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Deciduous woodland at Andersby, Eastern Sweden. Above-ground tree and shrub production

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Doctoral dissertation to be publicly discussed at the Institute of Ecological Botany, Uppsala University, on April 28, 1975, at 10 a.m. for the Degree of Doctor of Philosophy (according to Royal proclamation No. 327, 1969).

Abstract Primary production was studied in the tree and shrub layers of a heterogeneous deciduous woodland, including a *Quercus-Betula-Corylus* wood, *Betula*-wooded pastureland and a mixed woodland of *Tilia, Acer, Populus, Sorbus* and the above-mentioned species. The investigation area has long been used by man, but now less intensively. Production in three sampling areas was measured as the mean of five years' increment, the mean of three years' leaf fall and the mean of two years' fall of other litter. The sampling areas differed in tree-layer structure and density, also being in different successional stages. The representativeness of the sampling areas was checked by means of transect studies of the litter fall and of the tree structure in the whole investigation area.

Increment in branches was greater than in stems. Low precipitation during the growth period affected the increment. The growth in leaf area and in shoot length started at different times during May and June and in most species ceased during June. The greater part of the increase in diameter occurred during June and July. Much more leaf litter fell in tree groupings than in glades. The leaf fall, which in the densest parts amounted to 2.2 ton/ha, constituted, in the sampling areas, only between 40 and 70% of the total litter fall. The production of flowers and fruits varied between the individual years and formed a quantitatively important part of the litter fall, contributing greatly to nutrient cycling. Differences between soil profiles in different parts were recorded.

The sum of above-ground increment and litter fall of all kinds for the tree and shrub layers amounted to 3.4, 6.6 and 6.5 ton/ha in the three sampling areas.

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Contents

Preface

This study is part of an investigation in a deciduous woodland, with a complicated and unstable vegetation pattern and varying soil material. The intention of the investigation was to throw light upon dynamic aspects of production in a changing environment.

The investigation area, Andersby ängsbackar, has long been used by man. Most of the area is now in different successional stages between open meadow and closed forest, but some parts, remnants of haymaking, are still open. Other parts are overgrown since they were abandoned early this century. Parts of the area are still grazed. Before the investigation started, the southernmost parts were thinned. In these parts and also elsewhere in Andersby ängsbackar, a strong regeneration of aspen suckers occurs.

Andersby ängsbackar was, for these reasons, considered a suitable area for the accomplishment of the above-mentioned intention, which, however, has not so far been completely fulfilled.

The team of investigators included zoologists and botanists. One project was aimed at analyzing the flora and vegetation, at clarifying the background to their present state, and at shedding light on the effects of different steps in nature conservation and management (B.M.P. Larsson 1971a, p. 26). In the present project, which is part of the Swedish contribution to the International Biological Programme, primary and secondary production have been studied. The more specific aims of the zoological group, which dealt with secondary production, were to study the energy flow through populations of energetically important leaf-eating insects and soil animals.

The botanists measured annual production and the annual growth rythm. Hans Persson investigated field-layer and below-ground production, and the present author studied the annual cycle and sum of increment in the tree and shrub layers, and the litter fall. A less extensive part of the investigation was concerned with abiotic measurements (temperature and soil chemistry). Most temperature and other measurements, are, however, not given in this paper. Primary production was measured, in the main, in three sampling areas with different tree structure and tree density and comparisons are made between these areas.

The investigation commenced in 1968 and was carried out under the auspices of the Department of Ecological Botany at the University of Uppsala. The head of the department, Hugo Sjörs, initiated the investigation and I should wish to express my gratitude for his guidance and advice, his critical scrutiny of the manuscript and suggesting of many improvements and corrections. I am also greatly indebted to all my colleagues—Bengt M.P. Larsson, Hans Persson, Wolfgang Brunner and other botanists and to the members of the zoological team—for their cooperation, many discussions and kind permission to entrust as yet unpublished material to my disposal. Tord Ingmar and Mats Wærn have devoted considerable time to read specific sections of the manuscript. Einar Hansson, Österbybruk, and Ivar Nordlander, Andersby, have provided me with valuable information on former conditions at Andersby. Anna Bromberg, Carin Hulth, Regina Iwanicka, Villy Jungskär and Eva Swanstein worked carefully and patiently with the chemical analyses, the sorting of litter, the measurement of annual rings and other production measurements. Märta Ekdahl typed numerous drafts and re-drafts, the final manuscript and all the tables. Kerstin Johansson and Agneta Nordgren drew the majority of the figures. Folke Hellström developed and copied the photographs. Henry Letocha, B.A., translated and effectively made the MS more comprehensible. My hearty appreciation is also extended to editors Gunnel Sjörs and Erik Skye for advice and aid during the final stages of publication.

To all the above, and all other friends and colleagues both within and without the Department who have given me their support my warmest gratitude for their diligence and helpfulness.

I am most thankful to my wife, Brita, for all the understanding, patience and help she has afforded me during the course of the investigations.

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Uppsala March 1975
Håkan Hytteborn
Dept. of Ecological Botany, Univ. of Uppsala, Sweden

The study area

Location and size

Andersby ängsbackar are located in the province of Uppland, at a latitude of N 60°09′ and a longitude of E 17°49′. From the phytogeographic point of view, the area lies within the boreo-nemoral zone (Sjörs 1963) or the hemi-boreal zone (Ahti et al. 1968). One of the characteristic feature of this zone is that, within a landscape with dominant coniferous forests, there are more or less frequent stands of broad-leaved trees which have a southerly distribution. They grow mainly on land favoured by local climatic or edaphic conditions. The study area lies not far from the northern boundary for the boreo-nemoral zone, which is usually given as the northern limit for *Quercus robur* (Sjörs op.cit.). This limit runs approximately 70-80 km WNW of Andersby ängsbackar (at a latitude roughly 40 km to the north). The coast of the Gulf of Bothnia lies 35 km to the NE. Andersby ängsbackar lie adjacent to Lake Dannemora which is traversed by the small Vattholma River. The upper catchment of this river within the parishes of Dannemora and Film is characterized by an abundance of forests and groves composed of the above-mentioned southerly broad-leaved trees. In an area only 20-30 m higher and located about 1 km east of Lake Dannemora, these broad-leaved species are uncommon. Deciduous, "nemoral" (warmth-demanding), forest vegetation is, on the whole, limited in northern Uppland to land adjacent to lake systems and water courses (cf. Almqvist 1929).

The broad-leaved forest land situated in Andersby ängsbackar is, according to Göran Hansson and Tord Ingmar (1962), "probably the most extensive forest and wooded pasture area dominated by broad-leaved, deciduous trees in the whole of northern Uppland". Only 0.8 ha are dominated by *Picea abies* and 5.9 ha by *Betulae.*

The total area of the study area (see Fig. 1) is approximately 70 ha, of which roughly 8.5 ha are accounted for by arable land and 10 ha by treeless pastureland, moist meadowland and abandoned arable land. The remainder, approximately 50 ha, with which the present study is concerned, is made up of forest land or sparsely wooded land and glades.

