In addition, it may be pointed out that pine will not thrive as a young seedling in the mosses of unburnt spots (cf. Sirén 1948). A further hazard in these spots is an insect remarkably injurious to young seedlings, a weevil species, *Othiorrhyncus sp.* (Forsslund 1941) which is quite abundant (Sirén 1949). In spots burnt thorough, where germination is most successful, the young pine seedlings with no protective pile cover are threatened by heavy rains and soil clinging to the seedlings. In addition, the young pine seedlings seem liable to die of »damping off» (Vaartaja 1950, 1952, Mikola 1953) especially under poor illumination conditions. In their later stages of development the pine seedlings are susceptible to the destructive snow blight (*Phasidium infestans*) for a relatively long period (3—10 years). Especially in pine seedlings present in sparse spruce forests the snow blight is quite common and fatal. Where aspen suckers or seedlings occur on the same habitat as pine seedlings the latter mostly contract a difficult shoot cancer (*Melampsora pinitorqua*). Pine blister rust (*Cronartium sp.*) also is frequent in pine seedling stands on fresh sites. In dense broadleaved seedling stands the pines surviving the competition usually acquire a tuft-like crown and slender stem, which makes them more susceptible to snow damage. Besides whipping injuries, the mechanical damage caused by moose and reindeer should be mentioned. When spruce seedlings on the same habitat in due course leave the undergrowth stage and penetrate into the crown layer of the shelterwood they very often have mainly the fairly short-lived deciduous trees to conquer. Fairly young dead standing pines are often encountered in medium-aged and old HMT forests. They show no appreciable signs of snowbreaks, fungal diseases or other damage; the cause of their death is a riddle.

There may well be some other important factor contributing to the absence of pine that has remained unmentioned here, but the above may suffice to explain why the pine has relatively small chances of surviving as a scantily admixed species on burnt HMT sites in natural condition. The final result of the dynamics of tree species is probably a more or less pure spruce stand for sooner or later the relatively short-lived pioneer species disappear, incapable of regenerating properly (Fig. 3). Abundant formation of stump sprouts is not enough to secure the previous predominance of e.g. birch and sallow. It is evident that pine thrives naturally on HMT only in the event of its being the dominant or almost dominant tree species from the seedling stage onwards.

The most important of the forestless habitats[1] may be considered the open lands laid bare by violent forest fires. For reforestation burning-over for crops can be held to equal a forest fire at least; particularly in the eastern parts of North Finland the custom was widely spread until the end of last century. On open lands the primary qualities of the soil and the local climate, together with the coincidental colonization of plants, are decisive for the formation and development of vegetation including the trees. The starting-point offered by open land is in the first place comparable with the primary stage outlined by A. K. Cajander. The dynamic development of vegetations succeeding a fire, however, has been subjected to so many investigations that it is unnecessary in this connection to report on the main features of this phenomenon (cf. e.g. Kalela 1946). The prevailing silvicultural trend in this country is based to a remarkable extent on our knowledge of the dynamic changes of the stand composition. Heikinheimo already showed that the most viable stands have generally originated on soils treated by fire (cf. also Herlin 1913, Tkatschenko 1929, Tirén 1937, and Arnborg 1949).

A closer study of the effect of forest fires and burning-over on the forest dynamics of the wilds of Lapland reveals that practically all the forest soils have been burned.[1] Even in the very oldest secondary spruce forests, wood coal has been found in the border zone between the A-horizon and humus. In most of North Finland this suggests forest fires, but particularly in the communes of Salla, Kemijärvi and Kuusamo burning-over for cultivation has also been a fairly common practice judging from the tilled horizons. Even today old inhabitants living in the remote areas report having harvested rye from lands now covered by dense forest (the district of Vilmatunturi in the parish of Salla). In West Lapland burning-over aimed at providing pasture; typical burnt-over pastures are to be found e.g. in Kittilä, in the neighbourhood of the villages of Rouravaara and Nilivaara. These pastures now grow a mixed forest of birch and pine, and one of these stands is called, characteristically, Isokuusikko (Great Spruce Stand).[2] Of certain interest in this connection is the note of Airaksinen (1920, p. 74) that forest fires have been quite common in the eastern spruce area (see also the references mentioned by Regel 1940, p. 484). The importance of forest fires caused by lightnings has been stressed also by Saari (1923) and Keränen 1934).

Forestless sites may occur on unburnt areas also. A violent storm may fell and uproot the forest, laying bare the mineral soil locally yet

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[1] Logged forests are not discussed at all in the present investigation.

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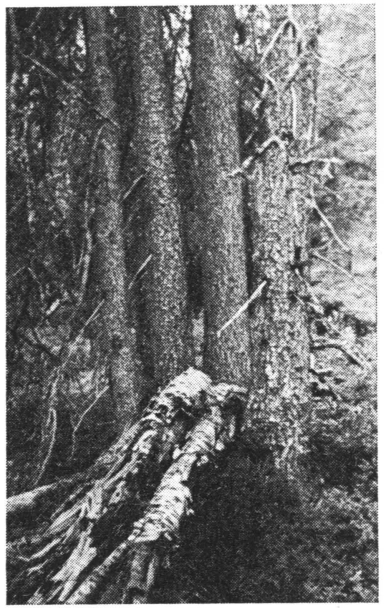
[1] A similar observation on the corresponding conditions of North Sweden has been made by Eneroth (1937).

[2] Burning-over for pasture was of course prohibited. The local inhabitants are reported to have replied to authorities inquiring into the cause of the fire, laconically: »*Ukko poltti*» (Thunder burnt). The Finnish *ukko*, the word used by the villagers on this occasion, not only means »thunder». It also denotes »the old man».



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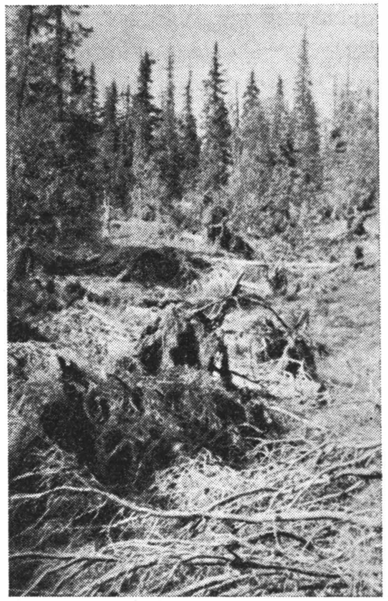

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Fig. 3. The old birch has succumbed and the stand has altered to spruce dominance. Sample Plot 22. Rautanaula, Kittilä.

Kuva 3. Vanha koivu on kaatunut ja metsikkö muuttunut kuusivaltaiseksi. Näyteala 22. Rautanaula, Kittilä.

Fig. 4. A wind-broken HMT spruce stand. Sample Plot 51. Tarpomapää, Sodankylä.

Kuva 4. Myrskyn kaatamaa vanhaa HMT-kuusikkoa. Näyteala 51. Tarpomapää, Sodankylä.

leaving the plant cover and humus cover in normal condition elsewhere (Fig. 4). Germination conditions on uprooted spots may with good reason be considered roughly as good as in the well fertilized mineral soil of the spots burnt through. On the other hand, the generally more extensive intact vegetation layer of the intervening spaces, with its thick layer of raw humus, affords but slender chances of both germination and later stabilization of young growth from tree seeds. Since storm-felled trees, lying off the ground, decompose very slowly, fallen trees take a long time to form a suitable germinating substratum. With the moss cover getting thinner the raw humus decomposing and disappearing, however, the regeneration gradually spreads uniformly over the area. The heavy growth of grass and herbs immediately after the storm damage also seems seriously to inhibit the establishment of reproduction, though only transiently. After a short and often explosive expansion, resulting in a quite effective covering field layer, mainly *Deschampsia flexuosa*, this ground vegetation enters on a regression stage which is accelerated by the appearance of birch on the habitat.

In other words, certain characteristics deriving from the previous forest generation are connected with the birth of a new tree generation after storm damage. Bearing in mind also that storm damage on the firm North Finnish soils, particularly on HMT, hits the old spruce forests hardest in which the moss layer is both dense and thick and thus an effective hindrance to regeneration, it is easy to understand that young growth makes its appearance almost exclusively in uprooted spots, in the neighbourhood of stumps and on sufficiently decomposed fallen trees; in exceptional cases only does the ground community afford an adequate germinating substratum for tree seeds. Considering these facts, it seems obvious that on a storm-devastated area the conditions of regeneration as a whole are poorer than e.g. on a fresh moraine site burned over by a fierce forest fire. In this connection it may be emphasized that the later development of a stand is greatly dependent on the conditions obtaining at its birth.

A stand of dead standing trees can hardly be considered a shelterwood competing with a new tree generation. Hence from the regeneration point of view such stands have been considered as forestless sites. In the majority of cases such dead standing trees are the consequences of insect or fungal damage. Where the damage has been severe and total the trees die within a very short period. Changed light conditions and fertilization from abundant litter — including the decomposition of dead roots — results in a temporary but strong increase in the luxuriance of the vegetation. This manifests itself e.g. in the occurrence of larger ecotypes, more abundant flowering and, sometimes, even in a greater variety of species. But in 5—20 years a distinct regression sets in and the vegetation soon becomes similar to that of slowly dying old spruce stands. The decomposition rate of raw humus is highly dependent on the composition the new forest generation happens to assume.

Old, physiologically overmature spruce stands usually die in a surprisingly short time, even though the »mass death» is usually preceded by a long phase of individual deaths. Mass death results usually in a stock

Fig. 5. Dying over-mature HMT spruce stand. Alikolkuttama, Kittilä.

Kuva 5. Kuolevaa yli-ikäistä HMT-kuusikkoa. Alikolkuttama, Kittilä.

of dead standing trees which soon fall, giving a forest picture highly reminiscent of the tangled thicket following storm damage (Fig. 5). In popular language, a fallen stand of dead trees is called *rutto* (the plague). The regeneration of these forests is scanty and accidental, but given enough time it results in a more or less unevenaged seedling stand which just covers the site, often slightly paludified in the course of the prolonged regeneration stage. Both the thickets resulting from storm damage and forests that have died of physiological maturity, i.e. »rutto», may catch fire, in which case regeneration naturally occurs in the same way as after a normal forest fire (cf. the place name *Ruttonpalo, palo* = fire).

A closer study in nature of the various potential ways of origination of HMT spruce forests, described above, showed that for practical purposes the following two alone need be noted: (1) regeneration together with other tree species on open lands devastated by fire, and (2) a scanty but general regeneration in old open spruce stands.

It is true that there are some storm-felled HMT spruce stands and some stands destroyed by insect and fungal damage, but the unbroken regeneration areas resulting from them seem insignificant both in number and extent. But on a smaller scale they are present in connection with the natural regeneration of almost all old spruce stands.

Due to the fact that the conditions for regeneration differ most on sites destroyed by fire and in old spruce forests in the process of natural regeneration, only these two instances have been taken in the present investigation as the starting-point for the study of the natural regeneration of HMT spruce forests. These ways of regeneration, surprising though it may seem, are the commonest in the whole of the North Finnish spruce forest area.

Since the National Forest Surveys have shown that spruce occurs in North Finland mostly on HMT it seemed appropriate to confine the study of the problems outlined above exclusively to the development of the spruce forests of this forest site type. Similarly, it has been found that HMT spruce stands admixed with birch are more frequent than those admixed with pine, for which reason only the birch-spruce mixed stands of the HMT forests that have originated after fire have been studied. In order to facilitate the collection of material and to make the different groups of stands comparable, only evenaged mixed stands were studied.

In view of the above mentioned facts the present investigation was limited to concern only:

1) The succession with a tree layer of birch and spruce in the first stages arising in virgin conditions after a forest fire.

2) The succession that follows when old mature spruce stands regenerate in virgin conditions without any intervening forest fire.

The sum of developmental stages which starts from the fire-denuded site and ends in a climax of the first spruce generation is termed the primary succession in this study.

The succession that starts with the second spruce generation without any intervening fire is in the following termed secondary succession.[1]

* * *

Territorially the study of the above forests is governed by the prevailing climatic and edaphic conditions. The beginning and end of summer and the sum of the daily temperature recordings of the growth period determine the northern and southern borderline of the district studied (cf. Keränen & Korhonen 1949, pp. 5—7, Maps 3, 4 and 6). In humidity too, the district is highly uniform (cf. Aaltonen 1933, p. 5, Kujala

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[1] Thus the definitions differ considerably from those applied by Cooper (1913), Clements, (1916, 1949), and others.

1936, p. 13 and A. Sirén 1949). An area in which the summer in normal years begins May 10—20 and ends Aug. 20—Sept. 1 and where the total effective temperature (i.e. the sum of the daily temperature recordings exceeding 5° C) averages 600°—800° C is considered climatically uniform (cf. Fig. 8). The area outlined above is edaphically interesting in that the spruce forest areas proper are generally situated in fell districts above the marine line, abounding in mica slates and basic rocks (cf. Heikinheimo 1920 b, and Aaltonen 1940, p. 28). The area belongs mainly to soil formation region 1, i.e. old, strongly leached soil where moraine is the typical soil of the fell districts (c.f. Aaltonen op.c. p. 207).

In Sweden the corresponding forest site type (Arnborg 1945: frisk blåbärs-ristyp — tjockmosstyp, Malmström 1949: risskogstyp med mossa), according to some estimates, is considerably more common than in Finland, primarily due to the greater altitude. The object of the study may be of certain interest also for Norwegian, Russian and Canadian forest researchers, due to the fact that the thick-moss type seems to be problematic in their countries too.

Investigation methods

The study of the above mentioned problems naturally pressupposes special methods for each aspect. The birth and development of spruce forests must be described. The factors affecting the dynamics of these forests must be ascertained. The former task can be tackled with the customary descriptive methods by studying representative sample plots. The latter part of the investigation aims at causality and therefore requires the application of relatively advanced, complex ecological investigation methods. To place the discussion of the subject on a firm basis we will confine ourselves first to the methods of the descriptive part only.

As trees develop relatively slowly compared with man the synthesis in investigations into the succession of forests must generally be built on momentary observations of sample plot stands at various stages of development. This is the method adopted by most researchers dealing with problems of this type. In the present investigation this method will be used to provide a reply to the problem of the origination and development of HMT spruce stands.

In connection with the search for fairly extensive HMT stands in natural condition during the summer of 1949 it was found that the development of these forests could best be studied in forest compartments of which a part had been destroyed by forest fire, storm or some other agent and which thus had been divided up into two or more parts of distinctly differing dynamic condition. Consequently the sample plots were placed contiguously on both sides of the generally surprisingly distinct borderline between the stands (see the typical example in Fig. 6). In order to obtain at least a satisfactory guarantee of the comparability of the various parallel sample plots the general standard required of the older stand was its absolute HMT character both in ground flora and in growing stock. Where both stands represented younger stages of development the extant remains of the old forest had to be sought in some other part of the same compartment. The plant associations to be compared were only accepted as typical HMT plant associations after a summary comparison with typical plant

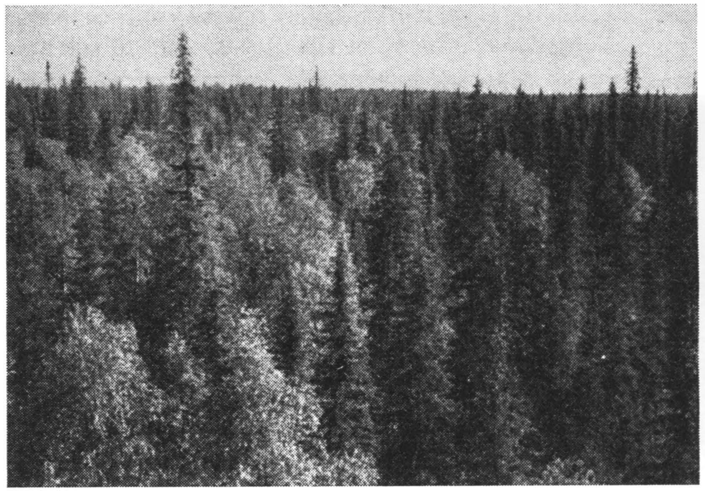

Fig. 6. Left, a middle-aged; right, an old primary stand. Sample Plots 32 and 43. Hevosvaara, Pelkosenniemi.

Kuva 6. Vasemmalla keski-ikäistä, oikealla vanhaa primäärimetsikköä. Näytealat 32 ja 43. Hevosvaara, Pelkosenniemi.

associations compiled on the basis of investigations by Cajander (1917), Heikinheimo (1922), Lakari (1920 a), Kujala (1921, 1938) Ilvessalo (1937), Teivainen (1952), etc. Due to the fact that relatively eutrophic species are included in the plant lists of these investigators it was considered necessary to compile a basic list from which both the most eutrophic (*Geranium*, *Dryopteris*) and the most oligotrophic (*Cladonia*, etc.) species of plant associations obviously foreign to HMT are excluded or in which they are only weakly represented. Obviously this basic list is a compromise based on the investigations of the above authors.[1]

In order to avoid including habitats of different site quality in the material — which might have been possible if for instance a recent severe forest fire in an HMT spruce stand had been arrested at the HMT limit — it was considered necessary to carry out preliminary observations of the soil before drawing the borders of the sample plot.

The older part of the parallel sample plot stands was not accepted for inclusion in the material in all cases. The reason for exclusion was usually the high occurrence of openings in these old spruce stands representing the typical HMT plant association. In these exceptional cases the ground vegetation was subjected to the most critical study possible.

Due to the rigid insistence on the sample plot stands being in natural condition they were almost all sited in forests that had escaped entirely the effects of civilization; as a result the majority of the sample plots are situated in the remote backwoods. Only a sample plot dominated by birch (No. 4), in which a part of the spruce storey may possibly have arisen from forest cultivation constitutes the exception from the general rule; its inclusion in the material, in spite of this suspicion, is due partly to the paucity of young sample plot stands available and partly to the general indication of the natural condition of this particular stand. In a few individual cases have minor reconstructions been effected for some broken tree individuals or some trees felled in hunting. On one sample plot certain healthy trees quite recently felled by storm were counted among the living tree stand.

The distance between the sample plot pairs was over 300 m in exceptional cases (3), in most cases 10—50 metres. The square, rectangular or, in exceptional cases, polygonal sample plots vary in area, depending on the age of the stand and number of stems, generally between 0.1—0.5 ha. In very young stands some sample plots smaller in size than this lower limit were marked out, and in the very oldest stands the sample plot exceeds 0.5 ha.

* * *

After the selection and demarcation of the sample plot according to the principles mentioned above came a detailed study of the vegetation, tree stand and soil.

The vegetation was described according to the method developed by Sarvas (1948). The frequency and the coverage of the various species on twenty evenly distributed square metre patches was graded 0—10 and respectively 0—100. Species found on the sample plot, but missing from the patches, were also entered in the list. Lichens, liverworts and mosses were counted as belonging to the bottom layer, as were the small areas covered by litter or without vegetation for some other reason. Grasses, sedges, horsetails, ferns, herbs and dwarfshrubs constituted the field layer. No special shrub layer was distinguished due to the poverty of shrubs on North Finnish fresh sites.

Maps showing the territorial distribution of the vegetation were made of some sample plots. Society and patch-society (cf. Arnborg 1943 and A. Kalela 1949) was selected as the smallest phytosociological unit.

Description of the vegetation also included measuring the heights of the most important mosses and dwarfshrubs. In each square meter patch four determinations of the mean value (one per quarter patch) per species were effected; hence the mean

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[1] The compilation of the list was greatly hampered by the mutual irreconcilability of the descriptions of vegetation.

values as a rule are based on 80 mean value readings per sample plot. A general report was also made out for each sample plot, with entries of the special features of the vegetation.

The phytosociological terminology is mainly based on that employed by A. Kalela (1949), and the nomenclature follows mainly that of Magnusson (1936), Weimarck (1937) and Hylander (1941).

* * *

The tree stand has been described and measured by the customary mensurational methods. As the purpose of the present investigation was more biological than mensurational the measurements were confined to counting the trees and to measuring the diameter at breast height (DBH), height, taper and bark thickness. The volume of the growing stock on the sample plots was calculated by means of Ilvessalo's tables (1947). Investigations into the growth were not considered necessary at this stage, and this mensurational aspect of the problem will be dealt with later in a separate investigation. In most cases primary data for growth calculations were for future needs collected from the sample plots. The biological classification of trees was also tentatively effected on some sample plots, utilizing a modification of L. Ilvessalo's method (1929)[1].

In the general description attention is devoted also to the viability, occurrence of cones, diseases and injuries, distribution and age of the trees. Especially the last-mentioned characteristic was thoroughly studied because of its decisive importance in determining the stage of development of the various sample plot stands. The combined age determination method previously advanced by the present author (1950) proved the most serviceable. Some representative sample trees of the dominant crown layer were removed, with roots, in each stand. The trees were split along the pith from the origo up to the first ocularly certain annual shoot (see Fig. 7). The lengths of the annual shoots from origo to top were also measured, to an accuracy of 1 cm, from the split trees. In order to throw light on the history of the stand it was often necessary to determine the age of fallen trees by splitting. The amount and age of the seedling stand was studied separately, and a map was often drawn of representative sample plots with seedlings.

One of the most important questions was determining the density of the stand. The method based on the crown projection of trees, employed by Lönnroth (1925), Ilvessalo (1927, 1937), Lappi-Seppälä (1930) etc. has certain inherent weaknesses in principle to which those authors, Kallio (1936), Sarvas (1945) and others have devoted attention. It is probably certain that the mathematical ratio between the area of the sample plot and the total of the measured or estimated crown projections is always less reliable than the ratio between the former value and the basal area of the growing stock of the same sample plots. As conclusively shown by Ilvessalo (1950), the diameter of a tree can doubtless be measured more exactly than the diameter of the more inaccessible and usually irregularly shaped crown. The point method employed by Sarvas (1953) does eliminate subjectivity in the determination of density but it does not do away with the error in principle since the determination applies to the density of the crown canopy and not that of the growing stock.

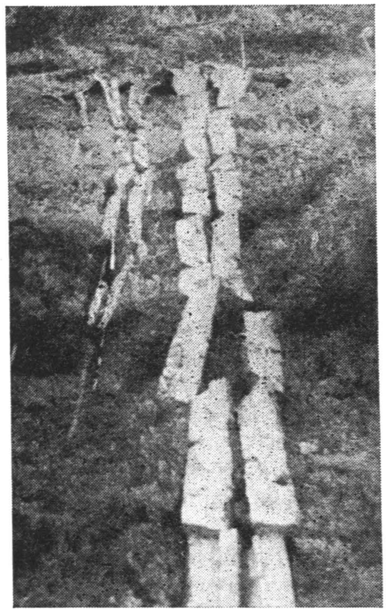

Fig. 7. The determination of the age and height growth of trees by splitting.

Kuva 7. Puiden iän määritys ja pituuskasvun tutkiminen tapahtui halkaisemalla runkoja ydintä pitkin.

In spite of the fact that the present method suffers from obvious weaknesses compared e.g. with the density determination method based on the basal area of the stand, the common method employed by Ilvessalo (1927) has been used slightly modified in this study. The main reason for this is that comparability with Ilvessalo's (1937) investigation results was considered more important than a more exact method of determining density that probably is more objective but seemed too much of an end in itself in this connection. Hence the crowns, in the present investigation, were projected and mapped on millimetre paper, upon which the ocularly estimated density was checked by a control comparison (cf. Lönnroth 1925, p. 142). A separate comparison was made with the basal area of the sample plot's growing stock; the totals of the basal area corresponded to the various density classes as follows:

Growing stock density class	0.7	0.8	0.9	1.0
» » basal area, sq.m/ha	< 24	24—27	27—30	30 <

---

[1] The crown layers of the spruce storey were distinguished ocularly by comparison with the dominant height, as follows:

dominant trees	height	> 85 %	of	dominant	height
co-dominant trees	»	65—85 %	»	»	»
intermediate trees	»	45—65 %	»	»	»
suppressed trees	»	25—45 %	»	»	»
undergrowth	»	< 25 %	»	»	»

Classification by basal area is arbitrary in a way, although the principle of the decision is based on results obtained by Lönnroth (1925) on South Finnish pine stands. They show that the basal area increases to only a small extent in fully stocked VT pine stands after the stand has reached the age of 80 years. — The over-dense stands of the present investigation, irrespective of the basal area (variation range 32—39 sq.m/ha), have been referred to density class 1.0+. Consideration of the basal area in density determination, particularly for mixed stands, has the valuable advantage of giving a more reliable picture than ocular estimation of the parts played by the different tree species. The checking with the aid of basal area naturally applies only to stands past medium age.

The method, however, has its own minor weaknesses which need not be discussed in this connection.

The method applied here is thus contradictory in a way to the author's personal view, but special weighty reasons justify the acceptance of a tried method. Another point deserving mention is that the density in some borderline cases was denoted in the field by two figures, e.g. 0.6—0.7. In connection with the final treatment of the material the density value arrived at in these cases, with a single exception, was the higher. In no case need it be assumed that the figures indicating density might be too low. The one exception in the treatment of the above borderline cases is Sample Plot 32 (Hevosvaara). It should by its basal area have been referred to density class 1.0 but because of a major opening in the sample plot was actually placed in class 0.9.

The description of the vegetation and the tree stand has followed the same lines on all the sample plots, including the Siulionpalo sample plots for special ecological studies.

* * *

The soil of the sample plots was investigated as follows.

The thickness of the humus and soil profile was measured from a 0.55 m deep pit in the middle of each quarter of a sample plot. The maximum and minimum values and the mean value of 8 observations of the thickness of the different layers were recorded for each pit; in addition, soil samples of 1 cu.dm were taken from the bottom of each pit in waxed cardboard containers.

The general report on the sample plot includes notes on the macroscopic structure of the humus, on the mycelial felt, wood coal remains, humus fauna, abundance of sclerotiae and other essential points. In addition to recording the thickness of the A- and B-horizons notes were made on ocular observations of the mechanical composition of the soil at different depths, its colour and possible pan formation, and of the occurrence of roots.

Stoniness of the soil, according to Viro (1947), affects the site quality. In order to ensure mutual comparability of the sample plots their stoniness was determined according to Viro by measuring the depth which a steel stick could be thrust into the ground, i.e. the depth index. The spacing of these sounds varied from 5—8 m. In a control determination of 16 sample pits (25 × 25 × 50 cm) Viro's method was found to give a true picture of the stoniness in the case tested. In studying the results it must be borne in mind that the thickness of humus is not included in the reading of the depth index; hence the values obtained are not directly comparable with those obtained by Viro in South Finland. The stoniness index (Si) is here calculated as by Viro (1952).

As mentioned before, ocular observations on the occurrence of roots were made in connection with the description of soil profiles. To obtain a more objective picture of the occurrence of the roots both of the trees and of some important species of ground vegetation in the various soil layers it was considered necessary to carry out a detailed study of root systems on nine sample plots representing different stages of development. Finding the roots in the raw humus layer was the most difficult part of the task. It could only be done by carefully crumbling samples 25 × 25 cm in size. The roots in the mineral soil were exposed by the water screening method discussed later (see p. 130).

Fallen trees were examined in connection with the study of raw humus. Their decomposition was graded according to Arnborg (1943, p. 16); a class interval of 5 cm was employed in diameter classification. Fallen trees were assumed to be of some help in reconstructing the forest-dynamic phenomenon of olden times.

The site quality of the swamps surrounding firm forest lands is known to be quite closely correlated with the fertility of firm forest land. Consequently, the determination of the types of swamp surrounding HMT forest lands in the present investigation was effected according to Lukkala and Kotilainen (1945). In the majority of cases sketch maps have been drawn to show the location of the different swamp types in relation to the HMT forest land in the vicinity.

The mechanical composition of the soil was studied in all the soil samples; the method employed has been described by Aaltonen (1941 b). The basic mineral index, which has a fairly constant ratio to lime on the old lands of North Finland (cf. Aaltonen 1939, p. 50), was determined by the method developed by Tamm (1934). The determinations of exhangeable lime, potassium and phosphorus were effected by the Agricultural Research Centre, Department of Soil Science (about the methods, see Vuorinen 1953). In addition, it may be mentioned that comparative recordings of soil temperature were effected on some parallel sample plots in the summer of 1951. All the detailed studies listed above were also made on the sample plots for special ecological studies in Siulionpalo.

The material and its classification

General features

A total of 83 sample plot stands were studied to illuminate the birth and development of spruce forest. They were all situated in a climatically uniform district (Fig. 8) where the total effective temperature during a growing season average 600°—800° C. The soil of the sample plots was fine-sand moraine with few stones (cf. Ilvessalo 1933, p. 18), with the exceptions listed below. In the pedologic respect the region in question is fairly rich in basic minerals (cf. Aaltonen 1937 a, pp. 38, 44). Most of the sample plots finally chosen were situated on gentle slopes with a NW — N — NE — E or SE exposure, as can be seen from Appendix 1 (cf.also Teivainen 1952, p. 70). Almost all the objects of study were situated above the post-glacial marine line, however not higher than 300 m (cf. map published by Aaltonen 1940, p. 467). The comparability with Ilvessalo's material (1937) is considering the altitude thus fairly good. Owing to the fact that the character of the investigation presupposes the absolute certainty of the mutual comparability of the sample plots the following requirements were made of the sample plots selected for inclusion on the final material:

(1) The soil had to be fine-sand moraine of similar mechanical composition throughout the sample plots.
(2) The degree of stoniness had to be normal, i.e. correspond to Class II according to Viro (1952). Permissible range of variation of the depth-index (Si): 12.1—21.0.
(3) Permissible variation range of the basic mineral index: 5—25.
(4) The nutrient conditions at a depth of 55 cm had to show a high degree of comparability.
(5) The moisture conditions of the soil had to be as equal as possible. The incidence of plants indicative of a high degree of paludification (Sphagnum etc.) was not to exceed △ : △ (frequence : coverage).

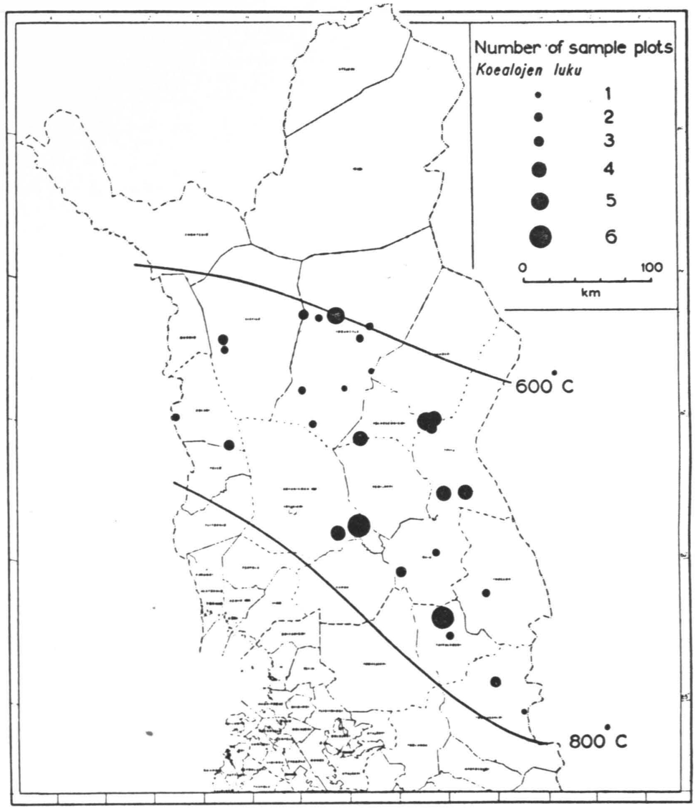

Fig. 8. Location of the sample plots, and curves for the total of the effective temperature during the growing season in the area studied.

Kuva 8. Näytealojen sijainti ja kasvukauden tehoisan lämpötilan summakäyrät tutkimusalueella.

(6) The control associations were not to include any species foreign to HMT. In addition a general condition made was that the parallel sample plots had to be located close to one another (cf. p. 39 above).

Due to the above requirements for comparability 12 sample plots had to be rejected in the subsequent detailed consideration, for the following reasons (cf. Table 1).

Hence in six cases the soil was far too stony and in two cases of a mechanical composition putting it in the sandy soil class. In two cases plants too eutrophic for HMT were present in such profusion that the forest site type must be considered superior in fertility to normal HMT. In the

Table 1. List of rejected sample plots.

Taulukko 1. Luettelo hylätyistä näytealoista.

Name of sample plot *Näytealan nimi*	Reason for rejection — *Hylkäämisperuste*
Hevosvaara c	Too stony, $\mathrm{Si} = \sim 3.0$, forest site type EMT-HMT *Liian kivinen* *metsätyyppi EMT-HMT*
Seipäjärvi b	» $\mathrm{Si} = \sim 7.0$, control sample plot too far away *vertailunäyteala liian kaukana* (> *1.0 km*)
Tarpomapää b	» $\mathrm{Si} = \sim 5.0$, forest site type EMT-HMT *metsätyyppi EMT-HMT*
Pahtavaara d	» $\mathrm{Si} = \sim 7.0$, » »
Nutukkaselkä a	» $\mathrm{Si} = \sim 7.0$, control sample plot too far away *vertailunäyteala liian kaukana*
Riipijärvi a	» $\mathrm{Si} = \sim 7.0$, » » »
Vaisko b	Sandy soil, $\mathrm{Si} = \sim 29.0$, » » » *Hiekkamaa*
Takakangas	» $\mathrm{Si} = \sim 28.0$, » » »
Ahmajärvi b	Too many openings, density only 0.5, (secondary forest) *Liian aukkoinen, tiheys vain 0.5, (sekundäärimetsä)*
Kuusivankka b	The stand included too much pine, site type EMT-HMT *Sekapuuna liian paljon mäntyä, metsätyyppi EMT-HMT*
Siulio j	Site type HMT-DMT, *Dryopteris, Geranium* too strongly represented *Metsätyyppi* » *Dryopteris, Geranium liian runsaasti edustettuina*
Kaihua e	» » » » » » »

remaining two cases the tree stand was too mixed with pine or, as regards density conditions (primarily because of the number of openings), unsuitable for the purposes of the present investigation.

It is obvious that the mensurational characteristics of the rejected sample plot stands differed somewhat from those of the HMT stands considered typical. In too stony stands, for instance, the volume was strikingly low. In the two HMT—DMT stands this characteristic naturally exceeded the average considerably. Vaisko b and Takakangas were very typical HMT forests and quite representative sample plot stands, but a closer study of the soil revealed that the mechanical composition differed too much from the other sample plots. The other sample plot at Vaisko should also have been rejected actually, because of its too high basic mineral index, but its unsuitability was noticed too late (computing error!), besides which laborious root studies had been made for the sample plot.

* * *

Cut down for the above reasons, the material therefore comprises only 71 sample plots (Appendix 1). The main criterion for the grouping of these sample plots was the way of origination of the stand and its present condition. The density conditions of the spruce storey have been taken into account in the same way, in principle, as in Kalela's (1936) investigation into mixed stands of spruce and grey alder. The three groups of the material are characterized by the following features.

Group I covers all the sample plot stands that have originated immediately after a forest fire, burning-over or broadcast burning. All of them had or had had a practically fully-stocked birch storey or one with few quite small openings. (In the oldest sample plot stands this could be concluded from the decayed and fallen trees.) The invasion of spruce into the burnt area had mostly taken place simultaneously with or just a few years later than the invasion of birch, even though in some cases the spruce did not arrive in the birch stand until 10—40 years later. According to Melechow (1934) spruce may appear in a burnt area even some few years before birch, (for the reasons, see e.g. Tkatschenko 1929, pp. 125—126), though this entails no essential changes in the dynamics of the tree species of the stand. Owing to the fact that the number of spruce varied greatly in the different stands, the sample plots were classified into three groups according to the number of spruce:

(a) Sample plots in which the spruce storey is rather sparse
(b) » » » » » » » » medium dense
(c) » » » » » » » » dense (for technical reasons of description, however, the term over-dense will be applied in the following).

In eight younger sample plot stands the proportion of spruce is so small that all these stands are referred to group (a). Sample Plot 12 (Roukuma) has also been included in this group. Five of these nine sample plots, however, grow such young stand that there is good reason to assume that the spruce storey will be supplemented. Reasons for the inclusion of Sample Plot 6 (the ecological sample plots of Siulionpalo) will be given later (p. 164). Enough spruce were present also on Sample Plots 7, 8 and 12 to suggest that they will form a closed stand after the stand has reached the age of, say, 200 years. It is obvious that the younger spruce individuals gradually appearing in them will supplement the stand to some extent, thought of course at the expense of evenagedness.

The differentiation between the sample plots of medium dense and over-dense spruce storey is shown in Fig. 9. The method employed is

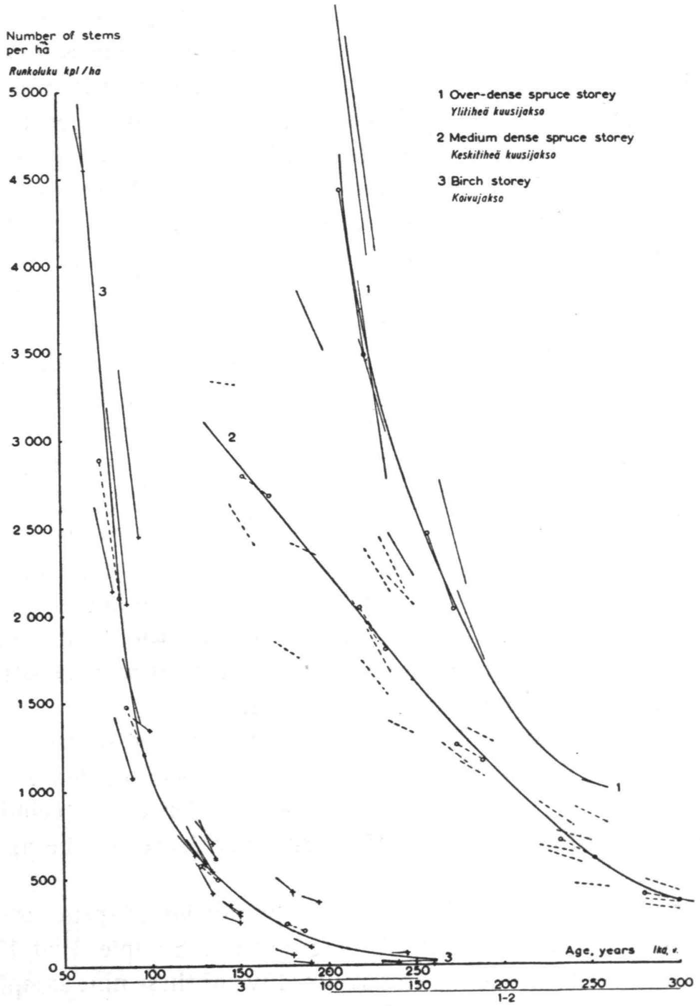

Fig. 9. Grouping of sample plot stands on the basis of the stem number of birch and spruce and the number of dead standing trees.

Kuva 9. Näytealametsiköiden ryhmittyminen koivun ja kuusen nykyisen runkoluvun ja pystyyn kuolleiden puiden lukumäärän perusteella.

that of Kalela, however with the difference that the living trees plus the standing dead trees supply a summary idea of the number of trees at a given time, which time is further removed from the present moment than from the moment of death of the dead standing trees that have been dead longest. In addition, it has been necessary to allow for the slower decomposition of trees in North Finland. From field observations on the rate of decomposition the conclusion arrived at for spruce is that the tree individuals alive at present and standing dead supply a rough idea of the number of the living trees of the stand some 10—15 years ago. Because of the much more rapid rate of decomposition and falling to ground of birches the corresponding figure for medium-sized birches has been assessed at 10 years.[1] In addition, the number of trees in the birch storey seemed to be independent, to a surprising degree, of the density of the spruce storey (cf. Kalela 1936, p. 77).

Whether or not a tree remains standing may naturally depend greatly on the size of the tree and on its degree of decomposition. On the other hand, it must also be borne in mind that the forces contributing to the falling of a tree are different at the timber stage and at the small-pole stage, e.g. the significance of wind and snow differ widely. After prolonged deliberation the present author finally arrived at a solution similar to that suggested by Kalela, no better means of solving this classification problem having been discovered to date. However, the different density conditions produced by the different ways of origination of the stands cannot be ignored. It is self-evident that the development and self-thinning of the stand starts later in sparse than in dense stands, not to mention over-dense stands. The primary stands, excluding the oldest, were very sound. — In the following the stands that have started after a forest fire, i.e. belonging to the primary succession, will be called alternatively first tree generation.

Group II covers sample plots representing different degenerative phenomena of primary stands. No stand characteristics proper can be given for such dying or dead stands, partially levelled, but these tangles must be included since they represent the transitional stage before the secondary tree generation. They are of great forest-dynamic interest.

Group III covers exclusively sample plot stands that have regenerated after a preceding spruce generation without any intervening forest fire. The most important criterion, in addition to the absence of a fresh carbon layer, was sometimes the almost totally decomposed large fallen trees, sometimes the overmature old trees from the previous tree generation still growing on the site. The new generation has appeared mainly in the

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[1] From observation it has been found that fairly small trees, diameter < 5 cm remain standing for some 5 years only.

uprooted spots, on fallen trees and in the spots with little moss in the gaps between trees. The density conditions of these sample plot stands are not always ideal, due to poor regeneration facilities. Their demarcation in the field was greatly affected by the fact that they were locally limited by the borders of burnt areas. Through force of circumstances, therefore, it was necessary to be content with the material available in the immediate neighbourhood of the burnt areas. A study of tabular Appendix 1 shows that the average densities of primary stand groups a, b and c are 0.80, 0.87[1] and 0.99., in secondary stands only 0.79. The oldest forests were badly damaged by rot. — For secondary stands the term second tree generation will be employed alternatively in the following.

The number of the sample plots of the three above mentioned successional groups is presented in Table 2.

The 44 sample plots of the primary forests are distributed by the density of the spruce storey as follows:

(a) inadequate spruce storey 9 sample plots
(b) medium dense » 26 » »
(c) over-dense » 9 » »

The material collected from the various sample plots is shown in Appendix 2.

In addition, observations on the various individual aspects of the investigation have been made on numerous excursions. A stay in the backwoods of Pomokaira and in Sompion-, Siulion- and Vilmankaira contributed greatly towards understanding the development of natural forest. Interesting observations were also made at Kivalo, in the backwoods of Kuusamo and Taivalkoski, and in the region between Lake Kiantajärvi and the eastern frontier.

Table 2. Number of sample plots of the various successional groups and age classes.

Taulukko 2. Näytealojen lukumäärä eri suksessio- ja ikäryhmissä.

Successional groups *Suksessioryhmät*	Age class, years — *Ikäluokka, v.* 0–49	50–99	100–149	150–199	200–249	250–299	300 +	Total *Yhteensä*
	Total number of sample plots — *Näytealojen lukumäärä, kpl*							
Primary stands — *Primäärimetsiköt*	5	8	11	8	3	5	4	44
Transition stage — *Ylimenovaihe*	—	—	—	—	—	—	7	7
Secondary stands — *Sekundäärimetsiköt*	2	2	2	6	2	5	1	20
Total — *Yhteensä*	7	10	13	14	5	10	12	71

Homogeneity of material

To collect a sufficiently homogeneous material for a biological investigation is difficult and in many cases quite impossible. In most cases the researcher must content himself with a summary similarity between some of the most important properties. The difficulty of collecting homogeneous material for a study of the properties of forests is particularly great, as Cajanus (1914) was the first to note when attempting to compile pure pine stands with a growing stock belonging to identical stem distribution series (see also Ilvessalo 1920 a, Lönnroth 1925, etc.). Homogeneity of the growing stock, however, is not in itself sufficient, as has been emphasized by Lönnroth (op.c.). The test of the intrinsic comparability of the contents of a material must be sought in the conditions under which the stand has originated and developed. Hence, it must be ensured that e.g. sample plots referred to a given group have formed in the same way and that their environmental conditions have enabled identical development.

As regards this last-mentioned point, it has been established that all the sample plots of the present material are situated in an area where the macroclimate can be considered fairly uniform throughout. But as far as the microclimate is concerned, dependent to a very great degree on the exposure (cf. Appendix 1), we have not been so successful.

Great attention has been devoted to the homogeneity of the soil of the sample plot. However, it must be pointed out that the factors studied, viz. stoniness, soil conditions, mechanical composition, mineral index, some important nutrients and acidity, do not guarantee the similarity of the other properties of the soil. It is true that mechanical composition is an indicator of the water capacity of the soil, but a significant dissonance may still occur in some other point not studied.

The characteristics of the physical and chemical properties of the soil listed above have been determined in the present investigation by the methods described (see p. 43). As far as the above properties are concerned the comparability of the sample plots representing different tree generations is illustrated in tabular form. The Tables 3 and 4 give the mean,

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[1] Excluding Sample Plot 44.

Table 3. Mechanical composition of the mineral soil in the primary and secondary HMT stands.

Taulukko 3. HMT:n primääri- ja sekundäärimetsiköiden näytealojen mineraalimaan raekoostumus.

Sample plots *Näytealat*	Percentage of soil fraction — *Maalajitteen sadannes*																	
	2—0.5			0.5—0.2			0.2—0.05			0.05—0.02			0.02—0.005			0.005—0.002		
	M_1	σ	$\varepsilon (M_1)$	M_1	σ	$\varepsilon (M_1)$	M_1	σ	$\varepsilon (M_1)$	M_1	σ	$\varepsilon (M_1)$	M_1	σ	$\varepsilon (M_1)$	M_1	σ	$\varepsilon (M_1)$
Primary stands — *Primäärimetsiköt*																		
All sample plots *Kaikki näytealat* . .	12.69	4.03	0.64	21.46	5.01	0.80	39.00	5.18	0.83	12.14	4.13	0.66	12.50	4.28	0.68	2.21	0.75	0.12
Parallel sample plots *Rinnakkaisnäytealat*	11.99			21.71			39.48			12.75			11.78			2.29		
Secondary stands — *Sekundäärimetsiköt*																		
All sample plots *Kaikki näytealat* . .	11.30	2.93	0.71	20.30	3.36	0.81	40.02	5.16	1.25	13.01	2.62	0.64	13.40	2.54	0.62	1.97	0.82	0.20
Parallel sample plots *Rinnakkaisnäytealat*	11.31			20.25			40.12			12.89			13.60			1.83		

M_1 = mean — *keskiarvo,* σ = standard deviation — *hajonta,* $\varepsilon (M_1)$ = standard error — *keskiarvon keskivirhe.*

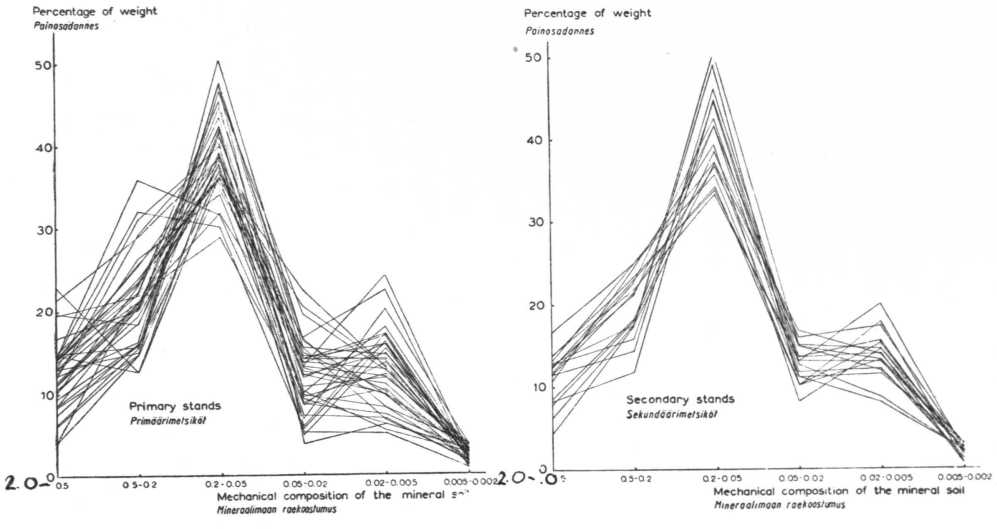
standard deviation and standard error of the mean value, and illustrate the internal homogeneity of the groups of the material.

As regards the mechanical composition of the soil, the material can be shown mathematically to represent fine-sand moraine (see Aaltonen 1940, p. 85 and 1941 c, p. 14) and, in addition, to be remarkably homogeneous (Table 3). The principal groups of the material, i.e. the sample plot stands of the first and second tree generation, prove well comparable mutually. A study of the mechanical composition of the soil of individual sample plots, however, gives a picture of somewhat less favourable appearance from the point of view of homogeneity, particularly with the primary stand sample plots (cf. Figs. 10 and 11). On the other hand, it must be borne in mind that the composition of moraine soils varies considerably. In previous separate investigations into the mechanical composition of the soil, however, even soils considerably more different mutually have been referred to one and the same class of moraine soil (cf. Aarnio 1938, Kivinen 1941 and E. Kivekäs 1946). Hence the reduced material described above, with the sandy soils eliminated, must be considered homogeneous enough in the mechanical composition of their soil for the purposes of the present investigation. It should be pointed out, incidentally, that Hesselman (1937, p. 557) has managed to collect a moraine soil material more homogeneous still though more limited.

The stoniness of the sample plots is also very similar. Excluding a few exceptions (10.5 and 21.6 cm, see Appendix 1), the depth index varied between 12.0 and 21.0 cm (Table 4). The inclusion of sample plots differing but little from the permissible limit values was a necessity owing to their great value in the present study as parallel sample plots. Incidentally, the moraine soils of the district under review are among the least stony in Finland (cf. Ilvessalo 1933, pp. 12, 19 and Aaltonen, 1941 a, p. 35).

The depth of the A-horizon indicates that the sample plots are sited on strongly leached (cf. Aaltonen 1941 a, p. 21) but nevertheless comparable areas (cf. Table 4).

As regards the chemical properties of the sample plot soil (Table 5), the rapid method employed only establishes the comparability of the sample plot groups. As this and only this is the issue in question the values obtained can probably be considered as indicators of the comparability of the principal groups of the material. The results gained from adjacent parallel sample plots are highly similar in all the properties studied, a fact that adds considerably to the reliability of the results. It may be mentioned that Tamm (1940, p. 59) considers basic mineral index values between 15—20



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Figs. 10 and 11. The mechanical composition of the mineral soil of the primary (Fig. 10) and secondary (Fig. 11) sample plot stands.

Kuvat 10 ja 11. Näytealojen mineraalimaan koostumus primäärimetsiköissä (kuva 10) ja sekundäärimetsiköissä (kuva 11).

Table 4. Stoniness of soil, thickness of A-horizon and the percentage of the coarse and fine soil fractions.

Taulukko 4. Maan kivisyys, A-horisontin paksuus sekä karkeiden ja hienojen maafraktioiden sadannes.

	Depth index, cm *Syvyysindeksi, cm*			Thickness of A-horizon, cm *A-hor. paksuus, cm*			Mechanical composition *Raekoostumus* > 2 mm			< 2 mm		
	M_1	σ	$\varepsilon(M_1)$	M_1	σ	$\varepsilon(M_1)$	M_1	σ	$\varepsilon(M_1)$	M_1	σ	$\varepsilon(M_1)$
	Primary stands — *Primäärimetsiköt*											
All sample plots *Kaikki näytealat*	17.2	2.46	0.37	8.0	1.68	0.25	16.56	4.71	0.74	83.44	4.71	0.74
Parallel plots *Rinnakkaisalat*	17.1	2.06	0.40	8.5	2.08	0.57	15.24	3.74	1.02	84.76	3.74	1.02
	Secondary stands — *Sekundäärimetsiköt*											
All sample plots *Kaikki näytealat*	16.4	3.69	0.82	9.0	3.53	0.79	16.84	4.70	1.16	83.16	4.70	1.16
Parallel plots *Rinnakkaisalat*	17.3	2.47	0.67	9.2	3.90	1.06	15.75	4.63	1.26	84.25	4.63	1.26

Table 5. Comparability of the soil as regards some chemical properties of sample plots belonging to different successions.

Taulukko 5. Eri suksessioihin kuuluvien näytealaryhmien vertailukelpoisuus maan eräiden kemiallisten ominaisuuksien perusteella.