Topography and substrate

The study area lies between 25 and 35 m above sea level and was completely submerged during the early and mid-postglacial period. To the west, the area skirts Lake Dannemora, along which runs an esker. East of the esker, the larger part of the area is composed of a mosaic-like pattern comprising till-covered hillocks and sedimented depressions. The difference in height between the eminences and depressions is rarely more than a few metres. The prime constituent of the till is sand (Höjer in Larsson, B.M.P., in preparation) but boulders are abundant on the hillocks. The sediment layer in the depressions is shallow, at the most a couple of metres deep, and consists, for the most part, of calcareous glacial clay, on top of which lie about 5 cm of down-washed material, containing stones and gravel. Above this material but beneath the humus is to be found a 5 cm thick layer of unstratified clay; it is, however difficult to ascertain whether this clay is postglacial sediment or glacial clay which has been translocated.

Gillberg (1967, 1968) has made a study of the distribution of limestone gravel (2-0.6 cm) and the calcium content in the coarse sand (0.2-0.02 cm) and in the fine material (<0.02 cm) in the till in the province of Uppland. The till samples were taken at a depth of approximately 5 dm. The limestone and greater quantities of calcium in general, originate from the Cambrian-Silurian area located north of Uppland on the bottom of the Gulf of Gävle. The Andersby area is located outside the distribution zone of limestone gravel (Gillberg 1967, Fig. 9).

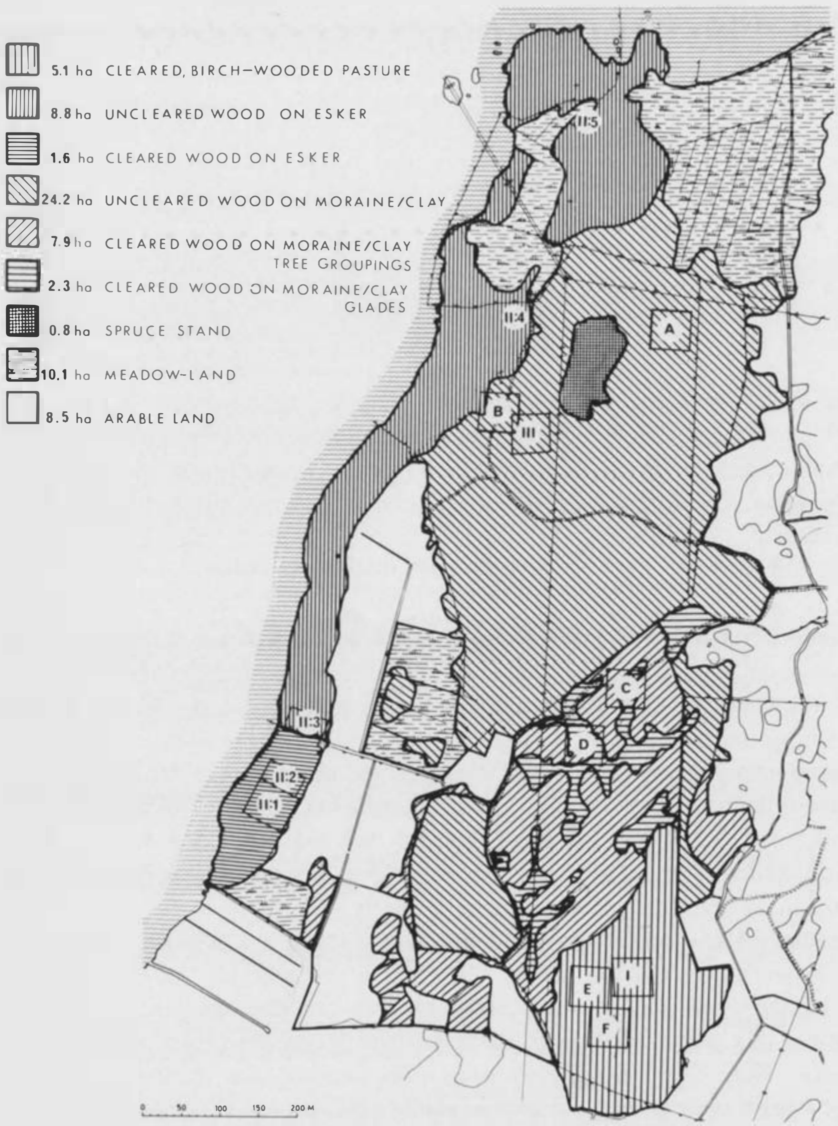


Fig. 1. Map of the study area, Andersby ängsbackar. Sampling areas I, II:1–5 and III were used for botanical sampling and sampling areas A-F for zoological sampling. To the west, the area borders Lake Dannemora.

Nevertheless, the coarse sand and fine material display raised contents of calcium. According to Gillberg, Andersby ängsbackar lie in an area where the amount of calcium in the fine material is of the order of approximately 1.6-1.9% (1967, Fig. 10) and in sand, approximately 1.2-1.5% (1968, Fig. 9).

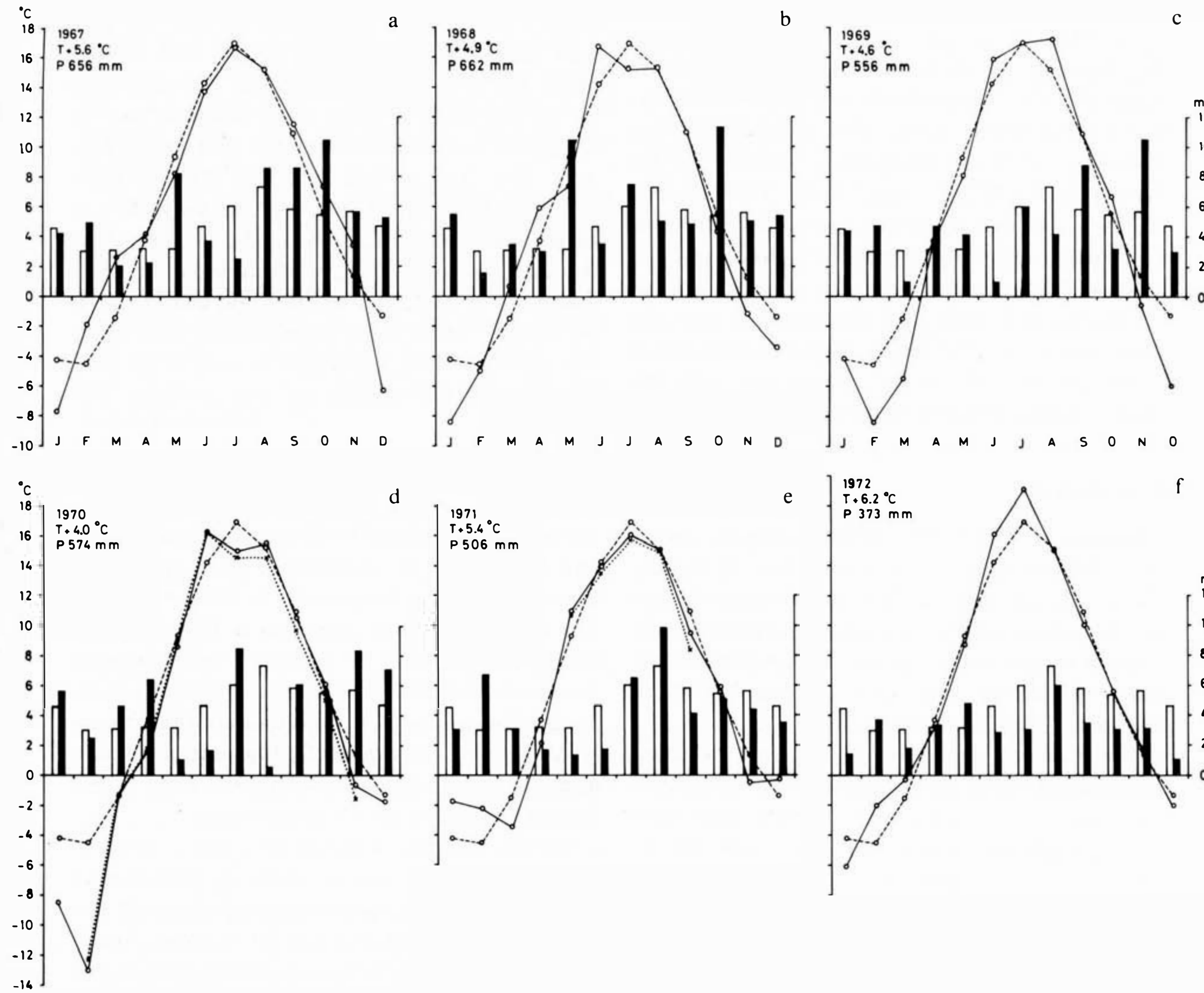
Certain sections have a surface layer which is composed of organic soil types. The most low-lying parts (generally not yet wooded to any greater extent) are covered by lake sediments exposed after the lowering of Lake Dannemora. For further information concerning the area's topography and Quarternary Geology, reference can be made to Larsson, B.M.P. (1971a and in preparation).