	Basic mineral index *Emäsmineraali-indeksi*	Water-soluble *Vesiliukoinen* $CaCl_2$	Calcium *Kalkki* $CaCO_3$	Potassium *Kali* K	Phosphorus *Fosfori* P	Acidity *Happamuus* pH
		kilograms per hectare — *kg/ha*				
Primary stands — *Primäärimetsiköt*:						
All sample plots — *Kaikki näytealat*	13.29	221.7 [1]	105.7	114.4	47.0	6.14
Parallel sample plots — *Rinnakkaisnäytealat*	12.08	—	124.6	108.3	51.7	6.17
Secondary stands — *Sekundäärimetsiköt*:						
All sample plots — *Kaikki näytealat*	13.86	299.2 [1]	115.0	101.5	52.9	6.01
Parallel sample plots — *Rinnakkaisnäytealat*	13.35	—	122.1	100.0	51.7	6.07

indicative of fairly good nutrient conditions from the viewpoint of minerals. On the other hand it is surprising to note that the values obtained are of the same magnitude as Aaltonen's findings from similar old northern soils (1939, p. 47 and 1941 c, p. 27).

The majority of earlier investigations has shown the comparability of the habitats by means of ground flora. As the subject matter of the present investigation is the comparison of successions, and the significance of ground flora as an indicator of site quality only assumes the power of evidence (in the light of the forest site type theory) after the stand has reached the climax stage, the present vegetation on the sample plots of the younger stands could not be utilized as proof of the similarity of the sites. The phytosociological equality of the control stands of these sample plots and of the sample plots in old stands has been considered the only correct criterion in this respect. The list of plants (Appendix 3) shows that the material is unusually homogeneous in the old stands.

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[1] The study does not concern all samples. — *Määritys koskee vain osaa näytteitä.*

The list do reveal some exceptions from the so-called climax associations. A nutrient content somewhat exceeding the average may be suspected on Sample Plots 9, 18, 19, 25, 34, 38, 56 and 70, and the opposite phenomenon, nutrient content less than normal, on Sample Plots 6, 7, 8, 13, 24, 30, 35, 40, 52, 67, 69. A comparison of the soil chemical properties studied reveals a slight dissimilarity. But the phytosociological divergence in particular is so small, especially compared with the extensive variation within a particular forest site type reported in previous investigations (cf. e.g. Lakari 1920 a, Kujala 1921, Teivainen 1952), that this divergence has been taken as a normal feature of even a uniform biological material.

The list includes moisture indicator plants. All researchers studying the vegetation of HMT have accepted roughly the same amount (Arnborg 1943) or considerably more (Lakari 1920 a, Kujala 1921, Ilvessalo 1937) of plants indicative of increased paludification in their typical associations. Thus the sample plots under review meet at least the customary requirements for similarity of moisture conditions in the sites. It may be pointed out that in itself the mechanical composition of the soil of the sample plots is a fairly good indicator of moisture conditions on level lands. Due to the fact that the majority of the sample plots are situated on slopes with moving water, the slight occurrence of hydrophytes must be considered to indicate that the hydrological conditions of the sample plots studied are roughly comparable.

Table 6. Quality of the swamps surrounding the sites studied.

Taulukko 6. Tutkimuskohteita ympäröivien soiden laatu.

	Spruce hardwoods peat-moors *Korpia*				Pine-bogs *Rämeitä*				Bogs *Nevoja*		Fens *Lettoja*		Total *Yhteensä*
	LhK [1]	RhK	VK	RääsK	LeR	IR	SR	RR	SsN	KN	VL	RiL	
	Percentage — *Sadannes*												
Swamps bordering on primary stands *Primäärimetsikköihin rajoittuvat suot*	5.5	11.1	13.9	1.4	11.1	16.7	11.1	2.8	13.9	1.4	9.7	1.4	100.0
Swamps bordering on secondary stands .. *Sekundäärimetsikköihin rajoittuvat suot*	6.7	13.3	11.1	2.2	11.1	11.1	13.4	4.4	11.1	—	15.6	—	100.0

Connected in a way with hydrological conditions are the swamps surrounding the sites of the sample plot stands. Lukkala (1919) and Ilvessalo (1934) found a definite positive correlation existing between the fertility of the firm soils and of the adjacent swamps. Consequently, the swamps in the vicinity of the sites studied were classified.

Table 6 shows that both the secondary and primary forests as a rule border on swamps that can be considered of good fertility. The eutrophic character of the swamps must mean that the firm lands in the neighbourhood also are fertile, irrespective of the condition of the existing stand. In spite of minor differences the primary and secondary forests under review, on the basis of the table above, may be considered significantly similar.

From the foregoing the mutual comparability of the habitats studied may be considered as at least satisfactory.

* * *

In an investigation to illustrate the development of a plant association composed of one or several tree species the criterion of homogeneity of the material must, however, be broader than that of just habitat. The difficulties that earlier researchers have had to overcome in attempting to collect from forests in natural condition materials homogeneous above all as regards the properties of the stand have been indicated above.

The material collected for the present investigation has been classified in the way described by the degree of dissimilarity of the tree stand on the sample plots. The most important considerations in the classification were the way of origination of the spruce storey and the degree to which the natural removal varied due to different densities. The intrinsic homogeneity of the various groups of each tree generation can be shown by means of different stem distribution series. Due to the limited size of the material, reliable series representing the different stages of development could not be collected from groups other than the primary stands with medium dense spruce storey. Fragments of series indicative of the general trend and justifying conservative conclusions can, of course, be collected also for over-dense spruce storeys and, above all, for secondary stands. The material collected, however, does not on all points suffice to warrant the drawing of any final, purely mensurational conclusions. Since it is only a comparison

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[1] LhK, etc. refers to Finnish swamp types.

between medium dense primary and secondary stands that is in question, the material may be adequate enough to ascertain the homogeneity of expressly these material groups. As the stem and volume distribution series will be quoted later (pp. 71 and 92) it may be mentioned in this connection that the material on these points may be considered to meet the requirements of satisfactory homogeneity.

The dynamics of *Hylocomium-Myrtillus* type forest

Stand development

In discussing the various ways in which spruce stands are born, it was found most appropriate to concentrate on the development of stands that originated after forest fires and those regenerated immediately after old spruce stands without an intervening fire catastrophe. Combining original data, collected from various sample plots, into series according to age gives a roughly representative idea of the characteristics of stands belonging to different successions. Although the theme of the present investigation is biological it has been impossible to avoid forest-mensurational concepts in reviewing numerous factors. Due to this biological character of the investigation it has not been considered necessary to give e.g. the exact numbers of trees in the different diameter classes; accuracy to the nearest 10 stems has been found to provide an adequate general idea. A comprehensive study of the internal structure of mixed stands of spruce and birch in the mensurational sense would require considerably more extensive material than that collected for the present investigation.

Stem number

Before embarking on the study of the development of the number of trees, it is necessary to recall Ilvessalo's (1937) statement on the wide amplitudes within which it varies in the pure stands of North Finland. As the present investigation deals, to a considerable extent, with mixed stands of ever varying species composition, it can hardly be expected that the stem distribution series will be more regular than in Ilvessalo's investigation. Similarly, considerable variation occurs in the number of stems in both Lappi-Seppälä's (1930) and Kalela's (1936) sample plot material from mixed stands of other types.

The development of the total stem number of spruce and birch storeys of primary stands of varying density has already been reported on in connection with the classification of the material (Fig. 9, p. 48). The original data on which this diagram is based are given in Appendix 1, which also contains the numbers of stems of secondary stands.

Due to the fact that the stem number in earlier Finnish literature (cf. Ilvessalo 1920 a, 1937), has been defined as a concept of sometimes extensive, sometimes concise limits, it has been considered necessary in the present investigation to effect the classification separately for the two principal tree species, as follows: trees of the dominant crown layer, trees of the dominated crown layer, trees of the undergrowth, and impurities.

This classification makes it possible to describe the stem number of each sample plot as follows:

1) spruce plus birch plus impurities (m) = N_T = total stem number of the sample plot
2) N_T less (m = N_P = stem number of principal tree species
3) N_P less undergrowth = N_M = stem number of main stand
4) N_M less dominated trees = N_D = stem number of dominant crown layer

Member (m), representing tree species other than spruce and birch, of equation (1) can be considered a normal and negligible impurity (< 10 %) of biological materials of this kind; it has been disregarded in the following. Hence we arrive at equation (2) in which individuals belonging to the undergrowth still have a special significance. Ilvessalo (1937, p. 34), however, considers undergrowth a factor disturbing the stem number of the principal main stand. Evidently, on the basis of the biological uniformity of the stand structure of evenaged pure stands, he has excluded undergrowth trees in calculating the stem number of mature stands. For the sake of comparability the same procedure has been adopted in the present investigation, and the part of the stand distinguished in this way is termed the main stand, or principal growing stock.[1] Since the dominating species in a mixed birch-spruce stand changes with age, the present author has found it necessary also to consider the variations

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[1] All tree individuals shorter than a quarter of the dominant height, however not more than 5 metres high, have been taken as undergrowth.

in the number of trees belonging exclusively to the dominant crown layer (N_D) in the different periods of age.

It is difficult to make a reliable comparison of the different stem numbers given above with the corresponding stem numbers from earlier investigations. The present author's material actually starts approximately where Kalela's (1936) material of mixed stands of spruce and grey alder on fresh sites ends, and is only partly (mainly MT spruce storey) comparable with Lappi-Seppälä's (1930) material which is also from South Finland. Ilvessalo's (1937) material of HMT spruce stands, in fact, mainly covers the 180—230 year age classes, which means that the possible role of birch in the formation of the tree stand in the earlier stages of stand development does not emerge. Ilvessalo (op.c.) does mention in another context that young HMT forests often grow birch.

The stem number curves of the main stands, plotted from the mean values for groups of stands, give levelled values for the different tree species and different tree generations (Table 7). Some main stand stem numbers supplied by Ilvessalo (op.c.) and computed in the same way are included in the table to facilitate comparison.

Table 7 reveals clearly that the over-dense spruce storey of primary stands contains some 50 % more stems belonging to the main stand than that of medium dense storey, the proportion of birch remaining approximately equal in both density classes. On the last mentioned point the result concurs with Kalela's finding on the stem number of grey alder (Kalela 1936, p. 77, Fig. 4). As regards medium dense spruce storeys it can be seen, in addition, that where the spruce storey has entered the stand slightly later than birch (case a) the number of spruces belonging to the main stand has been very low initially. When the stand is about 100 the spruce storey, by then no less than 60 years old, is about to catch up with birch and grows in dominance the older the stand becomes. Furthermore, it is striking that in approx. 120-year old stands the differences between spruce storeys evenaged with birch and those even slightly younger than birch in the number of individuals belonging to the main stand seem to disappear. The rapid removal of birch at the age of 80—120 years evidently has its significance in this respect.

As to primary stands, it may be pointed out that the stem numbers of medium dense spruce storey evenaged with birch (case b) are to some extent reminiscent of the stem numbers given by Ilvessalo (1937) for pure HMT spruce stands, particularly at the age of 80—200 years. It must be noted, however, that in such stands developing after

Table 7. Levelled number of stems of the main stand (N_M) in primary and secondary stands on HMT.

Taulukko 7. Päämetsikön tasoitetut runkoluvut (N_M) HMT:n primääri- ja sekundäärimetsiköissä.

Age *Ikä*	Primary stands — *Primäärimetsiköt*					Secondary stands — *Sekundäärimetsiköt*				Ilvessalo's stem numbers *Ilvessalon runkoluvut*		
	Spruce storey *Kuusijakso* Medium dense *Keskitiheä*		Spruce storey *Kuusijakso* Over-dense *Ylitiheä*	Birch storey *Koivujakso*	Medium dense (spr; b+bi) Total *Keskitiheä (ku; b+ko) Yhteensä*	Spruce *Kuusi*	Birch — *Koivu*		spr + bi; c Total *ku + ko; c Yhteensä*	HMT spruce *HMT kuusi*	HMT birch *HMT koivu*	MT birch *MT koivu*
	a	b					c	d				
	Levelled number of stems per hectare — *Tasoitettu runkoluku, kpl/ha*											
60	~ 500	~ 1 800		5 600	~ 7 400			(5 500)		3 500	—	4 200
80	~ 750	~ 1 650		2 200	~ 3 850			(3 000)		1 900	3 200	2 500
100	~ 1 100	~ 1 500	2 100	1 150	~ 2 650	1 700		1 800	> 1 700	1 500	2 000	1 550
120	1 340		1 850	730	2 070	1 450	(280)	1 100	1 730	1 220	—	—
140	1 180		1 660	440	1 620	1 100	300	550	1 400	1 050		
160	1 030		1 500	260	1 290	850	300	450	1 150	920		
180	880		1 340	160	1 040	700	260		960	830		
200	760		1 190	90	850	640	180		820	760		
220	660		1 040	40	700	620	100		720	720		
240	540		890	20	550	600	50		650	700		
260	440		740		440	580	40		620			
280	370				370							
300	(330)				330							

a = spruce younger than birch
ku nuorempi kuin ko
b = spruce evenaged with birch
ku samanikäinen kuin ko

c = moss-covered secondary stands
sammalpeitteiset sekundäärimetsiköt
d = secondary stands with scattered uprooted spots
sekundäärimetsiköt, joissa tuulenkaatopohjia siellä täällä
spr, *ku* = spruce, *kuusi* — bi, *ko* = birch, *koivu*

fire a notable number of birches is present, expressly in the age interval of 80—180 years, a feature not visible in Ilvessalo's material.

The stem numbers of the birch storey in themselves, as the table also shows, differ surprisingly little from the stem distribution series obtained by Ilvessalo for pure birch stands on MT and HMT (1937, p. 36). Admittedly, the stem number of birches in the 100-year old stand included in the present author's material only amounts to under 60 % of Ilvessalo's stem number for a pure HMT birch stand, and to approx. 75 % of that of a pure MT spruce stand. The competition of spruce, therefore, seems to have a fairly definite effect in primary stands as young as 100 years old.

The levelling of the stem numbers of sample plot stands belonging to secondary stands is considerably less reliable than the same calculation for primary stands. The main reason is the paucity of sample plots and the dissimilarity of their growing stocks. For instance, secondary stands originating after storm devastation contain considerably more birch (case d) than secondary stands originating in some other way (case c). The material assembled, it is true, only contains a couple of sample plots to support this point. A number of other interesting details emerge from the stem distribution series of secondary tree generation.

The stem number of the spruce storey in the main stand of secondary origin is found to be, up to 120 years of age, of the same size class and even slightly higher than that of medium dense primary stands. This may be due to the fact that the spruce regeneration, although relatively sparse, has mostly been free from competition by birch (case c), and practically all the spruce trees present on the site have remained to form the main stand. It is true that where the elements uprooting trees have exposed mineral soils, birch has invaded the extremely good germination substrata and in scattered groups has become a dominant species on these sites. Where this has happened ample space has been left for spruce, primarily in the gaps between the exposed spots, but spruce growing in the uprooted spots, in due course, pushes its crowns through the crowns of birch. Another interesting point is the number of trees where the stand is over 220 years old. By then even the individuals which in the regeneration stage were somewhat belated in appearing from the reproduction phase have had time to develop as members of the principal stock. In a sparse forest slightly younger seedlings too manage to survive. In addition, it must be borne in mind that sprout birches, primarily *Betula pubescens*, of relatively rapid growth, to some extent increase the number of stems in the main stand in the later stages of development also.

A comparison of the total stem numbers of secondary stands e.g. with those quoted by Ilvessalo for HMT reveals but a slight similarity in the age period 180—240 years. Due to the fact that Ilvessalo's material was probably collected from the purest possible spruce stands birch, an impurity in his material, is not shown at all in the tables. Hence, a comparison involving birch is not feasible. According to the general mensurational custom it is probable that birch in these circumstances has been included in Ilvessalo's stem numbers. In comparing the stem distribution series given with Ilvessalo's results the slight incomparability caused by the different age determination method must be borne in mind (cf. Ilvessalo 1937, p. 18 and Sirén 1950, p. 44). Ilvessalo's material probably ought to be taken as 20 years older for the comparison.

Table 8. Levelled number of stems (N_D) of trees belonging to the dominant crown layer.

Taulukko 8. Vallitsevaan latvuskerrokseen kuuluvien puiden tasoitetut runkoluvut N_D.

Age *Ikä*	Primary stands — *Primäärimetsiköt* Spruce — *Kuusi* a	 b	 Birch *Koivu*	Secondary stands — *Sekundäärimetsiköt* Spruce *Kuusi*	 Birch — *Koivu* c	 d
	Levelled number of stems per hectare — *Tasoitettu runkoluku, kpl/ha*					
80	∼ 500	∼ 500	1 400			750
100	∼ 620	∼ 620	860			500
120	∼ 650	∼ 650	580	600	90	340
140	∼ 650	∼ 670	360	520	110	240
160	∼ 600	∼ 620	200	450	150	170
180	520	∼ 580	100	410	120	120
200	460	∼ 500	50	380	70	70
220	400	(470)	40	360	20	20
240	330	(450)	20	350		
260	280	(430)		340		
280	250	(420)		330		
300	230	(410)		320		

a) stands with medium dense spruce storey
kuusijaksoltaan keskitiheät metsiköt
b) stands with over-dense spruce storey
kuusijaksoltaan ylitiheät metsiköt
c) moss-covered secondary stands
sammalpeitteiset sekundäärimetsiköt
d) secondary stands with uprooted spots here and there
sekundäärimetsiköt, joissa tuulenkaatopohjia siellä täällä

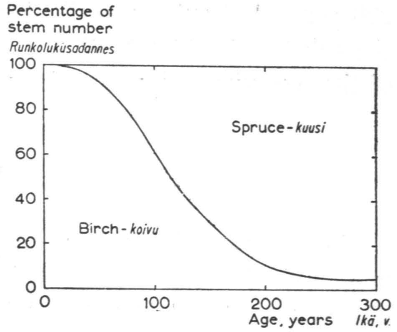

Fig. 12. Percentual distribution of birch and spruce stem number of the dominant crown layer in primary stands at various ages.

Kuva 12. Primäärimetsiköiden vallitsevan latvuskerroksen runkoluvun prosenttinen jakaantuminen koivun ja kuusen kesken eri ikäkausina.

An indication of this is the age determinations, carried out for the purpose (cf. p. 110 below), of spruce seedlings that have reached stump height. Taking these points into account, the stem distribution series of the spruce storey of secondary stands possibly assume a high degree of similarity to the stem numbers of HMT spruce stand given by Ilvessalo.

Forest is often assessed for mensurational purposes according to the tree stand forming the dominant crown layer. For this reason it has been considered necessary to give the levelled stem numbers (N_D) for this part of the stand also (Table 8). This table reveals above all the high proportion of birch in the dominant layer of young primary stands on HMT. But another notable feature is that in primary stands the medium dense spruce storey in the dominant crown layer represents approximately the same proportion as in over-dense storeys. Dominant and co-dominant spruce trees might be expected, at least in theory, to be definitely more numerous in over-dense than in stands of medium dense spruce storeys. But this was not the case in the stands studied.

The most important observation concerning spruce of the dominant crown layer is probably that their absolute proportion increases up to the approximate age of 120—140 years when, evidently due to competition within the species, the stem number begins to fall. But the relative proportion of spruce grows from beginning to end due to the removal of birch (cf. Fig. 12, which refers to primary stands). The figure also reveals the small proportion of birch in stands over 180 years old. The biological superiority of spruce is as indisputable on HMT sites in North Finland as on fresh forest site types in South Finland (cf. e.g. Kalela 1936, 1946).

For secondary stands it may suffice to say that the number of dominant spruce trees is slightly lower than in primary stands up to approximately

220 years, but subsequently slightly higher, perhaps primarily because of the smaller size of the dominant trees and openness of the spruce storey of the secondary succession in the earlier stages of development.

Diameter

In customary stand mensuration the diameter can usually be recorded more reliably than e.g. the height of trees. For this reason the average diameter at breast height including bark of the trees of the sample plot stands can be considered a fairly dependable characteristic of the stand. In forest-mensurational investigations quite important calculations have in fact been made on this basis. In the present investigation, however, only average diameters weighted by stem number will be given. Ilvessalo (1937) also employs average diameter weighted by stem number, which facilitates comparison.

The smoothed curves showing the average development of the mean diameter (including bark) of the different spruce and birch storeys of primary and secondary stands are given in Figs. 13, 14 and 15. Tables 9 and 10 give the corresponding levelled values.

From the numerical values obtained for the spruce storey of primary stands it can be seen that the mean diameter from the beginning has grown quite evenly up to 200 years, reaching peak values at approximately 240—260 years. This culmination is succeeded by a marked decline, a result of course of the continuous decrease in stem number and of arrested thickness growth, but above all of the fact that in the climax stage even big trees begin to dry up and fall.

No significant difference is observable in the mean diameter of the dominant[1] spruce trees of over-dense and medium dense storeys. The same applies to the spruces of the dominating crown layer. But a comparison of the mean diameters of the spruce storey of the main stands reveals a marked difference in favour of the sparser spruce storey. The difference remains approximately the same even when undergrowth is included in the calculation of mean diameter.

For birch, it is found that the mean diameter of dominant trees initially differs distinctly from that of all birches belonging to the dominating crown layers. But the difference diminishes from the age of 100 years

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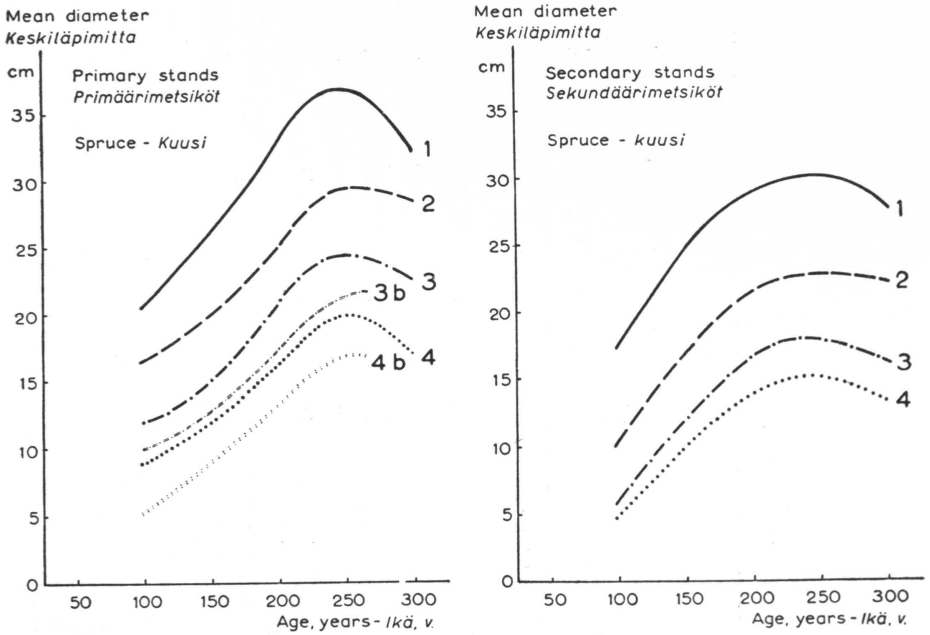
[1] Dominant trees = the 100 tallest trees within a hectare.

Table 9. Development of mean diameter in primary stands.

Taulukko 9. Primäärimetsiköiden keskiläpimitan kehitys.

Age *Ikä*	Spruce storey — *Kuusijakso*						Birch storey — *Koivujakso*			
	Dominant trees *Valtapuut*	Dominating crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*		Main stand + undergrowth *Päämetsikkö + alikasvos*		Dominant trees *Valtapuut*	Dominating crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*	Main stand + undergrowth *Päämetsikkö + alikasvos*
			Medium dense *Keskitiheä*	Over-dense *Ylitiheä*	Medium dense *Keskitiheä*	Over-dense *Ylitiheä*				
	Mean diameter, cm — *Keskiläpimitta, cm*									
60	15.5	13.5	10.5	.	7.0	.	15.0	9.5	7.0	6.5
80	18.0	15.0	11.5	.	8.0	.	18.0	12.0	9.5	9.0
100	21.0	16.5	12.0	10.0	9.5	5.5	20.0	14.0	12.0	11.5
120	23.0	17.5	13.0	11.0	10.5	6.5	21.0	15.5	14.0	14.0
140	25.5	19.0	14.5	12.0	11.5	8.0	22.0	17.0	16.0	16.0
160	28.0	20.5	16.5	13.5	12.5	9.5	22.5	18.5	16.5	16.5
180	30.5	22.5	18.5	15.0	14.0	11.5	23.0	19.5	17.5	17.5
200	33.0	25.0	20.5	17.5	16.0	13.5	23.0	21.0	18.0	
220	35.0	27.5	22.5	19.5	18.0	15.5	23.5	22.5	17.5	
240	36.5	29.0	24.0	21.0	19.5	16.5	24.0	23.5		
260	37.0	29.5	24.5	21.5	20.0	17.0				
280	36.0	29.5	24.0		19.5					
300	32.5	28.5	22.5		17.0					



13 14

Figs. 13 and 14. Development of the mean diameter in the different parts of the spruce storey in primary and secondary stands.

Kuvat 13 ja 14. Primääri- ja sekundäärimetsiköiden kuusijakson eri osien keskiläpimitan kehitys.

1 = dominant trees — *valtapuut.*
2 = dominating crown layer — *vallitseva latvuskerros.*
3 = main stand, medium dense —*päämetsikkö, keskitiheä.*
3 b = » » over-dense — *päämetsikkö, ylitiheä.*
4 = all trees, stand medium dense — *kaikki puut, metsikkö keskitiheä.*
4 b = » » » over-dense — » » *ylitiheä.*

onwards as only the most competitive birches (primarily *Betula verrucosa*) survive in the stand.

The curve representing the main stand of birch reveals a close similarity to the mean diameter curve for birches belonging to the dominating crown layers up to 150 years. From this age onwards, however, the influence of the sprouts replacing the removed birches begins to make itself felt to such an extent in the mean diameter of the birch storey that, to avoid confusion, the curves have not been continued. As these stump sprouts

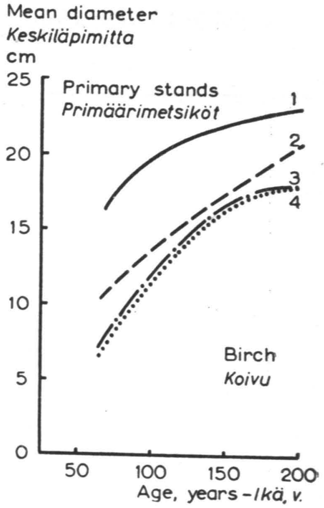


Fig. 15. Development of the mean diameter in the different parts of the birch storey in primary stands. (About explanation of the figures; see figs. 13 and 14).

Kuva 15. Primäärimetsiköiden koivujakson eri osien keskiläpimitan kehitys. (Numeroiden selitys ilmenee kuvista 13 ja 14).

in the sample plot stands under review, as regards both size and age, may be included in undergrowth, they need not concern us here any further.

The mean diameters of secondary stands as seen in both Fig. 14 and Table 10 show considerably lower numerical values throughout than those of primary stands; the main exception is the birch, of which there are few in secondary stands and which at the age of 160 years seems to be of almost the same size class as in primary stands. The abundant undergrowth of spruce in over-dense primary stands accounts for the fact that the mean diameter of the whole spruce storey of the somewhat sparser secondary stands, especially in the younger age phases, is of the same size class.

Comparison of the above mean diameters with those given by Ilvessalo for HMT warrants the following conclusions.

The main stand of the over-dense spruce storey in the primary succession has a mean diameter series somewhat similar to that of Ilvessalo's pure HMT spruce stand 180—240 years old. Bearing in mind, however, that the primary stands of the present investigation always included or have included a birch storey with a mean diameter series similar to that of Ilvessalo's pure GD(M)T and MT birch stands, this similarity between the spruce storeys cannot be taken as an indicator of the equality of the stands. If all tree individuals (i.e. the undergrowth too) are included in the comparison, the mean diameter series of the medium dense spruce storey also of primary stands is somewhat reminiscent of the series given by Ilvessalo. However, the comparison suffers

Table 10. Development of mean diameter in secondary stands.

Taulukko 10. Sekundäärimetsiköiden keskiläpimitan kehitys.

Age *Ikä*	Spruce storey — *Kuusijakso*					Birch storey — *Koivujakso*		
	Dominant trees *Valtapuut*	Dominating crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*		Main stand + undergrowth *Päämetsikkö + alikasvos*	Dominating crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*	Main stand + undergrowth *Päämetsikkö + alikasvos*
			By present author *Tekijän mukaan*	Referring to Ilvessalo (1937) *Ilvessalon mukaan*				
	Mean diameter, cm — *Keskiläpimitta, cm*							
60	11.0					12.5	5.5	4.0
80	14.0	9.0	3.5	3.4	3.0	13.0	6.0	4.0
100	17.5	11.0	6.0	6.3	5.0	13.5	6.5	5.0
120	20.5	13.5	8.5	9.0	7.0	15.0	8.0	6.5
140	23.5	16.0	11.0	11.3	9.0	16.5	10.5	9.0
160	26.0	18.5	13.0	13.3	11.0	18.0	14.0	12.5
180	28.0	20.5	15.0	14.9	12.5			
200	29.0	21.5	16.5	16.4	14.0			
220	30.0	22.5	17.5	17.5	14.5			
240	30.5	23.0	18.0	18.6	15.0			
260	30.0	23.0	18.0	19.5	15.5			
280	29.0	23.0	17.5		15.0			
300	27.5	22.5	16.0		13.5			

from the fact that, for reasons indicated above, the undergrowth is excluded from Ilvessalo's series. The birch storey, too, confuses this comparison. In addition, the mean diameter of birches definitely exceeds that of Ilvessalo's pure HMT birch stand although it evidently does not include the birch undergrowth. One explanation of this is that spruce-birch mixed stands contain a relatively higher proportion of birch individuals in the dominant crown layer than a pure birch stand.

A comparison of the mean diameter series of the spruce storey in the main stand of the secondary succession with that given by Ilvessalo for HMT spruce stands reveals a remarkable similarity, particularly if the 20-year correction (cf.p. 64) is borne in mind. The mean diameters of the incomplete birch storey of secondary stands also differ less from the mean diameters of Ilvessalo's HMT birch stand than the birch storey of primary stands described above.

The main result of the study may be summed up as follows: The mean diameter series of primary stands, for the two main species, differs so

definitely from the HMT mean diameter series given by Ilvessalo that no mutual similarity is observable. But an obvious similarity exists between the mean diameter series of the spruce storey in the main stand of the secondary succession and Ilvessalo's series.

Stem distribution series

Changes in two stand characteristics of the principal tree species of primary and secondary HMT stands have been reported on above. Supplementary to one another as they are, they afford a very real picture of stands in different stages of development; the picture, however, may be improved further by combining the characteristics in question — stem number and diameter — into so-called stem distribution series.

Such series may be worked out in many different ways and to serve different ends. Using probability calculation and statistical mathematics e.g. Cajanus (1914), Ilvessalo (1920a) Lönnroth (1925), etc. have computed levelled stem distribution series with the aid of which the most extreme samples, which disturb homogeneity, have been eliminated from the original material. In the present investigation this study of homogeneity has been effected by the simple adjustment method developed later by Ilvessalo (1937).

The adjustment of primary materials leads as a rule in biological materials to the formation of fairly distinct groups or series. Repeated adjustment, however, may sometimes lead so far from the original material that false conclusions are possible.

Since the values computed according to Ilvessalo's adjustment method (1937) did not differ appreciably from the mean values computed by age classes from the primary values (cf. example below, Table 11), a stem distribution series based directly on the mean values obtained from the various age classes of the original material was considered in better accordance with the facts. By this method adjustment errors, seen against the whole, are fairly limited and the conclusions drawn are based on true material alone. It should also be borne in mind that the special characteristics inherent in the structure of mixed stands may disappear if too many adjustments are carried out.

The advantages and weaknesses of the method employed are seen from the following examples covering the 125—137 year age class of primary stands (Table 11).

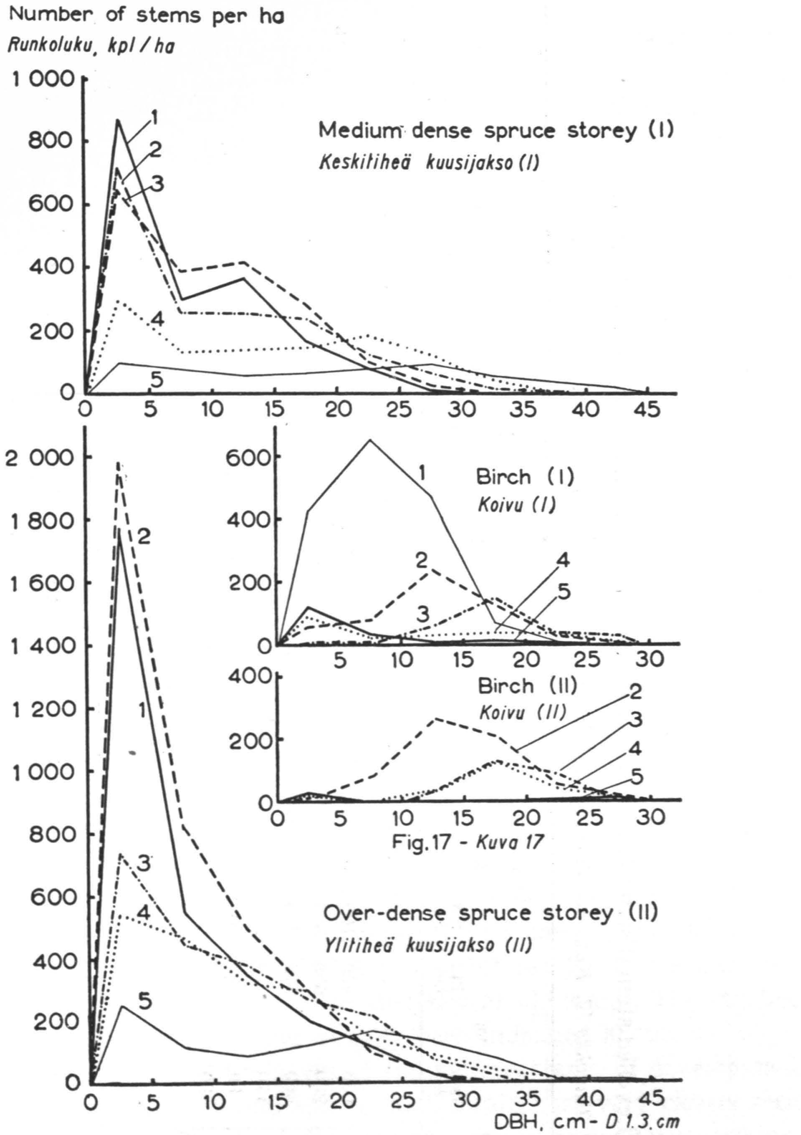
Table 11. An example of the calculation of the average stem distribution series of a certain age class (125—137 years).

Taulukko 11. Esimerkki tietyn ikäryhmän (125—137 v.) keskimääräisen runkolukusarjan laskemisesta.

Sample Plot No. *Näyte-alan No.*	Diameter class and tree species — *Läpimittaluokka ja puulaji* 0—5 spr *ku*	0—5 bi *ko*	5—10 spr *ku*	5—10 bi *ko*	10—15 spr *ku*	10—15 bi *ko*	15—20 spr *ku*	15—20 bi *ko*	20—25 spr *ku*	20—25 bi *ko*	25—30 spr *ku*	25—30 bi *ko*	30 + spr *ku*	30 + bi *ko*
	Number of stems per ha, medium dense spruce storey *Runkoluku, kpl/ha, kuusijakso keskitiheä*													
17	450	165	425	215	450	225	390	130	110	5	10	5	—	—
20	400	—	230	10	370	180	310	110	130	60	100	50	—	10
22	975	100	430	80	355	360	205	145	115	15	35	5	10	—
23	500	—	365	100	570	320	325	165	55	25	30	5	10	—
24	950	20	510	45	365	125	190	105	125	55	—	—	10	—
Mean value *Keskiarvo*	655	57	392	90	422	242	284	131	107	32	35	13	6	2
	Number of stems per ha, over-dense spruce storey *Runkoluku, kpl/ha, kuusijakso ylitiheä*													
16	2785	—	740	100	510	275	375	200	120	55	45	—	—	—
18	2550	35	1200	65	465	300	315	235	115	15	—	—	—	—
19	1285	10	585	135	490	250	250	185	100	85	50	40	—	—
21	1420	—	740	20	540	230	225	210	70	65	30	10	5	—
Mean value *Keskiarvo*	2008	10	825	80	502	264	292	207	102	55	31	13	1	—

A comparison of the individual figures with the mean values reveals wide differences on some points and, on the other hand, striking similarities between Sample Plots 24 and 19 which belong to different density groups. The intrinsic homogeneity of each group, however, is approximately the same in degree as in the material collected by Ilvessalo from the pure pine stands of North Finland (cf. e.g. Ilvessalo 1937, Fig. 10, sample plots of EVT, age 70 and 74 years).

Stem distribution series achieved in the way described above for certain periods of age are shown in Fig. 16 and 17. The primary stands of the different groups reveal a certain regularity in the stem number of the different diameter classes of both birch and spruce storey; the number of



Figs. 16 and 17. Curves illustrating the stem distribution of spruce and birch in primary stands of different age.

Kuvat 16 ja 17. Eri ikäryhmiin kuuluvien primäärimetsiköiden kuusen ja koivun runkojakaantumissarjat.

Age of the stands — *Metsiköiden ikä*

1= 90 — 100 years — *vuotta*
2= 125 — 137 » »
3= 150 » »
4= 180 — 200 years — *vuotta*
5= 240 — 270 » »

Table 12. Levelled stem distribution series for primary stands with a medium dense spruce storey.

Taulukko 12. Kuusijaksoltaan keskitiheiden primäärimetsiköiden tasoitetut runkolukusarjat.

Diameter class, cm *Läpi-mitta-luokka, cm*	Age of the stand and the tree species — *Metsikön ikä, v. ja puulaji*															
	50		90		130		150		170		190		230		250	
	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*
	Number of stems per hectare — *Runkoluku, kpl/ha*															
1— 5	?	6 300	600	420	100 (700)	70	80 (600)	20	— (400)		— (300)		— (200)		— (100)	—
5—10		2 500	300	650	390	90	260	30	190	10	130		(90)		(75)	
10—15		200	360	470	420	240	260	70	200	50	140	25	100		50	
15—20		—	170	75	290	130	240	150	260	90	150	40	110	10	60	—
20—25			80	15	100	30	130	40	200	50	190	40	140	10	80	—
25—30			20	—	30	15	80	30	100	25	130	20	150	10	110	—
30—35					10	—	30	—	40	5	50	10	60	10	70	—
35—40							10	—	15	—	20	—	40	—	50	—
40+													10	—	35	—
Total *Yhteensä*		9 000	1 530	1 630	1 340	575	1 090	340	1 005	230	810	135	660	40	500	—

lower diameter class trees decreases with the advancing age of the stand, the stem number of the higher diameter classes simultaneously increasing somewhat. Only the younger sample plots (90—100 years) of over-dense spruce storeys seem to have been slightly sparser than those of the 125—137 year group; the small trees in particular were fairly few. The low incidence of diameter class 5—10 cm in all (except the oldest age-classes) of the stands with a medium dense spruce storey emphasizes a slight irregularity of the spruce storey, perhaps one of the special characteristics of the internal structure of birch-spruce stand. A closer study of the primary materials revealed that some cases may involve a phenomenon resulting from a slight unevenagedness; comparison with stands with an over-dense spruce storey indicates the same trend. In addition, removal is fairly great in this diameter class (cf. pp. 97, 101 further below). Another interesting feature is the high number of small trees in age class 240—270. For birch the increase is due to the abundance of stump sprouts. For spruce again, at this stage of development too, it is mostly a matter of old undergrowth individuals of stunted growth, although seedlings growing on decomposed fallen trees and stumps are also found.

Since stem distribution series also have a purely practical value there is some justification for reproducing e.g. the stem distribution series of primary stands with a medium dense spruce storey, adjusted once on the basis of the mean values of the age classes of the original material (cf. Table 12).

In diameter class 1—5 cm, in fairly young stands in particular, a considerable number of the spruces also belongs to the main stand and birches belong to it almost without exception (birches 4—5 cm in diameter may often be 5—6 m high); the figures in brackets indicate the stem number including spruce undergrowth. A prominent feature is the low incidence of diameter class 5—10 cm in the 90-year old stand. The possible causes of this phenomenon have already been indicated above.

The internal structural changes of the various stages of development of a mixed stand of birch and spruce, incidentally, are very clearly seen from this table too. The rapid decrease of birch is particularly striking: e.g. in a 90-year old stand birch and spruce belonging to the main stand are approximately equal in number; a hundred years later birch numbers but one-sixth of the spruce individuals. The shift in mean diameter, however, is similar for both tree species.

Stem distribution curves have also been drawn on the basis of the mean values of certain age groups of secondary stands (Fig. 18). The curves

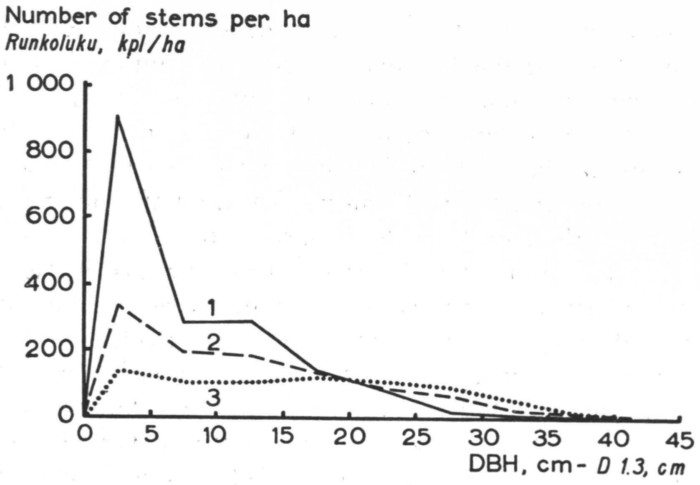


Fig. 18. Curves illustrating the stem distribution of spruce in secondary stands of different age.

Kuva 18. Eri ikäryhmiin kuuluvien sekundäärimetsiköiden kuusen runkojakaantumissarjat.

Age of the stands — *Metsiköiden ikä*

1 = 120 — 150 years — *vuotta*
2 = 170 — 180 » »
3 = 270 » »

have a structure highly similar to those for primary stands, even though they are somewhat flatter for the larger diameter classes. This point emerges from a comparison of curves roughly comparable as far as the age of the different groups goes (Fig. 19).

Stem distribution series for HMT have previously been published only by Ilvessalo (1937), and even then only for spruce stands approx. 200 years old. The material of the present investigation does not permit direct comparison; the mean value of the closest age class is not near enough to 200 years. Interpolation, however, gives us the following comparable figures (Table 13).

The series reveal that the structure of the primary stand mentioned in the example differs even more in its spruce storey from the structure of the HMT spruce stand described by Ilvessalo than from that of the secondary spruce stand. The secondary spruce stand, moreover, contains considerably less birch. Particularly in the biggest diameter classes, most decisive for the structure of the stand, the similarity is obvious.

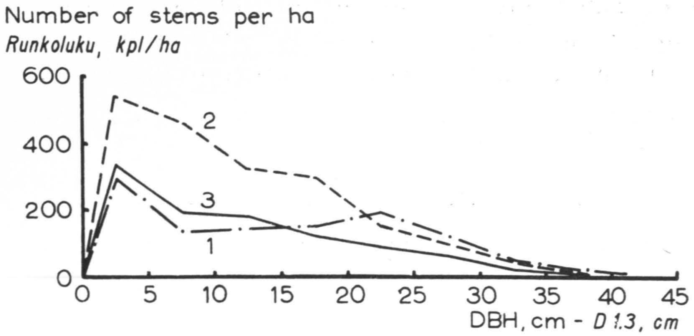


Fig. 19. An example of the structural difference of the stem distribution of the spruce storey in primary and secondary stands at an age of about 180—200 years.

Kuva 19. Esimerkki primääri- ja sekundäärimetsiköiden kuusijakson runkojakaantumissarjojen rakenteellisista eroista noin 180—200 v:n ikäisissä metsiköissä.

1 = primary stand, medium dense spruce storey — *primäärimetsikkö, keskitiheä kuusijakso*
2 = primary stand, over-dense spruce storey — *primäärimetsikkö, ylitiheä kuusijakso*
3 = secondary stand — *sekundäärimetsikkö*

Table 13. Comparison of the stem distribution series of an approx. 200-year old HMT spruce stand (Ilvessalo 1937) with those of evenaged primary and secondary stands.

Taulukko 13. Noin 200-vuotisen HMT-kuusikon (Ilvessalo 1937) ja samanikäisten primääri- ja sekundäärimetsiköiden runkolukusarjojen vertailua.

Stands compared *Vertailumetsiköt*	Diameter class, cm — *Läpimittaluokka, cm*							Total *Yht.*
	< 10	10—15	15—20	20—25	25—30	30—35	35 +	
	Number of stems per hectare — *Runkoluku, kpl/ha*							
Ilvessalo's material *Ilvessalon aineisto*	220	119	144	135	85	38	19	760
Secondary stand *Sekundäärimetsikkö*	180	160	140	100	80	40	20	720
Primary stand *Primäärimetsikkö*	110	130	140	180	140	55	25	780

Table 14. Examples of the stem distribution of birch at different periods of age according to different authors (Ilvessalo's HMT birch stand and the present author's birch storey in primary stands).

Taulukko 14. Esimerkkejä koivun runkojakaantumisesta eri ikäkausina eri tutkijain mukaan (Ilvessalon HMT-koivumetsikkö ja tekijän HMT-primäärimetsikön koivujakso).

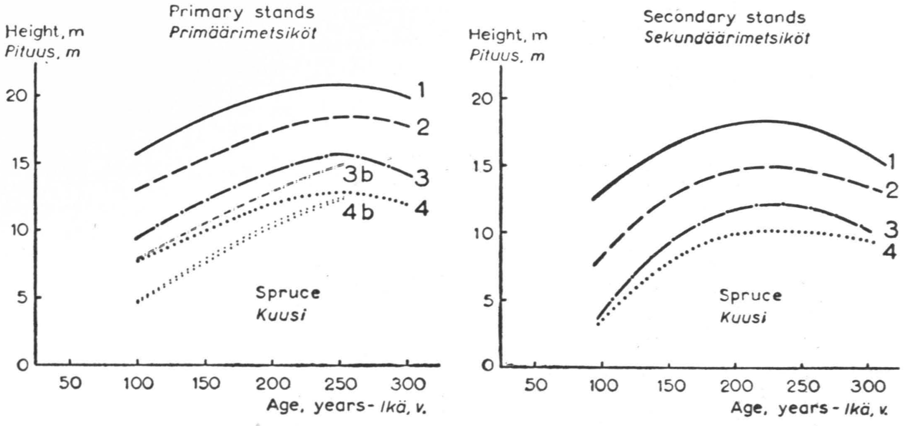
Author *Tutkija*	Age of stands, years *Metsiköiden ikä, v.*	Diameter class, cm — *Läpimittaluokka, cm*				
		< 10	10—15	15—20	20—25	25 <
		Number of stems per hectare — *Runkoluku, kpl/ha*				
Ilvessalo	80	3 272	628	88	12	—
	105	1 360	760	300	68	12
Present author — *Tekijä*	90	1 070	470	75	15	—
	130	160	240	130	30	15

The stem distribution series given by Ilvessalo for HMT birch stands also afford a chance of comparison (1937, p. 57). Although interpolation is necessary in this case too the comparable figures can probably be considered reliable. A closer study shows with surprising clarity the rapid decrease in the proportion of birch in mixed stands on HMT. A comparison of e.g. the 80- and 105-year old HMT birch stands described by Ilvessalo with the mean values obtained from the 90-year and 130-year age groups of the present investigation gives the following figures (Table 14).

The difference in stem number is evident. On the other hand, the internal relations of the various diameter classes do not seem to differ very much. The lower stem number of the birch storey in mixed stands means, however, that trees of large diameter begin to be relatively more frequent in stands older than 100 years, when spruce begins to assume the dominant position, resulting in a rapid disappearance of the smallest birches.

Height

The average height of a stand is quite a good indicator of its general development. This characteristic may be weighted in different ways and applied to different parts of the stand. Here the following average heights of both the principal tree species will be given:



20 21

Figs. 20 and 21. Development of the average height in the different parts of the spruce storey in primary and secondary stands. (The figures refer to Figs. 13 and 14.)

Kuvat 20 ja 21. Primääri- ja sekundäärimetsiköiden kuusijakson eri osien keskipituuden kehitys. (Numeroiden selitys ilmenee kuvista 13 ja 14.)

(a) the average height of all trees exceeding 1.3 m H_P (cf. p. 60),

(b) of the trees belonging to the main stand (H_M),

(c) of the trees belonging to the dominant crown layer H_D,

(d) the so-called dominant height.[1]

All average height values have been weighted only by the stem number of each diameter class. The smoothed curves of Figs. 20—22 show the mean values of the heights of the two main tree species, and Tables 15 and 16 the development of the average height in the stands of different successions.

The development of the average height in primary stands shows that the birch storey of the main stand has been higher than the spruce up to the age of 130 years, after which the spruce storey finally grows through the crown canopy of birches. But the spruce trees of the dominant crown layer and the dominant trees of the spruce storey are higher than the corresponding members of the birch storey from the age of 60—80 years onwards, and the difference continues to increase with the age of the stand. This paradox is a natural result of the lengthy period

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[1] Represented by the mean value of the height of the 100 highest trees within a hectare.

Table 15. Development of the average height of primary stands.

Taulukko 15. Primäärimetsiköiden keskipituuden kehitys.

Age *Ikä*	Spruce storey — *Kuusijakso* Dominant trees *Valtapuut*	Dominating crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö* Medium dense *Keskitiheä*	Main stand *Päämetsikkö* Over-dense *Ylitiheä*	Main stand + undergrowth *Päämetsikkö + alikasvos* Medium dense *Keskitiheä*	Main stand + undergrowth *Päämetsikkö + alikasvos* Over-dense *Ylitiheä*	Birch storey — *Koivujakso* Dominant trees *Valtapuut*	Dominant crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*	Main stand + undergrowth *Päämetsikkö + alikasvos*
	Average height, m — *Keskipituus, m*									
60	11.5	10.5	7.0		6.0		11.0	9.0	8.0	9.3
80	13.5	12.0	8.5		7.0		13.5	11.0	9.5	11.6
100	15.5	13.0	9.5	8.0	8.0	5.0	14.5	12.0	10.5	13.9
120	16.5	14.0	10.5	9.0	8.5	6.0	15.0	12.5	11.0	(15.0)
140	17.5	15.0	11.5	10.0	9.5	7.5	15.5	13.0	11.5	
160	18.5	16.0	12.5	11.0	10.5	8.5	15.5	13.5	12.0	
180	19.5	16.5	13.5	12.0	11.0	9.5	15.5	14.0	12.0	
200	20.0	17.0	14.5	13.0	11.5	10.5	15.0	14.5	12.5	
220	20.5	17.5	15.0	14.0	12.5	11.5				
240	21.0	18.0	15.5	15.0	13.0	12.5				
260	21.0	18.5	15.5	15.5	13.0	13.0				
280	20.5	18.5	15.5		13.0					
300	20.0	18.0	14.5		12.0					
330	17.0									

Table 16. Development of the average height of secondary stands.

Taulukko 16. Sekundäärimetsiköiden keskipituuden kehitys.

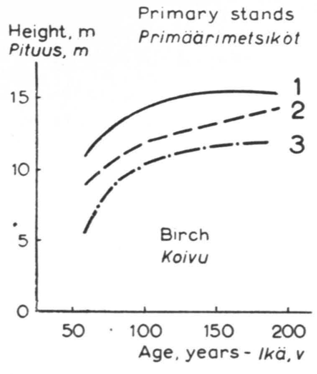
Age *Ikä*	Spruce storey — *Kuusijakso* Dominant trees *Valtapuut*	Dominant crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö* Present author *Tekijän mukaan*	Main stand *Päämetsikkö* Referring to Ilvessalo *Ilvessalon mukaan*	Main stand + undergrowth *Päämetsikkö + alikasvos*	Dominant height, Ilvessalo *Ilvessalon valtapuut*	Birch storey — *Koivujakso* Dominant trees *Valtapuut*	Dominant crown layer *Vallitseva latvuskerros*	Main stand *Päämetsikkö*	Referring to Ilvessalo *Ilvessalon mukaan*
	Average height, m — *Keskipituus, m*									
60	10.0					6.5				
80	11.5					9.0				7.2
100	13.0	8.5	4.0			11.0	7.0	9.0	5.0	9.3
120	14.5	10.0	6.5			12.7	8.0	10.0	6.0	10.7
140	15.5	12.0	8.5		(7.5)	14.2	10.0	11.5	7.5	
160	16.5	13.0	10.0		8.5	15.6	13.0	13.5	10.5	
180	17.0	14.0	11.0	10.4	9.5	16.8	15.5	15.5	14.0	
200	18.0	14.5	12.0	11.2	10.0	17.9				
220	18.5	15.0	12.5	11.9	10.5	18.8				
240	18.5	15.0	12.5	(12.5)	10.5	19.5				
260	18.0	14.5	12.0		10.0	20.0				
280	17.0	14.5	11.5							
300	16.0	14.0	10.5							

of dominance of the birch storey, during which the dominant crown layer is almost exclusively composed of birch. The rapidly developing spruces, growing in the gaps between the birches, emerge before long like thorns in the even birch crown canopy. Spruces growing in groups of birches have on the contrary seldom been spared the whipping injuries that interfere with their height growth and have also seldom been able to penetrate into the dominant crown layer. Most individuals of the spruce storey usually remain in a dominated position until the heavy removal of birches at about the age of 80—120 years suddenly increases the spruce's chances of attaining a dominant position.

In addition, distinct differences exist in the average height of main stands representing the different density classes of the spruce storey. Due to the higher stem number, the average height of over-dense spruce storeys initially at least remains smaller than that of medium dense. The difference increases if the individuals belonging to the undergrowth are included in the calculation of average height.

A comparison of the different successions reveals that comparable average height values in one and the same age class of main tree species almost without exception are higher in primary stands than in secondary stands. This finding warrants the following conclusion: In so far as height can be considered a characteristic of soil fertility, as is customary in Central Europe and in the Scandinavian countries, the greater height of primary stands indicates better growth conditions although the original qualities of the sites are identical.

In a comparison of the average heights of HMT stands as reported by Ilvessalo with those given in the present investigation attention is aroused, firstly, by the greater height of the birch storey of primary stands. But it must be remembered that Ilvessalo's birch stands were pure, without an appreciable mixed tree species accelerating the removal of the suppressed birches. In other words, the structure of Ilvessalo's birch stands differed considerably from that of the birch storey in the primary stands of the present investigation. Fig. 22 in fact reveals that the frequency of dominated birch individuals cannot have been very high as the average height of the main stand was only 1.5—2.0 m below that of the dominant birches. — Ilvessalo's dominant height of the HMT spruce stand, which offers another point of comparison, was not, because of its method of determination, fully comparable, with the



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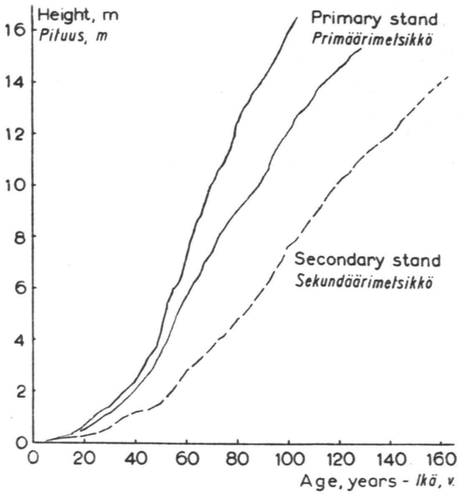

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Fig. 22. Development of the average height in the different parts of the birch storey in primary stands. (The figures refer to Figs. 13 and 14).

Kuva 22. Primäärimetsiköiden koivujakson eri osien keskipituuden kehitys. (Numeroiden selitys ilmenee kuvista 13 ja 14).

Fig. 23. An example of the different height growth rate of representative dominant trees in adjacent primary and secondary stands.

Kuva 23. Esimerkki edustavien valtapuiden erilaisesta pituuskasvusta rinnakkaisissa primääri- ja sekundäärimetsiköissä.

dominant height computed in the present investigation. This may be another reason why a considerable difference — admittedly one that decreases with age — is observable.

A comparison of the average heights of the main stand in Ilvessalo's investigation (1937) and of different successions in the present investigation reveals that only the series describing the average height of secondary stands has some similarity to Ilvessalo's series for the average height of HMT spruce stand. In spite of the disputable comparability of the dominant height, a certain similarity is observable in this characteristic too.

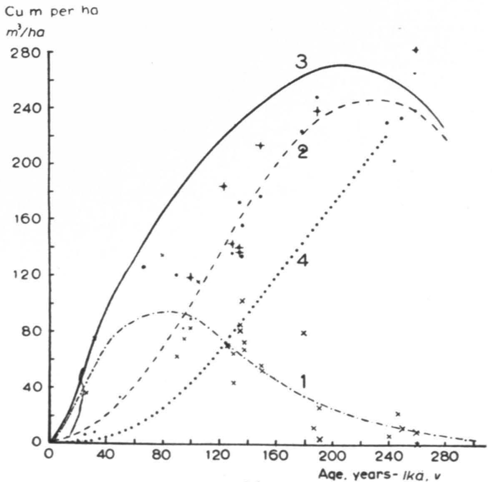
One to three stem analyses of the spruces belonging to the dominant crown layer were made in connection with age determination on the sample plots in both primary and secondary stands. The material thus collected cannot be published in its entirety in this place however. A typical example of the dissimilarity of height growth in the different successions is shown in Fig. 23 with curves illustrating the development of the height of three representative dominant trees selected from adjacent sample plots. All the parallel sample plots reveal a similar picture of the height growth. The dominant trees of the spruce storey in primary stands were usually considerably more rapid in growth than their counterparts in secondary stands.

Volume

The development of both the diameter and height of trees in HMT stands of different successions and partly of different density groups has been described in the foregoing. These characteristics are, besides the stem number, the most important part-characteristics of stand volume that have to be known for a calculation of the volume of the growing stock. The fourth factor required for volume determination, taper, has been measured in the way presupposed by Ilvessalo's volume tables (1947). It does not in itself require a detailed study in this connection.

Due to the fact that the density figures (cf. p. 41) of primary stands with a medium dense spruce storey vary between 0.7—1.0, it was considered appropriate to divide the material for this part into two groups: density classes 0.7—0.8 and 0.9—1.0, normally-stocked respectively fully-stocked sample plot stands. The plots with an over-dense spruce storey naturally form a special group; further below (p. 85) the conclusion is arrived at that they are in the first place comparable with fully-stocked sample plots. A similar grouping would naturally have been appropriate for secondary stands too, but this would have meant over-dispersion of the limited material as the densities vary no less than 0.6—1.0. However, in order to achieve some kind of comparability with the normally-stocked primary stands at least the extreme density classes of secondary stands, 0.6 and 1.0, have been excluded from the graph of the original material, the only purpose of which is to enable a comparison of the different tree generations based on unadjusted original material.

The volumes of the sample plot stands are shown in Appendix 1. The same table also includes cautiously corrected values for the volume of sample plot stands not completely stocked, to make them comply with true circumstances. Its purpose is to indicate the potential minimum volume of the stand in question assuming it to be fully-stocked with the present composition of tree species. To illustrate the material, diagrams describing volume development in stands representing different successions and density classes are given, with the original, uncorrected values, in Figs. 24—26.



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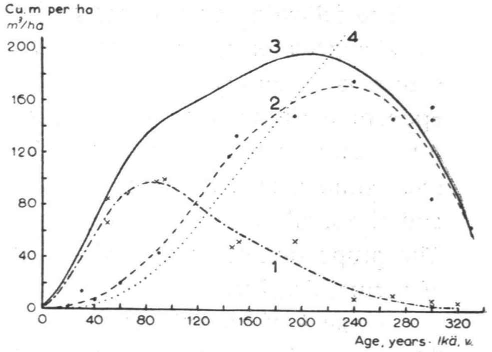

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Fig. 24. The development of the growing stock in primary stands on the basis of original values from fully-stocked sample plots. The signs + represent stands with over-dense spruce storey.

Kuva 24. Primäärimetsiköiden säilyvän puuston kuutiomäärän kehitys täysipuustoisten näytealojen alkuperäisarvojen perusteella. Pystyristit edustavat näytealametsiköitä, joissa kuusijakso on ylitiheä.

1 = volume of birch storey — *koivujakson kuutiomäärä*
2 = volume of spruce storey — *kuusijakson kuutiomäärä*
3 = volume of both storeys together — *molempien jaksojen kuutiomäärä yhteensä*
4 = volume of HMT spruce stand according to Ilvessalo — *HMT-kuusikon kuutiomäärä Ilvessalon mukaan.*

Fig. 25. The development of the growing stock in primary stands on the basis of original values from normally-stocked sample plots. (The figures refer to Fig. 24.)

Kuva 25. Primäärimetsiköiden säilyvän puuston kuutiomäärän kehitys normaalipuustoisten näytealojen alkuperäisarvojen perusteella. (Numeroiden selitys ilmenee kuvasta 24.)

From the dots of Fig. 24 (fully-stocked stands) it is found that no great difference is observable between the volumes of the spruce storeys of different degrees of density; the lower stem number of sample plot stands with a medium dense spruce storey is compensated by a slightly greater mean diameter and average height (cf. Baker 1953). Mathematically, the curves reveal a high degree of similarity. For this reason a single volume curve, independent of the density of the spruce storey, is given for fully-stocked stands (0.9—1.0). Normally-stocked (0.7—0.8) sample plots (Fig. 25) contain only a medium dense spruce storey.

The following points emerge from the diagrams:

The peak of the volume curve of the spruce storey in fully-stocked stands is definitely higher than that of normally-stocked stands, but it appears at the same age in both cases. The course of the volume curve of the birch storey is on the other hand similar in both density classes. The causes seem simple: the higher absolute amount of spruce accounts for the former and the similarity of the birch storey in both density classes for the latter. The proportion of dominated birches in the volume is low even in stands of normal density.

The peak of the volume curve of birch seems to come at approximately 80 years, independent of the density conditions mentioned, upon which a relatively slow decrease, due to the gradual removal of birch, sets in and persists until the final stages of development of the succession in question. The removal, which cannot be discussed in any greater detail in this connection, consists initially of the trees of the birch storey that at any given time are smallest, but as early as between the ages of 150—200 years plenty of dominant birch trees also are removed. The ensuing stump sprouts do but little to replace the volume loss.

The volume curve of spruce indicates that spruce develops considerably more slowly in the early stages than birch. However, the increase in the volume of spruce storey is even, reaching its peak at 220—240 years. Subsequently a slow starting decrease in the growing stock sets in, accelerating rapidly into a veritable »crash».

A stand of trees, roughly evenaged from the outset, which has reached maturity cannot for biological reasons (cf. e.g. Paech 1940) remain a more or less static colonnade for ever. The general physiological weakening resulting from advancing age leads before long to the death of individual trees, even if secondary causes of death can vary widely from tree to tree. To begin with, the trees die singly, but before long the majority of the trees begin to wither. They soon fall, either dried up or sometimes still surviving in their old age, battered by storms, leaving the remaining trees still more exposed to the final catastrophe. Similar destruction of old living stands has been reported by e.g. Iwashkevitsh (1930) and Jones (1945).

On this point the diagrams based on the original material therefore call for a reconsideration of the general opinion on the natural development of spruce forests, i.e. that it ends in a static state of climax (cf. e.g. Kalela 1945).

The curve of birch and spruce together, showing the development of total volume (the impurities = mixed species of minor importance are disregarded) rises sharply up to the age of 80, after which the volume grows evenly up to the age of 220 years. From the above separate surveys of birch and spruce such a development seems self-evident.

A comparison of the above curves with Ilvessalo's volume curve for HMT spruce stands reveals that the curve of the total volume of normally-stocked stands with medium dense spruce storey throughout differs from the curve published by him. The difference is greater still for fully-stocked stands, where the volume curve (cu.m solid measure) of the spruce storey only runs a considerably higher course than that of Ilvessalo's HMT spruce stand (1937, p. 70).

The diagram of the growing stock in secondary stands based on original values (Fig. 26) reveals the following:

The general course of the volume curve of the spruce storey is similar to that in normally-stocked primary stands, though somewhat flatter, particularly at the outset. Culmination occurs in secondary stands also at about 220 years, with a subsequent sharp fall in volume. The climax stage, moreover, seems of shorter duration than in the primary succession. Rottenness is probably a very important factor in this connection (cf. e.g. Tikka 1932, 1934 etc.). For birch, the material seems to indicate a fairly modest proportion in secondary stands. This is comprehensible, considering the poor chances of regeneration; the vast majority are sprout birches of poor growth.

Because of the low proportion of birch, the curve for both storeys together naturally cannot assume nearly the same shape as that for normally-stocked primary stands. The former is considerably flatter. This helps to emphasize the dissimilarity between primary and secondary successions. Comparison with the volume curve (cu.m solid measure) of Ilvessalo's HMT spruce stand shows that it runs a slightly higher course than the volume curve of the spruce storey of secondary stands of normal density but is slightly flatter than the total volume curve of the secondary stands. As Ilvessalo's curve apparently includes the mixed tree species of minor importance too the similarity is no less than surprisingly great.

The comparison of the volume curves of different successions, however,

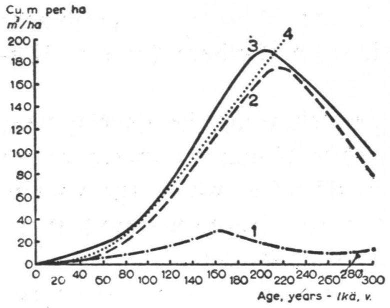

Fig. 26. The development of the growing stock in secondary stands on the basis of original values from normally-stocked sample plots. (The figures refer to Fig. 24.)

Kuva 26. Sekundäärimetsiköiden säilyvän puuston kuutiomäärän kehitys normaalipuustoisten näytealojen alkuperäisarvojen perusteella. (*Numeroiden selitys ilmenee kuvasta 24.*)

can only be effected on a realistic basis after the material has been made comparable as regards density. For instance, normally-stocked primary and secondary stands have been compared above. However, a vast majority of the sample plot stands representing primary stands were fully-stocked. In order that these stands too may be included in the comparison the whole material must be corrected to terms of full density (Appendix 1). The original curve of fully-stocked primary stands and the corrected curve of all primary stands are very nearly identical. But the conversion of stands to full density values affects the diagrams of secondary forests somewhat more markedly. Secondary stands originate when the primary overmature stands have become ruined, a fact for which allowance has been made in the diagram below. The birth of the seedling stand that will in due course constitute the principal growing stock of the secondary tree generation has been reckoned from the time that the primary tree generation attained the age of 300. At that time a considerable amount of unoccupied space is available in a ruined primary stand. This gives a development cycle consisting of two successions covering a period of 600 years. At the very first glance it discloses a point of remarkable interest (Fig. 27).

A comparison of the extant stands of primary and secondary origin shows that the timber yield capacity of stands belonging to the primary succession, i.e. stands originating after forest fire, is considerably higher than the timber yield capacity of spruce stands of the secondary succession, i.e. stands following immediately on the primary succession without an intervening fire. Should the study be extended to cover the total growth, the above difference is accentuated, for natural removal, particularly in the case of birch, is exceedingly high in primary stands.

In view of the above it seems possible that Ilvessalo's (1937)

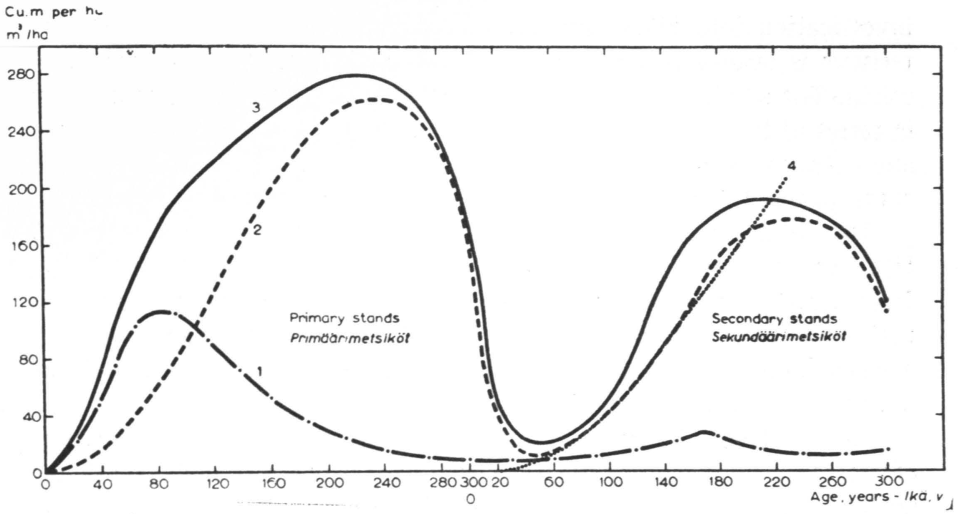

Fig. 27. Development of growing stock volume from origo after forest fire up to the secondary post-climax stage in HMT stands converted to full density.

Kuva 27. Täystiheiksi muunnettujen HMT-metsiköiden säilyvän puuston kuutiomäärän kehitys metsäpalon jälkeisestä primäärivaiheesta sekundääriseen post-klimaksvaiheeseen saakka.

Table 17. Comparison of the volumes of the growing stock of different HMT stands.

Taulukko 17. Erilaisten HMT-metsiköiden elävän pystypuuston kuutiomäärän vertailua.

Age *Ikä*	Primary stands *Primäärimetsiköt*		Secondary stands *Sekundäärimetsiköt*		Ilvessalo's HMT spruce stand *Ilvessalon HMT-kuusikko*
	spruce storey *kuusijakso*	main stand *pääpuusto*	spruce storey *kuusijakso*	main stand *pääpuusto*	
	Volume of growing stock, cu.m per hectare — *Puuston kuutiomäärä, m³/ha*				
40	16	70	5	15	4
80	60	180	26	36	24
120	127	218	64	80	64
160	198	250	119	145	114
200	250	276	170	188	168
240	262	278	178	190	(210)
260	250	260	170	180	—

investigation into HMT spruce stands and their mensurational characteristics is largely based on material collected from stands of secondary origin. The similarity is more evident still from the following comparison in terms of figures between the different tree generations on the one hand and between them and the figures obtained from Ilvessalo's volume curve (Table 17) on the other.

The table reveals above all the similarity between Ilvessalo's HMT spruce stand and the secondary stand described in the foregoing. Also apparent are the slow development of secondary stands and their small volume at culmination, i.e. at about 240 years of age. The most marked difference is between Ilvessalo's HMT spruce stand and fully-stocked primary stand in the present investigation.

Further below, in connection with the description of the development of vegetation on HMT, it is suggested that primary succession phases should not be considered plant communities of HMT so much as of MT. To illustrate the point, the primary stands of HMT are compared with GDMT (spruce) and EVT (pine) (Table 18). Unfortunately no data are available on the MT of North Finland. In addition, the table includes the volume figures of MT pine stands and spruce stands in South Finland.

Table 18. Comparison of the growing stock volume of the primary stands on HMT with Ilvessalo's volume of the spruce stands and pine stands on different forest site types in North and South Finland.

Taulukko 18. HMT-primäärimetsiköiden puuston kuutiomäärän vertailua Ilvessalon Pohjois- ja Etelä-Suomen eri metsätyyppien kuusikoiden ja männiköiden kuutiomäärään.

Age *Ikä*	HMT (present author) *tekijä*		GDMT	EVT	Age *Ikä*	MT South Finland *Etelä-Suomi* (Ilvessalo)		% B/D	% E/F
			North Finland *Pohjois-Suomi* (Ilvessalo)						
	spruce storey *kuusijakso* A	main stand *pääpuusto* B	spruce *kuusi* C	pine *mänty* D		spruce *kuusi* E	pine *mänty* F		
	Volume of growing stock, cu.m per hectare — *Puuston kuutiomäärä, m³/ha*								
40	16	70		(110)	20	21	60	59	30
80	60	180		243	40	114	200	73	57
120	127	218		272	60	249	313	*80*	*79*
160	198	250	165	285	80	366	407	*88*	*90*
200	250	276	257	294	100	445	472	*94*	*94*
240	262	278	(330)		120	480	507		

A comparison between the present author's HMT primary tree generation and Ilvessalo's GDMT[1], a forest site type considerably superior to MT[2], indicates that Ilvessalo's growing stock volume on northern MT might be even smaller than that of the present author's primary stands on HMT, at least up to the age of 200 years. A comparison with EVT[3], inferior to MT, shows that pine on EVT gives a better yield than spruce plus birch (Column B) in primary stands on HMT. However, the ratios indicate clearly that in time spruce forest catches up with the gain made by pine in its early years. This phenomenon is also visible in the South Finnish forests which develop much faster, at approximately double the above rate; by way of examples may be mentioned the spruce stands and pine stands of MT (Ilvessalo 1920 b). The similarity of the percentages of these stands justifies the assumption that HMT growing pine really gives — as assumed long ago by Heikinheimo, Lakari and Ilvessalo — a timber yield at least equal to that of EVT. This is in a way verified by investigations. Due to the fact that the pine stands studied for this very purpose are artificially regenerated (mainly by Prof. Olli Heikinheimo), the volume of their growing stock even slightly exceeds that of naturally regenerated EVT (cf. Sirén 1952).

This brings up the question of whether HMT, if growing pine after a forest fire or controlled fire, develops into EVT and whether EVT growing spruce develops into HMT. This problem, however, falls outside the range of the present investigation and must be left to future research. Either one of the two forest site types may well, by the present definition, prove to be, as a forest site type reflecting the timber yield capacity of a site quality, a variant of the other depending on the tree species occupying the site.

The results reported above permit the following conclusions:

The volume of the growing stock of the first birch-spruce generation after fire, i.e. of the primary HMT stands, is considerably greater in all stages of development than that of the corresponding stand of the next generation, i.e. of the secondary HMT stands. It is beyond dispute, therefore, that natural regeneration of spruce to replace an old spruce forest leads to a stand of deficient yield.

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[1] GDMT = *Geranium-Dryopteris-Myrtillus* type.
[2] MT = *Myrtillus* type.
[3] EVT = *Empetrum-Vaccinium* type.

That Ilvessalo gained an unfavourable impression of the site quality of North Finnish HMT is evidently due to the fact that his investigations apparently were mainly concerned with secondary stands on HMT, and these at the present moment are still in many places prominent on the fresh sites of North Finland. The potential site quality of these fresh sites, however, is definitely higher in reality than the actual site quality established by Ilvessalo. It is probable that primary stands growing spruce have as a rule been referred to MT whereas secondary stands have been classified under HMT.

The succession curves of growing stock volume indicate that HMT as a forest site type is dynamic and not static, both in its composition of tree species and its yield. A comparison between EVT pine stands and HMT primary stands indicates, furthermore, that the site quality classification of North Finnish forest site types requires revision.

Volume distribution series

The primary and secondary stands studied in the foregoing have been found to differ considerably in many respects. To establish the difference between the various successions requires a study also of the volume distribution series of the sample plot stands concerned. Volume distribution by diameter classes has been given primarily in terms of mean values for age groups. To indicate the internal variation of the material the primary distributions of the sample plot components of a certain age group are quoted. Since the distribution of volume into different diameter classes in a way emphasizes certain important points better than the distribution of diameter, it is interesting to see the extent to which the former characteristic sheds new light on the structure of the growing stock of the different tree generations already reviewed from other angles.

The study can well be based on the diagrams (Fig. 28) of volume distribution by diameter classes drawn from the mean values of age classes in the original material.

The most prominent difference is that primary stands with a medium dense spruce storey reveal a wider amplitude of diameter variation than those with an over-dense. The transition to the larger diameters with advancing age, apart from a few irregularities, follows largely the rules which Cajanus (1914), Ilvessalo (1920 a) and Lönnroth

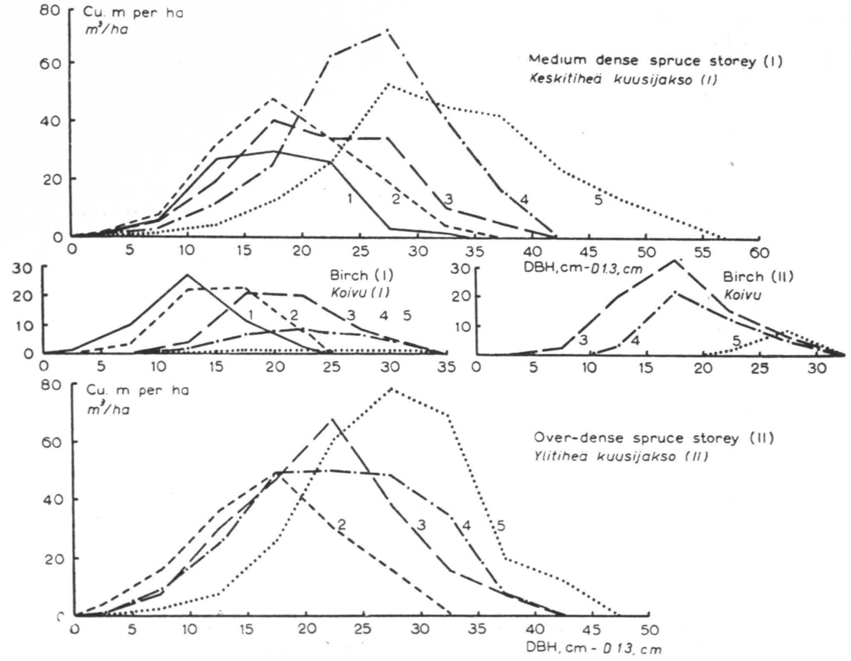


Fig. 28. Curves illustrating the volume distribution of spruce and birch in primary stands of different age. (The figures refer to Figs. 16 and 17.)

Kuva 28. Eri ikäryhmiin kuuluvien primäärimetsiköiden kuusen ja koivun kuutiomäärän jakaantumissarjat. (Numeroiden selitys ilmenee kuvista 16 ja 17.)

(1925) found to govern pure stands. It is particularly interesting to find that the volume of birch is composed almost exclusively of big trees once the stands are approximately 180 years old; however, birches remain definitely smaller in diameter than the biggest spruces.

The main feature disclosed by the volume distribution series of secondary stands is the insignificance of birch and the slow initial development

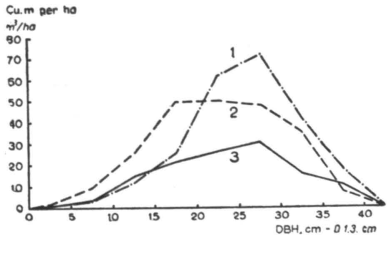
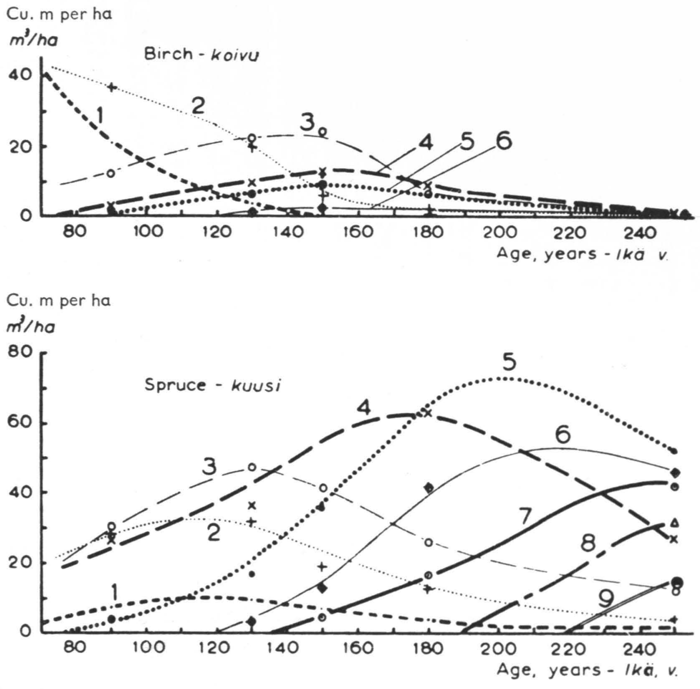


Fig. 29. An example of the structural difference of the volume distribution of the spruce storey in primary and secondary stands. (The figures refer to Fig. 19.)

Kuva 29. Esimerkki primääri- ja sekundäärimetsiköiden kuusijakson kuutiomäärän jakaantumissarjojen rakenteellisista eroista. (Numeroiden selitys ilmenee kuvasta 19.)



Figs. 30 and 31. Adjustment of the volume of the different diameter classes on the basis of primary values of birch and spruce storey.

Kuvat 30 ja 31. Koivu- ja kuusijakson eri läpimittaluokkien kuutiomäärän tasoitus primääriarvojen perusteella.

Diameter classes, cm — *Läpimittaluokat, cm*

1 = 0—10
2 = 10—15
3 = 15—20
4 = 20—25
5 = 25—30
6 = 30—35
7 = 35—40
8 = 40—45
9 = 45 +

of spruce. To provide an illustrative comparison, Fig. 29 shows the average volume distribution by diameter classes in approximately evenaged primary and secondary stands.

It is comprehensible that the highest proportion of large trees occur in stands with a medium dense spruce storey. It is also natural that the proportion of the lowest diameter classes in over-dense spruce storeys, both absolutely and relatively, is considerably greater than in medium dense spruce storeys. Both diagrams indicate also that the volume of primary stands considerably exceeds that of secondary. Naturally the quantities are not fully comparable, mainly due to the slightly different density of the stands, but not even a conversion to full density values would change the essential features of the results.

It is of course possible to give numerical volume distribution series based on mean values computed by age classes, but obviously even then coincidental factors may over-accentuate a detail and produce a misleading impression. This is why some sections of the series have had to be smoothed.

Here too a somewhat simplified modification of Ilvessalo's (1937) adjustment method has been employed in working out the distribution of volume by diameter classes.

The necessary adjustment can be effected directly on the basis of the primary values or the mean values of age classes. In this case the number of operations is reduced to one. Figs. 30 and 31 show examples of this method. They reveal that the principle of correcting for the biological shift of diameter has led to an indisputable marking down of the original values only for 20—25 cm diameter spruce in the 150 year age class. The birch volume diagram everywhere adheres to the mean values given. The volume distribution table worked out from these diagrams assumes the following form (Table 19).

Table 19. Distribution of the volume of spruce and birch into diameter classes, based on one adjustment of primary stands values.

Taulukko 19. Primäärimetsiköiden yhteen tasoitukseen perustuva kuusen ja koivun kuutiomäärän jakaantuminen läpimittaluokkiin.

Diameter class, cm *Läpimittaluokka, cm*	Age and storeys of the stand — *Metsikön ikä ja jaksot*									
	80		120		160		200		240	
	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*
	cu.m per hectare — *m³/ha*									
10	5	40	10	7	6	—	2	—	1	(1)
10—15	24	41	32	27	20	4	9	2	5	1
15—20	23	11	44	22	37	19	21	6	15	1
20—25	20	2	37	9	60	12	55	7	34	2
25—30	1		13	6	46	9	72	6	58	2
30—35			0	1	22	2	48	2	50	2
35—40					9	—	26	—	43	—
40+							7	—	42	—
Total *Yhteensä*	72	94	138	72	200	46	240	23	248	9

Almost all the figures given above are identical with those arrived at by Ilvessalo's adjustment method.

The greatest importance of stem and volume distribution series lies in their deciding whether or not the collected populations of the original material belong to identical series. Only mathematically we can reach an unequivocal decision. Since the material of the present investigation is rather limited for statistico-mathematical study it was considered best to abandon the attempt. Hence the homogeneity of the growing stock can only be assessed from the diagrams given. Considering the character of the stands studied, the course of the diagrams, apart from the irregularity mentioned above, is surprisingly even and follows the customary mensurational rules of diameter shift. In other words, as regards growing stock too the material may be considered at least satisfactorily homogeneous.

Natural removal

It has been seen how the growing stock of primary stands on HMT reaches its climax stage in some 220—240 years. The equilibrium attained is not, however, permanent. Continuous changes persist in the structure of the stand, however, and result before long in rapid deterioration. The climax stage of a primary stand, therefore, constitutes a state of unstable equilibrium followed — after an intervening mass death — by a new succession in the form of a secondary stand.

The deterioration of the matured stand is in fact only natural removal of unusual intensity. »Lack of space», due to competition, comes into play at a fairly early stage in dense stands; it results in the death of the tree individuals weakest at any given time. The number of dead standing trees at a point of time therefore reflects the intensity of the natural removal resulting from a »lack of living space» caused by the growth of the tree individuals.

Because dead trees do not remain standing very long, it is important to know also the number of dead trees in different stages of decomposition that have fallen to the ground. Combining these two figures gives some idea of the structure of natural removal.

The dead standing trees were counted in connection with the tree-tally on the sample plots. As many individuals had lost their bark it was preferred for the present purpose to group together in 5 cm classes the trees originally classified by 1 cm classes. The mean values, by age groups, are given in Table 20 by successions, tree species and diameter classes.

Table 20. Average number per hectare of dead standing trees in primary and secondary stands.

Taulukko 20. Primääri- ja sekundäärimetsiköiden pystyyn kuolleiden puiden lukumäärä keskimäärin hehtaaria kohden.

Diameter class, cm *Läpimittaluokka, cm*	Primary stands — *Primäärimetsiköt*																	
	Age groups and densities of spruce storey *Kuusijakson ikäryhmät ja tiheys*											Age groups of birch storey *Koivujakson ikäryhmät*						
	80—104		125—137		145—150		180—195		240—270		300—330	50—51	80—104	125—137	145—150	180—195	240—270	300—330
	I	II	I	II	I	II	I	II	I	II								
	Average number of dead standing trees per hectare — *Pystyyn kuolleita puita keskimäärin, kpl/ha*																	
< 1.3 m	48	120	13	277	23	120	8	120	8	0	14							
1—5	11	220	166	842	137	325	56	186	20	24	21	1 035	311	6	1	1	10	2
5—10	3	20	51	47	13	5	10	54	12	8	9	10	185	74	4	2	5	1
10—15	2	—	1	4	4	—	13	17	5	16	15		12	64	20	21	2	2
15—20			(3)	—	2	—	8	—	5	8	14		2	19	20	13	2	—
20—25			(2)	—	—		1	10	5	8	13		—	—	3	4	—	1
25—30									4		17		—	—			1	
30+									10		15		1	2				
Total *Yhteensä*	74	360	231	1 150	179	450	96	387	69	64	118	1 045	511	165	48	41	20	6

Diameter class, cm *Läpimittaluokka, cm*	Secondary stands — *Sekundäärimetsiköt*					
	Age groups of spruce storey — *Kuusijakson ikäryhmät*				Age groups of birch storey — *Koivujakson ikäryhmät*	
	120—150	170—180	260—270	300	170—180	200—270
	Average number of dead standing trees per hectare — *Pystyyn kuolleita puita keskimäärin, kpl/ha*					
< 1.3 m	48	10	9	5	13	1
1—5	164	16	5	12	19	11
5—10	85	10	5	6	9	4
10—15	35	5	4	11	27	7
15—20	18	1	5	—	15	1
20—25	3	3	3	6	4	2
25—30	5	4	7	5	1	2
Total *Yhteensä*	358	50	38	45	88	28

I = medium dense — *keskitiheä,* II = over-dense — *ylitiheä.*

The table shows, firstly, that only for spruce, and then only partially, is a comparison of stands of different successions possible. The removal in primary stands with a medium dense spruce storey is fairly high, reminiscent of that in secondary stands; the only difference is that a considerably higher number of large trees is removed from the former at a late age. Fairly large trees may be removed from young secondary stands too; but they are then usually relicts of the former tree generation.

A study of the removal shows further that in primary stands the removal from over-dense spruce storeys is considerably heavier, quite naturally, than from medium dense. Removal in the former stands affects more small trees proportionately than in the latter. With advancing age the diameter of the dead standing trees increases. For spruce, the removal seems to be at its heaviest numerically between approx. 80—200 years, lightest during the climax stage. Deterioration of a spruce storey manifests itself as a heavy removal of large trees, especially at the age of about 300 years, during the post-climax period.

For birch, the sharpest fall in stem number occurs at a very early stage. The diameter of the removed trees increases and their number drops simultaneously to a fraction of what it was, say, at the age of 50 years. In the oldest age classes the overall result is disturbed by the early removal of numerous stump sprouts.

Few numerical series are available on secondary stands; however, they reveal approximately similar trends for the different tree species as the series on primary stands.

The dead trees, as pointed out above, remain standing for a short time only; the small birches especially last a few years only, and a living spruce may often fall down straightaway without passing through an intervening stage of dead standing tree. This makes it necessary to include the dead fallen trees in a determination of the total removal. The interval elapsing from the time of death can be estimated approximately from the state of decomposition of the tree. In the present instance the classification was made according to Arnborg's (1943, p. 44) grading, however with the difference that in assembling the results it was found preferrable to refer the four »youngest» stages to a single class and the next two to one class. This reduced the number of classes for spruce to four (Table 21).

Table 21. Ratio between the state of decomposition and the »age» of fallen spruce trees.

Taulukko 21. Kuusi-maapuiden maatumisasteen ja »iän» väliset suhteet.

Decomposition class by — *maatumisasteet* Present author — *Tekijän*	Arnborg — *Arnborgin*	Description of fallen tree — *Maapuun kuvaus*	Approx. »age» of fallen tree, years — *Maapuun »ikä», v.*
1	1—4	Wood hard — fairly soft *Puu kovaa — pehmeähköä*	0—20
2	5—6	Wood soft — disintegrating *Puu pehmeää — murenevaa*	about 35 *noin*
3	7	Semi-decomposed and sunk into ground — *Puoleksi maatunut ja maahan vajonnut*	about 50 *noin*
4	8	Almost totally decomposed, barely discernible — *Miltei kokonaan maatunut, vain vaivoin eroitettavissa*	over 70 *yli*

The rate of decomposition naturally depends on a number of factors; the most important among them are the tree species, size, freshness of the tree, and position in relation to the soil surface and protection from rain. For instance, a dry fallen tree does not decompose nearly as soon as a fresh one of the same size. Birch decomposes much more rapidly than spruce; only the bark of the birch is very durable. This point is illustrated e.g. by the fact that large pieces of birch-bark are found in the lower part of the raw humus in secondary forests even. The following periods of years corresponded to the different degrees of decomposition of birch:

(1) hard wood; maximum of 10 years after death
(2) disintegrating wood; maximum of 25 years after death
(3) decomposed wood; some 40 years or more after death.

This classification applies primarily to trees 10—20 cm in diameter. The decomposition of very small trees (diameter less than 5 cm) takes approximately half the time. Bearing in mind the slow rate of decomposition in North Finland, primarily due to the cold climate, the above degrees of decomposition are well comparable with the results published by Sarvas for stumps in South Finland (1944) and North Finland (1950).

Due to the fact that it was sometimes difficult to measure the diameter of fallen trees (decomposed birches in particular had broadened), the

Table 22. Number of fallen trees in primary and secondary stands of different age, by tree species and degree of decomposition.

Taulukko 22. Eri ikäryhmiin kuuluvien primääri- ja sekundäärimetsiköiden maapuiden lukumäärä puulajeittain ja maatumisasteittain.

Age of stands, years *Metsiköiden ikä, v.*	Primary stands (medium dense spruce storey) — *Primäärimetsiköt (kuusijakso keskitiheä)*								
	Fallen trees of spruce storey — *Kuusijakson maapuut*					Fallen trees of birch storey — *Koivujakson maapuut*			
	Degree of decomposition — *Maatumisaste*				Total *Yhteensä*	Degree of decomposition — *Maatumisaste*			Total *Yhteensä*
	1	2	3	4		1	2	3	
	Number of fallen trees per hectare — *Maapuiden lukumäärä, kpl/ha*								
80—104	35	36	55	(14)[1]	140	138	243	500	881
125—137	97	45	(8)[1]	(20)[1]	170	116	221	288	625
145—150	54	36	19	21	130	45	176	255	466
180—195	115	51	13	14	193	21	123	208	354
240—270	120	87	80	57	344	9	17	92	119
300—330	380	136	229	·	>745				
	Secondary stands — *Sekundäärimetsiköt*								
	Number of fallen trees per hectare — *Maapuiden lukumäärä, kpl/ha*								
80—150	87	68	113	187	455	1	16	28	45
170—180	35	25	40	155	255	10	30	30	70
250—270	23	13	77	115	228	1	2	6	9

diameter at assumed breast height was assessed by 5 cm class intervals only. From this separate study the degrees of decomposition and age classes of the tree species of different tree generations are given in Table 22.

It is of interest to note that young secondary stands particularly have more fallen spruces than primary stands. In addition, the vast majority of the trees concerned are quite old, large and at least semi-decomposed, i.e. individuals of the preceding primary tree generation that fell some 50—150 years ago. For the spruce of primary stands, the number of the freshest fallen trees in particular increases fairly regularly with advancing age.

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[1] The values are probably far too low, due to the rapid decomposition on account of the small size of the removed trees. — *Arvot ovat luultavasti huomattavasti liian pieniä, johtuen poistuneiden puiden pienestä koosta ja nopeasta maatumisesta.*

Table 23. Number of fallen spruces in primary stands of different age, by diameter class and degree of decomposition.

Taulukko 23. Eri ikäryhmiin kuuluvien primäärimetsiköiden kuusimaapuiden lukumäärä läpimittaluokittain ja maatumisasteittain.

Age of stands, years *Metsiköiden ikä, v.*	Diameter class and degree of decomposition — *Läpimittaluokka ja maatumisaste*														Total *Yhteensä*	
	0—5 cm		5—10 cm		10—15 cm		15—20 cm		20—25 cm		25—30 cm		30 + cm			
	1—2	3—4	1—2	3—4	1—2	3—4	1—2	3—4	1—2	3—4	1—2	3—4	1—2	3—4	1—2	3—4
	Number of fallen trees per hectare — *Maapuiden lukumäärä, kpl/ha*															
80—104	40	25	23	7	—	12	—	6	2	13	6	5	—	—	71	69
125—137	70	1	46	1	16	4	5	8	3	7	2	7	—	—	142	28
145—150	62	8	22	6	6	1	—	10	—	14	—	—	—	1	90	40
180—195	66	3	48	3	26	4	9	2	11	4	5	6	1	7	166	27
240—270	24	7	44	5	18	13	27	31	44	29	30	28	20	24	207	137

The number of fallen trees belonging to the very oldest age class is exceedingly high. Due to an oversight on one sample plot, however, mean values comparable with the above can be only partly reported.

By contrast, the number of fallen birch trees, irrespective of the degree of decomposition, decreases in primary stands very markedly with the advancing age. Due to their tough bark the number of almost totally decomposed fallen birches has increased beyond that of the other classes.

In order to obtain a more comprehensive picture still of the removal represented by the fallen trees, the number of fallen spruces in primary stands, by diameter classes, classified under two degrees of decomposition only, is given by way of an example in Table 23.

The diameter distribution of fallen spruces shown in the table can of course, due to the nature of the matter, be considered at the most a series of observations indicative of the trend and supporting the findings already established. In spite of this, it may be concluded that the removal of spruce 0—10 cm in diameter is at its most intense in the period between 80—195 years of age. Similarly, the earliest removals of large trees do not occur until beyond the 200-year limit.

By adding together the living trees and the standing dead trees at a given point of time we get stem numbers which, on classifying the material, correspond approximately to the stem number at a certain earlier period. If the number of fallen trees of a certain degree of decomposition is added to the figure thus determined we can go still further back in time. Using

Table 24. Stem number and removal from the spruce storey of the main stand at different age.

Taulukko 24. Pääpuuston kuusijakson runkoluku ja poistuman suuruus eri ikäkausina.

Stand component *Osapuusto*	Age of stands — *Metsiköiden ikä* 80—104	125—137	145—150	180—195	240—270	300—330
	Average number of trees per hectare *Puiden lukumäärä keskimäärin, kpl/ha.*					
Living trees - *Elävät puut* . .	1 580	1 250	1 020	840	470	330
Dead standing trees - *Pystyyn kuolleet puut*		230	180	100	70	120
Fallen trees - *Maapuut*:						
died about 0—20 years ago *kuollut n.* 0—20 *v. sitten*			50			
» 0—35 »		140		170		
» 0—70 »					340	·
Total - *Yhteensä*		1 620	1 250	1 110	880	>450
Comparable age *Vertailuikä*		90	130	150	185	250

this method, the present material gives the following picture for spruce (Table 24).

The totals of the table seem to agree well with the average stem numbers for the different age classes and increase considerably the value of Table 22 — showing the degree of decomposition and number of fallen trees — as evidence of the dynamics and deterioration of the stands investigated.

It may be pointed out that the fallen trees are fairly large in size even in a stand aged 240—270 years; as a result decomposition proceeds quite slowly. In the 300—330 age class the number of fallen trees definitely exceeds 410 (340 + 70) per hectare, due to the slow rate of complete decomposition. The total is greatly affected also by trees falling across other trees during the period of heaviest removal, resulting in an unusually slow decomposition of the uppermost trees.

* * *

An extremely interesting stage in the dynamics of HMT spruce stands is represented by the seven sample plots of the intermediate succession stages.

Fig. 32. A stand of dead trees that has fallen forming a »rutto». Lauttaselkä, Sodankylä.

Kuva 32. Maahan kaatunutta kelokkoa eli »ruttoa». Lauttaselkä, Sodankylä.

Of these sample plots, No. 45 (Kaihuanvaara) represents the most intense stage of degeneration. A third of the total number of trees on this sample plot are dry standing trees, and the majority of the spruces still surviving are in a precarious state. It seems obvious that the stand, aged approx. 280—300 years, will be completely dead within the next 20 years.

The development is a step further advanced at Lauttaselkä and Siulionpalo (Sample Plots 46 and 47). Part of the spruce stand, tall-stemmed before, has died standing, a part has fallen while still somewhat green (cf. Fig. 32). At the moment the sample plots (some 0.5 ha) have perhaps ten living old spruce trees each, of different sizes. However, a new tree generation has not been able to make any noticeable start. Apart from lack of seed, this is probably due more than anything to the slight decomposition of the fallen trees. Similar graveyards of spruce stands that have dried up standing have been encountered at Sompionkaira and Vilmankaira, and around Lake Tulijärvi in the district between Lake Kiantajärvi and the eastern frontier.

However, spruce stand may die standing at a considerably more rapid rate than in the cases reported above. Fairly large stands almost completely destroyed by bark beetles (*Ips sp.*) have been found in two places. The approx. 200 years old secondary forest of Pahtavaara was a pure spruce

Fig. 33. A storm-uprooted old spruce stand Tarpomapää, Sodankylä.

Kuva 33. Myrskyn kaatamaa vanhaa HMT-kuusikkoa Tarpomapää, Sodankylä.

stand until some 3—4 years before the inventory, when it succumbed to serious destruction. The sample plot had no more than ten living trees left. As a result of the destruction the ground vegetation, particularly *Deschampsia* and some herbs, grew exceedingly luxuriant, and the activity of the humus proved from a separate determination of the CO_2 respiration to be approximately twice that of the living stand close by. The Kivalo area is smaller but exactly similar in nature; the rankness of the ground flora is perhaps still more conspicuous thanks to the fertility of many species (cf. also Arnborg 1943, p. 55). For the causes of the phenomenon see e.g. Watt & Fraser (1933), Romell (1934), Romell & Malmström (1945) and Kalela (1948).

A third variant of the intermediate stage is found in the two sample plots of Tarpomapää and Siiselkä. In the former area a storm had raged (1943), practically denuding an area of some 3—4 ha (thicket of windthrown trees). Birch and some spruce, sallow and aspen had already reproduced in the uprooted spots but the intervals showed only old stunted undergrowth seedlings which already showed signs of recovery (Fig. 33).

At Siiselkä development was some 20 years advanced from the stage described above (Fig. 34). The uprooted spots were full of seedlings, including spruce, and a sparse growth of spruce and birch had invaded the gaps.

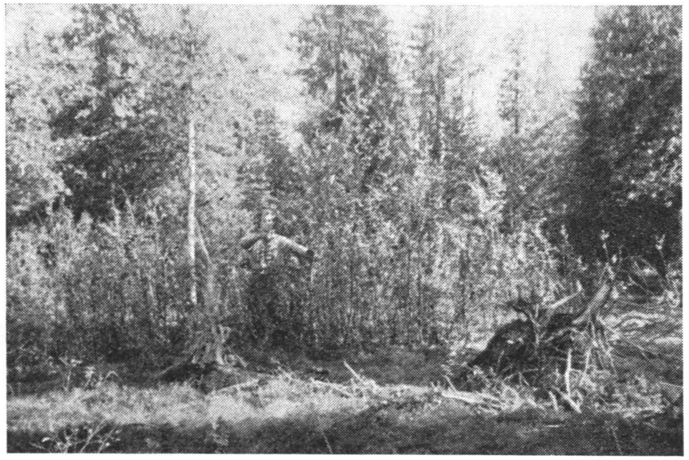


Fig. 34. Birch and spruce invading an old storm-uprooted area. Siiselkä, Sodankylä.

Kuva 34. Koivu ja kuusi metsittämässä vanhaa myrskynkaato-aluetta. Siiselkä, Sodankylä.

The sample plot of Takakangas incidentally, excellent in itself but rejected for its sandy soil, represented mature forest after storm devastation. The forest, approx. 140 years old at the moment of survey, was almost completely closed; its initial development had been slow but it had later improved its growth considerably.

These results of the intermediate stages of the degeneration of primary stands differed considerably from one another in reproduction conditions. Only the oldest had become stocked with young growth. Removal of old stand had thus led to the birth of a new tree generation. This interesting phenomenon, actually implying a change of tree generation, will be discussed in the following.

Natural regeneration

Among the special features of North Finnish spruce forests their repeatedly demonstrated weak regenerating capacity must be mentioned. Previous investigations show that young growth occurs in the forests primarily only in uprooted spots, on fallen trunks in the process of decomposition (Fig. 35) and in the spots where the present ground layer of the

Fig. 35. A typical row of spruce seedlings on and beside a fallen semi-decomposed trunk. Hevosvaara, Pelkosenniemi.

Kuva 35. Tyypillinen rivi kuusen taimia maapuun päällä ja vieressä. Hevosvaara, Pelkosenniemi.

vegetation has a weak moss cover. The seedling stand thus born, relatively sparse, uneven and mainly of stunted growth, is often insufficient to form a closed stand. Similar observations have been made outside Finland also; great attention has been devoted to the problems of regenerating northern spruce forests, especially in Sweden and Norway. The following references may be made to the extensive literature on the subject: the investigations by Holmgren (1914, 1942), Eide (1926 a), Mork (1927), Nordfors (1928), Eneroth (1928, 1931 a, 1934, 1937), Berg (1929), Holmgren and Törngren (1932), Wretlind (1932), Olofsson (1941), Arnborg (1943, 1947, 1952) and Tirén (1949, 1950—51). In the Soviet Union these problems have previously been studied by e.g. Tkatschenko (1929) and Sokolovskij (1908) (according to Airaksinen 1919), and Regel (1935—1941), who gives examples of bad regeneration in the southern part of the Kola Peninsula, which forms the direct continuation of the region studied in Finnish Lapland. Later on e.g. Letkovskij (1952), Novikov (1948) and Nekrasova (1948) have investigated some special aspects of the regeneration of spruce forests. In some mountainous districts of Central Europe also the natural regeneration of spruce forests seems to be quite insufficient (cf. e.g. Fröhlich 1935); on the Prussian plains too the results are poor (cf. Wiedemann 1937, p. 234).

However, the northern spruce forests are not a phenomenon peculiar to Eurasia only, the occurrence of the plant communities in question being practically circumpolar. Forests reminiscent of the thick-moss spruce stands, difficult of regeneration, occur also in Canada and in the mountainous districts of the U.S.A.; examples are mentioned by Ilvessalo (1929), Korstian (1937), Raup (1946), Candy (1951), Hustich (1950) and other authors. Grace (1950) points out that regeneration is difficult also in *Picea Engelmanni* stands with their thick dry peat layer, particularly after clear cutting, for which reason he recommends selective cutting as the best regeneration measure. It may be pointed out that this method has been abandoned in the Fennoscandian countries.