The soil conditions (see the chapter on the substrate) in the till sections vary from place to place and the variation coincides partly with the topography, with the result that the soil profile on the upper parts of the small hillocks is more podzolic than on their lower parts. The development of the humus layer varies between more or less typical mull and moder-like types, except for the spruce stand, where the humus type is a mor. The most typical earthworm mull is to be found on the clay in the moister sections of the study area. Chemical analyses (see under substrate) have been carried out on samples of the humus layer from each of the sampling areas and from a few other places.

Climate

The temperature at Andersby ängsbackar was recorded from June 1969 until the end of November 1971. The measurements were taken in a standard screen placed in an open field with a Lamprecht thermograph working on a weekly basis and maximum and minimum thermometers. Precipitation was measured during the course of shorter periods in 1970 and 1971. During the same years, Hans Persson measured precipitation 2 km north of the station at Andersby.

Precipitation and temperature have been measured since 1963 at the meteorological station,



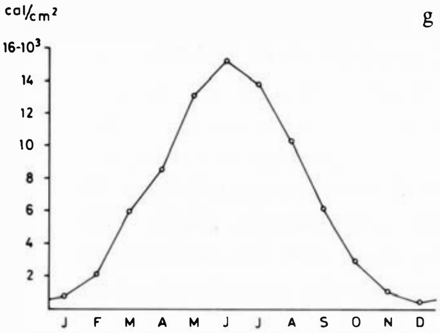


Fig. 2 a-f. Mean monthly temperature and precipitation at Dannemora 1967-72, from SMHI and mean values 1931-60, see text. InFigs. d and e, mean monthly temperatures at Andersby are given.
——— and filled columns: current year
- - - - - - - - and open columns: mean values 1931-60
. . . . Andersby ängsbackar.
g. Irradiation at Ultuna, mean values 1963-72.

"Dannemora", located in the eastern section of Österbybruk about 7 km NNE of Andersby ängsbackar and about 15 m higher. Previously only precipitation was recorded a mere kilometer to the W. The latter station lay at roughly the same height as the temporary one at Andersby. Both the meteorological stations and Andersby ängsbackar lie within the network of lakes and watercourses of the Dannemora and Österby area.

In Figs. 2 a-f are given the mean monthly temperatures and the monthly precipitation for the years 1967-72. With regard to the precipitation, the mean values for the period 1931-60 have also been included, as have interpolated values for the temperature during the same period. The interpolation was carried out between the station at Ultuna, located approximately 40 km SSW of Andersby, and that at Väsby, located roughly 28 km NW of Andersby. One took into consideration how the temperature recorded at the meteorological station "Dannemora" behaved in comparison with the above-mentioned stations during the period 1963-72.

Precipitation

The average annual precipitation during the period 1931-60 amounted to 566 mm (Modén & Nyberg 1965). The late winter and spring were characterized by the lowest recorded precipitation, approximately 30 mm/month, while a precipitation maximum occurred during the months of July and August, 60 mm and 73 mm respectively.

The station located at Österby recorded significantly higher annual precipitation values than the coast station, and somewhat higher ones than Central Uppland and the Lake Mälar region. According to Modén and Nyberg (op.cit.), annual precipitation reaches a maximum some 10-20 km from the coast. The Österby station lies within the western section of this zone. During the summer, however, Central Uppland receives a higher precipitation than Österby.

Precipitation varies within comparatively small areas, especially during thunderstorms and cloudbursts in the summer. Depending on small topographical differences, precipitation may also vary more regularly. Therefore, on a local, or short-term, scale, it is not possible to use the precipitation values recorded at Österby as entirely representative for Andersby ängsbackar.

The precipitation records from Andersby ängsbackar are too few for a detailed comparison between Andersby and Österby to be made.

Snow conditions. Northern Uppland is a region with a local maximum with regard to the duration of the snow cover and maximum snow depth, this being due to easterly and north-easterly winds which carry down large quantities of snow. According to Pershagen (1969), the mean number of days per year with snow cover during the period 1931-60 was about 125 in the Dannemora area. The mean date for the first cover of snow, which lasted at least 24 hours, was around November 20th and, for the last, April 20th. The average maximum depth of snow was approximately 50 cm. Approximately 20% of all precipitation comes down in the form of snow. However, during the years of investigation, snow conditions at Andersby deviated considerably from the average. Most years, the maximum snow depth was less than 50 cm. Local snow conditions are mentioned under Eco-temperature measurements: Soil temperature.

Humidity index and evapotranspiration. If humidity index is calculated according to de Martonne's method (see Hesselman 1932), a humidity index (l'indice d'aridité) of 36.5 is obtained, which agrees with Hesselman's interpolated values in Table 4 (op.cit.). This index of humidity, according to Hesselman, indicates the conditions of humidity existing between continental and subhumid regions. If humidity index is regarded as run-off, in accordance with O. Tamm (1959, formula 1), a value of 178 mm is obtained, a humidity factor which, according to Tamm, is that characteristic of a mildly humid region.

Wallén (1966) calculated the potential evapotranspiration issuing from a well-watered, short-grass surface with Pennmann's formula and arrived at a value of 541 mm for Uppsala. According to the map in Troedsson (1965), constructed after Mohrmann & Kessler, the water deficit in Eastern and South-Eastern Sweden during the growth period is of the order of 50-100 mm.

Temperature

The interpolated mean annual temperature for the period 1931-60 was approximately +5.5°C. The warmest and coldest months were July and February respectively, with mean monthly temperatures of approximately +16.9°C and −4.5°C. The amplitude was, thus, 21.4°C.

If the mean monthly temperatures for Österby are compared with those for a coastal station (Örskär) and those for a slightly more inland and southern one (Ultuna), it is clear that the temperature conditions at Österby are similar to those measured at the inland station. During winter, the mean temperature at Österbybruk was insignificantly higher than that at Ultuna while, during the rest of the year, it was somewhat lower. During spring, there is an observable retardation in florescence and foliation when compared with the Uppsala area (Ultuna) (cf. Persson, in press).

In Figs. 2 e-f are given mean monthly values from the temperature measurements carried out at Andersby ängsbackar. The mean temperatures are calculated according to SMHI årsbok 47 (1965).

During the autumn months, the mean monthly temperatures at Andersby were somewhat lower than those recorded at "Dannemora", the difference being at the most 1°C.

Table 1. Number of days per month, April-October 1970 and 1971, with minimum temperatures below 0°C at Andersby ängsbackar (standard screen) and mean values 1963-1972 at "Dannemora" station.

Year	A	M	J	J	A	S	O	Year
1970	14	5	0	0	1	3	10	
1971	22	7	2	0	0	8	14	
1963-72	16.1	4.7	0	0	0	1.2	8.4	157

In Table 1 is given the number of days with a minimum temperature below 0°C during the months April-October 1970 and 1971 at Andersby and also the mean values for the period 1963-72 from the Dannemora station. During the spring of 1970, the number of days with frost was less at Andersby than at Dannemora, while the opposite was true of the spring of 1971. During the autumn of both years, the number of days with frost was higher at Andersby than at Dannemora. However, the frost frequency is, to a great extent, dependent on local conditions and varies within Andersby ängsbackar as a whole. Obviously, the frequency is lower inside the woodland, at least at screen level, but in open spaces it is higher at ground or field layer level than at screen level.

Modén and Nyberg (1968) calculated the frequency of days with frost in Eastern Svealand during the period 1951-65. During the spring, the frequency of days with frost at the Dannemora station coincided with their calculations for the Lake Mälar region but during October, the frequency at Dannemora was somewhat higher than that in Lake Mälar region. The value of the comparison is, however, lessened by the fact that the periods of measurement are not the same.

Table 2. Growth periods expressed as number of days with mean temperature above certain temperatures and the global solar radiation for the same periods. Mean temperature at "Dannemora", 1963-72, and mean radiation at Ultuna, 1963-72.

Criterion	Period	Days	$Kcal/cm^2$
>0°C	26.3-18.11	237	78
>+3°C	13.4-1.11	204	66
>+6°C	28.4-15.10	170	61
>+10°C	19.5-19.9	123	48

Growth period. The number of days with a mean temperature above different temperature criteria is given in Table 2. These temperatures have been considered as suitable temperature limits for the growth period (Atlas över Sverige, Langlet 1936, Walter 1960, p. 66). The dates have been obtained from a graph which was drawn from the mean monthly temperatures, in accordance with Langlet. However, the real growth period of various plants can scarcely be estimated from the daily mean temperature measured at screen level. The growth period differs for different plants. The tree species start leafing at different times during May or the first days of June, and the autumnal leaf-fall starts during September and continues during the whole of October. Within an area such as Andersby ängsbackar, the growth period also varies because of the variable exposure, which causes, for instance, different conditions during thaw.

The use of mean temperature measured at screen level is also doubtful for the reason that the photoperiod, and probably the day and night temperatures as separate factors, are more decisive for the growth period than the mean temperature. Below-ground growth is, of course, dependent on soil temperature, which probably also effects above-ground growth.

Irradiation

The nearest station to the study area which records solar radiation is Ultuna. In Fig. 2g is drawn a graph with the mean monthly values for the period 1963-72. The annual total amounted to 81 $kcal/cm^2$ with the highest monthly value in June of 15.3 $kcal/cm^2$.

The irradiation totals measured at Ultuna for the respective growth periods based on temperature measurements at Dannemora are given in Table 2, see above. The differences in radiation between Ultuna and Dannemora seems to be negligible according to Wallén (1966).

Weather conditions during the years of study

Below is to be found, in connection with Fig. 2, a brief summary obtained, for the most part, from SMHI årsbok 49-54, Part 1.

1967. May was colder and had less rainfall than average; July also had a poorer rainfall. The summer months of June-August received approximately 80% of average year's precipitation. The autumn was milder and wetter than average. An early snow-fall occurred in the middle of October, when some leaves were still on the stems. The hazel stems were bent down by the heavy, wet snow.

1968. April was warmer than usual. The whole of May except the last week was very cold and rainy. June was one of the warmest this century, while July, on the other hand, was cold and wet. The first 10 days of September were warm. During October a greater amount of rain fell than usual. The summer months were drier than usual, the year, as a whole, was wet.

1969. April and May were somewhat chillier than usual. June was much warmer with considerably less rainfall than usual. Precipitation in July was low and drought conditions in Eastern Svealand more and more prevalent. In August, the weather was warm and dry up until the 20th, after which there followed a period of rain of considerable duration and intensity. Rainfall during the summer months was considerably less than normal, amounting to only 63% of the usual. There were two serious gales during September and a further one on the 1st and 2nd November. The year was exceptionally sunny, especially June-August and, to a lesser degree, also September.

1970. February was very cold. April was cold, wet and with less sunshine than usual. The winter 1969/70 was rich in snow and the last snow-patches melted during the first day in May. May and June were dry, June also being warm. July was colder and with more rain than normal. Rainfall during the month of August amounted to only 5 mm, as compared with 74 mm during an average year. The last two months of the year were wetter than usual. The summer months received only 59% of the rainfall during an average year but the year, as a whole, was normal from the point of view of rainfall.

1971. The winter 1970/71 was poor in snow with periods of bare ground. During the end of February and the greater part of March, the snow-depth was 20-30 cm. April, May and June were drier than normal. The period May 1st-20th was, with the exception of 1934, the warmest this century in Southern and Central Sweden. There was frost at the end of May with subsequent damage of oak and ash. In June, Eastern Svealand suffered from drought conditions. The drought continued until the end of July. August received greater quantities of rainfall than usual.

1972. May got more rain than usual, but all the following months were drier than normal. Of special note was the extremely low rainfall in December. The annual precipitation was only 66% of that for an average year.

During the five-year period 1967-71, i.e. the time which the study of increment in woody plants is concerned with, the average annual precipitation was somewhat higher than that for an average year. It was, however, somewhat lower during the months of May-August, and even more so, if one takes into account only the months of June, July and August. These three months received, on an average, 78% of the rainfall recorded during normal years. 1969 was extremely dry. There occurred two dry periods in 1970, one in June and one in August. In 1971, there was a period with low precipitation from the end of June until the middle of July.

During 1967-71, the mean monthly temperatures were, on an average, higher in June and August and lower in May and July than during the corresponding months during the period 1931-60.

Eco-temperature measurements

Measurements of temperature, especially in rather open stands, where irradiation conditions change rapidly both in time and in space, require a great number of measuring points. In this investigation, we chose to measure the temperature in a grove, in a glade, in a north-exposed edge and in a south-exposed edge, see Fig. 3, with the intention of illustrating the differences in the temperature conditions. The measurements were carried out in vertical profiles.