The regeneration of the spruce forests of the northern islands of Japan also seems to be very slow and inadequate (Sakai 1931).

However, the secondary sample plot stands included in the present material have originated naturally to replace old spruce stand. How this has been possible has already been explained in part.

Thanks to the investigations into the regeneration of the old spruce stands in South Finland (Hertz 1932, Heikinheimo 1931, Kalela 1948, etc.) it is known that spruce forests as a rule contain so-called latent regeneration material. Young growth usually exists, sometimes to a greater, sometimes a lesser extent, depending on the seed years and the rate of disappearance of the young growth. As enough growing space is liberated for one reason or another, the young growth on the site stabilizes itself and results before long in a visible group of seedlings. This gains in extent, joins the other seedling groups and, after the removal of the old stand, is ready to form a new stand.

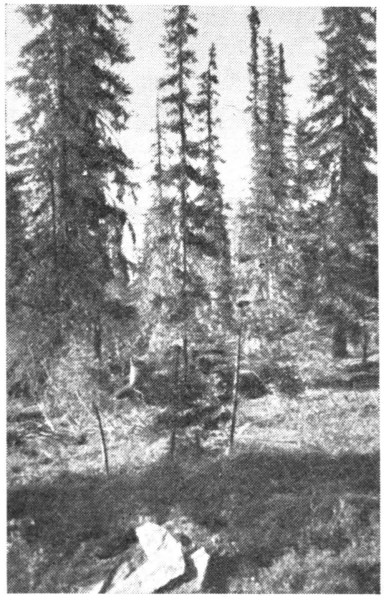
As seed years are rare occurrences in North Finnish spruce forests there is hardly any question of latent regeneration material. Hence seedlings reaching the stage of young growth are only found in the years immediately following seed years. As long as the main stand is closed no such young growth occurs in primary stands; especially in the 130—200 years age period there are hardly any seedlings at all. With the age of the spruce stand advancing, natural removal makes available permanently free growing-space and regeneration is possible. The establishment of reproduction in primary stands older than 240 years included in the present investigation can be seen from the following (Table 25):

Table 25. Average number of spruce seedlings per hectare in old primary spruce stands of different age.

Taulukko 25. Kuusen taimien keskimääräinen lukumäärä hehtaaria kohden iältään erilaisissa primäärikuusikoissa.

Age of the stands, years — *Metsiköiden ikä, v*			
240—300		300—330	
Average number of seedlings per hectare — *Taimien lukumäärä keskimäärin, kpl/ha*			
shorter than 1.3 m — *pikkutaimia alle 1.3 m*	Total *Yhteensä*	shorter than 1.3 m — *pikkutaimia alle 1.3 m*	Total *Yhteensä*
32	178	257	530

The general descriptions of the sample plots reveal that the »seedlings» of the 240—300 year old stands were usually old individuals of stunted growth and that young seedlings were almost completely missing; this is indicated by the figure of 32 seedlings per hectare. In the oldest stands the number of large trees is so small that relatively abundant light and free space is available for the young growth (Fig. 36). The amount of small seedlings also reflects well the improved regeneration conditions. The general descriptions show that regeneration has occurred mainly in the uprooted spots, on decomposed stumps and fallen trunks, as Heikinheimo, Eneroth, Mork, Arnborg (op. c.) have found in their investigations. The height of the seedlings is admittedly somewhat misleading — the oldest as a rule have taken root again at the butt (cf. Heikinheimo 1920 a, Hertz 1932 and Sirén 1950). The height growth also is very poor, only approx. 1—3 cm annually (see p. 110). In spite of their even height they in reality are very unevenaged — the majority of the seedlings younger than 30 years and another considerable portion generally 130—160 years old. These old seedlings have usually taken root again repeatedly at the butt and apparently derive from that development stage of the primary stands in which the old spruce storey was no longer capable of occupying immediately the growing spaces vacated by the removed birches and suppressed spruces. The seedling stand of the secondary succession is, however, already some ten years after the destruction of the old primary stand so complete that the formation of a new tree stand is possible (cf. Appendix 1).



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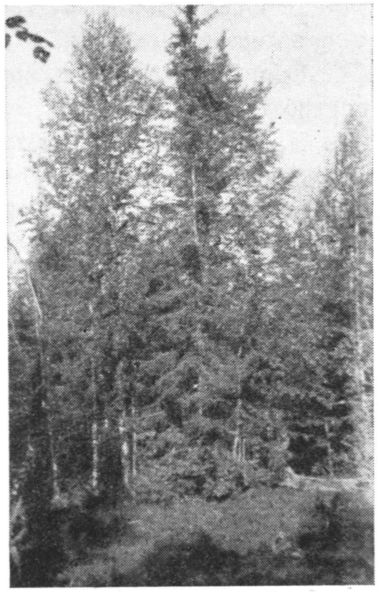

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Fig. 36. An old open spruce stand with some small old seedlings. Hevosvaara.
Kuva 36. Vanhaa aukkoista kuusikkoa, jossa harvakseltaan vanhoja taimia. Hevosvaara.

Fig. 37. A single spruce in a pure birch stand. Siulionpalo.
Kuva 37. Yksinäinen kuusi puhtaassa koivikossa. Siulionpalo.

The birth and development of the spruce storey of primary stands was partly discussed on pp. 27—35 Hence it will suffice here to point out that spruce seedlings make their appearance on the most thoroughly burnt spots of a fire area (cf. e.g. Petrini 1934, p. 258, Hesselman 1937, p. 556). Depending on the spacing and seeding capacity of the seeding stand and on certain limitations to this general minimum seeding factor (see Novikov 1948 and Nekrasova 1948), the seedling stand becomes more or less dense. E.g. Arnborg (1949) has published a series of illustrations depicting this regeneration occurrence very clearly. The sample plots reviewed in the present investigation are generally situated quite close to the burn limit. As a result the seeding conditions, judging by the stem number of the present stand, have probably been fairly good. On large burns, such as Siulionpalo, the middle parts, it is true, remain almost pure birch stands. Only after the spruces growing sparsely here and there begin to produce seed can the birth of a new forest-forming spruce generation be expected (Fig. 37).

The height growth of the spruce storey of primary stands has been found above to exceed distinctly that of secondary stands. As this difference is definitely visible throughout from the seedling stand stage onwards it has been considered appropriate to study how the dominant trees of the successions concerned on each sample plot have grown in their first ten years. As the age of the seedling at a height of 30 cm has a certain interest in the determination of tree age (cf. Sirén 1950) the average age at this seedling height has been selected as the basis of the study. The material includes a total of 81 trees from primary and 35 trees from secondary stand sample plot. The result of the comparison can be seen from the following (Table 26).

Apart from being sparse, the seedlings in secondary stands are also of slow growth. In addition, it may be mentioned that numerous crooks and re-rootings lead to the abandonment of considerable portions of the root systems (cf. e.g. Pöntynen 1929, Sirén 1950). This way provides various rot fungi with a good opportunity of attacking the trees. Spruce stands in fact are generally rather extensively rot-damaged (cf. Tikka 1928 etc.). It seems that the stands investigated in Lapland by Tikka have been in most cases of secondary origin.

Obviously, then, a spruce seedling stand appearing on the site of an old spruce stand during or after the period of deterioration must from its inception develop in conditions which, judging from the growth of the seedlings, are considerably poorer than on soils subjected to forest fire (cf. Hesselman 1927 and Eneroth 1928, 1931 a). The latter soils have neither appreciable vegetation, apart from sparse *Deschampsia flexuosa* and *Polytrichum sp.* (cf. e.g. Hertz 1931, p. 67), to inhibit regeneration nor any thick layer of raw humus, and this is a serious disadvantage in many respects. The freezing of spruce seedlings, greatly emphasized by Multamäki (1942), is a surprisingly unusual phenomenon on the burnt areas of North Finland. The regeneration rate, referring to the finding mentioned above, must consequently be considered to be quite superior in the early primary succession compared with the conditions of the secondary succession.

Table 26. The development of typical spruce dominants in the seedlings stage in primary and secondary stands.

Taulukko 26. Primääri- ja sekundäärimetsiköiden tyypillisten kuusivaltapuiden kehitys taimiasteella.

The stands — *Metsiköt*	Height of seedlings, cm *Taimien pituus, cm* 30	50	130
	Average age of seedlings, years *Taimien keskimääräinen ikä, v.*		
Primary stands - *Primäärimetsiköt*	11.5	16.6	28.3
Secondary stands - *Sekundäärimetsiköt*	22.1	31.3	53.7

Development of vegetation

In the previous chapters the dynamics of the tree stand has been elucidated to some extent. The vegetation of a site consists, however, of other layer communities than the tree layer. Due to the fact that the herbs, mosses and lichens have a shorter life cycle, changes in the ground layer are evidently to be expected sooner and more distinctly than in the dominant tree layer. In the following attention will be paid to the establishment and development of the herbaceous layer including dwarfshrubs[1] and the moss and lichen layer. For technical reasons the former will be named field layer and the latter bottom layer. With the aim of avoiding overorganized plantsociological terminology the following terms will be used:

association	tree layer		
	ground layer	field layer bottom layer	consisting of different societies due to successional development

Small irregularities in the societies will be noted as patch-societies. No further questions concerning plantsociological systems will be discussed in this report. The different successional stages have commonly used terms.

The methods of investigation and the most important findings as regards the tree layer have both been reported in previous chapters.

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[1] mainly ericaceous.

The other layers of the vegetation have been studied by the customary quadrat-inventory method. The plants of each sample plot were counted and their frequency and coverage determined on twenty quadrats of 1 sq.m each, of which the location was decided by the size and shape of the sample plot. Each quadrat represented an equal portion of the sample plot, and its mathematically determined location was changed only if it fell on an edaphide, such as stone, stump, log, etc., differing extremely from the vegetation in general. On the other hand, societies falling within crown projections were not counted as edaphide-societies but as patch -societies belonging to the ground community. Where a quadrat fell on such a differing patch-society an additional note to this effect was made.

The basic information gained by determining the frequency and coverage of the different plant species present was used to study the structure of the different components of the communities, both layer- and patch-societies. In the case of the latter, it was usually considered sufficient to distinguish the societies present in the crown projections of spruce from the ground community. The tentative mapping of the different layer-societies on certain sample plots naturally elucidated the composition of the association considerably. In addition, the vitality of the dominants was determined by measuring their height on each sample plot; the measurement was effected in the quadrats described by determining the average height of the plant concerned in a quarter quadrat. Arithmetic means were computed from the values obtained to serve as standards of frequency, coverage and vitality. The original material (except height) is compiled in Appendix 3.

A rough study of this list of plants shows that the floristic composition of the young succession stages of primary forests is remarkably similar to the picture given by Ilvessalo's MT stands and birch stands on HMT (1937, pp. 28—29). On the other hand, the floristic composition of Ilvessalo's spruce stand on HMT seems somewhat richer than that of the climax stage reported in the present investigation. The same applies of course to the descriptions of HMT vegetation by Teivainen (1952). (See also reference to literature supplied by Teivainen, op.c.) But there are other features of interest too.

Successional changes

Primary succession

Thanks to the employment in the present investigation of the method based on parallel sample plots it was possible to illuminate satisfactorily the main features of the invasion of the burnt areas of HMT. It usually takes some years for vegetation to appear on sites changed to a primary state by fire. This invasion occurs by two principal routes (cf. Kujala 1926 b, p. 29):

— the species with plentiful and light-weight diaspores spread more or less evenly throughout the site, carried by the wind, and

— from the edges of islets formed by plants surviving in the area active concentric expansion by means of either seeds or rhizomes particularly if species capable of strong vegetative reproduction have remained in the islets; the force of the invasion by these species is increased by generative reproduction (cf. e.g. Mc Minn 1951).

We know from earlier investigations that quite a large number of species usually participate in invasions of this kind (cf. e.g. Linkola 1916, Kujala 1926 b, Hesselman 1926, 1937, Högbom 1934, Sarvas 1937, 1938, Heiberg 1938, and Uggla 1949). Not all species, of course, arrive at the same time: they appear more or less haphazardly over a lengthy period. The ecological character and sociability of some species, however, suits the site poorly, particularly after the secondary changes brought about by plants more successful in competition come into play. A consequence of this lack of adaptation to the environment is the elimination of some species from the originally heterogeneous floristic composition. Sooner or later, however, the community, subject to many changes though it has been, reaches a certain state of equilibrium. But the changes induced by factors affecting the origin and development of plant communities will not be discussed here in any detail as e.g. Clements (1916, 1949), Sukatshev (1928), Yaroshenko (1946), Daubenmire (1947), Oosting (1950), Braun-Blanquet (1951) and McMinn (1951) have gone into the principles of the problem very thoroughly on the basis of both theoretical and experimental research. In addition to Cajander, especially Kujala (1926 b) and A. Kalela (1949) have studied the question expressly in relation to Finnish conditions.

From the foregoing the invasion stage might be expected to have turned

Table 27. Frequency and coverage of the plant species at the different development stages of the successions.

Taulukko 27. Kasvilajien yleisyys ja peittävyys suksessioiden eri kehitysvaiheissa.

Plant species *Kasvilajit*	Development stages of the vegetation and age groups of the sample plot stands *Näytealametsiköiden kasvipeitteen kehitysvaiheet ja ikäryhmät.*															
	Primary stands — *Primäärimetsiköt*									Secondary stands — *Sekundäärimetsiköt*						
	Invasion stage *Invasiovaihe*		Selection stage *Selektiovaihe*				Climax stage *Klimaksvaihe*		Post-climax *Post-klimaks*	Interregnum stage *Interregnumvaihe*			Climax stage *Klimaksvaihe*			Post-climax *Post-klimaks*
	6—8	25—32	51—65	80—104	125—137	145—150	180—195	240—270	300 +	32—40	60—90	110—150	170—180	210	250—270	300 +
	Frequency : Coverage — *Yleisyys* : *Peittävyys*															
Marchantia polymorpha ..	·															
Barbilophozia lycopodioides		2 : △	8 : △	7 : △	6 : 2	9 : 2	8 : 4	9 : 3	10 : 2	10 : 1	10 : 4	7 : 1	8 : 1	10 : 1	8 : 3	9 : △
Hepaticae			△ : △					△ : △			1 : △	1 : △	△ : △		△ : △	
Sphagnum Girgensohnii ..							△ : △	·	·	·	·	·	·			·
Dicranum sp.	1 : 1	4 : 2	9 : 4	10 : 6	10 : 5	10 : 5	10 : 7	10 : 5	7 : 1	10 : △	7 : 3	9 : 3	8 : 4	10 : 14	10 : 7	7 : 2
Pohlia nutans *Ceratodon purpureus* }	10 : 43															
Splachnum sp.		△ : △														
Aulacomnium palustre ..		1 : △	1 : △	1 : △			△ : △									
Brachythecium sp.	·	△ : △	8 : 1	2 : △	2 : △	1 : △	1 : △					△ : △	△ : △	2 : △		
Plagiothecium sp.			△ : △													
Ptilium crista-castrensis ..	1 : △		1 : △	4 : △	4 : 2	2 : 1	7 : 6	7 : 7	3 : △	3 : △	3 : △	2 : △	2 : 1	8 : 10	4 : 1	
Pleurozium Schreberi	1 : 1	4 : 3	10 : 15	10 : 17	10 : 14	10 : 24	10 : 30	10 : 35	10 : 55	10 : 56	10 : 42	10 : 31	10 : 27	10 : 43	10 : 38	10 : 36
Rhytidiadelphus triquetrus					1 : 1		·						△ : △			
Hylocomium splendens ..	1 : 1	2 : △	·	△ : △	10 : 41	10 : 49	10 : 42	10 : 40	10 : 32	10 : 25	8 : 21	10 : 46	10 : 42	10 : 30	10 : 36	10 : 35
Polytrichum sp.	9 : 26	10 : 36	9 : 13	8 : 4	7 : 9	8 : 7	6 : 4	6 : 4	9 : 4	9 : 12	9 : 6	8 : 8	7 : 5	3 : △	6 : 4	10 : 7
Nephroma arcticum	·		△ : △	·		·	△ : △	△ : △	·	4 : 2						
Peltigera sp.		△ : △	1 : △	△ : △	△ : △	1 : △	△ : △	△ : △	·	1 : △		1 : △	·		1 : △	·
Cladina sp.	5 : 1	1 : △	1 : △	△ : △	1 : △	△ : △	△ : △	△ : △	2 : △	6 : △	·	△ : △	△ : △	2 : △	1 : △	1 : 1
Cladonia sp.	·	4 : 3	2 : △	△ : △		△ : △	△ : △	1 : △	1 : △	6 : 1	5 : 3	2 : △	△ : △		3 : 1	4 : 2
Cetraria sp.	1 : △						△ : △	△ : △	△ : △	3 : △	4 : △	1 : △			1 : △	1 : △
Equisetum silvaticum		2 : △	1 : △				·	·	△ : △			1 : △	1 : △			
Thelypteris Dryopteris ..		△ : △				△ : △		1 : △				1 : △	△ : △			
Calamagrostis sp.	·															
Deschampsia caespitosa ..	·															
» *flexuosa*	9 : 18	10 : 24	10 : 19	10 : 6	9 : 3	9 : 4	9 : 6	10 : 7	9 : 12	10 : 23	10 : 18	7 : 7	10 : 8	10 : 8	10 : 8	8 : 6
Carex sp.	·	3 : 3	△ : △				△ : △			1 : △		2 : △				·
Luzula pilosa	1 : △	5 : 2	6 : 1	4 : △	3 : △	3 : 1	3 : 1	3 : 1	3 : 1	2 : △	2 : △	3 : 1	1 : △	9 : 3	1 : △	1 : △
Maianthemum bifolium ..	·			△ : △	1 : △	2 : △		2 : △				2 : △		·	△ : △	
Listera cordata		△ : △	·	1 : △			△ : △	△ : △			1 : △			·	△ : △	
Goodyera repens						△ : △	·	△ : △		·		·	△ : △		△ : △	
Rubus saxatilis			△ : 1							·		·			·	
Geranium silvaticum		·	·												·	
Chamaenerion angustifolium	9 : 22	5 : 2	5 : 2	2 : △	△ : △	·	·		·			·	·			
Cornus suecica		1 : △						1 : 1			3 : 3		·	·	1 : 1	
Trientalis europaea	·	6 : 1	△ : △	1 : △	·	1 : △	△ : △	2 : △			3 : △	1 : △	·	5 : 1	1 : △	
Melampyrum sp.		8 : 5	9 : 7	7 : 1	5 : 1	7 : 2	6 : 1	7 : 3	9 : 2	4 : 2	6 : 4	6 : 1	5 : 2	7 : 8	6 : 1	9 : △
Solidago Virgaurea	·	2 : △	3 : 3	4 : 2	2 : △	2 : △	1 : △	1 : △	·		2 : △	3 : △	△ : △	2 : △	△ : △	
Cirsium heterophyllum....			·													
Taraxacum officinale	·															
Hieracium sp.		△ : △	·	·												
Lycopodium sp.	·	3 : △	3 : 2	5 : 4	5 : 3	3 : 1	3 : 2	3 : 1	△ : 1		1 : △	1 : △	1 : △	3 : 1	1 : △	
Ribes rubrum			△ : △													
Pirola secunda		△ : △	1 : △	1 : △	1 : △	1 : △	1 : 1	1 : 1	△ : △	2 : △	1 : △	1 : △	1 : △	2 : △	·	·
Ledum palustre	1 : △	·	·		·	△ : △	1 : △	△ : △				3 : 2	·			1 : 2
Vaccinium Vitis-idaea ..	7 : 4	9 : 9	10 : 16	10 : 13	10 : 10	10 : 13	9 : 14	10 : 14	10 : 13	10 : 13	10 : 7	10 : 18	10 : 17	10 : 12	9 : 12	10 : 9
» *uliginosum* ..	1 : △	1 : 1	1 : △	△ : △	·	△ : △	△ : △	1 : △		2 : △	1 : 4	2 : 2	·		2 : 4	1 : 2
» *Myrtillus*	8 : 12	9 : 30	10 : 51	10 : 57	10 : 65	10 : 67	10 : 64	10 : 59	10 : 33	10 : 38	10 : 35	10 : 41	10 : 65	10 : 61	10 : 56	10 : 40
Calluna vulgaris	1 : △															
Empetrum sp.	·	3 : 3	2 : △	△ : △	△ : △	2 : △	2 : 1	3 : 1	9 : 11	7 : 3	9 : 11	7 : 1	5 : 1	1 : △	5 : 4	10 : 17
Linnaea borealis	2 : 1	1 : △	4 : 3	6 : 1	3 : 1	8 : 2	8 : 4	9 : 4	8 : 1	6 : △	4 : △	4 : 2	8 : 1	10 : 2	8 : 1	
Total of species in the different age classes *Lajien lukumäärä eri ikäryhmissä* ..	31	32	36	28	25	28	33	31	24	24	26	34	32	22	30	20
Total of species in the different successional stages *Lajien lukumäärä eri kehitysvaiheissa* ..	43		40				36		24	36			37			20

out fairly rich in species on the burnt areas of HMT. The original material collected from the sample plots, however, does not as it is seem to support this view (cf. Appendix 3).

In order to obtain a sharper general picture the mean values of the frequency and coverage of different species have been computed for each group of sample plots belonging to the same age class: this helps to emphasize the differences between the various stages of the succession (see Table 27 and Fig. 38).

The invasion stage in the present material has been split up into two sub-stages governed by the dominants: the *Chamaenerion-Pohlia* sub-stage and the *Deschampsia-Polytrichum* sub-stage; age classes 6—8 and 25—32 years.

The Chamaenerion-Pohlia sub-stage seems to follow immediately after a forest fire, even one that destroys the humus layer fairly thoroughly. The main species of this sub-stage are *Pohlia nutans* and *Ceratodon purpureus* in large unbroken patches in the bottom layer and *Chamaenerion angustifolium* in the field layer. Codominants, especially in less thoroughly burnt spots, are *Polytrichum juniperinum, P. piliferum* and *P. commune* in the bottom layer, where *Cladina* also occurs (cf. e.g. Tuomikoski 1948, p. 77), and in the field layer *Deschampsia flexuosa.* Other species that may be mentioned are *Marchantia polymorpha*[1], *Calamagrostis* sp., *Taraxacum officinale, Deschampsia caespitosa* and *Calluna vulgaris* which in the next, *Deschampsia-Polytrichum* sub-stage, disappear from the community.

The Deschampsia-Polytrichum sub-stage either follows the *Chamaenerion-Pohlia* sub-stage or commences immediately after fire, particularly where the fire has been so slight that *Pohlia* never becomes the dominant species at all. On this point, however, priority of appearance may be of importance: *Polytrichum* may sometimes easily and rapidly invade sites with an exposed mineral soil too. Where this occurs a dense *Polytrichum*-population appears on the surface of the scorched humus as well. The principal species are *P. piliferum, P. juniperinum, P. commune.* In the field layer *Deschampsia flexuosa* dominates and *Vaccinium Myrtillus* occurs occasionally as a codominant. The profusion of herbs is conspicuous. *Pohlia* is either absent originally or has disappeared almost completely, and the proportion of *Chamaenerion* is negligible.

The floristic composition of the *Deschampsia-Polytrichum* sub-stage is considerably richer in species than that of the *Chamaenerion-Pohlia* sub-stage, but as both these sub-stages are included in the invasion stage — the latter includes another 12 new genera — the number of species present at the whole invasion stage totals 43. It should of course be borne in mind that not all genera nor all species are present simultaneously.

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[1] *Equisetum* may occur together with *Marchantia* already in this sub-stage.

At the selection stage, divided into four transition sub-stages on the basis of the age of the sample plot stands, a characteristic feature is the intense propagation of forest mosses in the bottom layer. The slowly propagated *Hylocomium splendens* gradually becomes dominant by the latter half of the stage, finally catching up with *Pleurozium Schreberi.* The latter, however, may be considered codominant. Other constants are the *Dicranum sp.* (mainly *D. majus* and *D. fuscescens var. flexicaule*), and the *Polytrichum sp.* (primarily *P. commune*), which continue to decrease. In the field layer *Vaccinium Myrtillus* gains the position of a main species. Among the other dwarfshrubs may be mentioned *Vaccinium Vitis-idaea,* a codominant, and the *Lycopodium sp.* and *Linnaea borealis* present as constants. The proportion of grasses and herbs continues high, but *Deschampsia* decreases continuously and *Chamaenerion* disappears almost completely with the stand becoming increasingly spruce-dominated. The short period of profusion of *Melampyrum, Solidago Virgaurea* and *Luzula pilosa* seems to weaken towards the end of the stage.

A total of seven species new to the selection stage were found on the sample plots. Among them the endozoically dispersing *Ribes sp.* and *Rubus saxatilis* must be considered accidental species which might equally well have been present at the invasion stage already. *Cirsium heterophyllum* can probably be considered an impurity in the material, accidentally present at this stage; its anemochorous dispersal at least does not inhibit its occurrence (cf. Pettersson 1931) at the invasion stage, and the species has in fact been found in some other young birch stands following fire. As *Pirola rotundifolia,* present on a single sample plot, can probably be counted among the species foreign to the association of HMT the only newcomers proper left are *Rhytidiadelphus triquetrus,* which also with good reason might be considered fairly foreign to HMT association (see Kujala 1936), and *Sphagnum Girgensohnii* and *Goodyera repens.*

The table thus shows that the more or less permanent appearance of species invading the sites is made on burnt HMT areas mostly during the first ten-year period; however, the third decade even sees the arrival of a large number of new species. Even in a 50 year old stand species may be found which later on prove indisputably foreign to the final type association. Towards the end of the selection stage there is an important shift in the tree layer; birch loses its dominant position to spruce.

Before embarking on study of the climax-stage it may be stressed once again that the ground vegetation of the comparison stands of the sample plots at both the invasion and the selection stage definitely suggested an HMT climax association.

The climax association seems very uninteresting as regards ground vegetation. No new species appear. The dominance of certain constant species continues to increase considerably compared with the preceding stage, that of some others decreases. The former group includes *Barbilophozia*, *Ptilium* and *Linnaea*, the latter *Polytrichum*, *Deschampsia* and *Solidago*. The dominant species in the bottom layer are *Hylocomium* and *Pleurozium*, codominants *Dicranum* and the above-mentioned *Polytrichum* and *Ptilium*. In the field layer *Vaccinium Myrtillus* vanquishes the herbs and grasses almost completely. *Vaccinium Vitis-idaea* can be mentioned as codominant. A sort of basic list of the constants of the HMT type stage of primary succession can probably be compiled from Appendix 3 (cf. Arnborg 1943, e.g., p. 107 and Teivainen 1952, pp. 40—43). For practical reasons a list of plants is given at the same time, compiled from material collected from the climax of the secondary succession (Table 28).

As is shown by Table 28, no direct comparison is possible with HMT plant lists published previously. Lakari (1920 a), Heikinheimo (1920 b), Ilvessalo (1937) and Kujala (1921) have employed Norrlin's grading with non-equidistant intervals, and e.g. Cajander (1916) has only reported on the composition of the flora. Heikinheimo's (1939) material derived from cut forests, and Teivainen (1952) collected his material outside the main HMT area. However, the type association described by the present author seems slightly poorer in species than those described by the above authors — particularly Ilvessalo and Teivainen (Pisavaara HMT).

The post-climax stage is represented by a single sample plot. However, if the sample plots of the deteriorated stands between the primary and secondary succession are used to support this single very representative sample plot, the following conclusion can be drawn concerning the development of the vegetation of this stage:

An intense change occurs in the bottom layer because *Pleurozium Schreberi* becomes the main species at the expense of *Hylocomium splendens*. The proportion of *Polytrichum commune* also grows. *Ptilium* and *Dicranum*

Table 28. Composition of ground vegetation in the climax stage of different successions on HMT sites.

Taulukko 28. HMT:n eri suksessioiden klimaksvaiheen pintakasvillisuus.

Plant species *Kasvilajit*	Primary stands *Primäärimetsiköt*	Secondary stands *Sekundäärimetsiköt*
	Frequency : Coverage — *Yleisyys* : *Peittävyys*	
Barbilophozia lycopodioides	9 : 3	8 : 2
Hepaticae	△ : △	△ : △
Sphagnum Girgensohnii	△ : △	△ : △
Dicranum sp.	10 : 6	9 : 6
Aulacomnium palustre	·	△ : △
Brachythecium sp.	△ : △	△ : △
Ptilium crista-castrensis	7 : 7	4 : 2
Pleurozium Schreberi	10 : 33	10 : 34
Rhytidiadelphus triquetrus	·	·
Hylocomium splendens	10 : 41	10 : 38
Polytrichum sp.	6 : 4	6 : 4
Nephroma arcticum	△ : △	1 : △
Peltigera sp.	△ : △	1 : △
Cladina sp.	△ : △	1 : △
Cladonia sp.	1 : △	1 : △
Cetraria sp.	△ : △	△ : △
Equisetum silvaticum	△ : △	△ : △
Thelypteris Dryopteris	△ : △	—
Deschampsia flexuosa	9 : 7	10 : 8
Carex sp.	△ : △	·
Luzula pilosa	3 : 1	2 : △
Maianthemum bifolium	1 : △	△ : △
Listera cordata	△ : △	△ : △
Goodyera repens	△ : △	△ : △
Chamaenerion angustifolium	△ : △	·
Cornus suecica	△ : △	△ : △
Trientalis europaea	1 : △	1 : △
Melampyrum pratense » *silvaticum*	6 : 2	6 : 2
Solidago Virgaurea	1 : △	1 : △
Lycopodium sp.	3 : 1	1 : △
Pirola secunda	1 : 1	1 : △
Ledum palustre	1 : △	△ : △
Vaccinium Vitis-idaea	10 : 14	10 : 14
» *uliginosum*	△ : △	1 : 2
» *Myrtillus*	10 : 61	10 : 60
Empetrum sp.	2 : 1	5 : 2
Linnaea borealis	9 : 4	8 : 1

sp. decrease. In the field layer *Vaccinium Myrtillus* decreases very strongly, making room for *Deschampsia flexuosa* and the explosively expanding *Empetrum.* The changes in the relations between the species of this stage are attributable more or less directly to the destruction process in the spruce stand. Improved light conditions favour especially *Deschampsia, Empetrum* and apparently *Pleurozium* (as regards *Pleurozium,* see e.g. Tuomikoski 1948, p. 78).

Secondary succession

Dominance variations in the composition of species at the post-climax stage culminate during the tree regeneration stage of secondary succession. Particularly *Pleurozium Schreberi, Deschampsia flexuosa* and *Empetrum sp.* are at their most vigorous; correspondingly, *Ptilium* and the *Dicranum* species are still extremely scanty. The proportion of *Hylocomium splendens,* still present in profusion, weakens in the bottom layer. On the other hand *Vaccinium Myrtillus,* also profuse still, shows signs of stabilization; it grows in the field layer in approximately the same proportion as during the post-climax stage. No distinct *Deschampsia-Polytrichum* stage, not to mention *Chamaenerion-Pohlia* stage, can be observed of course, even though *Deschampsia* is relatively approximately as abundant as during the invasion stage in the primary succession. According to Hesselman (1917), *Deschampsia* is present in profusion where the humus decomposes slowly. Eneroth (1937, p. 222) among others, has described the reaction of the vegetation as approximately similar to that on the logging areas of the corresponding forest site type in Norrland, Sweden. *Pohlia nutans* and *Chamaenerion angustifolium* of course do not occur at all at this stage of natural reforestation except in uprooted patches. In the lengthy interim period between the regeneration and climax stages of the secondary succession a certain recovery of shade-tolerating species is observable while light demanders decrease in the ground layer.

On all important points the ground vegetation of the climax stage in the secondary succession is similar to the vegetation of the corresponding stage in the primary succession. Even the frequency and coverage of the species are of similar proportions (cf. Table 28) and the constancy[1] is practically identical (cf. Appendix 3). The differences are so insignificant that the only ones worth mentioning, probably, are: *Empetrum sp., Vaccinium uliginosum* and *Ledum palustre* occur in greater profusion in the climax stage of the secondary than of the primary succession; on the other hand the proportion of *Ptilium crista-castrensis* and *Linnaea borealis* seems to decline somewhat.

Sample Plot 71 is the only example of a detailed study of changes in ground vegetation concurrent with the deterioration of secondary stands. Hence it does not seem possible to generalize the conclusions reached from the observations. It may be said, however, that species usually growing on swamps propagate during this stage. Other observations made in various parts of North Finland are indicative of the same trend. It may be mentioned that the so-called PHMT forest site type is not seldom represented by old, dying spruce stands in the process of paludification. A general observation on the development of ground vegetation at the post-climax stage in secondary stands that may be offered, therefore, is: plants indicating paludification increase without the species composition gaining in richness. This developmental stage might perhaps be termed the first paludification stage, which in certain conditions may result in an irreversible retrogression of earlier firm forest land.

Vitality of dominants

In the chapter above on the frequency and coverage of species no attention is paid to the physiognomy of species. As it would have been too time-consuming to describe the different physiognomic features of all the species the present investigation is confined to certain dominants only, and even then to reporting the mean height only. From these mean values, group mean values have been computed to describe the relevant stage in the development of stands. The results thus obtained are shown in Table 29.

It is interesting to note that dwarfshrubs reach their full height at quite an early stage in the development of primary stands; mosses, on the other hand, seem to continue growing throughout the progressive stage of development. Only after the stand starts to dry up and to fall does a minor change occur in the vitality of the moss layer; *Hylocomium splendens,* which is intolerant of great changes in light (Hertz 1932), seems to decline whereas *Pleurozium Schreberi* seems to grow even more luxuriant. Of course the conclusion is very uncertain for the difference in the numerical values concerned may easily arise from small errors in measurement, but

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[1] Constancy is used here in the same sense as by Kalliola (1939).

Table 29. Mean heights of some dominant species of ground vegetation on the sample plots of the different age groups of the successions.

Taulukko 29. Kasvipeitteen eräiden valtalajien keskimääräinen korkeus suksessioiden eri ikäryhmien näytealoilla.

Species — *Kasvilajit*	Age groups of primary stands — *Primäärimetsiköiden ikäryhmät* 0—49	50—99	100—149	150—199	200—249	250 +
	Mean height, cm — *Keskimääräinen korkeus, cm*					
Hylocomium splendens ..	7.3	7.8	8.1	8.8	9.7	9.2
Pleurozium Schreberi	7.3	7.3	7.5	8.5	9.0	9.7
Vaccinium Myrtillus	20.1	24.0	24.0	24.2	24.4	23.7
Vaccinium Vitis-idaea ..	17.0	16.5	17.4	17.1	20.7	18.1

	Age groups of secondary stands — *Sekundäärimetsiköiden ikäryhmät* 0—49	50—149	150—199		250 +
	Mean height, cm — *Keskimääräinen korkeus, cm*				
Hylocomium splendens ..	7.7	10.0	8.3		8.6
Pleurozium Schreberi	7.8	9.7	8.0		8.3
Vaccinium Myrtillus	20.8	24.0	24.0		25.2
Vaccinium Vitis-idaea ..	16.8	20.5	19.1		19.0

observations in nature are indicative of the same trend. According to Tamm's investigations (1953 a, p. 30), a gradual improvement in light conditions should have a contrary effect on *Hylocomium splendens.* It is probable, however, that the reduced tree litter crop and supply of rain water from the canopy change the nutrient balance in a direction unfavourable to *Hylocomium splendens* (cf. Romell 1939, Tamm 1953 a). In secondary stands the initial height of mosses seems to exceed slightly that in primary stands. No appreciable difference is observable in dwarf-shrubs. The similarity is particularly striking in stands more than 150 years old.

Special features of type association

Another remarkable feature of type association to be mentioned is its mosaic character. This variation in the layer societies of ground vegetation is presumably due to the microlocal differences of the plant community. A habitat differing from its surroundings is often produced e.g. when the crown of spruce extends down to the ground. In HMT associations the patch-society occurring expressly under a spruce crown is one of the principal factors accounting for the mosaic character. Thanks to the investigation method employed, numerical data can be quoted for this phenomenon. Table 30 shows the respects in which the frequency and coverage of species belonging to a patch-society under spruce crowns differ from the ground community found in the gaps. The table covers only the most important constants of the type association.

The table shows that the drought and shade produced directly by

Table 30. Occurrence of the most important constants of HMT type association in the different societies.

Taulukko 30. HMT:n tyyppikasvuston tärkeimpien konstanttien esiintyminen erilaisissa kasvustoissa.

Species — *Kasvilajit*	Ground community *Peruskasvusto*	Patch-society in the crown projections *Latvusalustojen laikkuosakasvusto*
	Frequency : Coverage — *Yleisyys : Peittävyys*	
Barbilophozia lycopodioides	9 : 4	7 : 3
Dicranum sp.	9 : 6	8 : 6
Ptilium crista-castrensis	6 : 5	7 : 2
Pleurozium Schreberi	10 : 25	10 : 30
Hylocomium splendens	10 : 53	10 : 36
Polytrichum commune	7 : 5	6 : 4
Deschampsia flexuosa	10 : 8	8 : 1
Luzula pilosa	4 : 2	2 : △
Melampyrum pratense, & M. silvaticum	8 : 2	4 : △
Solidago Virgaurea	1 : △	1 : △
Lycopodium sp.	3 : 2	4 : 2
Pirola secunda		1 : 1
Ledum palustre	1 : △	1 : 1
Vaccinium Vitis-idaea	10 : 8	10 : 21
» *uliginosum*	1 : 1	·
» *Myrtillus*	10 : 61	10 : 51
Empetrum sp.	2 : △	1 : △
Linnaea borealis	8 : 6	6 : 1

spruce crowns have a reducing effect on the coverage of at least *Barbilophozia, Hylocomium, Ptilium, Luzula, Deschampsia, Melampyrum, Vaccinium Myrtillus, V. uliginosum* and *Linnaea*. The bottom layer suffers most. No less than 20 per cent on an average of the area of the habitat remains covered by litter, compared with approx. 2—3 per cent in most cases in the ground community of the gaps. Microclimatic and micropedological changes, however, do not reduce the coverage of all the species; there are species for which the change is directly or indirectly beneficial. The most typical of these species in the bottom layer is *Pleurozium Schreberi*, in the field layer *Vaccinium Vitis-idaea*. It may be pointed out that e.g. Stålfelt (1937, p. 48) found that *Pleurozium* requires approx. 50 per cent less light than *Hylocomium* to attain maximal assimilation. In addition, it may be emphasized that extensive areas are very often encountered in nature with a patch society under spruce definitely dominated by *Vaccinium Vitis-idaea — Pleurozium. Pirola secunda* and individual *Ledum palustre* also occur frequently on such patches. The result obtained seems to be partly contrary to the common opinion (cf. e.g. Arnborg 1943, p. 170 and Tuomikoski 1948, p. 79) but on the other hand Teivainen (1952, p. 115) concludes on the basis of references that *Pleurozium* is more drought resistant than *Hylocomium*.

Taking into account the autecological properties of the plants mentioned, the mosaic character is a completely natural phenomenon. The problem of the autecology of the plants occurring on HMT has been discussed by Teivainen (1952, pp. 107—122) in particular and he has also given a very comprehensive survey of the literature on the relationship of ground vegetation to spruce. Additional light on the autecology of feather mosses in particular and their importance in the formation of raw humus comes from the investigations by Romell (1939), André (1947), Tuomikoski (1948) and Tamm (1950, 1953 a, b).

Comparison and conclusion

The development of the frequency and coverage of species shows that a considerable difference exists between comparable stages of primary and secondary successions. The invasion and selection stages of the primary succession with their fluctuations are almost totally absent from comparable secondary stands (cf. Figs. 38 a and b). Bearing in mind that the initial situations are different, it is comprehensible that the ground vegetation of secondary stands retains a broadly speaking unchanged composition

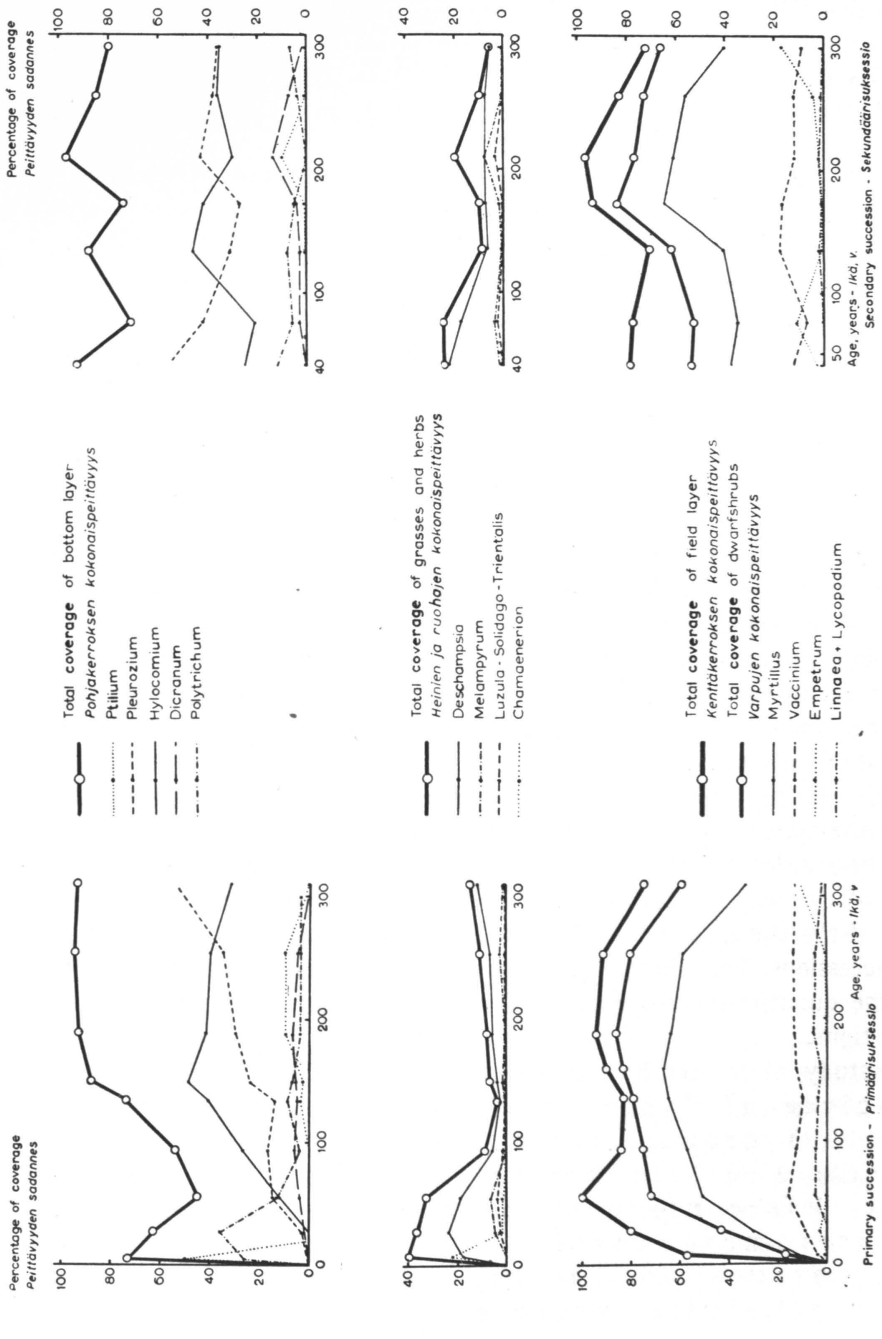

Fig. 38 a and b. Curves illustrating the development of the ground vegetation and its main components during the primary and secondary successions.

Kuva 38 a ja b. Kasvipeitteen ja sen pääkomponenttien kehitys primäärisen ja sekundäärisen suksession aikana.

of species. The raw humus accumulated in the course of years, with its moss cover, does not provide the necessary conditions for the invasion of newcomers. It may be mentioned that Attenberger (1951) has found similar characteristics in Central Europe in the *Myrtillus-Schreberi* associations of secondary spruce stands.

Similarly, it emerged above that spruce definitely affects the formation of ground vegetation. As the composition of tree species in primary and secondary stands is very different in the first 150 years, this difference too must be taken into account when the potential occurrence of the various plants during this period is assessed. Finally, in a climax-stage stand — as will be shown later — the thick raw humus layer may affect the habitat so much that the similarities in stand climate produced by the trees will not suffice to offset the ecological differences produced by accumulated humus in the properties of another principal factor of the habitat, the mineral soil. A comparison of the ground vegetation of primary and secondary stands in fact reveals that a slightly higher number of species indicative of paludification appear in secondary stands at the climax and post-climax stages than is present at the corresponding stages of the primary succession. From the forest site type theory point of view, however, the differences in ground vegetation are hardly big enough to warrant the introduction of a sub-type even. On the contrary, the associations disclose a surprising similarity, being practically identical on other points (cf. Table 28, p. 119).

This finding implies, in other words, that HMT as defined by the forest site type theory is still a reality, even though the reality contains an additional feature earlier overlooked. This special feature is the decisive effect of the way of origination of the stand on the association, not so much of the climax stage as that of the initial and transitional stages of the successions. This effect is particularly distinct on both the qualitative and the quantitative properties of the growing stock of the different tree generations.

A study of the results reported above shows also that the basic principle of Cajander's forest site type theory, viz. that ground vegetation of a certain type reflects a certain site quality, provided development has continued undisturbed long enough, requires more precise definition. The second main proposition of the theory according to which all similar vegetations imply habitats of equal value, is also subject to question in the light of the results reported. The extremely different growing stock of primary and secondary tree generations bear witness to different site qualities proper, in spite of the fact that associations present on habitats of equal potential site quality, classifiable under one and the same forest site type, are in question in both cases. The definition of forest site type, for HMT at least, therefore must be broadened to include the concept of succession, provided the aim is to define potential site quality by means of forest site types.

On primarily identical habitats, therefore, two associations may, different successions notwithstanding, reach a climax stage similar in forest site type without the growing stocks being even nearly equal in their quantitative properties. This means above all that the method of site quality assessment based on vegetation must be based on knowledge of forest dynamics also.

The investigation has also revealed indirectly that the application of the forest site type theory to North Finnish HMT presupposes in certain cases either an ability to predict without error the forest site type developing after approx. 0—150 years or a thorough knowledge of the plant associations of different succession stages. The latter alternative is probably worth noting, for few experts today are likely to be able to determine infallibly — without extremely good fortune — the association that will be present after, say, 100 years.

Root system changes

It is self-evident that the root conditions of a habitat are governed by the plants present on the site. It also seems evident that the dimensions of the root systems of e.g. the healthy individuals of one and the same species on habitats of equal value are generally more or less fixed in their ratio to the size and, normally, age of the trees. At the seedling stage the root system of a tree individual is restricted and superficial; depending on the number of seedlings the superficial parts of the soil, in spite of the small size of the seedlings, may be full of and even packed with roots. Natural thinning eases the competition between root systems but briefly, if at all. A root system that has reached its maximal density may spread more or less freely downward only. From horizontally extended root systems, as the tree grows older, a considerable amount of vertical roots penetrates from the superficial layers to greater depths, down to a certain limit governed by so far unknown factors; this limit is reached at a relatively early age in spruce stands (Kalela 1949, p. 32). In this connection it might be as well to stress that while humus in a natural state of fermentation continues to offer new nutrients the potential upward expansion of roots is nevertheless very limited. The keenest competition between tree roots therefore occurs, as Laitakari (1927, 1935), Kalela (op.c.) etc. have found, just in the humus layer and in the thin surface layer of mineral soil immediately under it. Unnecessary and weak roots die, and in so far as they are not replaced in time in some other direction the tree individual concerned runs the risk of being placed at a still further disadvantage in root competition. In old age — particularly when the tree reaches over-maturity — the death rate of the tips of the roots becomes supernormal and begins to exceed new root growth to such an extent that it causes, directly or indirectly, the death of the tree (Sirén 1950).

The root system of a seedling is structurally tiny to start with. Before long, as the tree grows, the roots extending from the butt gain in strength, gradually assuming an appearance more in keeping with their changing function; at the same time the uptake of nutrients, for instance, is performed exclusively by the fine roots which are present in increasing profusion. Mature trees show roots of greatly differing dimensions and type. Previous investigations have found root systems of coarse structure on habitats of low nutrient content while root systems relatively rich in fine, multiramified roots with a large number of root tips intended for uptake of nutriens, are found on good habitats (cf. e.g. Aaltonen 1920 a, Laitakari 1927, Eneroth 1937, Sirén & Olenius 1945, Kalela 1949 and Sirén 1950.

From this it can be assumed that a high percentage of fine roots in the total root system indicates a habitat of high nutrient content (unless the stand is very young) and, conversely, that a high percentage of fairly thick roots suggests either a site of poor quality or an old forest.

A special feature of root relations associated with the present material is concealed in the species composition of the tree stands studied. Laitakari (1935) has shown that the root system of birch lies deeper in the mineral soil than that of spruce. Bearing in mind, in addition, that the physiological life of birch is shorter than that of spruce, there is good reason to assume that some kind of incomplete utilization of the normal soil volume used by root systems will occur after the removal of birch from the stand (cf. also Brückner & Jahn 1932, p. 169, and Gaiser 1952 a).

A characteristic peculiar to HMT forests, as mentioned before, is profuse dwarfshrub vegetation combined with an unusually thick leached layer generally considered fairly poor in nutrients. Although these factors may not be of decisive importance for the development of the root systems of trees — e.g. Kalela (1949) found the A-horizon to have no special influence on the root relations of spruce stands on South Finnish MT — they are nevertheless worth studying because the A-horizon of HMT is considerably thicker than that of MT in South Finland; in addition, dwarfshrubs on the latter forest site type are considerably less numerous. In Germany Brückner & Jahn (1932) in fact found that the root system of spruce, expressly in thick raw humus and below it, becomes particularly superficial. In this connection it may be mentioned that also Laing (1932, s. 44) has observed that where peat is undecomposed the rootlets rest on or near the surface. On the other hand there are reliable observations proving that A-horizon does not in all cases indicate poverty in nutrients (cf. e.g. Wittich 1952). Aaltonen (1920 a, pp. 23—24) is so far as is known the only researcher, who has studied the root conditions of spruces in Lapland. He found the roots rather superficial.

The main purpose of the investigation into the root conditions of HMT forests was to study the amount of roots of the principal tree species, birch and spruce, in stands at different stages of development, their distribution into different thickness classes and soil layers, and their relationship to the roots of other plants, especially dwarfshrubs. The extensive literature dealing with root systems will not be discussed in any greater detail in this connection. In addition to the bibliography published by Dunning (1949), the papers by Laitakari (1927, 1935), Kalela (1949), Sirén (1950) and Yli-Vakkuri (1953) contain numerous references to the literature.

* * *

Ocular observations of the occurrence of roots were made on all sample plots in connection with investigation of the soil. As the subjectivity of the investigator may easily lead to erroneous conclusions it was considered necessary to carry out a special study eliminating as far as possible the subjectivity, tiredness etc. of the observer.

On sample plots situated close to flowing water, following the method employed by Kalela, four pits were dug as a general rule; from one side of each pit 10 cm thick soil layers measuring 25 × 25 cm were detached. The soil, cut with a small, straight-edged, sharp shovel, including all the roots, was placed in hemispherical screens. These were joined together, in pairs, into globes, a centre screen preventing the samples from mixing. This 2 mm gauge spherical screen was hung in flowing water to remove the fine soil particles. Since some of the finest roots, particularly those that on being cut ceased to be attached to the thickest roots, obviously also may have been lost in the process, repeated tests were made with fine roots specially marked. In all the washing tests, totalling over ten, the loss was less than 7.0 per cent, average approx. 5.0 per cent. After rinsing the root samples were bagged and sent to the laboratory for sorting, measurement, drying and weighing.

The root relations of the humus could not be clarified by water rinsing alone, for which reason the 25 × 25 cm clod of roots was either studied on the spot by picking or sent as it was to the laboratory where humus samples were always given priority. Some samples were preserved in formalin solution.

The root relations of a total of 8 sample plots were investigated in this way. In addition, the root relations of an HMT spruce stand situated at Kivalo were studied by Kalela's sorting method. Roots were dug from a total of 56 pits; on two sample plots samples were taken from 8 pits each and on the Kivalo sample plot from 16 pits. The depth of the pits was 50 cm in every case.

Before persuing the results, it may be useful to recall a few details of the tree stand of the sample plots studied (Table 31).

It may be pointed out once again that the proximity of flowing water decided the sample plots on which root system studies could be carried out. The studies were made in the period between August 15 — September 15, after the main growing season for roots in Lapland (cf. also Laing 1932, s. 62 and Ladefoged 1939, pp. 130—155).

To illustrate the method of study let us take first the representative records (Table 32) of the root relations of Sample Plot 6, Siulionpalo. The most significant point emerging from these tabulated notes is the small amount of roots obtained in the filtrate on water screening in the laboratory treatment and larger amount on mechanical sorting; hence the majority of roots were sorted manually.

The comparison of root weights will be discussed later. But it may be mentioned in this connection that roots exceeding 5 mm in thickness have not been included in the total weight of tree roots. Apart from the fact that the occurrence of such thick roots in the samples is accidental, this decision can also be supported by the fact that the roots or other underground parts of dwarfshrubs and other plants are generally less than 5 mm thick. In this way the material collected from each sample plot offers many possibilities for the study of various data. Like the rest of the material the root samples are deposited in the Silvicultural Institute of Helsinki University. Because of space problems the present paper will give only a few representative cases and tabulated compilations.

Table 31. Main characteristics of the tree stand on the sample plots selected for root studies.

Taulukko 31. Juuritutkimuksiin valittujen näytealojen puuston pääpiirteet.

Number of sample plot *Näytealan n:o*	Age of stand *Metsikön ikä*	Density of stand *Metsikön tiheys*	Special characteristics of species composition *Puulajisuhteiden erikoispiirteet* Percent of volume *Kuutiomääräsadannes* bi — *ko*	spr — *ku*	
6	51	0.8	90	10	spruce storey slight unevenaged *kuusijakso lievästi eri-ikäistä*
10	88	0.7	80	20	spruce storey 20 years younger than birch — *kuusijakso 20 v. koivua nuorempaa*
12	95	0.8	70	30	spruce storey grouped *kuusijakso ryhmittäinen*
19	135	1.0+	60	40	spruce storey very dense, small trees — *kuusijakso erittäin tiheä, pientä puuta*
22	137	1.0	40	60	birch storey not quite intact *koivujakso hiukan puutteellinen*
38	260	0.9	0	100	no more birch present *koivua ei enää esiinny*
60	170	0.8	10	90	secondary forest with some sprout birch — *sekundäärimetsä, jossa vesakoivua*
70	270	0.8	0	100	secondary stand *sekundäärimetsikkö*
71	300	0.7	20	80	secondary stand with a little sprout birch — *sekundäärimetsikkö, jossa vähän vesakoivua*

Table 32. Summary of the roots of a sample plot.

Taulukko 32. Yhteenveto erään näytealan juurista.

Soil layer *Maakerros*	Diameter classes of roots, mm — *Juurten läpimittaluokat, mm* Birch — *Koivu* < 1 fil-trate *suodos*	< 1 as a result of sorting *lajittelun tuloksena*	1—2	2—5	5 <	Spruce — *Kuusi* < 1 filt-rate *suodos*	< 1 as a result of sorting *lajittelun tuloksena*	1—2	2—5	5 <	Other roots, g/sq.m — *Muita juuria, gr/m²* Dwarf-shrubs *Varpuja*	*Deschampsia flexuosa*	*Polytrichum*
	Length of roots, m/sq.m — *Juurten pituus, m/m²*												
Humus + 4.4—0 cm	84.60	470.05	41.48	15.26	5.60	2.40	1.28[1]	1.08	0.96	—			
	Weight of roots, g/sq.m — *Juurten paino, g/m²*												
	.	*67.14*	*46.18*	*84.58*	*170.42*	—	*0.12*	*0.88*	*3.53*		*103.59*	*73.25*	*25.94*
0—10	44.10	268.42	32.16	12.80	6.50	3.00	2.90	0.56	0.22	—			
	.	*40.30*	*36.99*	*54.15*	*138.75*	—	*0.93*	*0.41*	*0.63*		*21.04*	*10.20*	*25.62*
10—20	22.90	175.72	21.90	4.92	1.38	1.00	1.92	0.50	0.10	—			
	.	*27.72*	*20.46*	*17.53*	*42.94*	—	*0.54*	*0.61*	*0.29*		*1.57*	*5.87*	*1.18*
20—30	12.50	100.66	20.90	2.94	—	—	—	—	—	—			
	.	*18.52*	*22.50*	*15.18*							*0.67*	*4.38*	
30—40	6.00	78.56	11.80	1.98									
	.	*14.32*	*12.51*	*8.39*							*0.04*	*2.62*	
40—50	4.30	44.02	7.50	1.84									
	.	*8.80*	*8.53*	*4.58*							—	*1.28*	

The roots of the stands

The study of the results follows largely the general lines taken by Kalela (1949) in order to enable at least some kind of a comparison. Kalela has e.g. considered it important to study the total amount of roots, their distribution in the different soil layers and their relationship to the volume of growing stock. These data are given in Table 33 a, b and c for each sample plot (cf. also Fig. 39).

Table 33 a and b. The amount of roots in sample plot stands investigated (primary material).

Taulukko 33 a ja b. Eri näytealametsiköiden juurimäärät (primääriaineisto).

Soil layer *Maakerros*	(a) Age of stands, years and tree species — *Metsiköiden ikä, v. ja puulajit* Primary stands — *Primäärimetsiköt* 50 birch *koivu*	50 spruce *kuusi*	88 bi *ko*	88 spr *ku*	95 bi *ko*	95 spr *ku*	135 bi *ko*	135 spr *ku*	137 bi *ko*	137 spr *ku*	260 bi *ko*	260 spr *ku*	Secondary stands *Sekundäärimetsiköt* 170 bi *ko*	170 spr *ku*	270 bi *ko*	270 spr *ku*	300 bi *ko*	300 spr *ku*
	Total length of roots, m/sq.m — *Juurten kokonaispituus, m/m²*																	
Humus	627	9	202	109	226	73	222	400	221	286	16	378	79	334	△	292	43	440
0—10	364	7	230	28	252	22	248	98	158	133	5	211	45	69		124	17	168
10—20	227	4	269	15	156	15	236	73	109	34	6	132	37	104		146	17	91
20—30	137	△	159	1	106	7	216	24	61	4	1	106	54	101		103	6	42
30—40	98	—	140	—	124	10	133	10	62	1	1	63	50	74		70	1	46
40—50	58		102		109	△	71	9	26		2	21	37	46		20	△	21
Total *Yhteensä*	1511	20	1102	153	973	127	1126	614	637	458	31	911	302	728	△	755	84	808
	(b) Percentual distribution of roots into different soil layers *Juurten prosenttinen jakaantuminen eri maakerroksiin*																	
Humus	41.5	45.0	18.3	71.2	23.3	57.5	19.7	65.1	34.7	62.5	51.6	41.5	26.2	45.8		38.8	51.3	54.4
0—10	24.1	35.0	20.9	18.3	25.9	17.3	22.0	16.0	24.8	29.0	16.1	23.2	14.9	9.5		16.4	20.2	20.8
10—20	15.0	20.0	24.4	9.8	16.0	11.8	21.0	11.9	17.1	7.4	19.4	14.5	12.1	14.3		19.3	20.2	11.3
20—30	9.1	△	14.4	0.7	10.9	5.5	19.2	3.9	9.6	0.9	3.2	11.6	17.9	13.9		13.6	7.1	5.2
30—40	6.5	—	12.7	—	12.7	7.9	11.8	1.6	9.7	0.2	3.2	6.9	16.6	10.2		9.3	1.2	5.7
40—50	3.8	—	9.3	—	11.2	—	6.3	1.5	4.1	—	6.5	2.3	12.1	6.3		2.6	△	2.6
Total *Yhteensä*	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0		100.0	100.0	100.0

In a 50-year old birch stand where spruce is present mainly as undergrowth, the total length of roots approximates 1500 m/sq.m. In an old spruce stand where birch in its turn is present as a mixed species, the corresponding figure for spruce approximates 900 m/sq.m. The latter figure is definitely of a different size class from that given by Kalela (1949) for MT spruce stands in South Finland. The dissimilarity naturally may have many causes; one of the most important may lie in the different investigation method. This is indicated above all by the different ratios of root thickness classes. Later, after he had developed his method, Kalela gave root amounts similar to those reported here (Kalela unpubl.).

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[1] After sorting the small broken roots were estimated by microscope; 9.2 m birch- and 3.3 m spruce roots were found.
Mekaanisen lajittelun jälkeen arvioitiin jäännöksen juurimäärä mikroskoopin avulla; tällöin löytyi 9.2 m koivun ja 3.3 m kuusen juuria.

Table 33 c. The amount of roots per cubic metre of growing stock.

Taulukko 33 c. Juurimäärä puuston kuutiometriä kohden.

Soil layer *Maakerros*	(c) Age of stands, years and tree species — *Metsiköiden ikä, v. ja puulajit*														
	Primary stands — *Primäärimetsiköt*										Secondary stands *Sekundäärimetsiköt*				
	50	88		95		135		137		260	170		270	300	
	birch *koivu*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	spr *ku*	bi *ko*	spr *ku*	spr *ku*	bi *ko*	spr *ku*
	The amount of roots per cubic metre of growing stock, km/cu.m *Juurimäärä puuston kuutiometriä kohden, km/m³*														
Humus	74.5	20.9	56.5	22.5	25.3	16.2	39.4	33.0	21.3	15.7	60.8	26.9	21.7	21.5	55.0
0—10	43.2	23.8	14.5	25.1	7.6	18.1	9.6	23.6	9.9	8.8	34.6	5.6	9.2	8.5	21.0
10—20	27.0	27.8	7.8	15.5	5.2	17.2	7.2	16.3	2.5	5.5	28.5	8.4	10.8	8.5	11.3
20—30	16.3	16.5	0.5	10.6	2.4	15.8	2.4	9.1	0.3	4.4	41.5	8.1	7.6	3.0	5.3
30—40	11.6	14.5	—	12.4	3.5	9.7	1.0	9.2	0.1	2.6	38.5	6.0	5.2	0.5	7.5
40—50	6.9	10.6	—	10.9	△	5.2	0.9	3.9	—	0.9	28.5	3.7	1.5	△	2.6
Total *Yhteensä*	179.5	114.1	79.3	97.0	44.0	82.2	60.5	95.1	34.1	37.9	232.4	58.7	56.0	42.0	102.7

Comparison with previous investigation results is further hampered by the composition of the species in the stands studied. The root relations of mixed stands have been little studied; hence the numerical values given in the table must be accepted at their face value without any possibility of comparison.

Some idea of the root relations of the principal tree species of HMT forests can be formed on the basis of the material collected. After the necessary adjustment[1] the following picture is obtained of the occurrence of roots at different age periods (Table 34):

The more or less accidental and vastly differing species compositions of the material naturally affect the picture of the root relations. The series quoted reflects the root relations of an HMT stand in which the spruce storey is first present as insignificant undergrowth and at climax stage of smaller volume than normally. However, the adjusted root amount, computed per volume unit of both species in the stand (Table 33, Section c), provides a criterion more or less independent of the species composition

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[1] The adjustment was greatly complicated by the fact that Sample Plot 19 (Mainua) differed considerably from the others in its spruce storey.

Table 34. Levelled total length of roots per square metre at various age periods in the stands investigated.

Taulukko 34. Tutkittujen metsiköiden juurten tasoitettu kokonaispituus neliömetriä kohden eri ikäkausina.

Tree species *Puulaji*	Age of stand, years — *Metsikön ikä, v.*									
	50	75	100	125	150	175	200	225	250	300
	Length of roots, m/sq.m — *Juurten pituus, m/m²*									
Spruce *Kuusi*	20	100	250	450	600	750	850	900	900	800
Birch - *Koivu*	1500	1250	1000	780	550	350	250	150	60	—

of the sample plots for the study of root relations in stands where both birch and spruce have originated in full density. If the optimal curve of volume development (cf. p. 89) is taken as the basis for such an — admittedly uncertain — study, we get a picture differing from the above of the root relations of spruce in particular (Table 35).

The series are surprisingly complementary mutually — the analogy with growing stock is naturally axiomatic. There is no intention, with such a restricted and relatively heterogeneous material, of ascertaining the absolute root amounts of birch-spruce mixed stands. Nor, in view of the problem under investigation, is there any reason for extensive speculation otherwise. It may suffice, therefore, to consider the series given as probable series only for the event of the two principal species of an HMT stand invading the habitat simultaneously and, as far as possible, stocking it fully.

Table 35. Average total length of roots per square metre, weighted by the average volume of growing stock.

Taulukko 35. Puuston kuutiomäärällä punnittu juurten keskimääräinen kokonaispituus neliömetriä kohden.

Tree species *Puulaji*	Age of stand, years — *Metsikön ikä, v.*									
	50	75	100	125	150	175	200	225	250	300
	Length of roots, m/sq.m — *Juurten pituus, m/m²*									
Spruce *Kuusi*	(480)	550	630	740	860	990	1100	1100	990	(500)
Birch - *Koivu*	1500	1400	1100	770	500	300	120	—	—	—
Total *Yhteensä*	∼1980	1950	1730	1510	1360	1290	1220	1100	990	(500)

On the basis of the above two series of the total root amounts, it may be concluded that

— the root amount of the birch storey per square metre of forest soil is at its highest at an early age (approx. at or before 50 years), and it is then definitely greater than that of the spruce storey.

— with the removal of birch from the stand the total root amount of trees in the soil decreases surprisingly little due to the simultaneous increase of spruce roots; e.g. in a 250 year old pure spruce stand the root amount equals approx. half that of a 50 year old mixed birch- spruce stand,

— the strongest decrease of birch roots takes place at an age (75—175 years) when the growth of the spruce stand reaches its highest rate (ct. p. 89),

— the total root amount of the spruce storey reaches its maximum at approximately 175—250 years and concurs well in this respect with MT spruce stands, developing twice as fast, of South Finland investigated by Kalela, in which the maximum coincides with the age of 100—120 years. Absolute figures naturally are comparable only for roots exceeding 1 mm in thickness.

The degeneration of the spruce storey after the climax stage is also distinctly visible in the sudden decrease in roots. In ocular observations the amount of dead spruce roots was found to be particularly high in just those stands which were older than 300 years.

* * *

The total root amount, however, is rather an approximate guide to root relations. It affords no idea at all of the distribution of the various thickness classes of roots in the different soil layers. It may be assumed from earlier investigations that the roots of spruce and birch, practically independent of thickness class, spread differently in the soil. A general idea of this distribution of roots into the different soil layers is supplied by Table 33 above, Sections a and b.

In order to draw the essential features into sharper focus still, the sample plots, irrespective of the way in which the stands were born, have been grouped in the table below by age, counting stands of 50—137 years as young and the others as old stands. The former are dominated by birch, the latter are either pure spruce stands or stands strongly dominated by spruce (Table 36).

Table 36. Percentual distribution of roots in young and old sample plot stands at different depths.

Taulukko 36. Nuorten ja vanhojen näytealametsiköiden juurten prosenttinen jakaantuminen eri maakerroksiin.

Soil layer *Maakerros*	Percentage of roots in young stands *Nuorten metsiköiden juurten sadannes*		Percentage of roots in old stands *Vanhojen metsiköiden juurten sadannes*
	Birch — *Koivu*	Spruce — *Kuusi*	Spruce — *Kuusi*
Humus	27.5	64.1	45.1
0—10	23.7	20.1	17.5
10—20	18.7	10.2	14.9
20—30	12.6	2.8	11.1
30—40	10.7	2.4	8.0
40—50	6.8	0.4	3.4
Total *Yhteensä*	100.0	100.0	100.0

The table gives the total root amounts present in each soil layer, by tree species, as a percentage of the aggregate root amount of the soil volume studied (1.0 × 1.0 × 0.5 m^3). From these percentages the following may be concluded:

The vast majority of the root systems of the birch storey is situated in the mineral soil, considerably deeper than the roots of the evenaged or only slightly younger spruce storey. These series of figures thus also confirm Laitakari's (1935) finding regarding the depth distribution of the roots of tree species.

The vast majority of the root systems of the spruce storey is situated in the humus layer, particularly in young stands. At greater depths (> 30 cm) spruce roots are only present nominally. Similar results have been obtained much earlier already (cf. e.g. Aaltonen 1920 a, Moore 1922 and Laing 1932). The superficial location of the roots is more marked still in the HMT stands than in the South Finnish MT stands investigated by Kalela (1949).

As the stand grows older and becomes spruce-dominated the root system of spruce evidently invades the deeper soil layers to some degree, but does not replace the dying birch roots more than partially.

The density of roots per unit of soil volume, consequently, does not grow nearly as great as in the period of birch dominance. On this point it has also been possible to find from separate observations that the roots of spruce penetrate to the lower soil layers along channels left by birch roots, an observation made earlier by Laitakari (1935). It may be mentioned that Rahteenko (1950) has made the same observation, but he found in addition, from short-term but comprehensive experiments, that spruce roots are particularly superficial in pure spruce seedling stands. The roots generally develop better in mixed seedling stands.

The percentages in the table also reveal that a surprising change occurs in the vertical distribution of spruce roots with advancing age of the stand in that the relative amount of roots in the humus decreases perceptibly — in spite of the fact that humus grows in thickness and is definitely thicker in old stands.

All the conclusions drawn above are based on the total root amount of the different soil layers. However, an example (Sample Plot 6, Siulionpalo, see Table 32) will show that the distribution of root thickness classes is not of the same kind in all the soil layers: thick roots are more frequent e.g. in the A-horizon (0—10 cm) than in the other layers. To illustrate this point the absolute amounts of roots of various thickness classes in each soil layer are given in Fig. 39, and the corresponding percentages in Table 37.

From the data in both Fig. 39 and Table 37, the following conclusions can be drawn regarding the birch storey:

— Humus contains the largest amount of fine roots, both absolutely (with two exceptions) and relatively.

— A fairly large amount of roots occurs in the A-horizon (0—10 cm), but of a coarser structure than the roots in the humus; i.e. fine roots are relatively fewer. The thickest roots (2—5 mm and over 5 mm) are both absolutely and relatively highest in amount in this layer. The low number of fine roots indicates probably poverty in nutrients or other disadvantageous conditions of the soil layer concerned.

— The B-horizon contains the highest percentage of fine (under 1 mm) roots after the humus. The proportion of thick roots (2—5 mm and over 5 mm) is also great; this means that short, thin (1—2 mm) roots have ramified a great deal.

— At a greater depth in the mineral soil the proportion of fine roots does not change appreciably. But the proportion of 1—2 mm roots increases at the expense of the thickest.

For the spruce storey also certain interesting features are observable, above all the following:

Table 37. Relative depth distribution of different root fractions in different age groups of stands.

Taulukko 37. Eri kokoisten juurten suhteellinen syvyysjakaantuminen näytealametsiköiden eri ikäryhmissä.

Soil layer *Maa-kerros*	Diameter classes of birch roots, mm *Koivun juurten läpimittaluokat, mm*						Diameter classes of spruce roots, mm *Kuusen juurten läpimittaluokat, mm*					
	< 1 fine *hento*	1—2 thin *ohut*	2—5 coarse *karkea*	5 thick *paksu*	Ratio *Suhde* < 1 / 1—2	< 1 / 1—5	< 1 fine *hento*	1—2 thin *ohut*	2—5 coarse *karkea*	5 thick *paksu*	Ratio *Suhde* < 1 / 1—2	< 1 / 1—5
	Percentage of total length of roots *Juurten sadannes kokonaispituudesta*						Percentage of total length of roots *Juurten sadannes kokonaispituudesta*					
Humus	young stands — *nuoret metsiköt*											
	87.0	9.6	2.4	1.0	9.1	7.3	78.9	16.5	3.9	0.7	4.8	3.9
	old stands — *vanhat metsiköt*											
	88.6	*6.0*	*3.7*	*1.7*	*14.4*	*9.0*	*70.5*	*19.3*	*7.2*	*3.0*	*3.7*	*2.7*
0—10	79.5 *76.0*	13.6 *10.0*	4.9 *9.0*	2.0 5.0	5.8 *7.6*	4.3 *4.0*	69.6 *62.6*	22.6 *24.2*	6.6 *10.5*	1.2 *2.7*	3.1 *2.6*	2.4 *1.8*
10—20	82.6 *86.0*	12.4 *12.0*	4.0 *1.5*	1.6 *0.5*	6.7 *7.2*	5.1 *6.4*	80.8 *70.6*	17.4 *23.5*	0.7 *5.5*	1.1 *0.4*	4.7 *3.0*	4.5 *2.4*
20—30	80.0 *89.0*	15.1 *9.5*	4.4 *1.5*	0.5	5.3 *9.4*	4.1 *8.1*	89.6 *69.6*	10.4 *25.5*	*4.4*	*0.5*	8.6 *2.7*	
30—40	79.5 *87.0*	17.5 *12.5*	2.9 *0.5*	0.1	4.5 *7.0*	3.8 *6.7*	. *72.3*	. *25.1*	*2.3*	*0.3*	*2.9*	
40—50	81.6 *94.0*	16.1 *6.0*	2.2	0.1	5.1 *15.7*	4.5 *15.7*	. *70.9*	. *26.5*	*2.5*	*0.1*	*2.7*	

— The vast majority of spruce roots occur in the humus (see Fig. 39); in old stands the humus also has a profusion of thick roots.

— In the A-horizon (0—10 cm) the proportion of the tiniest roots is lower than in any other layer, and this applies to both young and old stands (cf. Wiedemann 1937, p. 222); the percentage of coarse roots again is at its highest.

— The B-horizon (10—20 cm) in many cases contains fairly few roots. But their distribution into thickness classes is very similar to that of the roots in the humus; the fine roots important for the uptake of nutrients are relatively profuse.

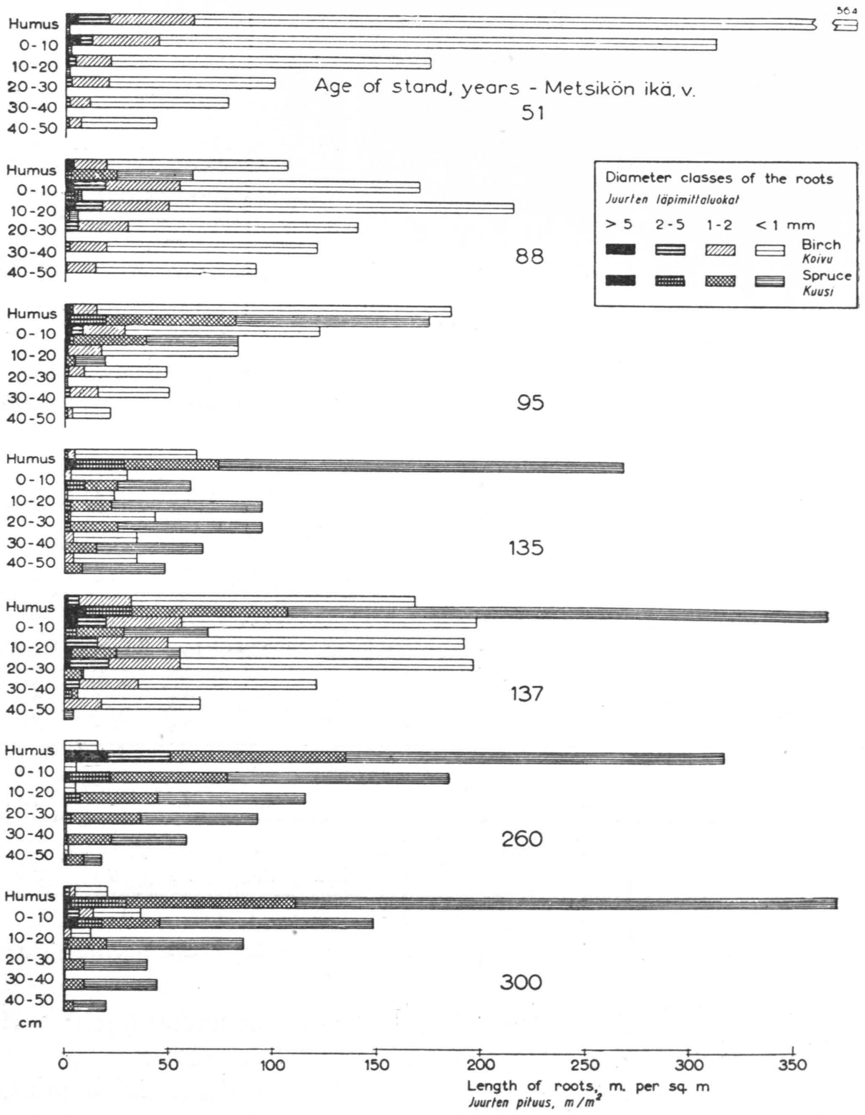

Fig. 39. The absolute amount of birch and spruce roots of various thickness in different soil layers on some of the sample plots.

Kuva 39. Eri paksuusluokkaa olevien koivun ja kuusen juurten absoluuttinen määrä eräiden näytealojen eri maakerroksissa.

— At greater depths the proportion of the finest roots in old stands remains at approx. 70 per cent, that of thin roots at approx. 25 per cent. The proportion of thicker roots in the higher layers is 5 per cent but decreases gradually with depth. In young stands the percentage of fine roots is high in the B-horizon and continues to increase towards the deeper layers. This of course is due, as e.g. Kalela (1949) has shown, to the general superficial location of spruce roots.

A comparison of the root diameters of spruce and birch reveals that birch has considerably more fine roots. The proportion of fine roots in the total root system is 80—90 per cent with birch, 70—80 per cent with spruce — except in the A-horizon where it is markedly lower. A fact striking at first sight is the ratio between the fine and coarse roots of birch, which varies between 4.5 and 9.4 except in the humus and deepest soil layers. Contrary to expectations, there are proportionately more fine roots in old than in young stands. The explanation seems simple. In the sample plot stands termed young the birch is already a large-sized tree; in old sample plot stands, on the other hand, there are plenty of small-sized sprout birches whose root systems are still fairly fine in structure. The spruce roots in old stands are coarser than in young stands.

* * *

A point to be borne in mind in studying the root conditions of trees is that root tips and fine roots are of the greatest importance for nutrient uptake. They are the most active of the roots, and their vitality and abundance reflects the growth conditions of the tree and the stand. In the present investigation, unfortunately, the number of root tips per length unit of fine roots was not computed, and only the total root length was measured. Nor were the important mycorrhiza investigated to an extent productive of reliable results.

The percentages of fine roots in relation to other roots in different soil layers are given in Table 37. As however, the absolute values may be of importance the following table gives from the primary stands studied the absolute amount of fine roots in the different soil layers, the root density on the humus layer and the length of roots per unit of growing stock volume (Table 38).

The following facts are revealed by this table:

— The amount of birch fine roots is exceedingly high particularly in young stands, and it is considerably larger than that of spruce, at least up to approximately 140—160 years.

Table 38. The amount of fine roots in the sample plot stands (primary stands).

Taulukko 38. Näytealametsiköiden hentojen juurten absoluuttinen määrä (primäärimetsiköt).

Soil layer *Maakerros*	Age of stands, years and tree species — *Metsikön ikä, v. ja puulajit*											
	50		88		95		135		137		260	
	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*	bi *ko*	spr[1] *ku*	bi *ko*	spr *ku*	bi *ko*	spr *ku*
	Total length of fine roots, m/sq.m *Hentojen juurten pituussumma, m/m²*											
Humus	564	7	174	87	195	66	190	294	204	206	16	247
0—10	312	6	175	18	192	17	192	70	130	91	5	133
10—20	199	3	219	14	128	13	186	47	90	28	6	87
20—30	113	—	130	△	84	6	160	16	50	4	1	70
30—40	85	—	120	—	97	6	97	4	47	△	1	40
40—50	48	—	87	—	93	△	52	4	21	—	2	12
Total *Yhteensä*	1321	16	905	119	789	108	877	435	542	329	31	585
	Total length of fine roots per cm of depth unit (cm) of humus, m/cm/sq.m *Hentojen juurten pituus humuksen paksuusyksikköä (cm) kohden, m/cm/m²*											
Humus	128.2	.	47.0	.	55.7	.	61.3	94.8	46.4	46.8	.	34.7
	The amount of roots per cubic metre of growing stock, km/cu.m *Juurimäärä puuston kuutiometriä kohden, km/m³*											
	156.8	.	93.7	(61.7)	78.6	(37.5)	64.1	42.8	81.0	49.1	.	24.3

— The vertical distribution of the fine roots underlines the superficiality of spruce nutrient uptake. In the oldest sample plot stand the influence of the sparse birch sprouts is visible.

— The density of fine roots in the humus layer is highest in the beginning of the succession and decreases as it seems with the age of the stands (= accumulation of raw humus). From this it may be concluded that the availability of nutrients in the humus layer has decreased.

— The amount of fine roots per cu.m of growing stock declines with advancing age of the stand — i.e., with increasing volume. The real value

of these figures is of course very small. The ratio fine roots: increment, or fine roots: assimilation surface would have been more instructive. Similar main features have been stated also by Kalela for spruce and pine in South Finland; only, there is a considerable difference between the root amounts of the different tree species. That the effect of the root system of birch, denser and of finer structure, emerges very clearly is comprehensible, particularly as the volume of the birch storey is often very low. When the growth of trees in due course decreases distinct signs of this decline phenomenon are visible in the root systems also; the renewal of root tips and fine roots is no longer capable of replacing the annual heavy losses, and increasing portions of root systems remain incompletely used and eventually die. This course of development should emerge from a comparison of the proportion of the finest roots with that of the longer-lived roots. This point is to some extent illustrated by the figures below of ratios based on the total length of two different root classes:

	Age of stand, years								
	50	88	95	135	137	260	170	270	300
	Birch roots								
Ratio: $\frac{\text{fine roots}}{\text{thin roots}}$	9.7	6.3	5.8	5.2	3.1				
	Spruce roots								
» »	7.2	4.8	5.6	3.3	3.4	2.5	4.4	4.0	2.4

The figures illustrate the development of root coarsening fairly well.

The absolute amount of spruce fine roots varies according to the density of the spruce storey of the stands. In certain cases it is considerable, totalling up to 500—600 m/sq.m in old stands. Compared with the figure obtained by Kalela for MT spruce stands in South Finland the amount of spruce fine roots in the present investigation is approx. 2—3 times higher. Bearing in mind that the percentage of these roots was found to vary between 70 and 80 per cent, the difference is understandable. Assuming that the percentage determined by Kalela averages 60 (cf. Kalela 1949, pp. 36—37), the following example will illustrate the deceptive character of the percentages:

$$\text{Total root amount } 100 \text{ — fine roots } 75;\ \text{ratio: } \frac{\text{fine roots}}{\text{others}} = \frac{75}{25} = 3.0$$

$$\text{» » » } 100 \text{ — » » } 60;\ \text{» » »} = \frac{60}{40} = 1.5$$

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[1] The spruce storey is over-dense — *Kuusijakso on ylitiheä.*

As there is good reason to assume that the differences in measurement of roots exceeding 1 mm in thickness are very small, it may be taken that the total root amount increases considerably (60 per cent) with fine roots increasing, let us say only from 60 to 75 per cent. With a fine root percentage of 80 per cent the total root amount increases 2.4-fold, provided the absolute amount of thicker roots is the same.

The roots of dwarfshrubs

It was pointed out above that the total root amount of spruce increases rather slowly in the humus layer with advancing age of the stand in spite of birch giving way to spruce. It will be remembered from the study of ground vegetation also that the proportion of dwarfshrubs was found to have grown considerably in old stands. Hence it was thought necessary to ascertain the extent to which the proportion of dwarfshrub roots had increased as the dwarfshrubs gained in profusion. The method employed made it possible also to collect the *Polytrichum* rhizoids and *Deschampsia* rhizomes and roots without additional effort. The amount of the roots of dwarfshrubs and other plants was determined by weighing. The root amounts of each sample plot are shown by soil layers in Table 39, which also gives the percentual vertical distribution. As the depth of humus in the various stands varied within wide limits, the root amount present in the humus has also been determined per cm of humus depth.

The table shows above all the overwhelming dominance of dwarfshrub roots, particularly perceptible in the humus layer of old stands. The superficial location of dwarfshrub roots is really remarkable; it is probably mostly due to the fact that humus, in addition to thicker roots, contains plenty of underground stalks which from the humus structure point of view are well comparable with roots. Into the mineral soil only very fine and, to a limited extent only, some thicker roots penetrate.

For *Deschampsia*, present primarily in young and in old open stands, the humus provided the best source of nutrient uptake for its rhizomes and roots. As, in addition, its roots on all the sample plots extend deeper than 50 cm, it is very well represented in each layer of the mineral soil (cf. e.g. Kivenheimo 1947, pp. 44—45).

For *Polytrichum* it may be mentioned only that its proportion in the humus is very small whereas in the A-horizon it is seemingly surprisingly high. Its rhizoids, by means of mycelium present, attach to the bottom

Table 39. The amount of the roots and other underground parts of dwarfshrubs (V), Deschampsia (D) and Polytrichum (P) in some sample plot stands investigated.

Taulukko 39. Varpujen (V), ahdelauhan (D) ja karhunsammalen (P) juurten ja muiden maanalaisten osien määrä tutkituissa näytealametsiköissä.

Soil layer *Maa-kerros*	Age of primary stands, years — *Primäärimetsiköiden ikä, v.*																		Age of secondary stands, years *Sekundäärimetsiköiden ikä, v.*							
	50			88			95			135			137			260			170			270			300	
	V	D	P	V	D	P	V	D	P	V	D	P	V	D	P	V	D	P	V	D	P	V	D	P	V	D
Amount of roots in different soil layers, g/sq.m — *Juurten runsaus eri maakerroksissa, gr/m²*																									
Humus	103.6	73.3	25.9	200.0	35.0	7.0	168.1	22.0	12.4	171.4	2.8	33.0	289.6	3.7	9.6	252.8	36.6	24.4	850.0	37.0	7.5	402.0	△	16.8	294.4	13.7
0—10	21.0	10.2	25.6	15.0	15.0	13.0	16.3	15.4	20.5	27.2	1.2	35.0	4.7	3.3	19.9	23.1	6.7	29.6	37.0	7.5	17.0	36.4		13.7	29.5	4.2
10—20	1.6	5.9	1.2	2.0	8.0	2.0	1.3	8.7	0.8	2.4	1.4	0.6	0.1	1.2	0.5	3.8	4.7	0.6	1.6	5.1	2.5	2.7		0.7	5.6	4.2
20—30	0.7	4.4			4.0		△	3.5	0.2	1.2	1.4	0.1	△	1.9		0.6	5.0		0.5	3.2		0.2	△	0.2	0.5	3.2
30—40	△	2.6			3.0		△	2.8	0.0	0.1	0.6		△	0.7		0.1	1.4		0.1	1.9		0.2		△	0.2	1.9
40—50		1.3			2.0		△	2.0		0.1	0.5		0.4	0.5		0.1	1.5		0.1	1.4		0.2				0.7
Total *Yht.*	126.9	97.7	52.7	217.0	67.0	22.0	185.7	54.4	33.9	202.4	7.9	68.7	294.8	11.3	30.0	280.5	55.9	54.6	889.3	56.1	27.0	441.7		31.4	330.2	27.9
Percentual distribution of roots in different soil layers — *Juurten prosenttinen jakaantuminen eri maakerroksiin*																									
Humus	81.6	75.1	49.1	92.2	52.2	31.8	90.5	40.4	36.5	84.7	35.5	48.1	98.2	32.8	32.0	90.1	65.5	44.7	95.6	65.9	28.0	91.0		53.5	89.2	49.1
0—10	16.5	10.4	48.6	6.9	22.4	59.1	8.8	28.3	60.5	13.4	15.2	50.9	1.6	29.2	66.3	8.2	12.0	54.2	4.2	13.4	63.0	8.2		43.6	8.9	15.1
10—20	1.3	6.0	2.3	0.9	11.9	9.1	0.7	16.0	2.4	1.2	17.7	0.9	0.1	10.6	1.7	1.4	8.4	1.1	0.2	9.1	9.0	0.7		2.3	1.7	15.1
20—30	0.6	4.5			6.0			6.4	0.6	0.6	17.7	0.1	△	16.8		0.2	8.9		△	5.7		△		0.6	0.2	11.5
30—40		2.7			4.5			5.1		0.1	7.6		△	6.2		0.1	2.5		△	3.4		△			△	6.8
40—50		1.3			3.0			3.8		0.1	6.3		0.1	4.4			2.7		△	2.5		△			△	2.4
Total *Yht.*	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0		100.0	100.0	100.0
Amount of roots per depth unit (cm) of humus, g/cm — *Juuria humuksen paksuusyksikköä (cm) kohden, gr/cm*																									
Humus	23.5	16.7		54.0	9.5		48.1	6.3		55.3	0.9		65.8	0.9		36.1	5.4		90.4	4.0		57.4	△	—	42.1	2.0

part of the thallus considerable amounts of fine soil particles, making it fairly heavy.

As regards the amount of dwarfshrub roots per depth unit of humus, this increases with advancing age and reaches its maximum in medium aged stands. In old stands, on the other hand, the amount of dwarfshrub roots per depth unit of humus seems to decline somewhat, possibly as a result of the increase in the moss remains of the raw humus. The absolute amount of dwarfshrub roots, however, is at its maximum expressly in old stands. Grass roots, comprehensibly, are more profuse in the early stages of the primary succession; unfortunately the root investigations were not extended at the young secondary stage sample plot stands which had plenty of *Deschampsia*.

A very interesting picture of the profusion of dwarfshrub roots is supplied by the series of figures quoted below. These give the weights of dwarfshrub and grass roots and of the basal parts of the thallus and rhizoids of *Polytrichum* as a percentage of the aggregate weight of all roots less than 5 mm thick (hence including tree roots) studied in each soil layer (Table 40).

The dominance of dwarfshrub roots in the humus seems surprising, particularly in the old stands. The great importance of dwarfshrub roots,

e.g. as competitors for water and nutrients, is known (cf. p. 153). It is comprehensible then that the relative proportion of spruce roots declines quite considerably in old stands compared with young. On the other hand, spruce roots are known to be at their maximum quantitatively in old stands in the climax stage. This, in combination with certain points ascertained previously, justifies the following conclusion.

Table 40. The ratio between root amount of dwarfshrubs etc. (V + D + P) and the total of the roots studied in young and old stands.

Taulukko 40. Varpujen ym. (V + D + P) juurimäärän suhde kaikkien tutkittujen juurten määrään nuorissa ja vanhoissa metsiköissä.

Soil layer *Maakerros*	Young stands *Nuoret metsiköt*	Old stands *Vanhat metsiköt*
	Dwarfshrub and other roots as a percentage of total root amount by weight *Varpujen ym. juurten painosadannes kaikista tutkituista juurista*	
Humus	55.0	74.0
0—10	25.0	31.6
10—20	8.5	11.9
20—30	6.2	6.4
30—40	4.7	4.5
40—50	4.9	5.8

In spite of the considerable qualitative changes occurring in the root systems of HMT associations during different successional stages, the absolute amount of roots expressed in weight units does not reach its maximum in the humus layer until during the climax stage.

This conclusion calls for a discussion of the fundamental features of the root dynamics of HMT stands.

Root dynamics

The root conditions of HMT stands were found above to correspond to conditions above ground. Initially there is a certain period of herb dominance in the field layer and of birch dominance in the tree layer both above and under ground. The herbs are soon suppressed by dwarfshrubs and when birch begins to disappear from the stand a corresponding decrease begins in the soil, ending with the almost complete disappearance of birch roots. Sprout birches are no longer capable, in the second tree generation, of regaining the lost position.

The most important result of this part of the investigation is the discovery of the different utilization of soil volume by the various tree species. Birch roots spread primarily in the mineral soil whereas the roots of spruce, especially in young and medium-aged primary stands, occur mainly in the relatively thin and well decomposing humus layer which evidently offers them somewhat more favourable conditions for nutrient uptake than the thick raw humus of old primary or secondary stands.

After the removal of birch from the stand the mineral soil space once used by birch roots might be thought to remain in a state of more or less incomplete utilization, due to the superficial location of spruce roots. While this may well be the case it must be pointed out that in stands where birch has occurred previously at some stage the roots of spruce go considerably deeper than in stands sparsely mixed with birch.

This is a definite indication that the deeper soil layers are increasingly utilized by spruce for the uptake of nutrients (cf. references on p. 129). On the other hand, tree growth, in the first place spruce growth, in the oldest primary and apparently in secondary stands in general no longer occurs at the same rate as during the first couple of centuries in primary stands when birch is plentiful in the stands. Among the numerous other factors associated with the function of roots that may be imagined to have a stimulating effect on growth, the nutrients conveyed by birch roots from the depths of soil and returned via easily decomposed leaves to the humus deserve most attention (cf. references on p. 287). In young stands the nutrients in question may be obtainable to a high degree from the soil surface; in old forests they may be either situated deep in the soil or bound in non-available form in the almost non-decomposed raw humus. Very remarkable is that the growth of spruce reaches its highest rate at a period when the decrease — and probably the manuring effect too — of the birch roots is strongest.

Kalela (1949) has shown that the root amount of the ground vegetation of a stand is inversely proportional to the root amount of trees. This seems natural, for the simple reason that the environment constituted by the tree stand is unfavourable in certain developmental stages for ground vegetation. Kalela's findings for South Finland may be assumed to hold good of the HMT stands of North Finland also. However, a closer study reveals that the considerable accumulation of raw humus either enables or induces, for dwarfshrubs above all, a continuous increase in total root amount up to the climax stage in spite of the fact that birch roots disappear at an early stage.

It was previously emphasized that the root systems of spruce in young and medium-aged primary stands are surprisingly superficial evidently due to the favourable conditions of nutrient uptake from the well decomposing humus layer. The question that arises now is whether the superficiality of the roots is smaller or not in young secondary stands. From earlier root investigation (Sirén 1950) we know that undergrown spruces in spruce stands have extremely few roots in the mineral soil. The ocular observations made in the young secondary stands investigated supported this earlier report strongly. Likewise the observations made in old secondary stands gave in most cases an impression of very superficial root systems. The amount of dwarfshrub roots is also considerably high during the whole secondary succession.

As a considerable portion of the roots of both trees and dwarfshrubs dies annually, in old stands in particular, the result of this development in North Finnish cold and humid conditions may influence the accumulation of raw humus to a high degree.

Accumulation of raw humus

The raw humus of HMT soils is composed mainly of dead plants or plant remains and dead animals decomposing into a physico-chemically more durable form. The humus-forming substances proper then are the more or less permanent remnants of the decomposition process, the remains of micro-organisms that have died and decomposed organic matter, and the new compounds, both biologically and chemically synthesized, formed on decomposition. In the present investigation attention has been focussed mainly on the plant debris conditional to the formation of forest humus.

Humus may accumulate both sedimentarily and sedentarily. The plant parts falling from trees and dwarfshrub stalks add to the litter layer on the surface of humus in the form of sediment. The dead plant parts contained within the humus, on the other hand, increase the humus material sedentarily. It is the sedimentary accumulation of humus that has usually attracted more attention.

It is evident that the association present on the habitat determines sedimentarily and mostly also sedentarily the quality of the resulting humus. It was pointed out above, in connection with the description of the development of HMT vegetation and tree stand that primary stands undergo an essential change with increasing age. It is natural to assume from this that consequential phenomena changing the character of the humus occur at the same time. As HMT evidently obtained its Finnish name expressly from its thick moss cover and thick raw humus layer, it was considered necessary to devote at least some study to the formation of humus on the forest site type in question.

As reported above, the humus was inspected ocularly on each sample plot. Its constituents were determined where possible, and its thickness was measured on all the sample plots. Chemical analysis, it is true, was only effected for some special sample plots, but the activity of humus was determined both on the sample plots of the ecological station established for the purpose and on some other sites.

An illustrative picture of the structure of humus changing according to the succession stages can be obtained from the general description of the sample plots, as the following examples show.

Siulio[1] 51 years — Humus composed of deciduous tree litter, basal parts of *Deschampsia* and dwarfshrub roots. Decomposed trunks in the soil locally numerous. Moss remains in the humus nominal. F-layer (2—7 cm) decomposing well. Insect excrement seems to have increased granularity, particularly in H-layer which in addition contains both sclerotiae and hyphae. H-layer especially well decomposed, thickness 1—2 cm, with an abundant content of dead birch roots; millipedes and nematods were observed. Plenty of birch bark at the bottom on top of a charcoal layer. Judging from the size and number of trunks lying in the soil the place was covered before fire by an almost pure spruce forest.

Vuojärvi 104 years — Humus composed of forest mosses, dwarfshrub roots and tree litter. The humus substance shows distinct variation: (A) in dense spruce groups, where ground vegetation is missing, the humus is thin, granular in structure and full of mycelium. The F-layer, however, dominated by needles, is fairly raw on the surface. (B) under the birches the main constituent of the humus is leaf litter; F-layer quite thin. H-layer very well decomposed, black and granular. (C) in the intervals, in addition to deciduous tree litter, remains of forest mosses and dwarfshrub roots locally form the components of humus. F-layer is relatively thick and humus brown in colour, degree of decomposition low. H-layer is seldom thicker than 0.5 cm. (D) locally the humus is composed exclusively of forest moss remains and dwarfshrub roots. In such spots the F-layer is almost undecomposed and often very thick. H-layer is present nominally.

In all cases charcoal is found at the bottom.

Mainua 135 years — Humus is composed of tree litter and decomposed trunks in the soil. Ground vegetation plays no great part, only remains of *Deschampsia* locally. Structure granular, yellow and white-grey mycelium occurs. F-layer thin. H-layer often begins directly underneath the litter layer. Soil fauna abundant; faeces plentiful. Immense amounts of roots (birch plus spruce), with plenty of mycorrhiza. Numerous sclerotiae. Charcoal at bottom.

Miehinkä 150 years — Mainly three types of humus: (A) mostly peat composed of dead mosses and (dwarfshrub) roots, with thick and raw F-layer, and underneath it a mostly thin H-layer which, judging from the birch-bark remains, is mainly composed of birch litter. (B) humus composed of dead mosses and *Deschampsia* remains. The F-layer of this type too is thick and raw, but the H-layer is thicker and more advanced in decomposition than in case (A). (C) raw peat composed of decomposed trunks, dead dwarfshrub roots and moss remains.

Hevosvaara 190 years — Humus relatively thin, but distinctly raw humus-like. Apart from crown projection area this raw humus is fairly uniform, composed of dwarfshrub roots, tree litter (birch) and moss remains. F-layer thin in some places, thick in others. Birch-bark present in lower part of H-layer, and the limit zone against the A-horizon is sticky »mud». Fauna is plentiful at this stage still (millipedes, nematods, slugs, weevils, spiders, ants, etc.). Dense fungal mycelium is also present, although not as a distinct layer, between A-horizon and humus. Under the spruce plenty of spruce needle fungus.

Vilma 240 years — Humus very thick in places, 13—14 cm, thin in others, 4—5 cm. Raw and brown F-layer is composed of moss remains and dead dwarfshrubs. H-layer thin, 2 cm, black-brown and contains birch-bark. Fine roots plentiful, similarly sclerotiae, visible soil fauna sparse. Charcoal present at the bottom as usual.

Siulio 300 years — Under the *Pleurozium-Hylocomium-Polytrichum* association is a 5—7 cm thick F-layer composed of moss remains and dwarfshrub roots. The proportion of dwarfshrub roots is nothing short of *immense*, great enough almost to justify terming the humus formation sedentary. Spruce roots are relatively few in the F-layer which also contains a small amount of fauna and their excrement, sclerotiae still present. H-layer 2—3 cm thick, well decomposed, lower part paste-like; locally there are unbroken 1—2 cm thick patches of mycelium.

Hevosvaara 300 years — Humus locally immensely thick, 16—20 cm (cf. Fig. 40), dense and raw. F-layer is almost exclusively composed of moss remains and dwarfshrub roots. Soil fauna extremely poor. H-layer pastelike, with local patches of mycelium.

Siulio 330 years — Humus 0—20 cm thick, depending on vegetation. Maximum thickness generally occurs under expanding *Deschampsia* and mosses (in spite of *Deschampsia* »eating» humus, cf. Arnborg 1943, p. 198). H-layer well decomposed and with pastelike lower part.

The raw humus investigated in secondary stands is similar in structure to that of the humus of the oldest primary stands; as a rule, however, it is rawer and a good deal thicker.

In spite of their in many respects summary and incomplete character the above examples permit the conclusion that the raw humus of young and even of medium-aged, primary HMT stands differs a great deal in its components, degree of decomposition and amount from the humus of old primary stands, not to mention those of secondary origin.

As regards the different remains, the association present on the site is a decisive factor. As long as litter and underground remains decompose readily and conditions favour decomposition, the quality of the humus also will be relatively good. But as soon as the litter type changes the decomposition process also undergoes a change, in a more unfavourable direction, a change that is emphasized by the ecological conditions being

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[1] Siulio is synonymous with Siulionpalo.

Fig. 40. Typical raw humus from old HMT spruce stands. Hevosvaara.

Kuva 40. Tyypillistä vanhojen HMT-kuusikoiden raakahumusta. Hevosvaara.

more unfavourable than before. The above examples reveal distinctly that humus becomes increasingly raw in quality as the stand ages and changes in its composition. In the transition period from the primary to secondary forest stage a slight strengthening of the decomposition process may, it is true, be imagined to occur. But considering the climatic conditions it seems to be of too short duration and too transient in character to change the habitat decisively towards the primary state. *Deschampsia* plays anyhow an important role in this transition period (cf. e.g. Wiedemann 1937 and Dimbleby 1952 a).

Other factors, too, than these indicated above suggest an unfavourable accumulation of humus. In connection with the discussion of the development of vegetation, e.g. the coverage and height of the dominants of the moss layer were found to increase with advancing age of the stand.

The accumulation of the moss carpet probably arises in the main from two factors: the ecological factors resulting from »sprucification» favouring mosses at the expense of other plants (cf. Tamm 1951 and Teivainen 1952), and the death and decomposition of the oldest parts of mosses in old forests not occurring, for one reason or another, as rapidly as in the earlier succession stages. However, the mosses, together with dwarfshrubs, consume considerable amounts of nutrients, as e.g. Tamm (1953 a) and Burger (1953) has shown. The latter gives an example (op. c. p. 119) — where dwarfshrubs and mosses together in a stand yielded more dry matter than the conifers yielded wood.

A good idea of the slow decomposition of dead moss leaves in old spruce forests is afforded by the bright brown colour of the raw humus; the F-layer often extend almost to the surface of the A-horizon.

At the same time as the mosses increase the proportion of grasses and herbs in HMT vegetation decreases. This cannot but have a negative effect on humus decomposition. Most decisive, however, is the influence of the rapid reduction in birch leaf litter, particularly at the age of 120—150 years. Just after this stage the mosses gain very greatly in strength (see p. 126 above). The beneficial influence of birch leaves on humus reaction, nutrient content of the soil and other growth factors is so well known that it need hardly be repeated in this context (cf. the references on p. 287). An interesting additional feature worthy of mention, however, is the quite considerable differences observable in the composition of microfauna between the young and old succession stages. The mites for instance, evidently of great importance for humus-decomposing fungus, proved both qualitatively and quantitatively different in the different stages (personal communication by Dr. E. Karppinen). Similar findings have been made by Gavrilov (1950). According to him, the ground fauna under spruce, both in species composition and numerically, was distinctly poorer than under birch. There is in other words some kind of dynamics observable in the microfauna and microflora too.

Another apparently very unfavourable factor in the formation of humus seems to be the profusion of dwarfshrub roots. A good idea of their poverty in nutrients, acidity etc. is supplied e.g. by Romell's investigation (1939). In addition, roots are the most important physical binders of the tough raw humus, which is disadvantageous in many respects.

Some of the factors deteriorating humus quality as the stand ages have been very briefly surveyed above. In another connection it is concluded that deterioration of quality is followed by a decisively slower rate of decomposition (cf. the chapter dealing with CO_2 respiration, p. 298). This again means that the rate of accumulation of the humus accelerates as the stand advances in age. The measurements effected prove the correctness of this assumption (see Fig. 41).