The temperature was registered once an hour with a battery-driven, multi-point recorder with clock switch (Grant miniature D). The measuring devices were thermistors of two types, one for air and one for soil. All twenty-eight thermistors were read off during 1 1/2 min. The accuracy of the thermistors, after appropriate corrections, was according to the manufacturer ±0.2°C and they were interchangeable. The amplitude was from −10°C to +50°C. The resistance of the thermistors did not change linearly

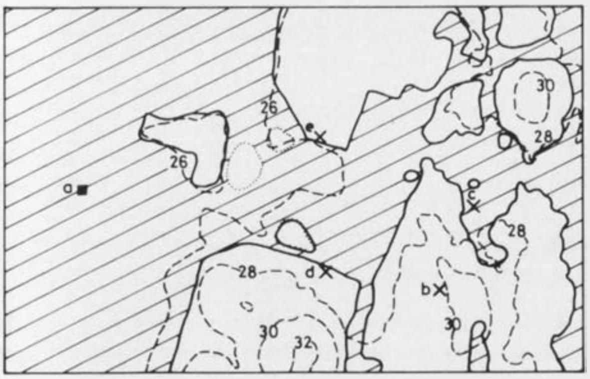


Fig. 3. Map of the places where eco-temperature measurements were recorded. a) the screen, b) the grove, c) the glade, d) the north-facing edge, e) the south-facing edge. The distance between the screen and the place of measurement in the grove is about 170 m. White areas—wooded ground, lined areas—open land. Dashed lines—2 m contours.

with temperature but described an S-shaped curve over the entire temperature range. Registrations are consequently corrected.

The irradiation shelters consisted of about 20 cm^2 aluminium foil. The latter was placed so that air could pass between the thermistor and the shelter.

Similar measurements with the same type of equipment have been made e.g. by Karlsson (1973, pp. 24-27 and Fig. 16).

In the grove, the N-facing and the S-facing edges, the uppermost thermistors were placed just above the crowns (17-19.5 m above ground) and those below in the middle of the crowns (11-13 m above ground). These thermistors were fixed on long bamboo canes. In the glade, the uppermost thermistor was placed 6 m above ground. In all places of measurement thermistors were arranged at 1.55 m and 0.1 m above ground, at ground level and at 0.1 and 0.6 m depth. Since the greater part of the root mass lies in the uppermost 10 cm and soil fauna is also most active in this stratum, the lowermost thermistors were moved up to a depth of 0.05 m on April 20th, 1971.

Fig. 4. Equipment used for measuring temperature up to 1.55 m. The glade. The edge in the background is situated about 12 m away from the measuring place. Photo: Bengt M.P. Larsson May 7th, 1970.

Consequently, six thermistors were placed in the glade, and seven elsewhere. One thermistor was suspended in the meteorological screen (see above).

In Fig. 5 four isopleth diagrams show the temperature course during June 24th, 1970. The hours are plotted on the abscissa. It must be emphasized that the temperature was registered only once an hour whereas the air temperature in the stands more rapidly. In the margin to the right, the minimum, mean and maximum temperatures and the amplitudes are given. The weather the weeks before was sunny and deficient in rain. High day temperatures were recorded, especially on June 19th and 20th. The 24th was rainless and could be characterized as a warm and clear summer's day with weak winds.

Air temperature

The grove. The highest temperature was measured 0.1 m above ground, where the temperature exceeded the temperature at standard height (1.55 m) by 4-5°C. This measuring point also had the highest amplitude. The double maxima show how irregular the course of the temperature was in a stand which partly permitted the entry of sunlight. Higher minimum temperatures were measured in the crown than at 1.55 and 0.1 m.

The glade. The temperature conditions were characterized by great variations, especially in the air layer just above the ground, at 0.1 m, where the amplitude was just over 35°C. The amplitude on the plant-covered soil surface, was 23.3°C. The amplitude at the standard height was greater in the glade than in any of the other measuring places. The topographical surroundings about the glade are somewhat higher and covered with trees. During calm days or days with weak winds, the air is trapped in the glade and is warmed up, while, in the

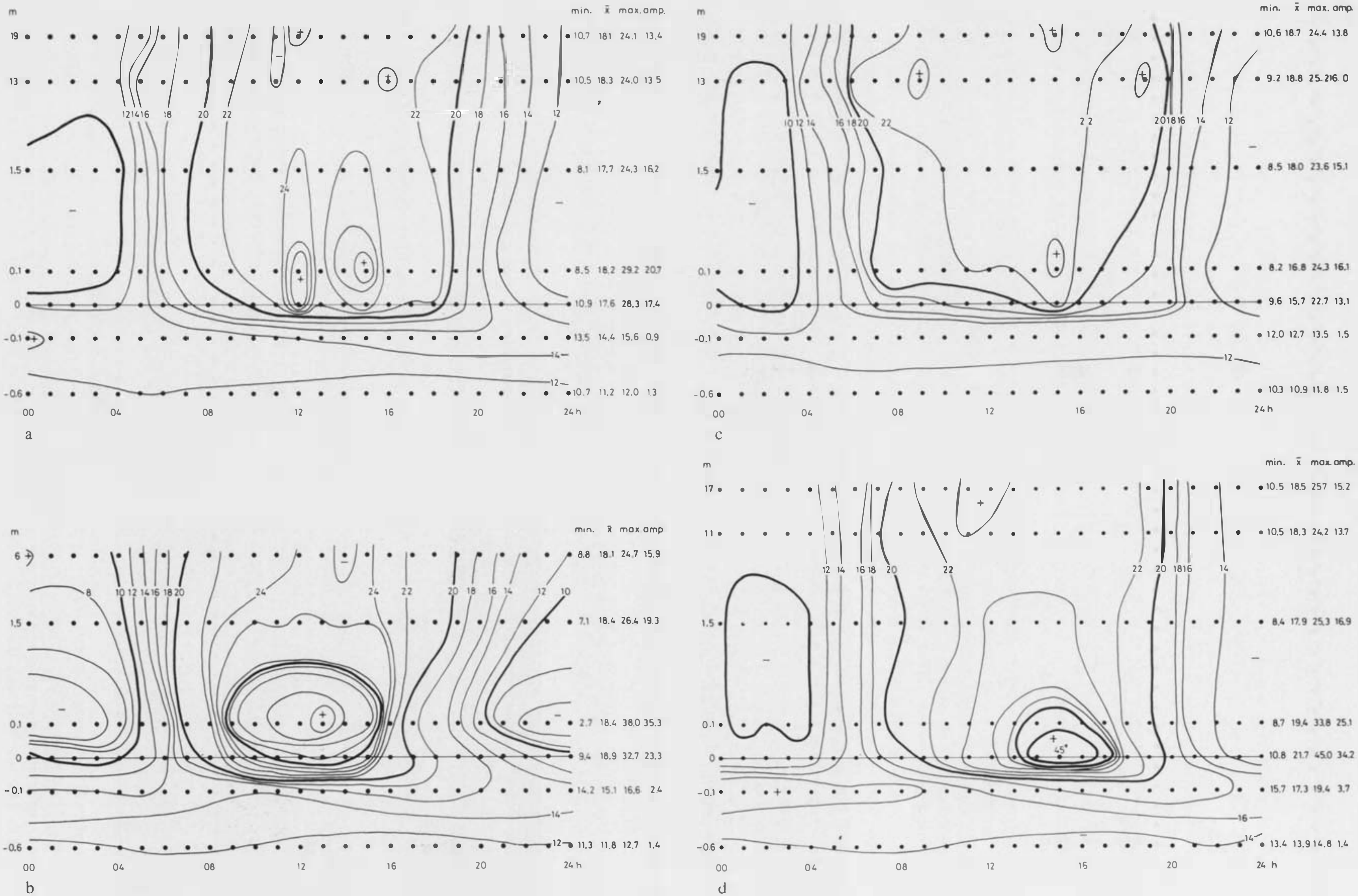


Fig. 5. Diagrams of temperature distribution June 24th, 1970 at different points. a) the grove, b) the glade, c) the N-facing, d) the S-facing edge. The screen temperature, see text. The temperature was registered once an hour (indicated with a dot). Solid lines each ten degrees. In Fig. d some fine lines have been omitted. The vertical axis height above ground are non-linear.