Figure 41 shows that humus grows very rapidly in some 20—50 years, up to a thickness of 3—4 cm in primary stands even. Naturally it is

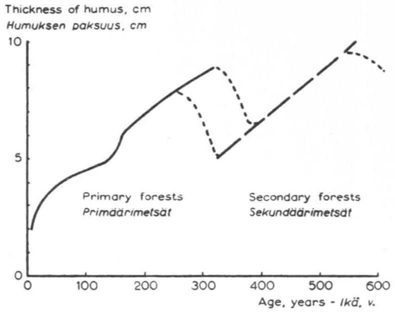

Fig. 41. Changes in the thickness of the raw humus layer during the primary and secondary successions.

Kuva 41. Raakahumuskerroksen paksuuden muuttuminen primääri- ja sekundäärisuksessioiden aikana.

possible that forest fire has destroyed the humus in part only, either in patches or the superficial layer only, in which case the initial thickness may easily amount to say 5 cm (cf. Heiberg 1938, p. 273). Subsequent accumulation is even, up to the age of some 140 years, when there is a sharp increase; that this can be coordinated with the change in tree species composition is obvious. After 180 years raw humus again grows fairly evenly in thickness, totalling 8—9 cm in spruce stands of 200—300 years. Hesselman (1937), Sweden, has attained similar results for the humus of primary succession. When the stand begins to thin at this stage and light conditions become unfavourable for the growth of mosses in particular and at the same time more favourable for the decomposition of humus, the humus gets considerably thinner as the primary stand degenerates into the secondary stage (cf. Sartz & Huttinger 1950). However, the raw humus layer has no time to become thin enough to provide ecological conditions for the vegetation of the secondary succession equal to those enjoyed by primary succession immediately after a forest fire. It must also be borne in mind that in secondary stages the humus covered by a moss layer is from the very outset composed of the slowly decomposing remains of spruce litter, mosses and dwarfshrubs, whereas the main content in primary stages is initially readily-decomposing leaf and grass. The result in secondary succession, therefore, is from the outset a raw and thick humus which, on the stand reaching its climax stage, may be as much as 10 cm thick. The secondary post-climax stage again entails a slight decay; in spite of this the tertiary stage probably begins in still more unfavourable conditions than the secondary succession.

Collation of results

The special investigation into the dynamics of HMT stands reported above is based on material divided into two main sections according to the way of origin of the stand on the forest site type under review, viz. sample plot stands of primary and of secondary origin. The former represent plant communities following immediately on a forest fire, the latter communities that developed naturally after deteriorated old primary spruce stands. The investigation describes the development of these communities with special attention paid to the tree layer representing different successions, and makes some comparisons. In order to establish tenable premises, the comparability of the habitats has been studied from a wide range of aspects. Primarily thanks to parallel sample plots, the comparability seems to be satisfactory. The internal homogeneity of the tree stands was also examined by means of various stem distribution series. Certain failings were found, but of no significant importance, and hence the material may be considered homogeneous and suitable for the purpose of the investigation.

A detailed review of the special investigations illustrating the development of HMT stands brings out the following main points.

The dynamics of the stands that developed on the sites investigated, i.e. on fresh forest soils after fire can be considered similar in the main to those e.g. on the fresh forest soils of South Finland (cf. e.g. Hult 1886, Cajander 1916, Kalela 1946). After a phase of intense expansion the proportion of birch and other deciduous trees in the primary stands begins to decline sharply at approximately 100 years. At 120—130 years, the originally birch-dominated stand becomes spruce-dominated. The birch storey which previously formed the dominant crown layer gets sparser and remains in a suppressed position. By the age of approximately 200 years the stand is, mensurationally, a pure spruce stand. Observations indicative of a similar trend in corresponding conditions have been made by e.g. Nordfors (1923), Hesselman (1937), Raup (1946), Arnborg (1949) and Moss (1953). Primary stands reach a climax stage of rather short duration at approximately 220—260 years. This is followed by a gradually accelerating deterioration of the growing stock which generally ends in the complete destruction of the stand. The fundamental idea behind the climax theory recently fashionable and to some extent still held, that of permanent static stands of trees, must therefore be considered a generalisation inapplicable, at least as far as primary spruce stands are concerned, to North Finnish conditions.

In the deterioration stage space becomes available for a new generation of trees as the existing forest recedes. The secondary tree generation consists from the outset of a birch-spruce mixed stand dominated by spruce, and thus it differs from the primary generation at this early stage. The slow development of secondary stands is a finding of the present investigation that must be considered remarkable. The most striking difference between the stands of the different successions is the superiority in growing stock of the primary stands at all developmental stages up to the climax period. This supports the views propounded by e.g. Högbom (1934), Bloomberg (1950) and Traunmüller (1952) on the influence of fire and on the quantitative differences of the growing stocks of different spruce generations.

Owing to the fact that the different tree generations involved in the present investigation occur on habitats equal in value as regards both the fundamental qualities and the vegetation of the site type phase (climax stage), the results attained mean that the fundamental conceptions — primarily the definition of forest site type — of Cajander's forest site type theory should be qualified by a precise definition of the origin of the stand.

Another noteworthy difference between the successive tree generations is the superior dominant height of the spruce storey in primary stands. This finding indicates that the methods of assessing forest soil quality by tree height alone also had their weaknesses, even in virgin forests — at least if applied to spruce forests in North Finnish and corresponding climatic conditions. In this context it may be mentioned that the firm correlation between dominant height and expressly the degree of soil podsolization pointed out by Keltikangas (1944, p. 98) in this particular case at least seems to be concealed by stronger factors. The depth and nature of the A-horizon of the primary and secondary stands investigated has been similar, particularly on parallel sample plots, and yet the dominant height has been far from equal in the different succession series. The view advanced by Keltikangas, according to which the leaching of Finnish mineral soils is considerable enough to be discerned even during one tree generation, does not seem to hold good in all cases, though a long-term slight impoverishment of forest soils is ascertainable (cf. Aaltonen 1940). There must be some causes other than the soil formation conditions to account for the dissimilarity in the dominant height of spruce stands of different successions (cf. also Zinecker 1950).

Another important finding is the mensurational similarity between the secondary forests of the present investigation and the HMT forests described by Ilvessalo (1937). Such similarity implies above all that the HMT defined by Cajander still exists and is still one of the most wide-spread forest site types on North Finnish moraine soils (Ilvessalo 1955)[1]. The spruce stands on HMT, however, are of secondary origin, and hence their yield conditions agree with the actual site quality conditions. Reduced to a primary conditions, i.e. burned, HMT is comparable in fertility, estimated on the basis of growing stock, with some of the best forest site types of North Finland. The effect of reintroducing the primary condition does not, either, seem to be confined to a few decades only, as some Scandinavian investigators contend (e.g. Tirén 1937, and Heiberg 1938), but lasts practically though indirectly up to the climax stage of primary succession. In reality this last-mentioned developmental stage corresponds to that stage of the phytosociological succession presupposed in Cajander's forest site type theory, on which the assessment of the potential site quality is to be based.

The ground vegetation in the stands of two different tree generations is phytosociologically similar in the type stages of the two successions studied. Considerably dissimilarities are observed, however, in the evolutionary processes leading to this state. Basing the forest site type determination on the physiognomic characteristics of two parallel plant associations of the primary succession, each of which are in a different developmental stage, presupposes a considerable ability to predict their development

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[1] Preliminary report from the third National Forest Survey (unpubl.)

up to the climax stage of the first tree generation. The correct assessment of the site quality of a secondary forest, again, presupposes an ability to interpret correctly the state of the ground vegetation retroactively. The criticism once levelled against the forest site type theory by Brenner (1922, p. 161) applies to some extent to this point. Letkovskij's (1952) final conclusion in his study of the dynamics of the vegetation of certain forest site types in Russia also tends to emphasize the difficulties of site quality assessment. In Letkovskij's opinion, plants may be considered indicators of the habitat (or rather micro-habitat) in tangible conditions, but for all that they cannot be taken to reflect the site quality of the site type. Although Letkovskij's conclusion is based in part on different premises, it does bring out beyond any shadow of doubt his observation of the contradiction involved in site quality, stand and ground vegetation, which occurs in certain cases reminiscent of the succession of HMT stands. In this connection it may be allowed to cite Attenberger (1951, s. 602): »In Myrtillus-Schreberi-Typ hat die Waldgesellschaft im Verlaufe einer jahrhundertelangen Fichtenwirtschaft eine so vollständige Überlagerung erfahren, dass die Bodenvegetation sich hier ausschliesslich aus acidiphilen Neuankömmlinge zusammensetzt, die der soziologisch hohen aufbauenden Kraft der Fichte ihr Dasein verdanken. Hier versagt die Identifizierung der Naturwaldgesellschaft—». Similar views have been advanced also by Chirita (1931) and Sarvas (1951).

A study of the uninterrupted span of development of the primary and secondary stands reveals an important characteristic of the dynamics of the vegetation. After the ground vegetation of the primary stand has passed the so-called selection stage the vegetation seems to remain more or less static for a surprisingly long time, just as Cajander presupposed. Only when the primary stand undergoes destruction and thus manifestly changes does the vegetation transiently assume new features (becomes overgrown with grass, etc.) but enters soon a state approximately similar to the type stage when the secondary stands reaches its climax. When the destruction of this tree generation sets in the ecological factors probably change so much that certain species indicative of paludification begin to occur in the plant association. Similar observations in moss-dominated virgin forests have been made e.g. by Sukatshev (1921, see Braun-Blanquet 1951, s. 12) in the regions around Lake Baikal in Siberia (cf. also Sukatshev 1932). All the findings concerning the development of primary succession into secondary succession and further agree surprisingly well with the theory of degeneration intuitively developed by Lundström (1897, 1902).

Many previous investigators have found the regeneration of HMT forests incomplete. In part, the present author arrives at the same conclusion. Regeneration follows largely the course outlined by Heikinheimo (1922), Eneroth (1937), Arnborg (1943) and others. In the present investigation, it is true, the living moss carpet, claimed to be the obstacle to regeneration, is found to increase little in thickness with the stand growing old. Instead, the raw humus grows very thick, in secondary forests in particular where it is approximately twice as thick as in a corresponding primary forest; in addition its structure is coarser and degree of decomposition less advanced than in the former. The proportion of dwarfshrub roots is remarkably high, especially in the raw humus of old HMT forests. If the most dominant layer society of the total plant association is determined on the basis of the quantity of roots and rhizomes present in the humus layer, there can be no doubt about the result in these cases; dwarfshrubs are the dominant society. During the first century the tree roots of primary stands account for the majority of the roots in the humus layer. Especially spruce roots are very superficial. Birch roots on the contrary occur mainly in the mineral soil, which after the removal of the birch in later successional stages may facilitate the penetration of spruce roots to deeper soil layers (cf. Laitakari 1935). Due to the accumulation of raw humus and the disappearance of birch roots it seems, however that the utilisation of the soil volume for nutrient uptake will be insufficient in the secondary succession.

The main conclusion to be drawn from the special investigation into the dynamics of HMT stands is probably that the growth conditions of primary and secondary stands are different, in spite of the fact that the chemical composition of the mineral soil justifies the assumption that the site qualities are equal in value (cf. e.g. Valmari 1921, Cajander 1921 and Ilvessalo 1923). However, the finding is in no way unique. The arrested growth of spruce stands is known as a very important phenomenon in Germany (cf. Wiedemann 1925, Wittich 1952). In Canada Raup (1946) and Bloomberg (1950) have found that the yield of secondary stands is generally inferior to that of forests originating immediately after fire. Lundström advanced the concept of the degeneration of forests as early as 1897 and 1902. Apart from studies by Wiedemann and Wittich, however, the causes of the changes in yield conditions have not been studied. Wiedemann connects the arrested growth of spruce stands in the German highlands primarily with drought. But Wittich attributes reduced growth mainly to slow humus decomposition; some important nutrients bound to the humus remain too long in a state in which the trees cannot utilise them. Wittich's view is supported by some Russian and French investigations (cf. e.g. Sukatshev 1932 and Duchaufour 1953).

These investigations carried out in other countries perhaps shed some light on the reduced yield of North Finnish spruce forests. Considering northern conditions, however, it is probably understandable that the low yield of the secondary stands cannot be explained from observations made elsewhere. It is a known fact that plant development is largely governed by the quality of the site substratum. Where two plant associations are present on soils of equal value the environment created by the plants themselves has a considerable influence on their development.

As sites growing secondary stands can be changed back by silvicultural measures into primary conditions with stands of high yield it is important to know at least some of the causes affecting the reduction in yield outlined above. For this reason it was considered necessary to devote a certain amount of study to the changes certain ecological factors, generally found to be of importance, undergo in the course of two consecutive successions of HMT forests.

II. THE ECOLOGY OF THE STANDS

Introduction

It has been shown in the preceding chapters that the primary mixed birch and spruce stand which arises after forest fires differs in its structure and development from the secondary forest generation resulting from natural regeneration in old spruce stands on HMT in the so-called post-climax stage. But as we are actually concerned here with forest communities on habitats so much alike in their primary characteristics and actual vegetation that, according to Cajander's theory of forest types, they can be referred to the same quality class, we automatically ask ourselves the causes of the contradiction between the potential and the actual site quality.

Since the method of selecting sample plot stands excludes the possibility of macro-climatic fluctuations in the last fifty years being the cause of the above mentioned contradiction, as propounded by Keränen (1943), Hustich (1945, 1948 a, b), Regel (1949 a, b), Ve (1951), Mikola (1952) and others, it seems natural to search for the causes in other quarters. The next step is to study certain significant conditions for the progress of forest trees. These are determined in the main by the two most important environmental factors: the soil and the climate. These extremely complicated factor-complexes, the latter limited in its effect to the climate of the stand only, will be studied more closely in the following.

One of the essential differences between primary and secondary spruce stands was found in the different environments of spruce seedlings and spruce undergrowth. In the primary stand spruce seedlings are merely scattered in a stand dominated by birch for the first century, with a thin humus layer and a vegetation comparatively rich in herbs. In the secondary stand the spontaneous young growth of spruce appears in an open but almost pure spruce stand with a thick moss and raw humus cover and poor vegetation otherwise dominated by dwarfshrubs; the contribution that these make to the litter, especially with regard to the normal supply of readily decomposed nutrients important for forest trees, must be considered particularly meagre (cf. e.g. Aaltonen 1950 and Tamm 1951).

It has long been known that forest soil and stand climate exhibit different characteristics depending e.g. on the dominating tree species (cf. e.g. Geiger 1925, 1926, 1941, Obolensky 1926, Amann 1932, Paeschke 1937 and Aaltonen 1940).

Numerous special investigations on the determining significance of the ecological factors for the structure and development of the forest community have been published abroad, especially in the last few decades. Let it suffice here to refer to a few of the most recent: Burger (1933, 1951), Clements (1949), Lundegårdh (1949), Geiger (1950), Oosting (1950), Mraz (1950). In Finland the same problems have been treated by Aaltonen in particular (1940, 1948); but Kalela (Cajander 1933), Keränen (1949), Sarvas (1952), Teivainen (1952), and others also have discussed the relationship between stand type and stand structure, and different ecological characteristics.

To investigate the ecological differences in primary and secondary stands from as many aspects as possible requires a thorough study of the ecological subfactors in a suitable number of parallel stands evenaged and comparable in every respect and representing different stages of succession. Unfortunately no such stands were available. However, in the wilds of Siulionpalo an extensive old secondary stand with typical HMT characteristics was discovered. Locally there was sparse young growth, of about 60—130 years standing; in vitality and height this growth was much inferior to the spruce interspersion in a neighbouring birch stand that had followed a forest fire at the turn of the century in the centre of the secondary stand (cf. Sample Plots 6 and 61). Close investigation revealed that spruce had formerly grown on the burnt area and that in many cases the ground was similar on either side of the fire line. On determining the age of representative, individual spruces in the two stands it was found that the young, 1—4 m high spruces in the old spruce stand (Sample Plot 61) had an average age of 66 years while the 5—12 m high spruces in the birch stand (Sample Plot 6) were 51 years old at the most (studied 1950). In the latter stand there was, in addition, an abundance of spontaneous new growth of younger age.

For lack of a more suitable plot, Siulionpalo was used to study the causes of the differences in seedling growth, not only in the two succession stages but also in the initial stages of the successions. Two sample plots were marked out in as pure stands as possible, on either side of the distinct fire line, in order to get as great ecological differences as possible. The birch sample plot selected was thus fairly free of interspersion of spruce; the sample plot in the secondary spruce stand was more similar to the surrounding forest with solitary over-mature individuals from a former tree generation and scattered unevenaged birch suckers (*Betula pubescens*). These stands were thus selected to serve as the basis of the ecological investigation, the main purpose of which is to shed light as far as possible on the divergences in the inner environments of primary and secondary stands. Clear cutting an area of 50 × 50 m where the sparse spruce stand was on the threshold of complete destruction gave a counterpart to the initial stage of the secondary succession. For the purpose of comparison, a similar clearing was cut in the birch stand. All the sample plots lay within an area of 2 hectares (Fig. 42). They had a slightly north-eastern aspect which, according to Heikinheimo (1920 b, 1922), Sartz & Huttinger (1950) and Teivainen (1952), is considered conducive to intense humus formation in this climatic region.

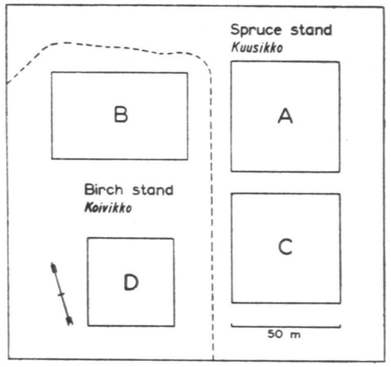


Fig. 42. The location of the four parallel sample plots in Siulionpalo. C and D open areas.

Kuva 42. Rinnakkaisnäytealojen sijainti Siulionpalossa. C ja D aukeita aloja.

The purpose of this comparative specialized study of the ecological factors is, in the first place, to reveal differences between the successions and to describe why conditions in the primary stand dominated by birch evidently favour spruce. It is regrettable that the very nature of the investigation excludes an inquiry into the selective influence of the different growth environments on the population variation of the new plant material. This interesting and obviously highly significant question (cf. Rohmeder 1953, pp. 501—505) is not only time-consuming to study but requires a special method of investigation and this is the main reason for failing to include it in the programme of the purely ecological field investigation. It is well known that a study of this kind requires genetically identical, or at least indisputably commensurable comparative objects. The question of the extent to which the dissimilarity in the development of primary and secondary stands is conditioned by the disparate genetic characteristics of seedling stands, a dissimilarity which is further accentuated by selection and which might possibly be disastrous for the secondary stands during the stage of germination and their early years of life and followed later by adaptation difficulties, has thus perforce been disregarded. The ecological causes of the degeneration of HMT habitats given in the following must, in consequence, be treated with a certain reserve in that there may be inter-individual, genetically significant differences between the spruce seedlings in young primary and secondary stands.

Investigation methods

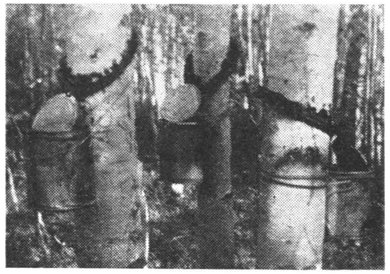
In order to reveal the causes of development of HMT forests, a temporary field station for ecological measurements was set up in the Siulionpalo area (67° 05′ N. lat.) at the east end of Pelkosenniemi. A pilot investigation was performed in summer 1950 and the main investigation in 1951. The former was rather a typical Lapland summer, only slightly warmer than normal, but the latter rainy and cold especially in June and July. During two vegetation periods, a large number of measurements were made daily of different ecological factors in the soil and in the stand climate. These data were recorded for four parallel sample plots in all; their location in relation to one another is given in Fig. 42.

The sub-investigations and the methods used were as follows:

Precipitation was measured with the summer rain gauge of the Meteorological Central Institute. Initially, two gauges were set up on each of the clear-cut Sample Plots C and D, but experience showed that the maximum variations between the two gauges was 0.1—0.2 mm, even in heavy rainfall, so ultimately one gauge was used on each open plot.

Sixteen rain gauges in square spacing were set up on each of the spruce and birch Sample Plots A and B. The decision to employ such a large number of gauges was prompted by the heterogeneous character of the stand canopy and the principle that standard error decreases roughly in inverse proportion to the square root of the number of observations. The instructions given by the Meteorological Central Institute for recording the volume, kind and time of precipitation were followed in the investigation. Run-off down the stem was measured as follows: a chute, about 5 mm broad and at an angle of about 45°, was affixed with pitch around 50 birch individuals of varying size and crown dimension. The chute terminated in a short spout leading the run-off water into a vessel hung on the stem. Each inlet was either protected or very small (Fig. 43). Chutes were placed on some spruce stems as well.

The vertical temperature and humidity conditions of the atmosphere were studied with the aid of three thermohygrographs placed at a height of 2.0 m on plots A, B and D, and with two Assman psychrometers. The rotation



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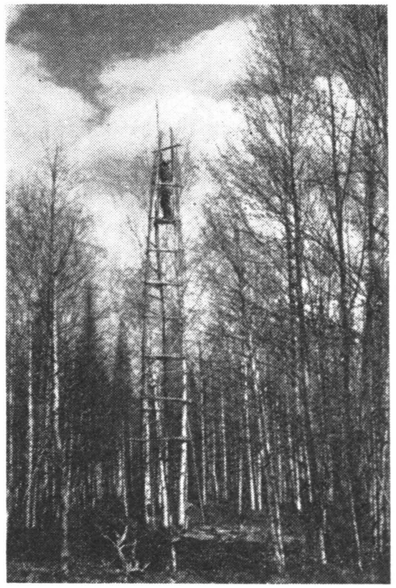

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Fig. 43. Arrangements for measurement of run-off down the stems.

Kuva 43. Runkojen valuveden mittausmenetelmä.

Fig. 44. Recording of wind velocity above the crown canopy.

Kuva 44. Tuulen nopeuden mittaus latvuskatoksen yläpuolella.

period of the thermohygrographs covered one week. The psychrometers were read three times daily, in the morning at 07 00, at 13 00 and in the evening at 21 00, at the following heights: 0.2, 0.5, 1.0, 2.0, 4.0, 6.0, 8.0 and 10.0 m. The temperature alone was also read at 0.5 and 1.0 m. For measurements at heights over 2 m, two towers were built (Fig. 44). No measurements were made above 2 m in the summer of 1950, and this also applies to the clear cut areas C and D in summer 1951. The measuring points were located in places representative of each stand. In the clear cut areas the measurements were made in the centre of the sample plot. Regarding the accuracy of the Assman psychrometers, the reader is referred to Franssila (1936, pp. 48—51).

Both day and night measurements were made irregularly, in total 11 times in the vegetation period 1951, and 9 times in 1950 at 07 00, 10 00, 13 00, 16 00, 20 00, 24 00, 04 00 and 07 00. — The methods advanced, used by Rossi (1933) and Franssila (1936), could unfortunately not be used mainly due to lack of equipments.

Wind conditions were recorded in connection with the daily meteorological

observations at 07 00, 13 00 and 20 00. Velocity and direction of wind were determined with Wild's apparatus. To obtain more exact and mutually comparable figures from the various sample plots, wind velocity was measured with an anemometer in connection with the psychrometer reading at 0.2, 2.0 and 10.0 m. As a reliable wind spectrum covering the 24 hour variation was found necessary, wind conditions were also measured at the other heights already mentioned for 24 days at intervals of 3 to 4 hours.

Additional vertical wind measurements were made at midday on approximately 20 windy days. Regrettably, no measurements were made in leafless birch stands.

Insolation in Siulionpalo were recorded in summer 1951 with a Robitsch actinograph.

Comparative measurements of the interior illumination in stands A and B were made with a lux-meter of Rektolux type. The measurements were made partly during the day (in cloudy weather), partly at night before and after leafing and after defoliation in the autumn. Light intensity measurements were taken at 5 m intervals in the stands. For practical reasons they were only recorded for 1.0 m above ground level, using a horizontal selenium membrane. Later in summer 1952, vertical light intensity measurements were taken at 0.2, 1.0, 2.0, 5.0 and 10.0 m. Light measurements were made in other stands in addition to those in the parallel sample plots.

The transpiration rate of tree stands was determined by the principles of the rapid weighing method used e.g. by Stålfelt (1944) modified in that whole trees (except the largest spruces) were the object weighed. Thus an important source of error, the approximation of the size of the transpiring surface, was largely excluded in the case of individual trees.

Five minutes (reckoned from the first axe stroke) was allowed for weighing, but as felling required some time no more than about 200 seconds actually remained for the procedure. With large spruces the sectorial method was employed; the object to be weighed varied in size between three-fifths and one-seventh of the crown. The total size of the crown was determined by weighing after the transpiration determination; ocular evaluation was considered satisfactory in some few cases. A Berchel scale, capacity 30 kg, accurate to 1 g, was used. Temperature and the relative humidity of the atmosphere, vapour pressure deficit, wind velocity and intensity of light during the process of weighing were also determined.

Evaporation was assessed with the aid of Wild's evaporimeter vessels and Sartorius balance scale, capacity 3 kg, accurate to 0.1 g. Four vessels were placed in pairs on Sample Plots A and B, one of the pairs in mutually comparable gaps, the other in groups of trees typical of both stands. The vessels were placed approximately in the centre of Sample Plots C and D. A transparent plastic cloth was spread 0.5 m above the vessels to protect them from rain. Weighing was performed on alternate days as a rule, on some days as often as every 3 to 4 hours.

The melting of the snow in the stands was measured with 100 rods with a centimeter scale, spaced out on the parallel sample plots in 5 m squares. Recording was started just before the highest snow level in March and continued at intervals of about 10 days up to the beginning of June when heavy rain removed the last snow patches. Only 8 measuring rods were used on the clear cut plots.

* * *

In addition to the sub-investigations concerning soil included in the succession study of all the sample plots, the following examinations were made of special Sample Plots A—D in Siulio.

Moisture conditions of the soil. Infiltration of rain water into the soil was observed and measured partly with the aid of lysimeters, 100 sq. cm × 10 cm deep, furnished with removable vessels for collecting water, placed immediately below the humus cover (cf. Stålfelt 1944, p.41), and partly with aid of Bouyoucos' plaster blocks. The lysimeter was inserted from the side, under intact humus. The number of lysimeters on the sample plots was: A 8, B 8, C 4 and D 4. They were checked and emptied as occasion demanded in connection with rain measurement. The results were unreliable. The moisture content of the mineral soil was studied with better success, however, with the aid of a resistance meter (Wheatstone's bridge) and plaster blocks (Bouyoucos 1947). The plaster blocks were placed at the following depths: on the border between humus and mineral soil (= 0 cm) and 10, 20 and 100 cm below the surface of the ground. On Sample Plots A and B, 8 series of 4 plaster blocks each were placed at the depths mentioned, and 4 series of 4 plaster blocks each on C and D. The plaster blocks of a particular series were placed beneath one another. The electric resistance was generally measured every second day in the summer of 1950 and every third day of good weather in the summer of 1951. Immediately after heavy rain, measurements were made each day for some 3—4 days.

The calibration of the plaster blocks was done partly in the laboratory according to the method of Bouyoucos and Mick (1940) and partly in the field, the true resistance being measured subsequent to continuous rainfall and drought. Samples of soil were taken with metal boxes size 100 cc from the ground in the immediate vicinity of the block in question. A reliable calibration material (cf. p. 246) was obtained by performing a sufficient number of control measurements. Soil moisture content was determined by weighing the samples before and after drying for three days at a temperature of 103° C.

The moisture variation in the humus was revealed to some extent by the resistance of the uppermost plaster block in the various series, but the investigation proper was based on the direct weighing of pieces of humus lifted from the mineral soil and then replaced on top of fine-meshed wire netting (wire diam. ~ 0.2 and width of mesh ~ 2.5 mm). A typical humus cake of this sort measured 20 × 30 cm × natural thickness; the total surface on the various sample plots was 0.54 sq.m on A and B, 0.24 sq.m on C and D. Weighing was performed on the above mentioned Sartorius scale, simultaneously with evaporation determination.

The soil temperature was measured continuously at only one point in the centre of the sample plots with four thermometers, 30 to 100 cm long, at depths of 0, 6, 20 and 50 cm. All the thermometers were inserted horizontally into intact soil. In the summer of 1951, the temperature was also taken at half the depth of the humus covering with a precision thermometer. Two maximum—minimum thermometers were placed in each sample plot under an approx. 1 cm thick and loose cover of moss for protection against radiation. All the thermometers were calibrated at 0° and + 20° C, the maximum—minimum thermometers at + 100° C in addition. To make sure, a number of sample-test temperature measurements were made at other points of the four parallel sample plots.

The temperature was read each morning, on the special days at intervals of 3 to 4 hours throughout the 24 hours.

Freezing and thawing of the ground was not studied methodically enough, which is regretted. However, especially in spring 1951, observations were made of the horizontal and vertical distribution of soil ice in Sample Plots A, B and D in connection with digging.

The pH variation in the soil. The acidity of the soil was measured fortnightly with Beckmann's apparatus. Samples of about 5 cc were taken from the F- and H-layers of the humus and at a depth of 5, 15, 25, 35, 45 and 55 cm in the mineral soil, from all sample plots. After vigorous shaking in 20 cc of distilled water the samples were allowed to stand for 24 hours and determinations of each test tube were made four times.

Nutrients. Besides the determinations of CaO, K_2O and P_2O_5 effected by the Department of Soil Science, Agricultural Research Centre, some special studies of the chemical properties of the litter, the roots, the raw humus and mineral soil were performed at The Department of Soils, Forest Research Institute.

The exchangeable ions were extracted with $CH_3COO\text{-}NH_4$(pH 4.65; 0.5-M CH_3COOH + 0.5-M $CH_3COO\text{-}NH_4$). After removing acetate, humus and silica the residue was dissolved in H_3NO_3 and an aliquote was taken for phosphorus determination. After this P, Fe, Al and Mn were removed. The residue was dissolved in a known volume HC1 (0.2-n) from which 5 cc was taken for determination of each Ca, K, Mg and Na. To each of these samples except Mg was added 0.25 cc of buffer solutions (cf. West & al. 1950). The quantities of CaO, MgO, K_2O and Na_2O were determined spectrophotometrically (Beckmann). Phosphorus (P_2O_5) was determined colorimetrically as phosphorusmolybdate. When total P was determined Mr. Halonen and Mr. Tulkki reduced the iron present to ferrous-iron before the treatment with molybdate. For total nitrogen analysis the Kjeldal method was applied.

Soil respiration. To determine the respiration intensity in samples of forest humus, a respiration apparatus was constructed according in the main to Marsh (1928) and Eidmann (1943) (see Figs. 45, 46). The respiration apparatus comprised four systems of four vessels, i.e. sixteen 5 litre vessels. The CO_2-free air was evacuated via the humus samples and absorption vessels with a vacuum pump, common to all the respiration vessels, its effect being regulated with valves. The air flow rate was checked three times per 24 hours — separately in each system. The normal CO_2 content of air, a highly variable value in urban and even in laboratory conditions, was eliminated by leading the inflowing air via Jena gas distribution tubes through concentrated NaOH solution (cf. Marsh op. c. and Mork 1938). Hence the carbon dioxide reacting in the absorption vessels derived from the respiration vessels only. It may be mentioned in this connection that the highly variable carbon dioxide content of urban air caused — at a flow rate of 20 l/h — an increase of 12 mg/h of CO_2 in the absorption result, which is equivalent to an increase of about 25 and 50 per cent in Sample Plots B and A respectively. In other words, absorption of the CO_2 content of the air proved necessary. Special control tests showed that purification of the air was effective in all instances. It may be mentioned that the air stream inlet was at the bottom of the fairly high respiration vessels; as is known, carbon dioxide is about 1.5 times heavier than the free air (for methods see also Waksmann & Starkey 1949 and Mork 1938).

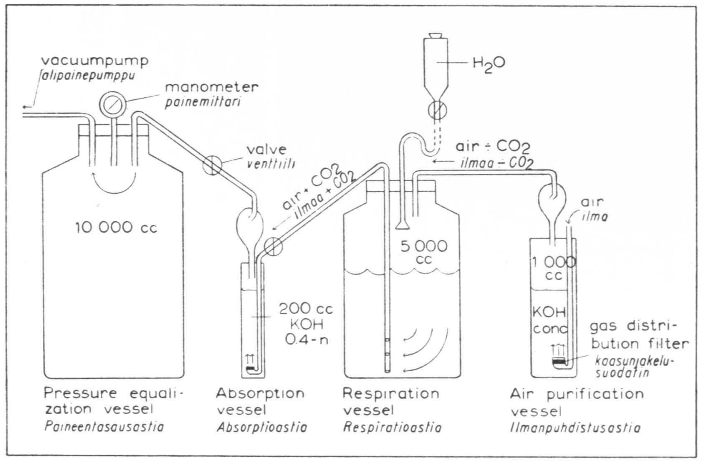


Fig. 45. Scheme of the soil respiration apparatus.

Kuva 45. Respiratio-kojeen kaavakuva.

The absorption vessels were coated with black varnish to prevent photosynthesis in the plants and parts of plants (seeds, suckers) which may have been included in the humus sample. The samples were watered with a built-in spray. The temperature in the laboratory was 21—22° C as a rule, limit values 19 and 25° C. Later, this great variation in the temperature proved detrimental and necessitated corrections. Another weak point in the method was the fact that naturally moist samples were used in the hope of showing from natural samples the significance of humidity for CO_2 respiration. In summer 1951, however, there was so much rain that this sub-investigation was a partial failure. On the other hand, the water content of the humus samples varied so slightly that it was of no significance for the other test series.

The effect of the temperature on the respiration intensity was studied by placing four respiration vessels in a refrigerator or hot cupboard on 5 different occasions, each of a different temperature. Arrangements for the purpose of revealing the effect of aeration were limited to regulation of the out-flow by means of valves. The regulation was effective and fullfilled the purpose.

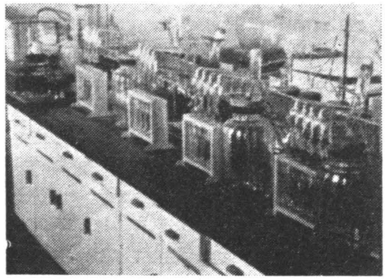


Fig. 46. Respiration apparatus in the laboratory.

Kuva 46. Respiratio-koje laboratoriossa.

The intensity of respiration was determined as follows. Each respiration vessel was filled with ten 1 sq.dm humus cakes of natural thickness. The 160 humus cakes required were taken at noon and transported on the same day to Rovaniemi and thence to Helsinki (Helsingfors) by the commercial plane; they arrived in the laboratory approx. 23 hours after they had been lifted. After stowing, the respiration vessels were hermetically sealed; the whole apparatus was connected up and the vacuum pump set to work. The amount of air was regulated separately for each vessel and, after wetting, the apparatus was allowed to work under continuous control for about 40 to 48 hours when one system at a time was closed for titration. The absorption fluid consisted of 200 cc of 0.4-n NaOH solution. This quantity proved sufficient to absorb the carbon dioxide exhaled from the humus samples in 48 hours. According to the formula $2NaOH + CO_2 \rightarrow Na_2CO_3 + H_2O$, 200 cc of NaOH can absorb 1760 mg of CO_2. Actually, this solution is capable of absorbing twice as much CO_2 since the absorption continues until the Na-carbonate is transformed into Na-bicarbonate, which has to be reduced to carbonate by the addition of suitable quantities of 0.4-n NaOH.

The titration was according to Winkler's method (see e.g. Kilpi-Tomula 1939), using 0.4-n HCl solution after precipitating the carbonate with barium chloride (40 cc concentrated $BaCl_2$ solution) according to the formula:

$$Na_2CO_3 + BaCl_2 \rightarrow BaCO_3 + NaCl.$$

Since the Na-carbonate is replaced by Na-chloride which does not consume acid, the free Na-hydroxide is directly measurable. The amount of CO_2-bound NaOH was obtained by subtracting from the original amount the remaining quantity of free NaOH revealed in titration. As the number of carbon dioxide equivalents is equal to the number of CO_2-bound alkali equivalents, there was no difficulty in working out the quantity of carbon dioxide absorbed. For evaluation of the various methods of determining CO_2 production see e.g. Waksman (1952, pp. 152—157).

Only a few tentative respiration determinations were made in summer 1950; the main investigation was concentrated in the summer of 1951. Five comparative determinations of respiration of the humus of sample plots A and B, covering a period of two weeks, were made. Complementary determinations were made in 1952 and 1953. As the study comprised the effect of seasonal variation, temperature, aeration and watering or irrigation (soil moisture) on the intensity of respiration, the various special investigations were performed as follows (Table 41):

In addition, a test was made to reveal the rate of respiration in the two main humus layers, the fermentation and the humification layers. In the summer of 1952, the CO_2 respiration of the mineral soil was determined, and in the summer of 1953 comparative respiration determinations were made on a number of different sites.

All the sample plots were represented in each determination by two respiration vessels; hence the average of the results obtained served as the starting point for comparison. The divergence between the vessels of any one pair was generally small, as can be seen from Fig. 82 (p. 302)which can be considered representative.

Soil aeration. Ventilation conditions in the soil were studied with the aid of a so-called sphygmomanometer to which was added a cylindrical steel socket 10 cm

Table 41. Scheme of the respiration study in summer 1951. T = temperature, W = watering, A = supply of air per system.

Taulukko 41. Respiratio-tutkimuksen suorituskaavio kesällä 1951. T = lämpötila, W = kastelu, A = ilmanvaihto systemiä kohden.

Seasonal variation *Näytteen ottoajan vaikutus*	Part of the special study — *Osatutkimus*		
	Influence of temperature *Lämpötilan vaikutus*	Influence of watering *Kastelun vaikutus*	Influence of aeration *Ilmanvaihdon vaikutus*
The ecological constants and variables — *Ekologiset konstantit ja variaabelit*			
T = 20° C	T = 2°, 6°, 10°, 15°, 26° C	T = 20° C	T = 20° C
W = 10 cc/24 h	W = 10 cc/24 h	W = 0, 10, 20, 40 cc/24 h	W = 10 cc/24 h
A = 20 l/h	A = 20 l/h	A = 20 l/h	A = 20, 10, 5, 2, 1 l/h

in height, the inner base measuring 10 sq. cm. The steel socket was driven vertically into the ground and air was pumped into the pressure chamber. At the moment when the soil in the socket let through air, the maximum pressure value was recorded. The pressure was allowed to diminish gradually until it regained balance with the ground resistance, when the minimum value was registered. In order to prevent irregularities in the pressure increase, pumping was done according to a time table. This method is suitable for comparative studies only. The author's views of this method, which are based on the results obtained, are less positive; as to the difficulties, see Rennie (1950).

The methods used for elucidation of the above ecological factors are mainly modifications of existing and tried procedures; hence a close study can be made of their errors and merits in connection with the original studies.

Lack of apparatus made it impossible to collect a more complete material. However, Fig. 47 gives a fairly good picture of how, and to what extent, the collection of the various ecological data was performed.

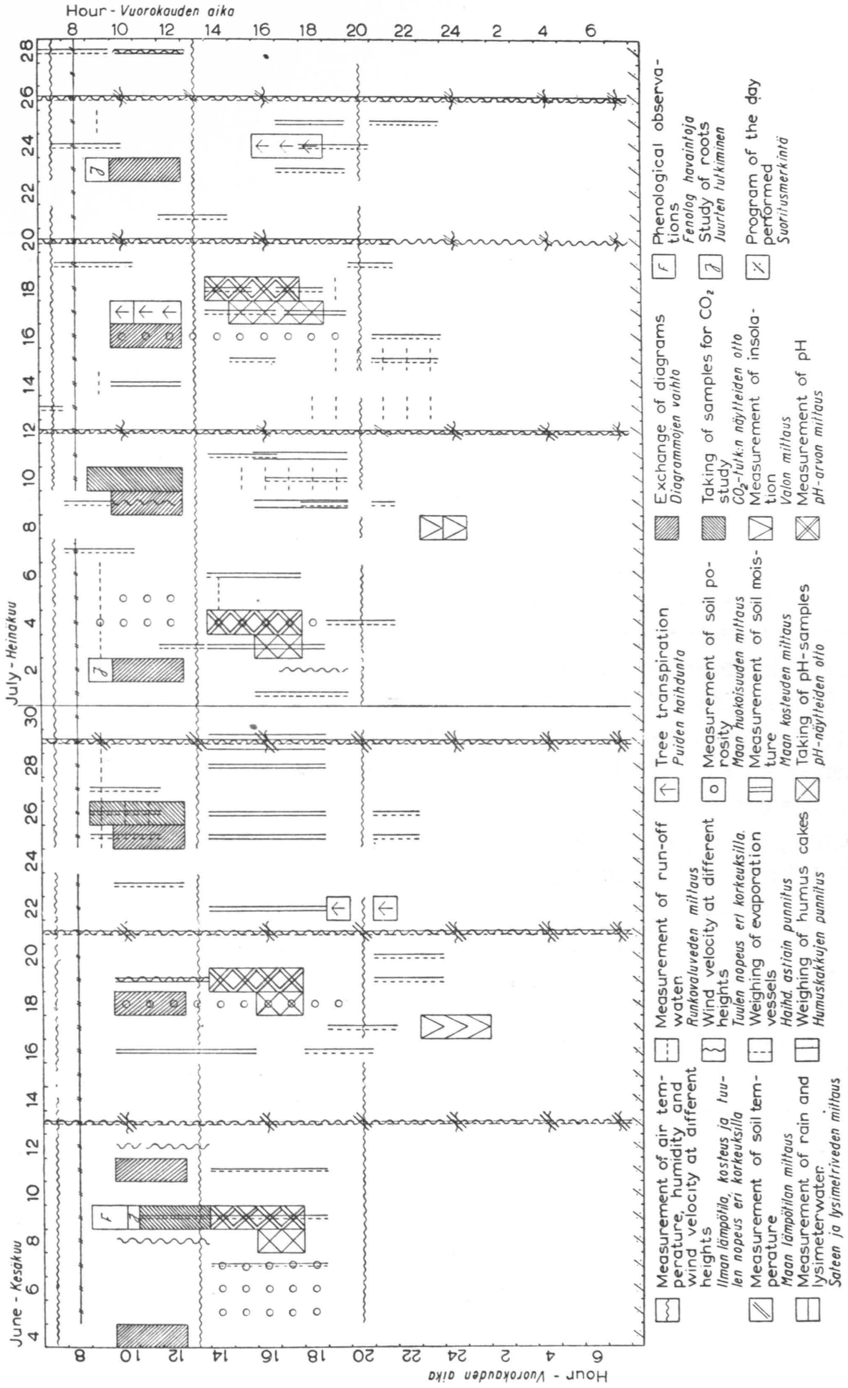


Fig. 47. Part of the programme carried out in the summer of 1951 at Siulionpalo.

Kuva 47. Osa kesällä 1951 Siulionpalossa suoritettua ohjelmaa.

Ecological changes in the stand climate

It is well known that the so-called stand or meso-climate gradually undergoes more or less distinct changes caused by the development of the stand itself. It is often difficult, however, to distinguish between cause and effect for the prevailing stand climate may, in its turn, bring about reactions in the forest-dynamic process which, under other meso-climatic conditions, might fail to appear or would be succeeded by other phenomena.

Light

In a tree stand the conditions of insolation can be studied to some degree by charting e.g. the seasonal variations of light conditions under the crown canopy.

Light is an ecological factor subject to particularly great changes, especially in spruce stands of the type studied in this investigation. Cajander (1916, p. 116), for instance, attached great importance to this factor, and some of his views have been verified by some modern research workers (cf. e.g. Geiger 1927, Aurén 1930, Lundegårdh 1949, Baumgartner 1952 and Hofmann 1952; see also the literature by Geiger 1950). The two representative parallel stands selected for specialized ecological studies differed in character to the extent that the light factor under the relevant crown canopies, for natural reasons, was also different then. A seasonal variation was to be expected in any case in the birch stand. In order to elucidate this detail, determination of the intensity of the interior illumination was made during two vegetation periods before, during, and after leafing; and after defoliation.

For further investigation of the extent to which the illumination changes with the stages of the succession, a number of light intensity measurements were made partly in primary stands included in the previously described series of sample plots and partly in some older, pure birch stands which do not belong to the series but have been included for the sake of comparison. It may be mentioned that on the whole very few light intensity measurements in stands have been made in Finland (cf. Sirén 1948, Kauttu 1952).

The results of the determinations of the light intensity in the two parallel stands are somewhat unfavourably affected, especially from the viewpoint of insolation, by the difference in crown structure: in the birch stand it is more uniform, in the spruce stand more irregular. This is evidenced, for instance, in the following example taken from measurements made during two light but cloudy summer nights, June 17 and July 18, 1951 (Table 42). (On the difference in principle between direct sunlight and diffuse light, see Trapp 1938, according to Geiger 1950, p. 305).

The figures in Table 42 must be taken as reliable, considering that the various determinations were made at the same points in the stands. There is no doubt about the change in the birch stand being significant, and, furthermore, the standard deviation reveals that the illumination in the birch stand was more even during as well as after leafing. From the crown projection maps and direct observations it was established that the soil surface in the birch stand studied actually receives less direct sunlight than that of the spruce stand. The difference between light and shade is sharper in the latter however. According to Sauberer (1937, p. 155), the radiation balance is fairly independent, however, of momentary radiation conditions, from which it follows that the marked contrast between light and shade cannot, due to the more or less slowly changing light conditions, be considered as significant as a first glance may seem to indicate. The light intensity values for full needle and leaf foliage, respectively, agree well with earlier results (cf. Lauscher & Schwabl 1934, according

Table 42. An example of the difference of illumination during and after leafing in the birch and spruce parallel stands.

Taulukko 42. Esimerkki valaistuksen erilaisuudesta rinnakkaismetsiköissä lehtien puhkeamisen aikaan ja sen jälkeen.

Stand *Metsikkö*	Date *Päivämäärä*	Degree of leafing *Lehtien puhkeamisaste*	Intensity of light, lux in average *Valaistuksen voimakkuus, lux, keskim.*		M_p $\left(p=\frac{100 \cdot s}{o}\right)$	σ_p	$\varepsilon(M_p)$
			in the open *avomaalla* M_o	in the stand *metsikössä* M_s			
Birch stand	17. 6. 51	30 %	1225	725	59.2	5.63	0.75
Koivikko	8. 7. 51	100 %	363	92	25.3	9.08	1.21
Spruce stand	17. 6. 51	~ 100 %	1050	409	38.9	11.19	1.12
Kuusikko	8. 7. 51	100 %	312	103	33.0	11.66	1.19

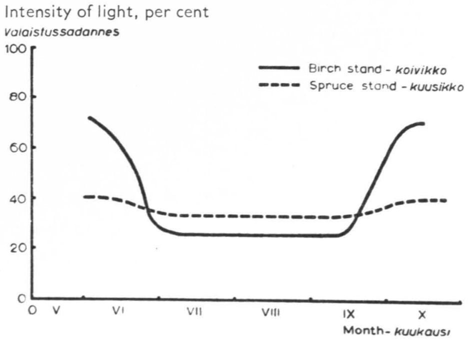
to Geiger 1950); the variation of the separate values, however, was smaller in the present investigation in the birch stand, contrary to the case in Nägeli's investigation (1940) in which the interior illumination of an old spruce stand and a beech stand were compared. Also, the degree of shade in the leafless stand seemed to be considerably less than 50 per cent, in the present investigation about 25 to 30 per cent (cf. Fig. 48).

In the north of Finland the soil temperature during the vegetation period, an important factor, is highly dependent on insolation conditions (cf. Keränen 1920, pp. 103—114, Mork 1933, p. 31, Lundegårdh 1949, p. 67, and others). For this reason it was considered appropriate to chart light conditions in both stands before, during and after the vegetation period. Fig. 48 shows the results of these measurements.

The light conditions in the birch stand definitely seemed to be worse during most of the vegetation period than in the spruce stand — provided reflected and diffused light is not considered to provide any particular qualitative benefit (cf. Knuchel 1914, Ångström 1925, Lundegårdh 1949). The light intensity in the birch stand was one-third, in the spruce stand one-fourth of the illumination in the open. On the other hand, before and during the first few weeks of leafing, the illumination in the birch stand was much greater than in the comparatively unchanging spruce stand (cf. Nägeli 1940).

The above results are surprising because spruce stands have generally been considered to provide more shade than birch stands. It must, of course, be remembered that the density and the age of the stand has a certain significance in the cases studied. To find out to what degree the development of the stand affects illumination conditions, a number of measurements were made in stands in full needle and leaf foliage of comparable density. Fig. 49 shows the relationship between tree species, age, and degree of shading.

The figure shows that illumination conditions at 1.0 m above ground level in birch-spruce primary stands, i.e. the conditions of the spruce seedlings, have changed radically in the first century. Primary stands of 80 to 140 years afford rather deep shade, after which increased light begins to seep into the stands in spite of the fact that spruce grows more dominating. The probable cause of this tendency is that the crown space of the receding birches is not filled by the surrounding spruces. The illumination in pure spruce stands, which increases with age following on the period with maximum shading, has already been studied by Mitscherlich (1940), and further details may be omitted in this connection. Comparing his results with those of the present study it must be borne in mind that the structure of spruce stands in the north of Finland is different and above all their development is considerably slower than in Germany. The principal similarity is however striking.



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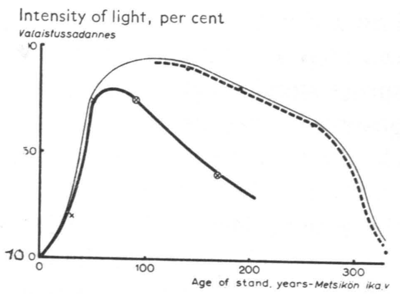

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Fig. 48. Interior illumination in the parallel stands in summer 1951.

Kuva 48. Rinnakkaisnäytealojen valaistusolot kesällä 1951.

Fig. 49. Interior illumination changes due to the age of birch and spruce stands. The fine line represents, broadly speaking, interior illumination conditions during the primary succession.

Kuva 49. Valaistusolojen muuttuminen koivikon ja kuusikon iän mukaan. Ohut viiva edustaa primäärisuksession valaistusoloja.

Comparison of stands dominated by spruces and birches is of interest. The latter have a short period of deep shading at the age of 50 to 100 years. But in the following century there is considerably less shading. At 200 years there is about three times more light than in comparable spruce stands. The spruce stand shows no considerable improvement of the interior illumination until towards the age of 300 years. Consequently there is no improvement of the insolation neither.

Against this background the ratio between the degree of shade in the spruce and birch stand at Siulio is easy to understand. The birch stand is in its stage of maximum shade whereas the spruce stand, which besides belongs to the secondary succession, is already sparser and permits a better penetration of light and more insolation.

The scattered vertical light measurements performed showed that no particular illumination changes take place between the heights of 0.2 and 1.0 m and of 1.0 m and 5.0 m in the two stands (cf. Trapp 1938 according to Geiger 1950, p. 305).

Evalution of the insolation conditions in the two stands should take into account the fact that the soil in the birch stand has been exposed to considerably stronger insolation up to high summer, from which time the spruce stand is actually somewhat lighter on the average. It must now be observed, however, that the illumination measurements were made in calm, cloudy weather; the effect of the wind — not to mention other factors — on the mobility of the crown layer, in the birch stand in particular, with the ensuing increased insolation (cf. Saharov 1949) is not visible in the results obtained. On the other hand, it is feasible, of course, that the crown layer of conical crowns in the relatively open spruce stand actually remains lighter in all circumstances than the birch stand in full leaf because a larger proportion of direct sunlight can penetrate right down to the soil. If this is the case, light cannot be a minimum factor for the weak spruce seedlings growing in the old spruce stand. The relative light minimum determined by Hesselman (1904, p. 311) lies far below the light intensity measured in the spruce stand. That spruce seedlings actually grow better in birch stands, in spite of the deeper shade in them during the latter part of the vegetation period, is explicable to some extent by the fact that tree height growth coincides with the first few weeks of the summer (cf. e.g. Wallen 1917, Romell 1925, Mork 1941 and Mikola 1950). In addition, other factors, both climatic and edaphic, in the birch stand, may lower the minimum light requirements of the spruce seedlings (cf. Pearson 1930 and Lundegårdh 1949, pp. 72—75).

To sum up the light factor, it may be said that the insolation to the soil in primary stands is comparatively good until the crown layer closes up completely. After a century-long period of dense shading the interior illumination, and consequenthy the insolation begins to increase when, at about 150 years, the spaces left by the crowns of receding birches are no longer filled by the spruce crowns. After the destruction of the spruce stand, insolation approaches the degree of insolation in the open. Studying of the inter-relationship between primary and secondary stands shows that in the latter insolation is considerably stronger during the first century except in spring and early summer.

About light conditions in the two parallel stands, subjected to specialized study, let it suffice to say that the differences observed cannot in themselves explain the differing vitality of the spruce seedlings.

The intensity of insolation, recorded by the actinograph will be discussed later in connection with the calculation of the heat exchange of the ground surface (cf. pp. 274—276). The influence of insolation upon stand transpiration is also briefly studied (pp. 259—261).

Temperature

In the preceding chapter on light conditions in the parallel stands it was observed indirectly that insolation before and during the greater part of leafing was decidedly better in the birch stand; in the spruce stand it was better after birch was in full leaf and needle foliation complete, i.e. during the major part of the vegetation period.

That a close correlation exists between temperature and insolation is known. It remains to discover to what extent this is reflected in the temperature conditions of the different stands. These conditions during the vegetation period constituted one of the main subjects to be studied at the Siulio ecological station. The method used has been described previously (p. 167). The literature dealing with stand climate in general, and temperature of air especially is so extremely vast that even a concentrated review would be too extensive. Especially Geiger has since 1924 published a large number of investigations (cf. Geiger 1927, 1950). Among other researchers in this field the following may be mentioned: Wallén (1917, 1928, 1932), Burger (1933, 1951) and Mork (1941). In Finland Multamäki (1942), Lukkala (1946), Kauttu (1952) and Teivainen (1952) have made same interesting studies of the stand climate. Multamäki also presents a short review of the literature.

* * *

The study of continuous temperature conditions on the parallel sample plots was based on thermographic recordings. Careful calibration preceded the siting of the instruments. Unfortunately this precision was partly offset during the rough journey to the remotely situated sample plots. In order — after renewed calibration in the field — to guarantee the comparability of the thermographic diagrams on the one hand and of these and the thermometric readings on the other control readings were made at least once daily with a precision thermometer, and once a week control calibration was performed with Assman's psychrometer thermometer. These repeated control recordings made possible the necessary correction of the instruments and diagrams. After two weeks the two Lambrecht thermo-hygrographs were completely reliable in operation. The Fuess thermograph also worked excellently, though the time error was somewhat greater than in the Lambrecht apparatus. All the instruments were tested on termination of the field work. The Lambrecht apparatus was found

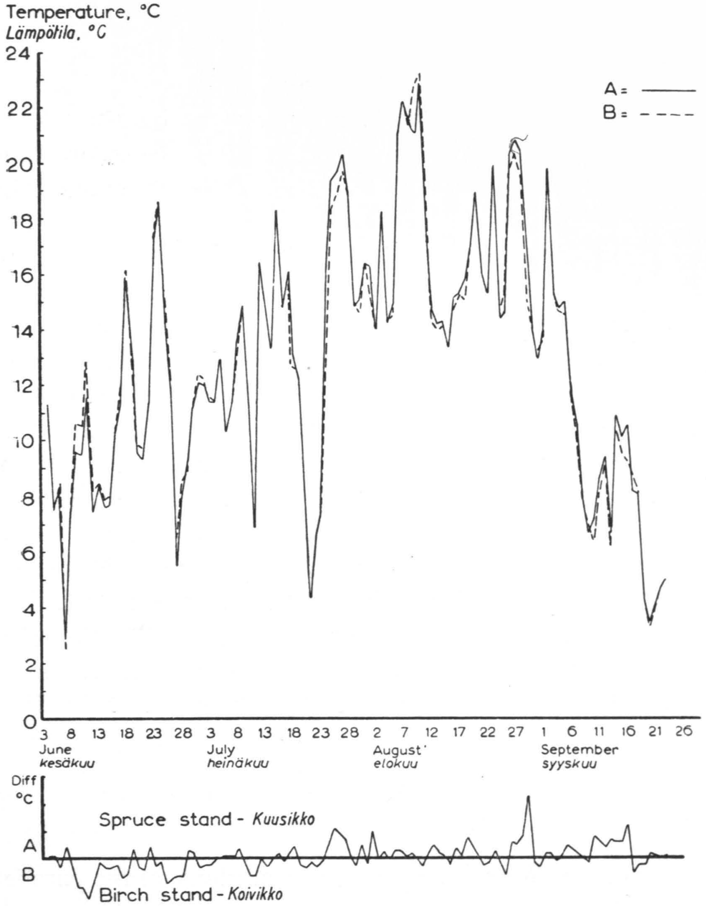

Fig. 50. Variation of day temperature in the parallel stands during growing season 1951.

Kuva 50. Päivän lämpötilan vaihtelu rinnakkaismetsiköissä kasvukautena 1951.

still to draw identical diagrams; the time divergence in the Fuess apparatus was only about 20 minutes a week. The time errors registered were readily corrected as the general course of the curves with numerous characteristic momentaneous values facilitated fixation of the desired recording times in connection with the calculation of averages.

The mean temperatures were calculated after correcting the temperature diagram readings: the mean day temperatures (T° d_1) were based on readings at 08_{00}, 10_{00}, 12_{00}, 14_{00}, 16_{00}, and 18_{00}, and the night temperatures (T° n_1) on readings at 20_{00}, 22_{00}, 24_{00}, 02_{00}, 04_{00} and 06_{00} hours. The diurnal temperature was obtained by working out the average of the twelve recordings. For control, the diurnal, the day and the night average temperatures were calculated with the aid of a planimeter. Maximum and minimum temperatures were read without regard to the hour of the day or night. As a rule, highest and lowest temperatures occurred somewhat later in the stands than in the open spaces. The cause of this delay has been studied e.g. by Geiger (1929, p. 51).

The material of the diagrams, treated as described above, produced a large number of curves for the entire vegetation period. The curves for the average day and night temperatures (Figs. 50—51) and the minimum and maximum curves from all the sample plots are of particular interest.

They give an instructive picture of temperature conditions in the various sample plots in Siulio. Except for four short periods of cold weather, the temperature rose steadily in the summer of 1951 to the end of July, and remained comparatively high throughout August and the first week of September.

Studying the average day temperature at a height of 2.0 m in spruce and birch stands, and especially the differential curve (see Fig. 50), it is seen that early summer was characterised by a higher temperature in the birch stand, late summer by a higher temperature in the spruce stand. The night temperature was lower in the first part of early summer in the birch stand, but at high summer (i.e. after leafing of the birch was complete) there was a radical change; the birch stand got warmer. The difference was levelled out at the end of July. Not until mid-September, when defoliation thinned out the crown canopy considerably, was the night temperature higher in the spruce stand.

The minimum temperature seemed to follow the same trend as the night temperature. By contrast, the maximum temperature, except in early summer, was definitely higher in the spruce stand.

However, these diagrams give no clear picture of the differences in temperature between the two parallel stands. To obtain the numerical differences in the stand temperatures requires other methods.

Setting out from the above mentioned four diagram-systems and the drimary diagrams obtained, the vegetation period was divided into weather phases, as follow:

The original diagrams for air temperature, relative humidity, and insolation were synchronised and compared with one another. All succes-

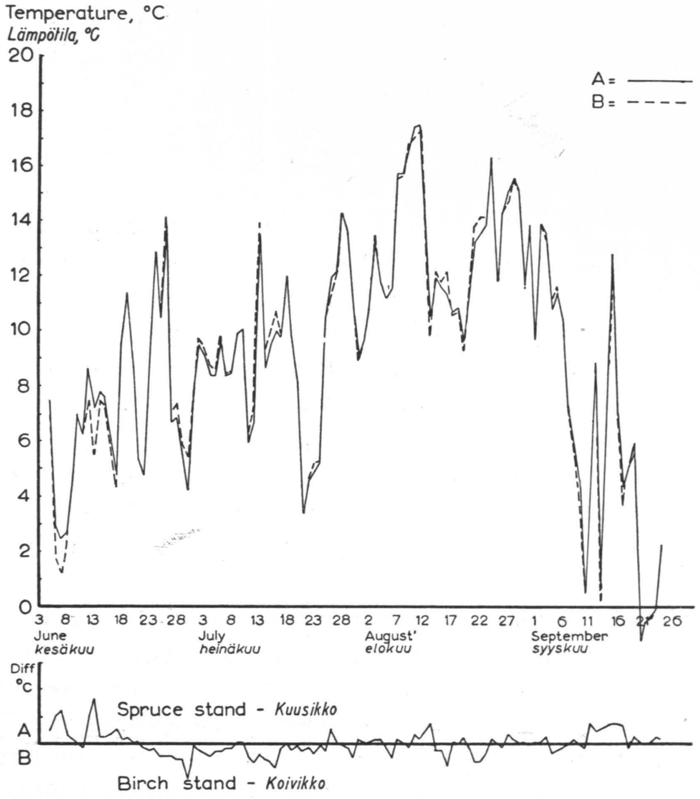

Fig. 51. Variation of nocturnal temperature in the parallel stands during growing season 1951.

Kuva 51. Yön lämpötilan vaihtelu rinnakkaismetsiköissä kasvukautena 1951.

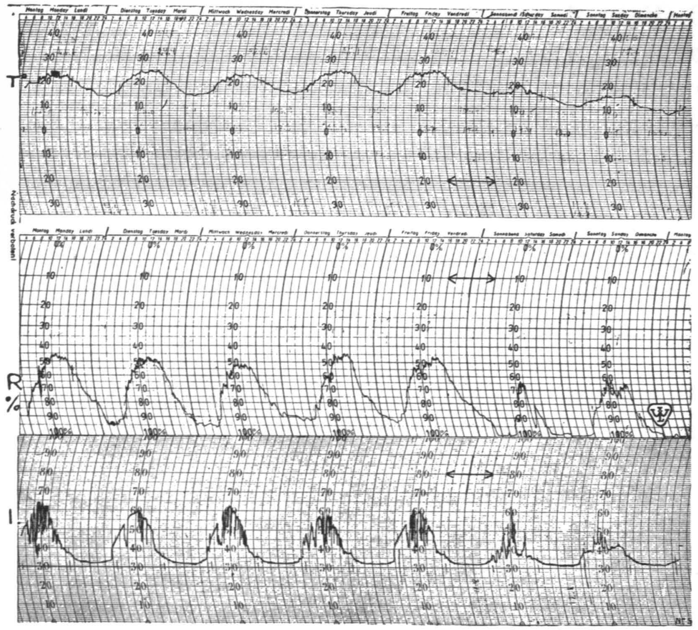

Fig. 52. An example of dividing in weather phases. T = temperature, R = relative humidity, I = insolation.

Kuva 52. Esimerkki sääjakson määrittämisestä. T = lämpötila, R = suhteellinen kosteus, I = säteily.

sive days showing almost similar weather, humidity, and insolation were referred to one and the same weather phase (see example in Fig. 52).

The day, night, and diurnal mean temperatures, humidity, and insolation intensity, respectively, calculated on primary treatment, formed the basis for determination of the averages for the various phases. Owing to lack of space, only temperature conditions in summer 1951 are shown in Table 43.

The table, whose approximate agreement with the diagrams in Figures 50 and 51 is self-evident, shows that the temperature at Siulio was comparatively low for the major part of the vegetation period. Permanent warm weather did not arrive until July 24, but it then persisted until September 5, inclusive. Before this warm period the average day temperature was over 15° C in only one weather phase. The average night temperature was likewise particularly low before July 24. Short and appreciable breaks in the continuous temperature increase in early and midsummer were caused by four cold periods: June 7 and 27—28, July 11 and 21—23. These breaks also show that a weather phase in the present investigation may cover a 24-hour period only. The cold period in September may be regarded as a normal phenomenon of early autumn.

The impression obtained from these phases of the temperature factor of the vegetation period in the various stands is still, however, too disconnected. These small units must be grouped together if they are to serve general survey purposes. The only overall characteristic that seems to emerge is the higher and wider temperature range of the cleared area.

Phenological and macroclimatic phenomena were selected to serve as

Table 43. Mean day, night, and diurnal temperatures determined by thermograph in spruce and birch stands and on open ground during the weather phases in summer 1951.

Taulukko 43. Kuusikon, koivikon ja avoalan keskimääräinen termografilla määritetty päivä-, yö- ja vuorokausilämpötila ns. sääjaksojen aikana kesällä 1951.

Weather phase, date *Sääjakso, pvm.*	Spruce stand *Kuusikko*			Birch stand *Koivikko*			Open area *Avoala*		
	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*
	Temperature °C — *Lämpötila °C*								
4— 6. 6	9.00	4.33	6.67	9.07	3.37	6.22	·	·	·
7. 6	3.00	2.70	2.85	2.50	2.30	2.40	·	·	·
8—13. 6	8.65	6.88	7.76	9.68	6.35	8.02	·	·	·
14—15. 6	7.65	6.90	7.28	7.95	6.55	7.25	·	·	·
16—17. 6	10.70	7.25	8.98	11.15	6.35	9.00	·	·	·
18—19. 6	14.50	10.05	12.28	14.55	9.85	12.20	13.85	9.80	11.83
20—22. 6	10.10	6.37	8.23	10.17	6.43	8.30	9.10	5.90	7.50
23—24. 6	17.85	11.60	14.73	18.05	11.85	14.95	17.30	11.15	14.23
25—26. 6	13.05	10.20	11.63	13.85	10.60	12.23	13.50	10.45	11.98
27—28. 6	6.70	6.15	6.43	8.30	7.65	7.98	7.20	6.75	6.98
29. 6—10. 7	11.80	8.32	10.06	12.08	8.56	10.32	11.82	8.54	10.18
11. 7	6.90	6.70	6.80	7.50	7.30	7.40	6.20	6.20	6.20
12—20. 7	14.27	9.39	11.83	14.27	9.68	11.98	13.09	8.76	10.93
21—23. 7	6.10	4.90	5.50	6.27	5.07	5.67	5.90	4.70	5.30
24—28. 7	18.94	12.26	15.60	18.28	12.38	15.33	18.98	12.28	15.63
29—30. 7	15.20	10.10	12.65	14.85	10.00	12.43	15.30	10.00	12.65
31. 7— 3. 8	16.23	11.50	13.87	15.95	11.45	13.70	16.03	11.35	13.69
4— 5. 8	14.55	11.40	12.98	14.40	11.70	13.05	14.50	11.75	13.13
6—10. 8	21.82	16.70	19.26	22.10	16.54	19.32	22.04	16.24	19.14
11—19. 8	15.27	11.27	13.27	14.99	11.22	13.11	15.02	10.81	12.92
20—25. 8	16.57	13.88	15.23	16.67	13.12	14.90	16.10	13.45	14.78
26—28. 8	20.53	15.37	17.95	19.90	15.13	17.52	19.87	14.37	17.12
29. 8— 5. 9	15.43	11.96	13.70	15.08	11.96	13.52	14.80	11.39	13.10
6—18. 9	9.03	5.78	7.41	8.68	5.42	7.05	8.45	4.72	6.59
19—23. 9	4.34	0.05	2.20	4.30	±0.00	2.15	2.94	—2.20	0.37

the criteria for grouping the phases into ecological periods. The time of snow melting, leafing, defoliation and other factors must of course be considered in assessing the climate of the stand.

Melting of the visible snow cover at Siulio ceased on June 7 at night, and no marked swelling of the birch bud occurred before this date. Leafing

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started about June 8, with intensified and rapid swelling of the buds into »mouse ears». The leafing process could be considered complete at Midsummer when the entire birch stand was in full leaf. The actual thermal high summer, June 23 to September 5, both dates inclusive, was divided, mainly on account of an essential difference in the temperature, into two ecological periods: June 23 to July 23 and July 24 to September 5. This division is supported by the difference in the insolation conditions recorded with the Robitsch actinograph. The first cold period in the autumn, September 6 to 18, accompanied by more or less continuous defoliation, formed a natural border period between summer and autumn, and the night of severe frost, September 19, ushered in the actual autumn.

The averages for the various ecological periods, grouped as described above, are presented in Table 44. They were calculated from the diurnal, day, and night temperature means. The temperature differences were included in the table to facilitate comparison of spruce and birch stands.

The figures definitely have the force of evidence and verify the statements made concerning the general trend of the temperature (pp. 182, 184). Interpretation of the numerical data may thus be limited to comment on the influence of the stand on the temperature.

Before June 8, the dark spruce crowns on Sample Plot A permitted a

Table 44. Mean temperature of the air during the ecological periods of summer 1951 in the parallel stands of spruce and birch recorded by thermograph at a height of 2.0 m.

Taulukko 44. Rinnakkaisten näytealametsiköiden ilman keskimääräinen lämpötila 2.0 m korkeudella termografilla määritettynä eri ekologisina kausina kesällä 1951.

Ecological period *Ekologinen kausi*	Spruce stand (A) *Kuusikko (A)*			Birch stand (B) *Koivikko (B)*			Temperature differences (A—B)[1]		
	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*	Day *Päivä*	Night *Yö*	Diurn. *Vrk.*
	Temperature °C — *Lämpötila °C*								
4. 6— 7. 6	7.50	3.93	5.72	7.43	3.10	5.27	+ 0.07	+ 0.83	+ 0.45
8. 6—22. 6	9.86	6.83	8.35	10.40	6.95	8.68	— 0.54	— 0.12	— 0.33
23. 6—23. 7	11.95	8.44	10.20	12.26	8.79	10.53	— 0.31	— 0.35	— 0.33
24. 7— 5. 9	17.05	12.73	14.89	16.80	12.74	14.77	+ 0.25	— 0.01	+ 0.12
6. 9—23. 9	7.73	4.19	5.96	7.46	3.92	5.69	+ 0.27	+ 0.27	+ 0.27

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[1] *Lämpötilaero (A—B).*

comparatively intense absorption of heat by day and prevented outgoing radiation at night. The leafless birch stand, in spite of intense absorption of heat at soil surface level (see p. 192), was less heated and simultaneously less able to prevent radiation at night. The start of leafing brought an essential change in the position (cf. e.g. Schubert 1929, pp. 77—78). In the daytime, the air was heated under the thin leaf-canopy up to an average of 0.54° C more than in the spruce stand whose conical crowns are evidently not as effective a barrier to air exchange within the stand. The rapidly heating soil in the birch stand is also of great significance (see pp. 256—257). The leaf-canopy, which slowly closes up, effectively prevents radiation and the result is that the night temperature is higher on an average than in the spruce stand. Wind conditions are probably a contributive factor since the cooling effect of wind is greater in the spruce stand which is more open at the top (see Figs. 53—55). The spruce stand, characterized by more marked shade conditions in spite of a higher average total insolation, shows a lower soil temperature (cf. Fig. 79) in addition, and this is reflected on the air temperature of the stand in some measure. The excellent heat-storing capacity of the spruce crowns (cf. Sauberer 1937) does not, it seems, suffice to level out the temperature differences in favour of the spruce stand. The average temperature of the birch stand is persistently higher than that of the spruce stand in the early part of high summer. The significance of the fully-developed leaf-canopy for the prevention of radiation during the unfavourable temperature conditions prevailing at the time is evident; the average diurnal temperature is 0.33° C higher than in the spruce stand. Only in the latter part of high summer does a slight shift occur in favour of the spruce stand. The daily temperature is then on an average 0.25° C higher in the spruce stand and night temperature conditions may be considered almost equal in the two stands. That the spruce stand shows higher day and night temperatures on the approach of autumn is natural considering that the leaves in the birch stand yellow and fall.

The essential difference in the temperature relations of the parallel stands during the vegetation period may be assumed from the above to lie in the ecological periods of early summer and early high summer. In these periods — so important for the growth of the trees in height and thickness (cf. Wallén 1917, Romell 1925, Eide 1926 b, Mork 1941, Mikola 1950, and others) — the average temperature is somewhat higher in the birch stand than in the spruce stand at a height of 2.0 m above ground level. Considering the unreliability of thermograph readings in general, however, the temperature differences obtained must be considered merely probable and not of conclusive significance.

It should be added, however, that the temperature difference between the two stands during the comparatively early and fine summer of 1950 favoured the birch stand considerably more than in the moist summer of 1951. This appears distinctly enough in the table below presenting the average differences in the ecological periods of the summer of 1950. (Table 45).

According to e.g. Mork (1941) these above mentioned temperature differences must have a significant physiological influence upon the growth rate of the trees — in favour of the trees in the birch stand.

From the viewpoint of the trees, however, the stand climate is of greater significance than the »forest climate» discussed above (i.e. the climate at a height of 2.0 m), although the latter often gives a good picture of the climate in the whole stand.

* * *

The conversion of thermographic diagrams to numerical data is known to involve potential errors, mainly caused by the thickness of the curve compared with the temperature scale. Reading errors of up to 0.1° C are

Table 45. Temperature differences in the parallel stands in the ecological periods of 1950.

Taulukko 45. Rinnakkaisten näytealametsiköiden ilman lämpötilaerot eri ekologisina kausina kesällä 1950.

Ecological period — *Ekologinen kausi*	Date *Pvm.*	Temperature differences (A—B) *Lämpötilaero (A—B) ° C*		
		Day *Päivä*	Night *Yö*	Diurn. *Vrk.*
Early summer, latter part of leafing .. *Varhaiskesä, hiirenkorva-aika*	12—18. 6	— 1.08	— 0.95	— 1.01
Early high summer .... *Keskikesän alkukausi*	19. 6—3. 7	— 1.14	— 0.60	— 0.87
High summer cold period .... *Keskikesän kolea kausi*	4. 7—12. 7	— 1.60	— 1.02	— 1.31
High summer .... *Keskikesä*	13. 7—3. 8	— 2.16	— 0.53	— 1.34
Late summer .... *Syyskesä*	4. 8—31. 8	+ 0.26	+ 0.57	+ 0.42
Autumn, commencement of defoliation *Alkusyksy, ruska-aika*	1. 9—24. 9	+ 0.13	+ 0.27	+ 0.20

at least possible. To obtain a better idea of the climate of the stand and, simultaneously, to check the thermographs the temperature was measured daily with a precision thermometer and psychrometer (protected against radiation) at 07 00, 13 00 and 20 00 hours at various heights above the ground. Furthermore, to ensure reliable comparability, temperature readings were taken both day and night at intervals of 3 to 4 hours for 9 days in the summer of 1950 and for 11 days in the summer of 1951. The method used for these temperature measurements has been described previously (p. 168).

Of the data thus obtained during the whole vegetation period, the day temperature at 13 00 hours at 2.0 m above ground level is probably the most suitable for comparison with the readings of the thermograph diagrams (Table 46).

Considering that the thermometer readings were made with the aid of psychrometers, well protected against radiation (accuracy of readings = 0.1° C), these data must be more reliable than those of the somewhat less sensitive thermographs. The wide differences between the thermometric and thermographic values in the two stands can probably also be attributed to some extent to the different micro-milieu. The thermometers were read in the open whereas the thermographs were enclosed in small shelters with intact roofs but spaced walls and floor boards.

That the thermometers showed higher readings during the early and high summer periods but almost equally high readings in the late summer and autumn can be explained by the fact that the raised temperature of air at noon during the unstable climatic conditions prevailing in the early summer was recorded more readily by the thermometers than by the less sensitive thermographs. During the latter part of high summer the stand climate was stable and the momentary divergences therefore apparently smaller. The essential difference between the thermometric and thermographic data is, however, the fact that the average thermometer recordings were higher in both stands and *that the higher temperature in the birch stand during early summer and the first part of high summer was further confirmed*. The difference may be considered significant thanks to the accuracy of reading. That even small differences in the temperature can be of decisive character has been stated earlier by e.g. Mork (1941) and Hustich (1948 c).

In many cases the climate of advanced stands may be characterised by the average values at the traditional height, 2.0 m above ground. Stand characteristics vary from case to case, however, and under such conditions the temperature records obtained at other heights than 2.0 m may be valuable. The actual stand climate comprises all air layers, from ground level to the upper surface of the crown canopy.

In Siulio, the temperature was measured three times daily at 0.2, 0.5, 1.0, 2.0, 4.0, 6.0, 8.0 and 10.0 m above ground level. Only some details of importance from the vast material thus assembled will be given in this connection. To facilitate the survey of the results the study will again be based on the ecological periods. Table 47 gives the average temperature at the three cardinal hours, at 0.2, 2.0 and 10.0 m. The observation towers were erected between the 4th and 7th of June, hence records from heights exceeding 2.0 m are not available for this earliest period. To facilitate comparison of the two stands, another table (Table 48) covering the differences has been worked out.

In addition to previous evidence of the more favourable temperature conditions in the birch stands during early summer and the first part of high summer, confirmed in the tables, they provide fresh information on temperature conditions in the stands. Comparison of the temperature readings shows, as is natural, that the air layer close to soil surface (0.2 m) often

Table 46. Mean temperature and differences between thermographic and thermometric readings at 13 00 hours in the birch and spruce stands during the ecological periods in summer 1951.

Taulukko 46. Rinnakkaisten näytealametsiköiden ilman keskimääräinen lämpötila päivällä klo 13 00 tarkkuuslämpömittarilla ja termografilla määritettynä eri ekologisina kausina kesällä 1951.

Ecological period, date *Ekologinen kausi, pvm.*	Birch stand *Koivikko*		Spruce stand *Kuusikko*		Difference — *Erotus*			
	Thermometer *Lämpömittari* a	Thermograph *Termografi* b	Thermometer *Lämpömittari* c	Thermograph *Termografi* d	a—b	c—d	a—c	b—d
	Temperature °C — *Lämpötila °C*							
4. 6— 7. 6	8.43	·	8.18	·	·	·	+ 0.25	·
8. 6—22. 6	11.74	11.67	10.79	10.66	+ 0.07	+ 0.13	+ 0.95	+ 1.01
23. 6—23. 7	13.59	13.47	13.06	12.80	+ 0.12	+ 0.26	+ 0.53	+ 0.67
24. 7— 5. 9	17.77	17.82	17.80	17.80	— 0.05	+ 0.00	— 0.03	+ 0.02
6. 9—18. 9	10.00	9.98	9.90	9.98	— 0.02	— 0.08	+ 0.10	+ 0.00

Table 47. Mean temperature in the parallel stands at different heights above ground level in the morning, at noon and at night during the various ecological periods in the summer of 1951.

Taulukko 47. Rinnakkaisten näytealametsiköiden ilman keskimääräinen lämpötila eri korkeudella aamulla, illalla ja keskipäivän aikaan ns. ekologisina kausina kesällä 1951.

Ecological period *Ekologinen kausi*	Spruce stand (A) — *Kuusikko (A)*									Birch stand (B) — *Koivikko (B)*								
	Height above ground (m) and hour of temperature reading *Lämpötilan mittauskorkeus (m) ja -ajankohta*																	
	0.2			2.0			10.0			0.2			2.0			10.0		
	07 00	13 00	20 00	07 00	13 00	20 00	07 00	13 00	20 00	07 00	13 00	20 00	07 00	13 00	20 00	07 00	13 00	20 00
	Temperature °C — *Lämpötila °C*																	
4. 6— 7. 6	3.38	7.55	4.00	4.13	8.18	4.48				4.32	8.10	4.90	4.35	8.43	4.67			
8. 6— 22. 6	7.85	11.51	9.27	8.04	10.79	10.05	7.64	10.66	10.48	8.39	12.15	9.68	8.31	11.74	9.99	7.54	11.21	10.72
23. 6— 23. 7	9.90	13.03	10.14	9.98	13.06	10.94	10.14	12.76	10.36	10.11	13.70	10.49	10.22	13.59	10.47	10.98	13.05	10.34
24. 7— 5. 9	13.59	18.45	13.43	13.64	17.80	14.09	13.86	17.28	14.62	13.24	17.37	13.55	13.25	17.77	13.94	14.14	17.59	14.54

Table 48. Temperature differences at various heights above ground level and at various hours in the parallel stands (A—B)

Taulukko 48. Rinnakkaisten näytealametsiköiden ilman lämpötilan erotus (A—B) eri korkeudella ja eri vuorokauden aikoina ns. ekologisina kausina kesällä 1951.

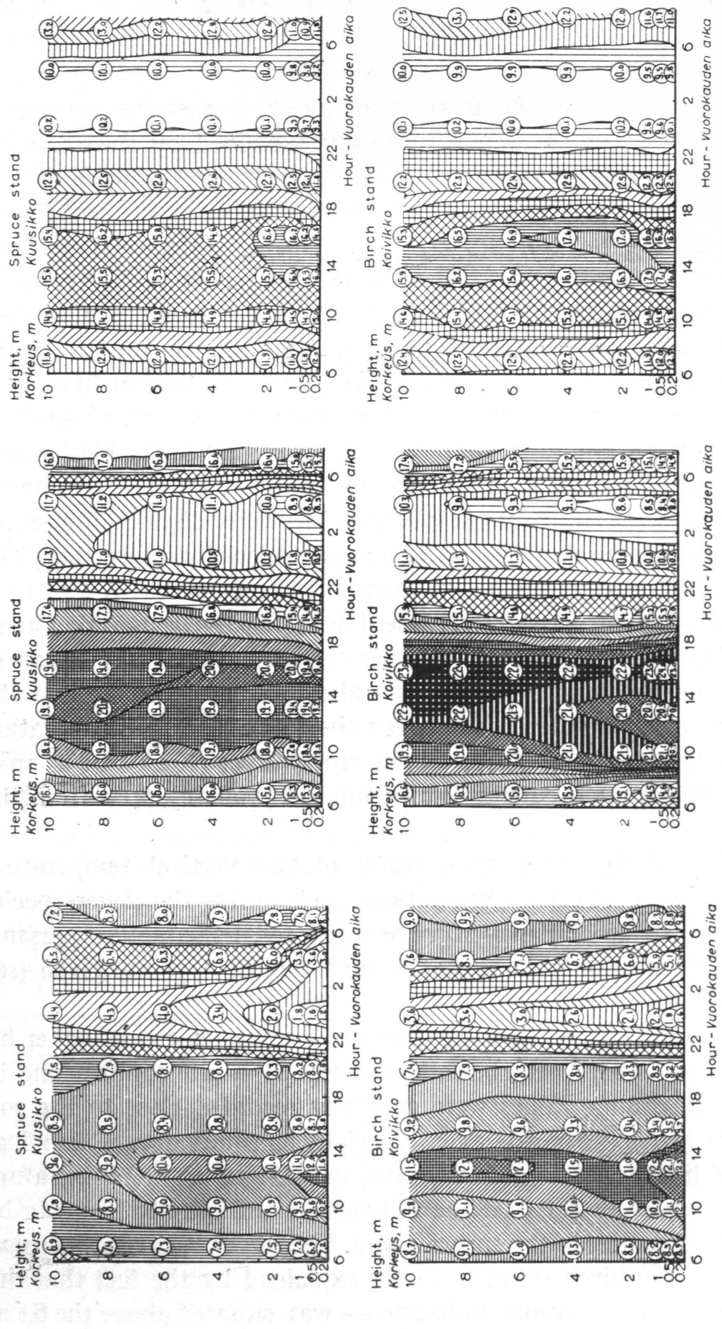
Ecological period *Ekologinen kausi*	Height above ground (m) and hour of temperature reading — *Lämpötilan mittauskorkeus (m) ja -ajankohta*								
	0.2			2.0			10.0		
	07 00	13 00	20 00	07 00	13 00	20 00	07 00	13 00	20 00
	Difference in temperature (A—B) °C — *Lämpötilan erotus (A—B) °C*								
4. 6— 7. 6	— 0.94	— 0.55	— 0.90	— 0.19	— 0.25	— 0.19	.	.	.
8. 6—22. 6	— 0.54	— 0.64	— 0.41	— 0.27	— 0.95	+ 0.06	+ 0.10	— 0.55	— 0.24
23. 6—23. 7	— 0.21	— 0.67	— 0.35	— 0.24	— 0.53	+ 0.45	— 0.84	— 0.29	+ 0.02
24. 7— 5. 9	+ 0.35	+ 1.10	— 0.08	+ 0.39	+ 0.03	+ 0.15	— 0.28	— 0.31	+ 0.08

registered the highest temperature. This appears to be a momentary phenomenon, however, as the temperature in the crown layer (10.0 m) of both spruce and birch stands is generally higher in the morning and at night. The fact that the temperature of the air layer near the ground was lower at midday in the autumn is naturally explained by the radiation from the ground at that season (cf. Homén 1896, and others).

Table 48 shows, further, that the difference between the stand temperatures close to the soil surface (0.2 m) was generally noticeable. Especially in spring and early summer — and sometimes in high summer — the 0.2 m air layer in the birch stand was evidently more effectively warmed than in the spruce stand. In the hot days of late summer conditions changed in favour of the spruce stand. At the normal height of 2.0 m above soil surface the differences are not so distinct as at ground level; in spring, early summer and high summer the temperature in the birch stand is distinctly higher, except at night. In late summer, on the other hand, the temperature of the spruce stand is higher. The fairly distinct differences between spruce and birch stands at 10.0 m are especially interesting. The significance of the topography of the canopy, as reported by Karsten (1922, pp. 235—244), is distinctly evident here. That the morning temperature during the leafing period is lower above the birch stand than in the spruce stand at the same height can also be understood against the background of the dissimilarities between the stands, partly in radiation and partly in the thermal capacity of the crown layer (Karsten op.c. p. 241). The differences occurring in the autumn probably arise from the same causes.

Tables 47 and 48 invite close study of the vertical temperature distribution in the stands. The observations made during the eleven special days in the summer of 1951 may serve as a pointer. For practical reasons, temperature charts of only three of the most typical days are given (see Figs. 53—55).

This investigation shows that the temperature was as a rule higher by day in all the air layers of the birch stand, except in late summer and in autumn. The maximum values were generally recorded close to the soil surface or in or above the crown layer, especially on sunny days. Physiologically harmful high temperatures were not noted. The night temperature minimum was generally noted at the soil surface and usually found to be lower and more constant in the spruce stand. The larger vertical dimension of night cold in the birch stand is partly explained by the fact that the crown layer — which prevents radiation — was situated above the 6.0 m



Figs. 53—55. Vertical temperature profiles in the parallel stands during three typical days, June 21, July 26, and August 17 in the summer of 1951.

Kuvat 53—55. Rinnakkaismetsiköiden ilman lämpötilan pystysuora jakaantuminen kolmena edustavana vuorokautena; 21. 6, 26. 7 ja 17. 8 kesällä 1951.

height. An incomplete crown cover in the close proximity of the observation tower may have affected the result to some extent (see Fig. 44).

The daily isotherms for late summer and early autumn give an excellent illustration (see for instance Fig. 55, Aug. 17) of the previously described levelling of temperature conditions in both stands (p. 188). It is striking that the temperature amplitudes are wider in the spruce stand during autumn, while the temperature fluctuations are wider in the various air layers of the birch stand during spring and early, high and late summer. »Potential isothermia» occurs at times, especially during late summer and the nights of autumn (cf. Karsten 1922, p. 241).

The results given above agree largely with earlier studies of temperature conditions in tree stands (cf. e.g. Paeschke 1937, Geiger 1941, Multamäki 1942 and Wallén 1928, 1932). Differences of detail will possibly be discussed later in a separate paper.

It may be added here that nothing essentially new emerged from comparison of the atmospheric temperature in stands and over open surfaces. The general views presented by Schubert (1900, 1929), Geiger (1927, 1950), Burger (1933), Multamäki (1942), Franssila (1949), Hofmann (1952), Maran & Lhota (1953), and others seem to apply to Lapland too.

To sum up the temperature conditions in the two parallel stands: — in the ecological periods most important for the physiological functions of the trees, early summer and early high summer, the temperature in the birch stand was definitely more favourable than in the spruce stand close to soil surface, in the air space of the stand, and in the crown layer.

Assessing the changes in the stand air temperature during a complete long succession, consideration should be given to insolation conditions. In primary stands heavily dominated by birch the stand temperature is probably higher in the early stages of succession than in later, spruce-dominated stages (cf. p. 179). This signifies that thriving conditions, as far as stand temperature is concerned, favour the trees in the first half of the succession. In other words, the spruces interspersed in birch stands generally enjoy better temperature conditions than spruce undergrowth in pure spruce stands.

It is difficult to make a similar comparison between primary and secondary stands in spite of each of the stands examined representing a separate succession. Considering the structure and composition of the tree species in stands typical of their respective succession stages, and the consequential insolation conditions, it might be assumed that a diagnosis of the temperature differences of the stands would involve no difficulty. However, insolation is not the only factor in the heat equation; large amounts of energy lie latent in the rising temperature of the soil and in evapo-transpiration from the soil surface. These problems will be treated later. All that remains to be said here is that the evidence indicates that the stand temperature — at least in the first half of the vegetation period is probably more favourable in the mixed primary stands than in comparable pure secondary stands dominated by spruce. This assumption is based on the studies of the atmospheric temperature in the stands and openings reported above. The present material does not reveal to what extent conditions change in favour of secondary stands after reduction of the birch interspersion to a minimum in the primary spruce stands.

Wind

It is well known that vegetation retards wind. As a rule friction is strongest close to ground level and decreases rapidly upwards from the ground (cf. Hellmann 1915, 1919 according to Geiger 1950). The intensity of friction depends on the height of the plant community, its density, and some other factors (cf. Paeschke 1937). Since one of the most important sub-factors of the forest climate, air exchange within the stand — important for evapo-transpiration and temperature — is highly dependent on wind conditions in the stand (cf. e.g. Geiger 1925, 1926, 1927, Leighly 1937, Schubert 1942, Burger 1951), comparative investigations between the birch and spruce stands had to be made at Siulio.

Three kinds of wind measurement were therefore performed:

1) According to the instructions of the Central Meteorological Institute, with Wild's Beaufort-meter, three times daily, above the canopy of the stands.
2) With an anemometer, in the stands, at 0.2, 2.0 and 10.0 m above ground, three times daily and diurnally three to four times a month.
3) With an anemometer, in the stands and in the openings (Sample Plots C and D), at 2 m intervals from 0.2 to 14.0 m above ground, an average of once or twice a week at noon.

Wild's apparatus is used, as is well known, only for the purpose of obtaining a general idea of macro-climatic wind conditions. Briefly, the results obtained show that in 1950 E-S-SW winds prevailed up to 70 per cent of the time, and in 1951 SE-S-W winds. Gales or strong winds were rare. The velocity of the wind generally varied between 0 and 3 Beaufort. No significant difference between the months was observed, though the wind in June and July was somewhat more gentle than in August and September, especially during the night, both in 1950 and 1951.

The comparative results of the study of wind conditions in the spruce and birch stands are based on wind velocity measurements at noon above the birch stand at 14 m above soil surface. The following classification was used: $<$ 1 m/sec, 1—2 m/sec, 2—3 m/sec, 3—4 m/sec and 4 m/sec. The results of the noon wind measurements at various heights above ground in 1951 are given in Fig. 56. The material collected in the summer of 1951 verified completely the observations of wind conditions at Siulionpalo during the pilot tests in the preceding summer. No essential difference was observed between wind velocity in the spruce stand with a number of small gaps and in the fairly even birch stand. At velocities over 2 m/sec the wind was slightly weaker in the birch stand up to 6—8 m above ground. Higher than 8 m, stand height had some influence; at 14 m there was no leaf canopy obstruction above the birch stand to act as a wind-break. In the open Sample Plots C (50 × 50 m) and D (40 × 40 m) the wind velocity was naturally of a different order from that in the stands. That the velocity of the wind was always somewhat lower in Sample Plot C is explained by the fact that the surrounding forest was about 5 — 6 m higher than around Sample Plot D, which was encircled by the low birch stand. Nothing new was observed in the comparison of stands and openings (cf. e.g. Schubert 1922, Paeschke 1937).

Since the difference between the spruce and birch stands at low wind velocities during the most unstable wind conditions at midday was insignificant the above evidence of the equivalence in wind conditions between the stands should be considered satisfactory. It has long been known (cf. Hellmann and others, see Geiger 1950) that the wind reaches its highest velocity at midday, slows down towards night, reaches its minimum after midnight, and rises again towards morning. It may be thought, however, that the difference in the structure of the stand might influence the rate of atmospheric currents, especially in the morning and at night. To establish the diurnal variations present, wind measurements were added to the so-called twenty-four-hour programme. As there were but 11 »complete» diurnal periods in the summer of 1951, the material was

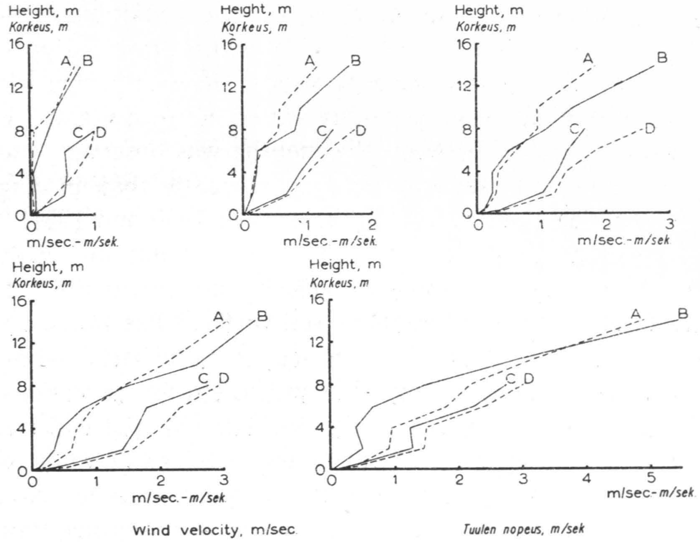


Fig. 56. Windprofiles at different wind velocities at Siulionpalo ecological station. A = spruce stand, B = birch stand, C and D = open areas.

Kuva 56. Tuuliprofiileja Siulionpalon ekologisella asemalla. A = kuusikko, B = koivikko, C ja D = aukeita aloja.

divided into only two groups: < 3 m/sec and > 3 m/sec. Curves were plotted for the mean values thus obtained at different heights above soil surface and at different times of the day (Fig. 57). These curves indicate in spite of wide individual variation that the wind velocity was somewhat less in the lower air layers in the birch stand than in the spruce stand during almost all hours of day and night, especially in the night. The maximum rate was generally noted at midday and the minimum in the early hours of the morning, between 00_{00} and 04_{00}. The daily wind measurements indicated a similar trend.

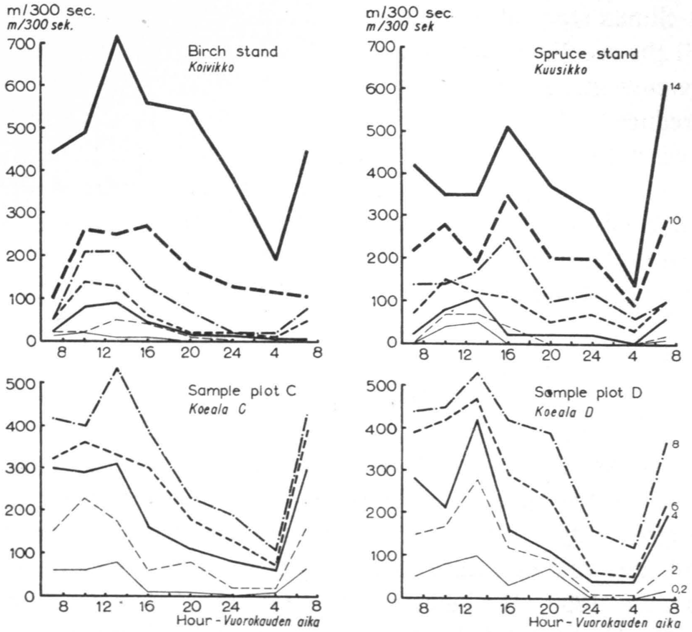


Fig. 57. Diurnal variation of wind velocity at different levels at Siulionpalo station. The figures on the right indicate level above ground.

Kuva 57. Tuulen nopeuden vuorokautinen vaihtelu eri korkeudella Siulionpalon ekologisella asemalla. Oikeassa laidassa olevat numerot osoittavat mittauskorkeutta.

That the wind velocity is lower in the birch stand after leafing may be of some physiological significance. According to Stålfelt (1932, p. 59) optimum assimilation occurs with low wind currents and high wind velocities may impede the process. The conflicting relationship between wind velocity and transpiration observed by the Japanese research workers Nakayama and Kadota (1949) will be discussed in a later chapter. On the other hand the higher wind velocity before and during leafing in the birch stand must have an extremely positive influence upon the evapo-transpiration rate from the soil cover (cf. e.g. Leighly 1937). Later it will be shown that this is a contributive factor to the higher soil temperature of the birch stand.

To sum up the wind conditions in the two parallel stands, the velocity after leafing was somewhat lower in the birch stand, particularly at night when the significance of radiation as a cooling factor is especially perceptible. It was, however, mentioned in the preceding chapter that the temperature in the birch stand was generally higher than the temperature in the spruce stand. This may be a sign that the structure of the birch canopy obviously promotes heat storage in the early summer and early high summer especially.

Comparison of the wind conditions in primary and secondary stands makes it fairly obvious — taking the above findings into account — that the wind circulates fairly freely in stands of spruce seedlings developing in the post-climax stage after the disappearance of the primary spruce stand. Not until the seedlings have grown sufficiently to form a closed stand are exchange currents, set up mainly by wind and vertical temperature differences, reduced. The spruce interspersion in the primary stands — first dominated by birch — grows except during the first part of the vegetation period from the outset in a somewhat calmer environment with narrower ecological amplitudes (cf. Geiger 1950, s. 323). In old primary stands dominated by spruce the wind velocity is exceptionally low compared with that over openings (cf. e.g. Tirén 1924, Geiger 1926).

Precipitation

Water — as is well known — is an ecological factor of paramount importance to plants. It is also well known that different forest communities affect differently water management above and below the surface of the soil. The vast literature on these questions includes detailed reports (cf. Hoppe 1896, Geiger 1926, 1927, Aaltonen 1940, Stålfelt 1944, Kirwald 1944, Kramer 1949, Burger 1951, and others). As precipitation represents the main debit side of the water management balance in forest communities on firm forest land, it seems appropriate to introduce the study of water problems in the stands with a discussion of general precipitation conditions.

The method used in this special study was described above (p. 167). The investigation was confined to the period June 1, 1950, to September 25, 1951, i.e. two vegetation periods and the interjacent winter season. The results, corrected according to Korhonen (1924), can be seen in Table 49. It may be mentioned in passing that very few studies of precipitation in tree stands have been made in Finland (cf. Heikinheimo 1912, Lukkala 1942, 1946, Teivainen 1952).

The precipitation at the Siulionpalo ecological station was considerable during the 1950 and 1951 vegetation periods, well above the mean observed rainfall in North Finland (cf. Korhonen 1951). Comparison of measurement made at the three neighbouring meteorological stations showed the local variations also to be wide (cf. Nakayama & Tasaki 1949, and Doyle 1952). During the winter season, on the other hand, there was no marked difference in this case. No general conclusions can be drawn as only two vegetation periods were measured, though it does seem natural that rain should be more plentiful at Siulionpalo owing to its higher altitude than e.g. Sodankylä and Kemijärvi.

Table 49. The monthly precipitation at Siulionpalo and mean precipitation at the three neighbouring meteorological stations, Sodankylä, Kemijärvi and Savukoski, from June 1950 to Sept. 1951.

Taulukko 49. Kuukauden sademäärä Siulionpalossa sekä kolmen lähimmän meteorologisen säähavaintoaseman (Sodankylä, Kemijärvi ja Savukoski) sademäärän keskiarvo kesäkuusta 1950 syyskuuhun 1951.

Place of observation *Havaintopaikka*	Year and month — *Vuosi ja kuukausi*															Mean *Keskimäärin*	Total precipitat. mm *Sademäärä yht. mm*
	1950							1951									
	June VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	Sept. IX		
	Monthly precipitation, mm — *Kuukauden sademäärä, mm*																
Siulionpalo (a)	92.9	51.9	19.2	67.8	60.5	41.1	29.8	25.8	8.1	25.6	62.8	23.4	87.2	175.7	55.8	60.0	55.5	887.6
The meteor. stations (b) *Säähavaintoasemat (b)*	47.3	52.3	14.7	64.7	54.0	32.5	34.7	25.3	11.3	29.0	56.3	24.3	89.0	150.3	58.7	42.3	49.2	786.7
Difference *Erotus(a—b)*	+ 45.6	— 0.4	+ 4.5	+ 3.1	+ 6.5	+ 8.6	— 4.9	+ 0.5	— 3.2	— 3.4	+ 6.5	— 0.9	— 1.8	+ 25.4	— 2.9	+ 17.7	+ 6.3	+100.9

Horizontal rainfalls, for instance, are more frequent at high altitudes (cf. e.g. Woelfle 1950).

However, the absolute precipitation is of minor consequence in this investigation; it is precipitation in the various sample stands that is of considerable importance. Snow melting, interception, run-off down the stems and evaporation in stands and soil surface are of special interest.

Melting of snow

In the winter of 1950—1951, precipitation was 130.4 mm at Ritaselkä in the neighbourhood of Siulionpalo. This corresponded to a snow cover of about 80 cm on the ground. The correlation of these determinations must be considered satisfactory in the light of the water value of the snow in this region (135 mm in March, 1951) as calculated by the Hydrological Institute at Helsinki (Helsingfors).

The depth of the snow cover varies widely in forests, depending on altitude and exposure, species of tree, density, height of stand and other factors (cf. Schubert 1914, 1917, Aaltonen 1919, Keränen 1920, Heikinheimo 1920c, Korhonen 1926, Ronge 1928, A. Sirén 1936, Kaitera 1939, Kalliola 1942, Burger 1951, etc.). For natural reasons, the snow cover is thinner in dense than sparse stands. The forests of Lapland also have snowless wells round the spruces whose crowns reach down to the ground. To form a fairly reliable conception of the depth of the snow cover over extensive areas involves counting the number of snowless wells and calculating their proportionate area of the surface, or measuring the snow depth with a large number of sounds or fixed measuring rods per unit of area. The latter method was used at Siulionpalo. Measuring was started in early April and continued until the beginning of June. The results are given in Fig. 58.

It is interesting to find that the slight snowfall before April 22 had no lasting influence on the depth of the snow cover on the open sites C and D, contrary to the case in the spruce and birch stands. That the average snow cover was less after the first snowfalls in the spruce stand than on the other sites may be considered normal, but it is largely due to the snowless wells around the spruces. The last phase of thawing reveals another aspect of the effect of the spruce stand on the snow cover. In spite of the snow depth being shallower on the average, thawing was slower in the gaps of the shady spruce stand than in the openings and in the birch stand (cf. e.g. A. Sirén 1936 and Kaitera 1939) where the ground, however, was completely free of snow about 10 days earlier (cf. Schubert 1914, p. 570). It may be mentioned that the last patches of snow in the spruce forest were always found on the north side of particularly dense and comparatively tall spruces; similar observations of the thaw in spruce forests have been made by e.g. Arnborg (1943) and Teivainen (1952). On the other hand it may be mentioned that the first snowless patches occured in the spruce stand, where the heat-absorbing crowns melted the snow to the south of the trees, enlarging the wells considerably (cf. Teivainen 1952, s. 84). In the particularly shady places the soil ice also persisted longer. The superficial layer of the A-horizon next to the humus was still frozen after Midsummer on June 26, 1951 (cf. Ronge 1928). This is natural because of the close correlation that exists between the reflecting capacity of the ground, the albedo, and the colour and type of the ground cover. Since the snow cover has a very high albedo (in the case of old snow, 2 to 3 times that of the ordinary ground vegetation, cf. e.g. Franssila 1949, p. 24), and as thawing is more rapid in the leafless birch stand owing to the absence of effective insolation barriers, the albedo of the spruce stand during the 10 days mentioned seems to be considerably higher than that of the birch stand. In the latter, moreover, heat is absorbed more or less directly and not through the filter-like canopies which cast a deep shade (cf. Ångström 1931, p. 129). However, the comparatively

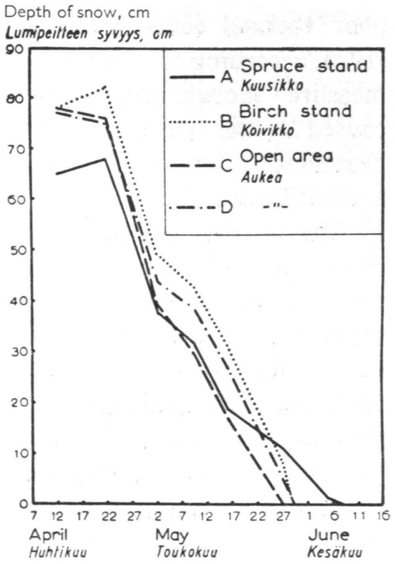


Fig. 58. Thawing of snow at Siulionpalo 1951.