less wind-sheltered places, the air movements prevent such strong heating. The night temperature was lower than in the other places of measurement depending on both the higher surroundings and the uncovered situation with freely outgoing radiation. The minimum temperature at 0.1 m level was about 6°C lower than at the three other measuring places. The glade, however, was not unique from the point of view of minimum temperature. During the autumn of 1971, similar conditions were observed in several glades in the study area. The crown cover was important. For example, a minimum temperature of −2.5°C was measured in the glade and +2.1°C at the edge of the glade under a hazel crown. The importance of the topography could be illustrated by the fact that a difference of over 4°C was measured from the top to the base of a hillock. The places of measurement were, on this occasion, situated beneath crowns.

The north-facing edge. The registered temperatures on the soil surface and at 0.1 m level in the air fluctuated less and were, during the day-time, lower than in the other measuring places.

The south-facing edge. The south-facing edge had the greatest temperature range at ground level, due to the lack of vegetation cover. The registered maximum temperature reached 45°C. As the measuring place was shaded during the morning, the maximum temperature was not registered until 3 p.m. The range was over 34°C. At the 0.1 m level, the amplitude was about 8°C higher than at the standard level, due to a higher maximum temperature.

The screen. The temperatures registered in the screen were lower than at the four measuring places. Min.: 8.0°C, mean: 17.2°C, max.: 23.1°C.

Comparison. Two measuring points were of special interest, viz. that at soil surface on the south-facing edge and that at 0.1 m level in the glade. At both points a range of 34-35°C was measured. In the screen, the range was only 15.1°C.

The field layer in the glade consisted of low grass and herbs. The thermistor at 0.1 m was, thus, in the upper section of this field layer. In accordance with several investigations (cf. Geiger 1966, pp. 279 et seq.) both the highest and the lowest temperatures were measured at this level. On the sparsely plant-covered south-facing edge, the range was, as mentioned, greatest on the soil surface. The temperature on the soil surface on the south-facing edge was, during the night, constantly somewhat higher than at 0.1 m and 1.55 m on the same site, and considerably higher than at 0.1 m in the glade. From the only partially analyzed material, this seems to be valid almost generally.

The south-facing edge thus differs from the glade by its higher night temperature and from the grove, by its higher day temperature (cf. Fritz Wilmers 1968, p. 121).

The above-mentioned temperature maxima were exceeded on several occasions. On the south-facing edge, over 50°C was measured on June 19th and 20th and, in the glade, 43.2°C on June 20th.

The temperatures recorded in the same places on an autumn day (Oct. 21th, 1969) with weak frost have been reproduced at an earlier date in a textbook by Sjörs (1971, pp. 74-75). A high temperature (12°C higher than the temperature measured in the screen) was noted even at that time of the year, during the afternoon on the soil surface on the south-facing edge. The same also applied to the spring. For example on April 20th, 1970, 20°C was recorded on the soil surface, when the maximum temperature in the screen was only 9.5°C.

Soil temperature

The soil temperature during June 24th, 1970, differed at the four measuring places. Higher temperatures were recorded on the south-facing edge, both at 0.1 m and 0.6 m depth. This edge had a greater temperature range at 0.1 m depth than the other places, partly resulting from the fact that irradiation to the soil surface was not hindered by a field layer.

At all places, a delay of the maximum and the minimum temperatures was registered in the soil, as compared with the conditions on the soil surface. At 0.1 m depth the delay amounted to between 1 and 8 hours and at 0.6 m depth to between 11 and 17 hours. The delay of the maximum temperature was somewhat greater than that of the minimum temperature.

In Table 3 the measurements of snow depth during the spring of 1971 are reported. The spring of 1970 showed the same tendency, namely that the south-facing edge was snow-free about 2 weeks before the three other places.

The S-facing edge is not unique in its early thaw-

Table 3. Snow depth (cm) at the four temperature stations during spring, 1971.

	3.3	10.3	17.3	27.3	31.3	2.4	13.4
Grove	33	21	21	23	+	15	0
Glade	38	25	24	27	+	18	0
N-facing edge	25	21	20	20	+	15	0
S-facing edge	23	10	2	6	0	0	0

ing but several places exposed to the south were snowfree at about the same time. The thinned part of the esker was, on the whole, snow-free at the same time as the south-facing slopes of the hillocks. General observations in the investigation area indicate that the glades and the north-facing slopes of the hillocks were snow-free latest, and that the snow in the thinned part thawed earlier than in the unthinned.

In these early snow-free places the spring herbs, in the main *Anemone hepatica,* start their development correspondingly earlier. April 24th, 1970 *A. hepatica* flowered on the S-facing edge, which had been snow-free since April 13th. The other measuring places were still covered with snow.

In Fig. 6, the soil temperatures at 0.1 m depth during the thawing period of 1971 are given. The temperature is a mean value for seven measuring occasions during the day. The S-facing edge was snow-free on March 31st and the other measuring points

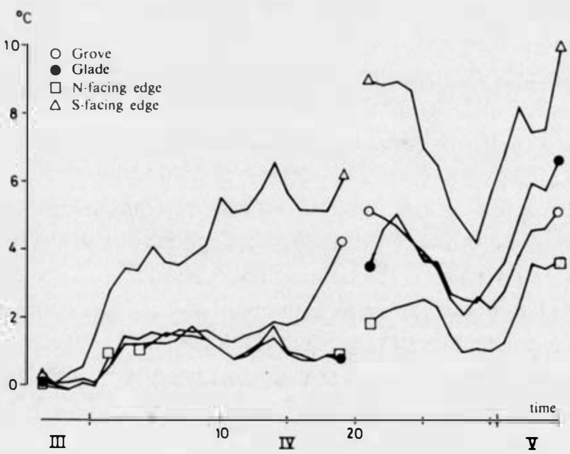


Fig. 6. Diagram of soil temperature at 0.1 m depth during the spring, 1971. The snow cover disappeared at the S-facing edge about May 31th and at the three other places about April 13th. The soil was frozen longer in the glade and at the N-facing edge than in the grove. The soil was dug up April 20th, see text.

on April 13th, at the latest, a time difference of about a half month.

The soil temperatures started to rise half a month earlier on the S-facing edge than in the grove and at least twenty days earlier than in the glade and on the N-facing edge. On April 20th the lowermost thermistors were moved as already mentioned from 0.6 m depth up to 0.05 m. The soil in the glade was then frozen down to between 5 and 16 cm and, on the N-facing edge, between 2 and 10 cm. In the grove and on the S-facing edge, the soil was unfrozen at that time.