Kuva 58. Lumen sulaminen Siulionpalossa 1951.

poor thermal conductivity of the leaf litter described by Schmidt (1925, according to Geiger 1950) offsets the absorption of heat in some measure, though not sufficiently to counteract the great loss of heat caused by the late thaw in the spruce stand. That ground covers vary in heat-conduction owing to differences in depth and structure is naturally a contributive factor.

The melting of snow in stands proceeds in varying ways depending on the factors mentioned above, but it is generally considered to be slower in spruce stands than in e.g. birch stands which, however, due to the thicker snow cover become free of snow later. The extensive investigation of Kaitera (1939) especially emphasizes this view. In the present study the melting of snow in the spruce stand was found to continue even after the birch stand was snowless. Since similar results have been obtained by Teivainen (1952) too, it seems that the question of the melting of snow in the Lapland forests requires further investigation.

Precipitation during the growing seasons

The major part of the precipitation in the summer months and in September came in the form of rain which, especially towards autumn, assumed the character of horizontal rain, i.e., the cloud cover was level with the Siulionpalo forest. For simplicity, all precipitation — irrespective of kind — during the vegetation periods will be termed rain.

Only some of the total precipitation over normally closed stands falls straight onto the ground — that is rain which is not prevented by the canopies from reaching the ground between the stems. The remainder is generally caught up by the crowns, and, depending on the density and dryness of the needle and leaf foliage and crown branches, and on other factors, large or small quantities of the rain are intercepted, partly adhesively but partly also absorptively, i.e. by cuticular and/or stomatal water intake (cf. Stålfelt 1944), the remainder running off along the stem or dropping onto the ground (cf. Hoppe 1896, Mitchell 1930, Stålfelt op.c. Lukkala 1942, 1946; see also the literature by Wood, 1937).

Unfortunately the two stands compared were of different density classes: the birch stand 0.9 and the spruce stand 0.8. Obviously, therefore, the number of rain gauges spaced between the trees and in the parts sheltered from rain differed proportionally in the two sample plots. In the spruce stand there were 10 unsheltered gauges and in the birch stand only 6. To a certain extent the spaces between the trees were also sheltered from the rain, depending on how the wind blew while the rain fell. Although, therefore, the distinction made between sheltered and exposed rain gauges is open to discussion in certain cases, it is a detail that need not concern us here. The exposed gauges showed considerably higher values than the sheltered gauges as a whole and in the individual instances. The differences can be seen from Table 50.

It should be observed that none of the 32 rain gauges were placed directly under a crown affording maximum shelter from rain. (The excellence of the shelter afforded by the spruce crown was proved by two additional gauges placed close to the stem of a big spruce.) A striking conformity between the exposed gauges is revealed by the figures in the table. It is also remarkable that the sheltered gauges in the spruce stand recorded higher precipitations than their counterparts in the birch stand in the summer of 1950. Close investigation of this phenomenon revealed that an old, dead, lichen-covered tree had acted as a water collecting apparatus during the few very heavy showers, and a rain gauge under this tree showed exceptionally high values. Another point to note is that most of the rain remaining in the spruces was actually retained (Hoppe 1896, p. 21) and slowly evaporated, whereas much of the rain adhering to the birches ultimately trickled down the stems. On the other hand, the spruce stand had considerably more gaps. On the whole, the results obtained conformed well with the precipitation rates measured by Burger (1951) in open spruce stands in Switzerland.

Table 50. Mean data showing the influence of sheltering trees on the results of precipitation measurements in the birch and spruce stands of Siulionpalo.

Taulukko 50. Sateelta suojaavien puiden vaikutus sademittaustuloksiin Siulionpalon koivikossa ja kuusikossa.

Year *Vuosi*	Rain gauges in — *Sademittarit*				
		birch stand — *koivikossa*		spruce stand — *kuusikossa*	
	open *aukealla*	exposed *vapaat*	sheltered *suojatut*	exposed *vapaat*	sheltered *suojatut*
	Precipitation, mm — *Sademäärä, mm*				
1950	100	90.0	71.0	91.0	78.0
1951	100	89.0	73.0	91.0	70.0

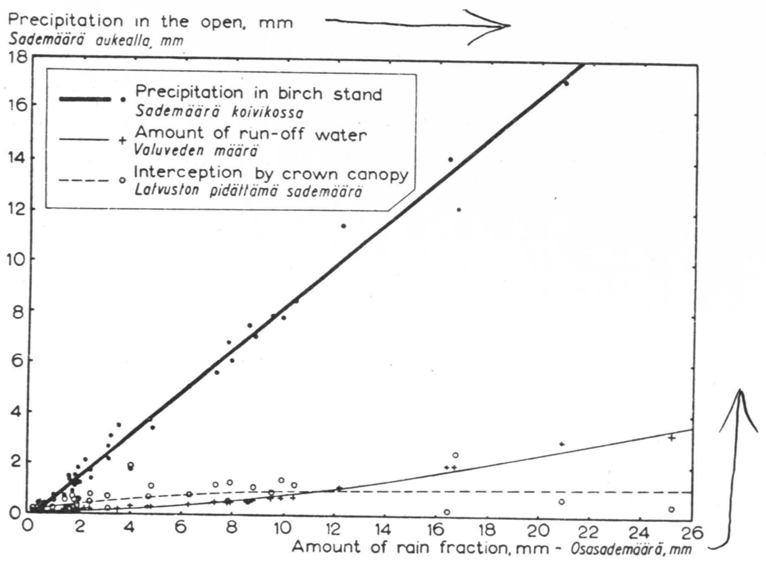


Fig. 59. Distribution of precipitation in a wet birch stand. The dots, circles and crosses indicate unadjusted values.

Kuva 59. Sateen jakaantuminen märkään koivikkoon. Pisteet, ympyrät ja ristit edustavat alkuperäisiä mittaustuloksia.

To obtain as comprehensive a view as possible of the distribution of rain in the several stands, measurements were made to determine the run-off down the stems. The method used was described on p. 167.

The run-off after 27 rain showers was recorded from a total of 47 birches, 2 to 12 cm in diameter. Three of the originally 50 sample trees were abandoned. The first preliminary measurements indicated that the run-off volume seemed to be closely related to the dryness of the leaf surface. Hence run-off in stands that were wet was differentiated from stands that were dry. The first results were noted in a coordinate system by diameter classes, and adjusted following usual statistical principles. The adjusted curves for each diameter class then formed the basis on which the run-off of the whole stand under all conditions of rain was calculated.

The primary values and adjusted curves can be seen from Fig. 59, which represents precipitation in wet birch stands. The run-off along the spruce stems was almost nil, even during heavy rain, because the branches of the northern spruce grow obliquely downward (cf. Mikola 1938). Any run-off along the stem is led off in a peripheral direction; only

Table 51. Interception by leaf canopy and run-off along stems at various rates of precipitation and wetness of the leaves in the birch stand studied at Siulionpalo.

Taulukko 51. Kokonaissademäärän ja koivun lehtien kosteuden vaikutus latvuston pidättämään sekä runkoja pitkin valuneeseen sademäärään Siulionpalon koivikossa.

Rain fractions *Sade-fraktiot*	Wet leaf canopy (B_w) *Märkä latvusto* (B_w)			Dry leaf canopy (B_d) *Kuiva latvusto* (B_d)			Difference ($B_w - B_d$) *Erotus* ($B_w - B_d$)		
Total rain in open, mm — *Sademäärä aukealla, mm*	5	10	15	5	10	15	5	10	15
Interception in birch stand, mm — . . . . . . *Latvuston pidättämä sademäärä, mm*	0.7	1.0	1.1	1.2	2.0	2.3	— 0.5	— 1.0	— 1.2
Run-off, mm — . . . . . . *Valuvesi, mm*	0.3	0.8	1.5	0.1	0.4	1.0	+ 0.2	+ 0.4	+ 0.5
Rain in birch stand, mm — *Sade koivikossa, mm*	4.0	8.2	12.4	3.7	7.6	11.7	+ 0.3	+ 0.6	+ 0.7
Total precipitation in birch stand, mm — *Kokonaissademäärä koivikossa, mm*	4.3	9.0	13.9	3.8	8.0	12.7	+ 0.5	+ 1.0	+ 1.2

really heavy rains and horizontal rains of long duration give a slight run-off (cf. e.g. Hoppe 1896, Stålfelt 1944).

The difference between the water remaining in the tree and the run-off in wet and dry stands is of special interest. The following figures give a clear idea of the volume of cuticular (or possibly stomatal, cf. Stålfelt 1944, s. 60—64) intake of water in the birch stand.

Fig. 59 and Table 51 show that the total amount of rain falling to the ground in the stand increases if the canopy is still wet after the previous shower, but the increase may be due to heavier run-off and decreased total retention (interception). The last line in the difference column (in Table 51) also shows the rainfall probably retented by cuticular or stomatal absorption. It is remarkable that the purely adhesively, i.e. superficially retained water in wet stands and the water probably absorbed after rainfalls in dry stands, seem to be of about the same order, at least judging by the values recorded in the table. The volume retained in defoliated birch

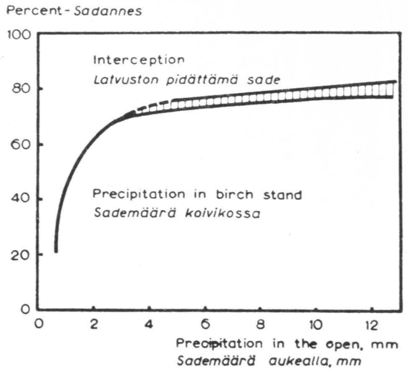


Fig. 60. Percentual distribution of precipitation in the dry birch stand (cf. Fig. 61).

Kuva 60. Sateen prosenttinen jakaantuminen kuivaan koivikkoon (vrt. kuva 61).

stands was not determined but was doubtless considerably smaller than in the stands in leaf (cf. e.g. Mitchell 1930).

Figs. 60, 61 and 62 give the percentual interception, run-off, and total precipitation in the stands. The total interception value is somewhat higher for the spruce than for the wet birch stand, which is quite natural since there was no run-off in the former.

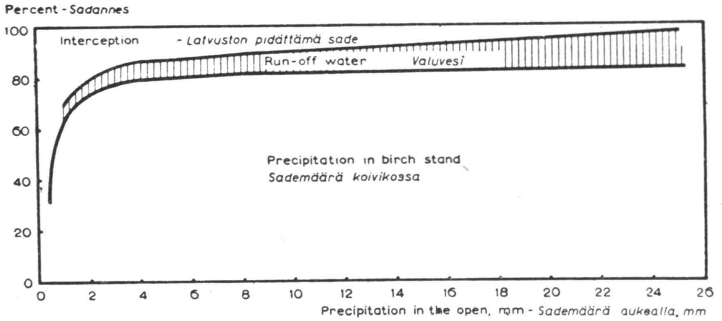


Fig. 61. Percentual distribution of precipitation in the wet birch stand.

Kuva 61. Sateen prosenttinen jakaantuminen märkään koivikkoon.

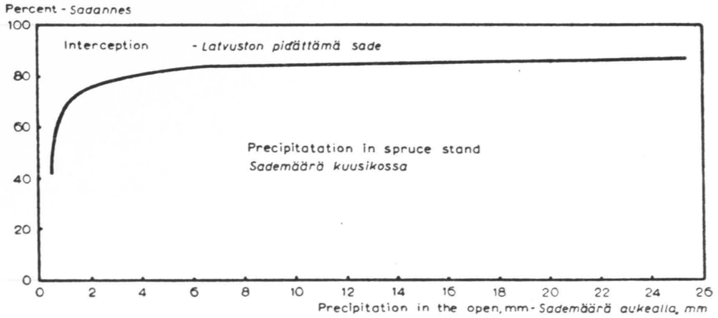


Fig. 62. Percentual distribution of precipitation in the spruce stand.

Kuva 62. Sateen prosenttinen jakaantuminen kuusikossa.

On the other hand, after fine, dry weather even larger amounts of rain were retained in the birch stand than in the spruce stand. The lower density of the latter, in the case examined, must be considered a factor decreasing retention. Also, the spruce stand holds more water after dry weather than after persisting rain; this is not an observation of recent date (cf. e.g. Hoppe 1896). That the interception curve for the spruce stand diverges somewhat from Hoppe's curve must be attributed to the fact that a stand with gaps is unable totally to absorb even drizzling rain. That the retention in the spruce stand studied by Lukkala (1946) was larger was probably due among other factors to its greater density. In principle the course of the curves agrees with that of Mitchell's (1930) curves. The interesting correlation between the rate and duration of rainfall on the one side, and interception on the other, will perhaps be treated in another paper. In the present study the question is of no importance. Besides, Nakayama & Tasaki (1949) and Linskens (1951) have discussed the problem.

After determination of total precipitation in the open the amount of rain in stands, run-off, and interception, it remains only to study the compilation of the various quantities (Table 52).

Table 52 reveals the significance of run-off and interception. Total interception in the birch stand during the two vegetation periods was somewhat less than in the sparser spruce stand where the retention capacity of the needle foliage seems to be slightly more effective, especially with regard to rain adhering to the trees. Of the monthly precipitation, that in September 1951 was of special interest. In spite of a low total precipitation rate, interception was considerable, particularly in the spruce stand. This was evidently because of the amount of horizontal rain in September.

By way of a final summary of the distribution of precipitation in the stands investigated in the summers of 1950 and 1951, the following may be pointed out:

In spite of the sparseness of the spruce stand, its interception exceeded

Table 52. Fractional distribution of rain on the sample plots at Siulionpalo in the summer of 1950 and 1951.

Taulukko 52. Sateen jakaantuminen eri fraktioihin Siulionpalon koivikossa ja kuusikossa kesällä 1950 ja 1951.

	Birch stand — *Koivikko*					Spruce stand *Kuusikko*	
Year and month *Vuosi ja kuukausi*	Precipitation in open, mm *Sademäärä aukealla, mm*	Rain in the stand, mm *Sade latvuston alla, mm*	Run-off along stems, mm *Valuvesi, mm*	Total precipitation, mm *Sade + valuvesi, mm*	Interception, mm *Latvuston pidättämä sade, mm*	Total precipitation, mm *Sade latvuston alla, mm*	Interception, mm *Latvuston pidättämä sade, mm*
1950							
June *Kesäkuu*	91.0	72.4	8.4	80.8	10.2	79.6	11.4
July *Heinäkuu*	50.7	38.6	3.5	42.1	8.6	39.0	11.7
August *Elokuu*	18.7	13.6	0.3	13.9	4.8	13.0	5.7
September *Syyskuu*	52.1	40.9	4.4	45.3	6.8	48.2	3.9
Total *Yhteensä*	212.5	165.5	16.6	182.1	30.4	179.8	32.7
Per cent *Sadannes*	100.0	77.9	7.8	85.7	14.3	84.6	15.4
1951							
June *Kesäkuu*	80.5	64.1	5.0	69.1	11.4	66.0	14.5
July *Heinäkuu*	175.7	138.5	18.0	156.5	19.2	147.7	28.0
August *Elokuu*	55.8	42.1	5.0	47.1	8.7	47.2	8.6
September *Syyskuu*	44.3	36.0	2.1	38.1	6.2	32.9	11.4
Total *Yhteensä*	356.3	280.7	30.1	310.8	45.5	293.8	62.5
Per cent *Sadannes*	100.0	78.8	8.4	87.2	12.8	82.5	17.5

the total amount retained by the birch stand and, in consequence, slightly smaller amounts of rain fell on the ground cover in the spruce stand. The difference was so small, however, that the water management cannot have been affected. The question of how precipitation which falls to the ground benefits the stands later in the season will be dealt with in connection with water management of the soil.

The density and species composition of the stand must be considered in applying the numerical precipitation data on the sample stands to the various succession stages of HMT spruce forests. It has been shown that dense birch growth predominates in the primary succession up to the age of about 130 years, after which the spruce gains definite dominance. Secondary stands are comparatively sparse up to the age of about 100 years, after which the canopy begins to close. From this it is highly probable that the amount of precipitation that falls to the soil surface in secondary stands exceeds that in primary stands at least up to 130 years in age. As primary stands in their later stages are markedly spruce-dominated and generally show a higher degree of crown closure than secondary stands, it may be assumed that the precipitation reaching soil surface persists at a higher level in the secondary succession.

Air humidity and conditions for transpiration

The previous chapter discussed the distribution of precipitation on the different sample plots of the ecological station. One thing that emerged was that the interception by spruce and birch stand varies considerably with the weather conditions and amount of precipitation. The type and duration of rain were not discussed as they proved to be of secondary importance for a preliminary comparison. Total interception throughout the vegetation period in the birch stand studied amounted to approx. 13 per cent and in the spruce stand to approx. 18 per cent of the total precipitation on open field (1951).

However, the water management of the stands involves considerably more numerous factors than the sum of the different precipitation fractions at soil surface level. The schedule of the distribution of precipitation in the stands worked out by Stålfelt (1944, p. 22) gives an instructive picture of the routes by which water circulation can occur. As this circulation is highly dependent on the capacity of air to absorb water molecules, the variation range of the relative humidity of air, vapour pressure deficit and evaporation from open water surfaces in the parallel stands involved would appear to form a profitable subject of study.

The air temperature and wind velocity, both of which are of decisive importance for the water absorption ability of air, have already been discussed in a previous chapter.

It may be expressly pointed out that this part of the investigation is more concerned with a comparison of the conditions for evapo-transpiration in the two parallel stands than with advancing opinions on the conditions for evaporation, the purely physical nature of which has been thoroughly described e.g. by Leighly (1937). He rejects vapour pressure deficit as a serviceable standard of the capacity of air to absorb water and introduces instead air turbulence, measured in terms of wind velocity, as the principal factor. In spite of this it can be assumed that vapour pressure deficit still plays a certain part in evapo-transpiration, and even in the purely physical process of evaporation. No evaporation is likely to occur in a closed system, for instance, however high the wind velocity, if the air passing over the evaporation surface is saturated and of the same temperature as the water surface. The difference in principle between transpiration and evaporation is still valid, in spite of Leighly's critical analysis of the climatic factors. The transpiration of living plants is not dependent solely on climatic conditions for the diffusion of water molecules through the laminar boundary layer into the turbulent air layers; the sufficiency of the water supply and, in addition, certain internal physiological phenomena also have their great significance (cf. e.g. Stålfelt 1928). As to climate, let it be remembered that »light increases transpiration more than evaporation, whereas wind increases evaporation more than it increases transpiration» (Daubenmire 1947). The connection between the rate of evaporation on the one hand and vapour pressure deficit and air temperature on the other is extremely conclusively illustrated e.g. by the experiments by Briggs & Schantz (1916).

In this connection it may be mentioned that air humidity in stands has long interested scientists. The observations by Homén (1897) were probably the earliest made in Finland. Related problems have been discussed e.g. by Hamberg (1876), Wallén (1917, 1932), and above all by Geiger in a long series of investigations. The studies by Paeschke (1937) and Burger (1951) are of a more recent date. In North America, in addition to the authors mentioned by Leighly (1937), e.g. Briggs & Schantz (1916), Sanderson (1950) and Thornthwaite & Mather (1951) have devoted a great deal of attention to evapo-transpiration. Evaporation studies have also been carried out by a large number of Finnish scientists, for instance Rossi (1933), Franssila (1936), A. Sirén (1936), Kaitera (1939) und Niinivaara (1953).

Because of the methods applied in the present study of the climate of the different stands, it seems suitable to start by plotting the diurnal variation in the relative air humidity (r), vapour pressure deficit (v) and evaporation (ev) during the observation days.

As it is impossible to publish the material of all the 9 (1950) plus 11 (1951) days in this brief report, only two observation days, fairly typical of the ecological periods they represent, will be studied in detail here. The combined (r), (v) and (ev) material is presented in Table 53 a, b and Figs. 63 and 65; the latter also have a curve of the ground cover evapo-transpiration.[1]

As regards the relative humidity of air (r) during the early summer day of June 21, 1951, the normal minimum is found immediately after noon and the normal maximum at soil surface during the early morning hours in both stands (cf. e.g. Homén 1897, Geiger 1927, 1950, Rossi 1933, Franssila 1936, Paeschke 1937, Burger 1951). Except at night, the air in the birch stand seems to be drier — relatively at least. A calculation of the absolute humidity (f) according to the formula $f = \frac{1.06\, e^*}{1 + \alpha t}$ (see e.g. Franssila 1949, p. 51) showed, however, that no significant difference existed between the stands; the lower relative humidity, therefore, is mainly due to the higher temperature of the birch stand. Perhaps the most striking feature is the dissimilarity of different levels above ground. In the spruce stand the maximum air humidity, practically without exception, is found down at soil surface throughout the 24-hour period (cf. Stocker 1923); in the birch stand the morning maximum close to soil surface shifts in the course of the day and evening to the crown canopy. A contributory reason naturally is the absorption of heat by the soil surface. Intense radiation of heat during the night hours raises the relative air humidity in the birch

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[1] Ground cover here refers to ground vegetation plus humus.

* e = vapour pressure
t = air temperature
α = coefficient of volume-expansion of gases (= 1/273)

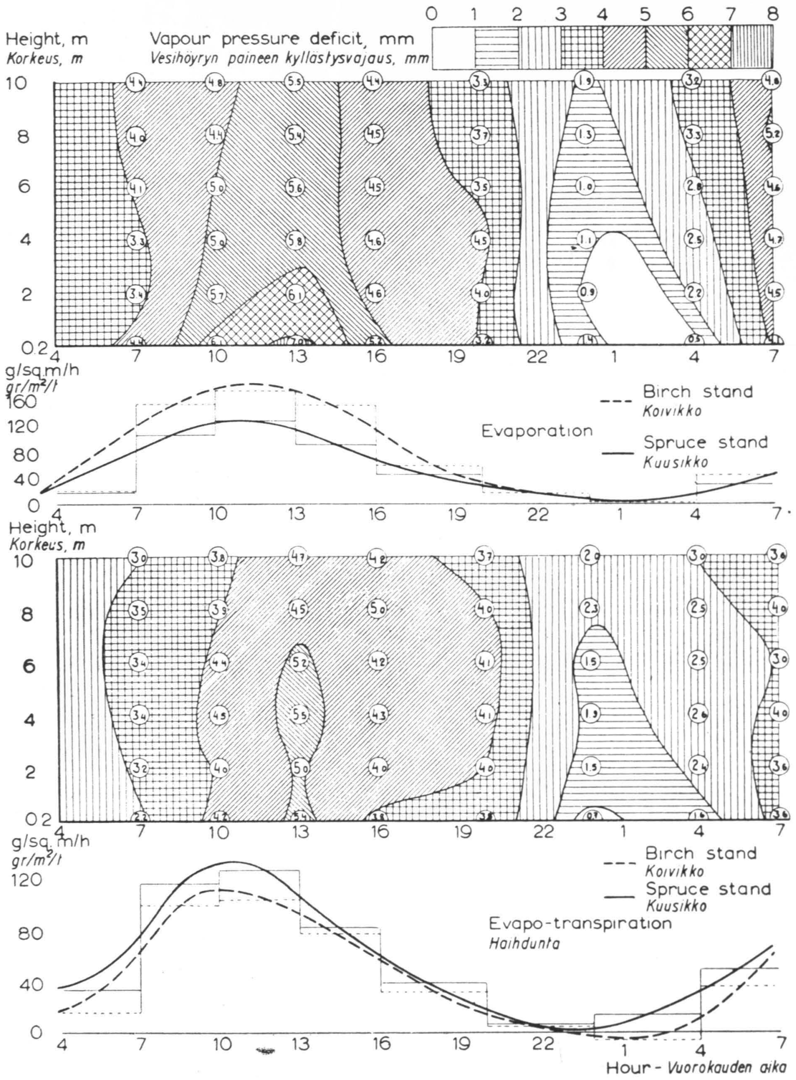

Fig. 63. Vertical distribution of vapour pressure deficit in the birch (upper part) and spruce (lower part) stand at Siulio. The curves refer to evaporation and evapo-transpiration. June 21, 1951.

Kuva 63. Ilman vesihöyryn paineen kyllästysvajauksen pystysuora jakaantuminen koivikossa (ylempi osa) ja kuusikossa (alempi osa). Käyrät osoittavat evaporation ja maapeitteen haihdunnan vuorokautista kulkua. Kesäkuun 21. 1951.

stand somewhat above that in the spruce stand; the maximum is reached at 04_{00} at soil surface and at midnight in the crown canopy.

If the relative air humidity alone governed transpiration, conditions on June 21, 1951, would justify the assumption that the air in the birch stand is capable during morning and day hours of absorbing somewhat more vapour than the air in the spruce stand, which again seems to be less saturated during the evening and night.

However, the relative air humidity (r) is not only a condition for evaporation and transpiration but also a consequential phenomenon of the total transpiration that actually occurs. A high (r) value, particularly in the evening, may also imply heavy transpiration in the few hours preceding the normal temperature drop towards night; high relative air humidity is known to restrict the further absorption of vapour at least in non-turbulent conditions. Unfortunately this vicious circle could not be broken even by introducing vapour pressure deficit (v) in microclimatology as a measure of the conditions for transpiration (see e.g. Livingston, 1917 according to Leighly, 1937). In one rare special case only is the transpiration directly proportionate to the vapour pressure deficit (Leighly, op.c. and Franssila 1949, p. 53). As a rule, however, there is a fairly reliable correlation between the two characteristics even though local conditions and other factors make it impossible to trace any regularity of indisputable diagnostic significance (cf. Briggs & Schantz 1916). In any case, vapour pressure deficit provides besides wind velocity and air temperature gradients a good picture of evapo-transpiration and transpiration conditions. That presumably both a prerequisite and a consequence are involved is another problem the detailed discussion of which must be postponed to a later specialized study.

Table 53 a and Fig. 63 show that the vapour pressure deficit in the birch stand reaches its maximum close to soil surface immediately after noon, at the same time as at the other levels too in the stand. During the day and evening up to midnight the vapour pressure deficit is greatest at soil surface. Not until the early hours of the morning, in the first place as a result of the almost horizontal insolation (sun was shining the whole night!), is there a radical shift up to the crown canopy. Simultaneously a pronounced minimum occurs close to soil surface where an insignificant deficit of $0._5$ mm indicates a very high relative humidity. This humidity arises primarily from the low temperature following the thermal radiation that occurs before midnight. Dew was also formed locally on the soil surface in the birch stand. The dew formation is also indicated by

Table 53 a. Vapour pressure deficit, relative air humidity and wind velocity in the spruce stand (A) and the birch stand (B) on June 21, 1951.

Taulukko 53 a. Ilman vesihöyryn paineen kyllästysvajaus, suhteellinen kosteus ja tuulen nopeus kuusikossa (A) ja koivikossa (B) kesäkuun 21. päivänä 1951.

Level above ground, m *Mittaus-korkeus, m*	Date, hour and place of recordings — *Päivämäärä, tunti ja mittauspaikka* June 21, 1951 — *Kesäkuun 21. 1951*															
	07 00		10 00		13 00		16 00		20 00		24 00		4 00		07 00	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
	Vapour pressure deficit (v), mm — *Vesihöyryn kyllästysvajaus (v), mm*															
10.0	3.0	4.4	3.8	4.8	4.5	5.5	4.2	4.4	3.7	3.3	2.0	1.9	3.0	3.2	3.0	4.8
8.0	3.5	4.0	3.9	4.4	4.5	5.4	5.0	4.5	4.0	3.7	2.3	1.3	2.5	3.3	4.0	5.2
6.0	3.4	4.1	4.4	5.0	5.2	5.6	4.2	4.5	4.1	3.5	1.5	1.0	2.5	2.8	3.0	4.6
4.0	3.4	3.3	4.5	5.0	5.5	5.8	4.3	4.6	4.1	4.5	1.9	1.1	2.6	2.5	4.0	4.7
2.0	3.2	3.4	4.0	5.7	5.0	6.1	4.0	4.6	4.0	4.0	1.5	0.9	2.4	2.2	3.6	4.5
0.2	2.2	4.4	4.2	6.7	5.4	7.0	3.8	5.2	3.8	3.9	0.7	1.4	1.6	0.5	3.6	4.1
	Relative air humidity (r), per cent — *Ilman suhteellinen kosteus (r), %*															
10.0	60	48	52	48	46	46	49	51	51	57	65	86	62	58	51	45
6.0	56	53	52	46	45	47	47	50	50	56	65	84	66	62	50	47
2.0	58	50	54	42	47	38	51	48	51	51	74	82	66	69	55	49
2.0[1]	56	50	47	43	42	38	47	45	51	50	79	82	71	70	50	48
0.2	61	50	53	42	47	37	55	51	53	56	84	81	75	92	59	53
	Wind velocity, m/min — *Tuulen nopeus, m/min*															
10.0	37	37	61	59	22	58	71	71	62	49	0	0	0	24	2	3
2.0	4	24	14	20	8	10	22	4	4	4	0	0	0	0	0	0
	Difference of vapour pressure deficit, mm — *Vesihöyryn kyllästysvajauksen erotus, mm*															
$v_{0.2}-v_{2.0}$	−1.0	+1.0	+0.2	+1.0	+0.4	+0.9	−0.2	+0.6	−0.2	−0.1	−0.8	+0.5	−0.8	−1.7	±0.0	−0.4
$v_{0.2}-v_{10.0}$	−0.8	±0.0	+0.4	+1.9	+0.9	+1.5	−0.4	+0.8	+0.1	+0.6	−1.3	−0.5	−1.4	−2.7	+0.6	−0.7

the vapour pressure curve at 24 00 (cf. Fig. 64). The differences of vapour pressure deficit at different levels above ground are markedly higher in the birch stand than in the adjacent spruce stand.

The spruce stand differs in many respects from the birch stand. Attention is first aroused by the smaller variation in the vapour pressure deficit

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[1] Refers to the hygrograph — *Hygrografin mukaan.*

Table 53 b. Vapour pressure deficit, relative air humidity and wind velocity in the spruce stand (A) and birch stand (B) on July 26, 1951.

Taulukko 53 b. Ilman vesihöyryn paineen kyllästysvajaus, suhteellinen kosteus ja tuulen nopeus kuusikossa (A) ja koivikossa (B) heinäkuun 26. päivänä 1951.

Level above ground, m *Mittaus-korkeus m*	Date, hour and place of recordings — *Päivämäärä, tunti ja mittauspaikka* July 26, 1951, — *Heinäkuun 26. 1951*															
	07 00		10 00		13 00		16 00		20 00		24 00		4 00		07 00	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
	Vapour pressure deficit (v), mm — *Vesihöyryn kyllästysvajaus (v), mm*															
10.0	6.6	4.8	9.2	7.7	11.2	10.5	11.1	14.6	9.4	5.1	2.5	2.0	3.7	1.4	8.6	6.0
8.0	6.4	4.5	10.1	8.4	11.8	9.8	11.4	11.2	8.8	4.3	2.2	2.0	3.3	1.0	8.7	5.8
6.0	6.4	3.7	9.4	8.0	10.3	9.6	11.4	11.2	8.7	3.8	2.1	2.0	3.1	0.7	7.7	4.3
4.0	6.3	3.7	10.1	9.6	10.1	9.2	11.9	10.7	8.3	3.9	1.8	1.7	3.2	1.0	7.5	3.8
2.0	6.0	4.9	8.8	9.3	10.3	9.8	10.3	11.3	7.4	3.4	2.0	1.4	1.9	1.2	6.8	3.8
0.2	4.9	4.0	9.3	7.5	10.1	9.4	10.0	13.2	4.3	3.8	2.3	1.6	1.1	1.1	6.4	3.0
	Relative air humidity (r), per cent — *Ilman suhteellinen kosteus (r), %*															
10.0	53	67	48	56	34	47	34	40	35	63	74	80	65	81	47	61
6.0	53	72	43	57	38	51	34	49	41	71	78	80	69	90	46	69
2.0	51	63	39	54	36	51	37	45	51	73	81	85	78	88	46	71
0.2	62	70	47	63	40	51	41	36	65	71	72	85	87	88	54	76
	Wind velocity, m/min — *Tuulen nopeus, m/min*															
10.0	17	22	69	24	13	20	18	0	22	19	74	11	0	3	61	42
2.0	0	0	30	2	7	4	0	3	0	0	2	0	0	0	6	0
	Difference of vapour pressure deficit, mm — *Vesihöyryn kyllästysvajauksen erotus, mm*															
$v_{0.2}-v_{2.0}$	−1.1	−0.9	+0.5	−1.8	−0.2	−0.4	−0.3	+1.9	−2.9	+0.4	+0.2	+0.2	−0.8	−0.1	−0.4	−0.8
$v_{0.2}-v_{10.0}$	−1.7	−0.8	+0.1	−0.2	−1.1	−1.1	−1.1	−1.4	−5.1	−1.3	−0.2	−0.4	−2.6	−0.3	−2.2	−3.0

amplitudes. As in the birch stand the maximum is reached at noon; but it is of shorter duration, especially close to soil surface. The amount of heat stored by spruce crowns (cf. Fig. 53, p. 194), however, seems to maintain the vapour pressure deficit during the evening and night at somewhat higher values than at the corresponding levels in the birch stand. Only at midnight is a minimum of short duration, of the same nature as at a somewhat later hour in the birch stand, observed close to soil surface.

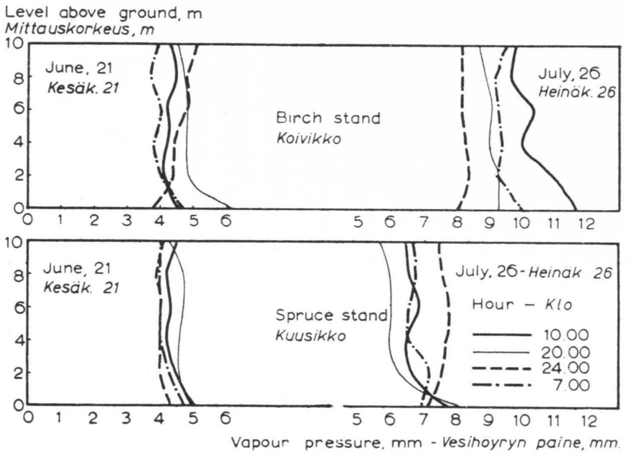

Fig. 64. Vertical distribution of the vapour pressure at different hours in the parallel stands during two typical days in the summer of 1951.

Kuva 64. Ilman vesihöyryn paineen pystysuora jakaantuminen rinnakkaismetsiköissä eri aikoina kahtena edustavana vuorokautena kesällä 1951.

The vertical distribution of the vapour pressure, however, indicates, no dew condensation at all.

This picture of the relative air humidity and vapour pressure deficit in itself indicates that during the major part of the 24-hour period conditions are obviously more favourable for evaporation and transpiration in the birch stand than in the spruce stand on the early summer day in question. Unmistakable proof of this is provided by the evaporation curves for the stands (cf. Fig. 63). The early morning hours of dew formation in the birch stand excepted, evaporation from open water surface is greater in this stand throughout the 24-hour period.

In spite of these excellent conditions for transpiration compared with the spruce stand, the evapo-transpiration from the ground cover was actually somewhat smaller in the birch stand (cf. the lower curves). Consequently, the amount of total transpiration is dependent also on factors other than the purely climatic. Among the important factors may be mentioned the water content of the substratum, its water and heat capacity, and the true transpiration surface (cf. e.g. Leighly 1937, Stålfelt 1944, Sanderson 1950, Thornthwaite & Mather 1951). The relevant problems will be discussed in detail in a later context; however, it may be pointed out that ground vegetation is probably the main reason for this dissimilarity. The mosses in the spruce stand apparently constitute larger surfaces which give up the water more readily than the sparse grasses and herbs in the birch stand. After rain the loss of water by evapo-transpiration from a *Pleurozium-Schreberi* cover is anyhow rather heavy during the first days (cf. Mägdefrau & Wutz 1951).

The second observation day (the late summer day of July 26, 1951, Fig. 65) selected for close study discloses a very different pattern from the early summer day. The birch stand, apart from a higher relative humidity and higher vapour pressure (see Fig. 64) almost throughout — particularly under the crown canopy — also shows lower vapour pressure deficit values than the spruce stand. However, there is an important exception in the afternoon: two maxima for this deficit are found in the birch stand, one at the heavily heated soil surface and the other up in the crown canopy. In both cases the vapour pressure deficit of the birch stand exceeds that at the corresponding level in the spruce stand. The difference in evaporation is also fairly great just at this date between 13_{00} and 20_{00}. The diurnal average of the vapour pressure deficit, however, is much higher in the spruce stand than in the birch stand. Irrespective of this, the diurnal evaporation is definitely lower than in the birch stand. Furthermore, the evaporation quantity was less on July 26 than on June 21 although the air temperature and vapour pressure deficit were higher on the latter date. In spite of similar wind conditions, the average air exchange coefficient of the two days were respectively 0.50 and 0.56 g/cm/sec, and this accounts to some degree for the difference in evaporation. The difference in evaporation between the stands, in addition, is less than during the early summer day. From the conditions on June 21 it could be assumed that evapo-transpiration from the ground cover in the birch stand in particular would decrease during the late summer day. This in fact was the case, but on July 26 evapo-transpiration from the ground cover was of the same order in both stands; it follows that the reduction was greatest in the spruce stand!

In spite of the fact that evaporation, the relative air humidity and vapour pressure deficit, in the light of the somewhat contradictory examples given above, cannot be considered unequivocal criteria of the conditions for transpiration, they do have a certain diagnostic importance.

The most striking feature is the similarity between evaporation (ev) on the one side and the vapour pressure deficit (v) and relative air humid-

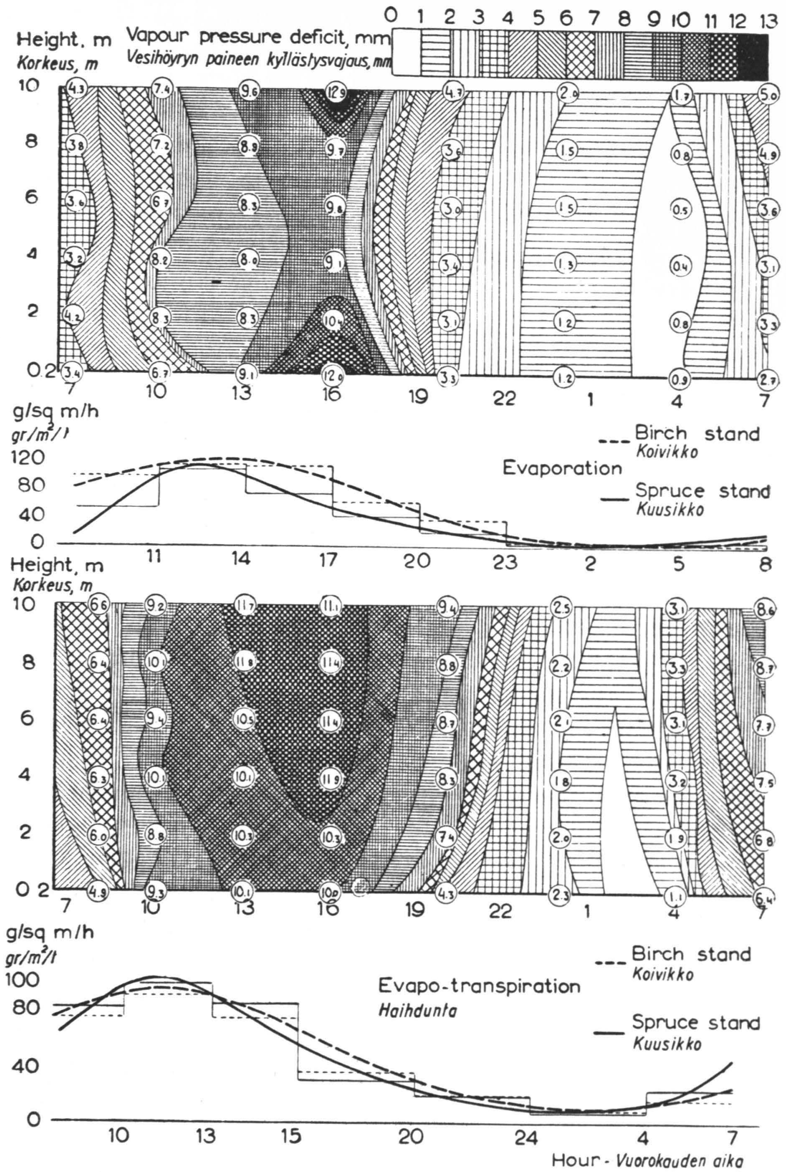

Fig. 65. Vertical distribution of vapour pressure deficit in the birch (upper part) and spruce (lower part) stand at Siulio. The curves refer to evaporation and evapo-transpiration. July 26, 1951.

Kuva 65. Ilman vesihöyryn paineen kyllästysvajauksen pystysuora jakaantuminen koivikossa (ylempi osa) ja kuusikossa (alempi osa). Käyrät osoittavat evaporation ja maapeitteen haihdunnan vuorokautista kulkua. Heinäkuun 26. 1951.

ity (r) on the other. Where the value of (r) is high (v) assumes a low value and (ev) too remains low. The conditions for evapo-transpiration are apparently optimal during the hottest hours of the day and minimal in the early hours of the morning when condensation even occurs. The dissimilarity between spruce and birch stand in evaporation is striking. Bearing in mind that the wind had in this case somewhat freer play (see p. 198) in the sparser spruce stand, the greater evaporation in the birch stand must evidently be attributed in the main to the more favourable temperature conditions and the high air exchange coefficient. Another, not unimportant, consideration is the different light conditions. The dense spruce crowns shade effectively both the soil surface and the evaporation vessels during some hours of the day at least, while the mobile leaf canopy of the birch stand results in more uniform insolation (cf. Saharov 1949). The remaining 18 observation days disclosed similar patterns of conditions for evapo-transpiration during the hottest hours of the day.

Summarizing the diurnal observations on the vapour pressure deficit, relative air humidity and evaporation, it may be said that the conditions for evapo-transpiration seem better in the birch than in the spruce stand at least in day-time. This applies especially to the early summer.

In order to find out the extent to which the evapo-transpiration conditions varied in the different stands during the various ecological periods of the 1951 vegetation period the author has compiled data on the relative air humidity (r), vapour pressure (e) and vapour pressure deficit (v) in the form of Tables 54 and 55.

Table 54. Relative air humidity in the parallel stands during the various ecological periods on the basis of hygrograph readings, summer 1951.

Taulukko 54. Rinnakkaisnäytealojen ilman suhteellinen kosteus eri ekologisina kausina hygrografilla määritettynä kesällä 1951.

Ecological period *Ekologinen kausi*	Birch stand — *Koivikko*			Spruce stand — *Kuusikko*			Difference — *Erotus*		
	Day *Päivä* a	Night *Yö* b	Diurn. *Vrk.* c	Day *Päivä* d	Night *Yö* e	Diurn. *Vrk.* f	Day *Päivä* a-d	Night *Yö* b-e	Diurn. *Vrk.* c-f
	Relative air humidity (r), per cent — *Ilman suhteellinen kosteus (r), %*								
4. 6—22.6	47.80	70.60	59.20	50.20	70.80	60.50	—2.40	—0.20	—1.30
23. 6—23.7	71.28	88.90	80.09	70.95	88.31	79.63	+0.33	+0.59	+0.46
24. 7—10.8	61.56	88.06	74.81	62.78	87.56	75.17	—1.22	+0.50	—0.36
11. 8— 5.9	81.54	97.04	89.29	80.92	96.88	88.90	+0.62	+0.16	+0.39
6. 9—23.9	81.94	98.33	90.14	83.22	98.50	90.86	—1.28	—0.17	—0.72

Table 55. Vapour pressure and vapour pressure deficit at noon in the parallel stands at Siulionpalo, 1951.

Taulukko 55. Rinnakkaisnäytealojen ilman vesihöyryn paine ja sen kyllästysvajaus keskipäivän aikaan Siulionpalossa v. 1951.

Level above ground, m *Mittaus-korkeus, m*	Ecological period — *Ekologinen kausi* 4.6—7.6		8.6—22.6		23.6—23.7		24.7—10.8		11.8—5.9		6.9—23.9	
	Vapour pressure (e) and vapour pressure deficit (v), mm *Vesihöyryn paine (e) ja vesihöyryn paineen kyllästysvajaus (v), mm*											
	e	v	e	v	e	v	e	v	e	v	e	v
	Spruce stand (A) — *Kuusikko (A)*											
0.2	5.25	2.63	5.84	4.43	8.19	3.67	9.46	6.85	10.60	3.74	6.38	1.74
2.0	4.80	3.40	5.56	4.54	7.72	3.86	9.04	7.24	10.25	4.35	6.33	2.08
10.0	·	·	5.22	4.67	7.19	4.30	8.81	7.84	9.71	4.60	5.86	2.54
	Birch stand (B) — *Koivikko (B)*											
0.2	4.95	3.00	5.07	5.94	8.14	3.35	10.81	5.70	11.36	3.12	6.71	1.42
2.0	4.60	3.75	4.82	5.96	7.78	4.00	10.30	6.06	11.05	3.95	7.09	1.67
10.0	·	·	5.14	5.18	7.71	3.71	10.18	6.77	10.95	4.05	6.86	2.03
	Difference ($v_A - v_B$) — *Erotus* ($\nu_A - \nu_B$)											
0.2		−0.37		−1.51		+0.32		+1.15		+0.62		+0.32
2.0		−0.35		−1.42		−0.14		+1.18		+0.40		+0.41
10.0		·		−0.51		+0.59		+1.07		+0.55		+0.51
	Open area (C) — *Aukea ala (C)*											
0.2		3.67		4.97		4.00		8.15		4.95		2.39
2.0		3.90		4.85		4.21		8.06		4.64		2.31

As a rule the relative air humidity (Table 54) in the warm or sunny ecological periods was greater in the spruce stand between morning and evening; the birch stand usually had more humid air during the night. In the early weeks after the melting of snow (r) was even a great deal lower in the birch stand, primarily due to the cooler temperature of the soil surface and air of the spruce stand and to the thaw in process. Later, the difference narrowed to some extent. Broadly speaking, the maximum relative air humidity values were reached in prolonged rainy periods and can probably be considered as unusually high on the average (cf. Burger 1951). There was often dew formation on humid and cold nights.

With the exception of the period immediately before Midsummer, it can probably be assumed from the slight difference between the relative air humidity at 2.0 m above ground level in the spruce and birch stands that no major dissimilarity in the conditions for transpiration was present. Yet the vapour pressure deficit values for the whole vegetation period indicate a fairly pronounced difference (cf. Table 55).

Table 55 gives general information on the variation in vapour pressure (e) and in the vapour pressure deficit (v) in the two stands in the summer of 1951. In the early summer the conditions for transpiration at noon seem particularly favourable in the birch stand. A contributory factor is that the vapour pressure deficit (v) is greatest down at soil surface where the air really absorbs water. The high vapour pressure just above the crown canopy of the birch stand (10.0 m) can probably be ascribed to crown transpiration. In the spruce stand the case is opposite. The deficit at soil surface is not only lower than in the birch stand, it is also lower than at 2.0 and 10.0 metres. Presumably a consequential phenomenon of the strong evapo-transpiration process is involved here, but in addition the values suggest simultaneous good air exchange within the stand and consequently also relatively good conditions for evapo-transpiration.

The birch stand is in full leaf at Midsummer, and in this the picture is changed to some extent. The spruce stand continues to show a smaller deficit down at soil surface than up in the crown layer but the values of this deficit are higher at all levels than in the birch stand. As evapo-transpiration from the soil surface is smaller in reality in the birch stand during high summer the low vapour pressure deficit mentioned above might well be explained as a result of the barrier to air exchange suddenly appearing when the birches are in full foliage (cf. also wind conditions, pp. 198—199).

That the vapour pressure deficit is greater at noon on the open areas is explicable in the first place from the higher temperature values in the lowest air layers.

Knowing that the above dissimilarity in the vapour pressure deficit during the hours of the day is most important for transpiration, it seems surprising at first that the evaporation was greater all the time in the birch stand. Admittedly the number of evaporimeters was small and they were not located to provide reliable mean values, but even taking into account the proportion of shaded and exposed surfaces in the two stands

Table 56. Evaporation in the different sample plots at Siulionpalo, summer 1951.

Taulukko 56. Evaporatio eli haihdunta vapaasta veden pinnasta Siulionpalon eri näytealoilla kesällä 1951.

Sample plot *Näyteala*	Location *Paikka*	Ecological periods — *Ekologiset kaudet*				
		8—22.6	23.6—23.7	24.7—10.8	11.8—5.9	6.9—21.9
		Average diurnal weight loss by evaporation g/sq.m/24 hours — *Vuorokauden keskimääräinen evaporatio, g/m²/vrk*				
Birch stand (B) *Koivikko (B)*	Gap — *Aukko*	1696	924	1160	436	208
	Shady group — *Varjoisa ryhmä*	1308	428	676	284	136
Spruce stand (A) *Kuusikko (A)*	Gap — *Aukko*	1308	776	1008	364	188
	Shady group — *Varjoisa ryhmä*	544	248	404	156	52
Open area (C) *Aukea ala (C)*	In open *Aukealla*	2784	2228	3344	1456	864
» » (D)	»	2484	2120	2880	1160	516

evaporation throughout the vegetation period in the birch stand exceeds that in the spruce stand by some 15 per cent (Table 56).

The difference between the evaporimeters was smallest in the gaps. Late leafing and early defoliation affected evaporation in shaded places in favour of the birch stand. During the long, light early summer days evaporation, incidentally, reached a maximum although the vapour pressure deficit was rather low. A detailed study revealed, in addition, that evaporation from free water surfaces was considerably greater in the birch stand in all weather conditions of the period. The abundant rainfall during June 23 — July 23 also left definite traces on the evaporation records: in both stands there was a heavy drop. During the latter part of high summer (July 24 — Aug. 10) it was expected that high temperatures and low precipitation would result in maximum evaporation in the stands. The maximum was reached on open areas C and D, but inside the stands the case was different. The rise in day temperature, long delayed and modified by the shade of the stands, was of insufficient duration (the insolation hours grew fewer and fewer) to increase evaporation to the early summer levels. Otherwise the differences in evaporation between the stand and the open surfaces were highly dependent on the weather in general and, broadly speaking, much greater than those found to obtain by Burger (1951) in Brandiswald (Switzerland).

That the evaporation inside the two stands is to some extent correlated with the vapour pressure deficit of the air of the stands is obvious. It may be that the wind velocity measured with more sensitive instruments than anemometers would have given a physically more correct correlation, as proposed by Leighly (1937). However, as the question is of a peripheral nature it will not be taken up for closer discussion in this connection. Geiger (1950) has discussed details associated with this problem and provides liberal references to the literature.

Parenthetically, it is interesting in this connection to note that the openings C and D provided somewhat different conditions for evaporation. Area C burned after Midsummer, surrounded by high, dark spruce forest, evidently due to a higher soil surface temperature, showed a better air exchange than area D in the midst of low birch forest, although the wind had freer play in the latter. It is also possible that the evaporation vessel on open area C was affected by the dark colour of the ground cover.

Summarizing the above facts on the vapour pressure deficit as a condition of evapo-transpiration, it may be said that conditions decisively more favourable for evapo-transpiration from the ground cover prevailed during the early summer in the birch stand than in the spruce stand. Once the foliage of the birch stand grew the difference was to some extent levelled out and even began to show in favour of the spruce stand. However, if evaporation is made the basis for assessing these conditions for evapo-transpiration, the birch stand can be considered to provide better prerequisites even throughout the whole growing season. The levelling out towards autumn can be considered of secondary importance.

* * *

The special study of humidity variation in the air of the stands and of the general conditions for evapo-transpiration has provided the answer to some minor questions. But, seen as a whole, the special study is of course incomplete. Under other macro-climatic conditions the results obtained would probably have assumed a very different character. The only conclusive fact from all points of view is that the birch stand shows decisively better conditions for transpiration in the early summer until the time of full foliage. In these circumstances it is of course risky to apply the results to the different successions. The first result of such an application would be an indication that conditions for evapo-transpiration are comparatively favourable in the birch-dominated stages of the succession in primary stands.