Former and present land use

In both of his works from 1971, Bengt M.P. Larsson has published historical cartographic material concerning Andersby ängsbackar, which reveals the use the land was put to in times past and present. The oldest map is from the year 1739, the others from the 1870's and 1922. A good deal of information about the vegetation is to be found on these maps. The following description is based on commentaries made by B.M.P. Larsson in one of his works (1971a). The oldest map shows that those areas which are nowadays arable land were, in the beginning of the 18th century, hay-meadows and even certain sections of the present wooded areas were also used for haymaking. An area in the south is denoted in such a way that one is led to believe that shifting cultivation and burn-beating occurred: charcoal has been found in several places in this area. In the 1870 map, which gives a detailed picture of the land use, a large number of the sediment-covered depressions in the wooded areas are denoted as hay-meadows. According to Hansson & Ingmar (1962), haymaking took place as late as the First World War. However, the 1922 map shows that the hay-meadows had then been abandoned, a fact which has been corroborated orally by several elderly persons.

Verbal information claims that grazing ceased in the northernmost section, i.e. the section lying to the north of the northern fence, in the year 1918. It was also stated that the section of the esker which lies between the two central fences has not been grazed at all during the course of this century. The part of the area located on the till was partly cleared, including hazel, in 1921 and, since then, almost uninterrupted grazing has taken place in its southern section, i.e.

that section which was again partly cleared in 1967-68. The section north of the latter plus the adjacent esker (north of the central fence) were used for grazing mainly horses during the 1920's. However, afterwards, the latter sections were grazed only sporadically. Verbal information is unfortunately not too reliable on this particular point. In 1939, a number of oak-trees were felled in the southern section of the esker and elsewhere: this is attested to by verbal information and by the presence of stumps. During the period when this study was carried out, the southern and nowadays partly cleared section has been grazed by approximately 10 head of dairy cattle.

During the course of this century, the tree and shrub vegetation has become denser and was, at the time of the clearing operations in 1967-68, in varying stages of closedness. The grazing in the southern section had not prevented this regrowth process to any appreciable extent. A considerable number of spruces grew up in different parts, including in the grazed southern section.

During the winter of 1967/68, approximately one third of the study area was partly cleared in an attempt to recreate the former structure. The clearing operations, which affected only the southern section of the area, also included the southernmost part of the esker, see Fig. 1.

Five hectares in the south-east were cleared more intensively. In this section, which was dominated by *Betula verrucosa* and *B. pubescens*, roughly two thirds of the trees, corresponding to one half of the basal area of the stand, were felled.

The section immediately north of the latter was cleared somewhat disparately depending on the topography and the distribution of the tree layer. Less cutting took place on the till hillocks while, in the sediment-covered depressions, almost all the trees and shrubs were removed. All spruces and nearly all aspens were felled. The southern deciduous species were left standing in preference to birch and rowan. The less common deciduous shrubs were mostly spared, but many junipers and some hazel shrubs were removed.

The southerly section of the esker was thinned with the result that all previously multistemmed tree individuals were made single-stemmed. Small and suppressed trees were also removed, as well as all spruces, the majority of the aspens and a large number of hazel shrubs. The few examples of *Crataegus* and *Rhamnus* were left standing.

Branches and tops were burnt after the thinning. In order to check the growth of adventitious vegetation, the burnt patches were sown with rye. Germination was poor and few growing shoots of rye resulted, if any at all.

During the spring of 1968, the tree stumps were painted with a mixture of phenoyacetics and diesel oil, and lopped hazel shoots were sprayed with the same preparation. The vegetation growing within a radius of some metres from the sprayed hazel stumps was to some degree damaged. The preparation proved fairly effective in the case of all species except *Populus tremula*, from the root system of which numerous suckers appeared.

Subsequently, the farmer has thinned the easterly privately owned strip, which was not incorporated in the thinning 1967/68. He left some *Picea abies* trees, among others standing.

Tree and shrub flora

According to Bengt M.P. Larsson (1971a), the flora of the study area is richly endowed with southerly and south-easterly species. This applies not only to the trees and shrubs but also to the field-layer species. As regards the field-layer species, reference is made to Waldemarson & Larsson, S. (1970) and Hans Persson (in press).

Andersby ängsbackar are characterised by a large number of broad-leaved tree and shrub species. As regards vascular plants, the nomenclature is in accordance with Hylander 1955 and 1966.

The most recurrent tree species are *Quercus robur* and *Betula pubescens* and *B. verrucosa*. *Betula pubescens* is more plentiful than *B. verrucosa*, at least in the southerly section. Of special note is the rather rich abundance of *Acer platanoides*. *Tilia cordata* is also rather abundant. *Ulmus glabra* ssp. *glabra* and *Fraxinus excelsior* occur only sporadically within Andersby ängsbackar but are somewhat more numerous immediately to the north. A few examples of *Malus silvestris* grow in the area. A few specimens of *Sorbus intermedia* have been found and have probably spread from the farm.

Other species are *Alnus glutinosa*, *Populus tremula*, *Prunus padus*, *Salix caprea*, *S. pentandra*, *Sorbus aucuparia* and the coniferous species *Picea abies* and *Pinus silvestris*.

Of special note among the shrub species are *Rhamnus cathartica, Rosa dumalis* and *Crataegus calycina*, all of which grow in the vicinity of their northerly limit. *Crataegus monogyna* also occurs within the area but has probably spread from the surrounding farms (cf. Almquist 1929, p. 553). Also to be found are *Daphne mezereum* (common), *Lonicera xylosteum* (abundant), *Rhamnus frangula, Ribes alpinum* (abundant), *Rosa majalis, Salix cinerea, S. myrsinifolia, S. repens, Viburnum opulus* and *Juniperus communis*.

Vegetation

The vegetation of the area is being investigated by Bengt M.P. Larsson (in preparation), who has already produced a description (1971a). However, the vegetation in Andersby was studied earlier, e.g. by Göran Hansson and Tord Ingmar, who carried out an inventory for the purpose of nature conservation within Dannemore commune (Hansson & Ingmar 1962). They came to the conclusion that the area was of great botanical value, partly because of the flora and partly because of the different vegetation types. They also maintained that the conservation of the wooded pastureland was of interest from the point of view of agricultural history.

During the course of 1969, Eva Waldemarson and Stig Larsson, working together with Bengt M.P. Larsson, analyzed sample plots which had been placed systematically in a square grid pattern with intervals of 50 m. Both the field layer and the tree and shrub layers were analyzed (Waldemarson & S. Larsson 1970). Using the results of the analyses as a guide, they divided the tree-covered parts of the study area into six vegetation types or categories. This division agreed in the main with the one carried out by Hansson & Ingmar some eight years before.

In the above-mentioned work by Bengt M.P. Larsson, further vegetation types were recognized, e.g. fringe vegetation, epilithic moss vegetation and epiphytic moss and lichen vegetation.

During the spring of 1971, Wolfgang Brunner carried out a belt and line survey in the area. He analyzed the tree layer in 5 m wide belt transects and the shrub layer along a line located in the middle of the transect (Brunner 1972). He also used the same line transects as the present author during a sampling programme for leaf litter during the autumn of 1970.

The entire study area was divided into subareas, according to the density and composition of the tree layer. Later, as a result of litter sampling and Brunner's survey, the division was altered so that the esker was distinguished from the remaining forest-bearing land. The final division can be seen on the map, Fig. 1. The degree of variation is great, even within the subareas. Furthermore, the mosaic-like structure makes the fringe areas very extensive. Since the latter possess qualities which distinguish them from both glades and closed forest, they ought to have been treated as special ecosystems.

The survey lines were laid in a NW-SE bearing, starting out from a point which had been chosen at random. This particular direction was chosen since the lay of the land in certain areas displays a marked N-S or E-W tendency. In the unthinned sections of the study area, the lines were laid at intervals of 200 m, while in the thinned sections, they were laid at intervals of 100 or 50 m. Brunner employed lines with 100 m intervals in the thinned sections in his particular investigation.

The following points from Brunner's methods can be summarized: "Within the tree layer were included all tree species which had a diameter at breast height, i.e. 130 cm from the base, of at least 5 cm. All trees, which stood within 250 cm of the survey line were recorded..." (translated from Brunner p. 4). The tree individuals were classified into species and their diameters and heights were measured. *Betula pubescens* and *B. verrucosa* were classified under the common designation, *Betulae*.

Within the shrub layer, which also included trees with a diameter at breast height of less than 5 cm, were recorded according to species and cover all living parts or sections of trees and shrubs which were intersected by the line or by its imaginary vertical projection. The number of centimetres on the tape covered by each individual species was registered (Brunner op.cit. p. 4). A direct result of the latter procedure is that individuals with branches jutting outwards are overrepresented. The bushes and trees in the shrub layer were divided into three classes—<1 cm, 1.0-2.9 cm and $\geqslant 3$ cm. The diameter was measured at a height of 0.3 m above ground level. *Corylus avellana* was divided in exactly the same way except that a further diameter class was added, viz. $\geqslant 5$ cm. Variations in the topography were noted.

Brunner divided the transects into sections 25 m long and measurements from each section were collated. For each member of the tree layer he calculated a volume index, expressed either as D^2h or as parabolic volume, i.e. $\frac{1}{2}\pi R^2 h$. The latter were added together in each section. By Brunner's kind permission, some of these maps have been published in this work, see Figs. 7 and 8.

Thinned birch-wooded pastureland

Most of the birch-wooded pastureland is located on flat, morainic land. The present tree density and basal area can be gauged from Table 4. Sampling area I lies within this birch-wooded pastureland. A section almost equal in area to sampling area I has

Table 4. Basal area (m^2) and number of trees in the transects in different parts of Andersby ängsbackar. Modified from Brunner 1972.

	Birchwood thinned		Mixed deciduous forest on till and clay thinned[a]		unthinned		Mix. decid. forest on esker unthinned		Spruce stand	
	m^2	No	m^2	No	m^2	No	m^2	No	m^2	No
Acer platanoides	0.15	3	0.19	2	0.28	14	0.27	16	.	.
Alnus glutinosa	.	.	.	.	0.41	11	0.25	11	.	.
Betula pub + verr	0.84	13	1.38	22	2.61	66	0.45	9	0.13	2
Picea abies	.	.	0.06	2	0.33	19	0.10	5	0.51	12
Pinus silvestris	.	.	.	.	+	1	0.07	1	.	.
Populus tremula	0.02	5	+	1	0.72	48	1.50	15	.	.
Prunus padus	.	.	.	.	+	2	0.02	4	.	.
Quercus robur	0.23	6	1.39	20	4.01	67	1.59	15	0.26	5
Salix caprea	.	.	+	1	0.08	7	0.06	1	+	2
Sorbus aucuparia	.	.	0.14	3	0.19	14	0.64	31	0.03	2
Tilia cordata	.	.	0.42	6	0.75	40	0.69	8	0.01	2
Total	1.24	27	3.59	57	9.40	289	5.65	116	0.95	25
Length of transects (m)	476		721		960		409		85	
Total/ha	5.2	113	10.0	158	19.5	602	27.6	567	22.4	588

[a] Only wooded hillocks; open glades excluded.

Table 5. Percent coverage in the shrub layer. Slightly modified from Brunner 1972. (Brunner did not separate the esker from the till and clay and only the three most common species have later been re-counted to the two different sites.)

<table>
<tr><th></th><th>Birchwood thinned</th><th colspan="4">Mixed deciduous forest</th><th>Spruce stand</th></tr>
<tr><th></th><th></th><th colspan="2">on till and clay thinned</th><th colspan="2">on esker unthinned</th><th></th></tr>
<tr><th></th><th></th><th>glades</th><th>hillocks</th><th></th><th></th><th></th></tr>
<tr><td>Corylus avellana</td><td>2.0</td><td>11.8</td><td>22.1</td><td>34.4</td><td>33.1</td><td>1.9</td></tr>
<tr><td>Daphne mezereum</td><td></td><td></td><td>x</td><td colspan="2">x</td><td></td></tr>
<tr><td>Juniperus communis</td><td>1.3</td><td>1.7</td><td>5.5</td><td colspan="2">0.5</td><td></td></tr>
<tr><td>Lonicera xylosteum</td><td>2.1</td><td>0.4</td><td>1.2</td><td>2.4</td><td>6.4</td><td>0.9</td></tr>
<tr><td>Rhamnus frangula</td><td>0.1</td><td>0.5</td><td>0.5</td><td></td><td></td><td></td></tr>
<tr><td>Ribes alpinum</td><td>0.1</td><td>0.3</td><td>1.0</td><td>2.9</td><td>4.8</td><td>1.9</td></tr>
<tr><td>Rosa sp.</td><td>x</td><td>x</td><td>x</td><td></td><td></td><td></td></tr>
<tr><td>Salix sp.</td><td></td><td>1.2</td><td>0.2</td><td colspan="2">0.1</td><td></td></tr>
<tr><td>Viburnum opulus</td><td></td><td></td><td></td><td></td><td></td><td>0.4</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Acer platanoides</td><td></td><td></td><td>0.3</td><td colspan="2">0.8</td><td></td></tr>
<tr><td>Betula spp.</td><td>0.5</td><td>0.6</td><td>0.6</td><td colspan="2">0.6</td><td>x</td></tr>
<tr><td>Fraxinus excelsior</td><td></td><td></td><td></td><td colspan="2">x</td><td></td></tr>
<tr><td>Picea abies</td><td></td><td></td><td></td><td colspan="2">0.1</td><td>1.2</td></tr>
<tr><td>Populus tremula</td><td>0.8</td><td>1.3</td><td>0.8</td><td colspan="2">1.2</td><td>1.6</td></tr>
<tr><td>Prunus padus</td><td>x</td><td></td><td></td><td colspan="2">1.3</td><td></td></tr>
<tr><td>Quercus robur</td><td>0.6</td><td>0.4</td><td>1.7</td><td colspan="2">1.5</td><td>1.2</td></tr>
<tr><td>Sorbus aucuparia</td><td></td><td></td><td>0.1</td><td colspan="2">1.1</td><td>0.2</td></tr>
<tr><td>Tilia cordata</td><td></td><td></td><td>0.3</td><td colspan="2">1.7</td><td>8.4</td></tr>
</table>

been used for analysis by means of transects. By means of this transect method, a greater number of trees per ha were recorded but the basal area registered was somewhat lower. The area is dominated by a sparse population of birches, with occasional oak, linden, rowan, aspen and maple. All spruce has been thinned out. The shrubs are scattered, see Table 5, with sporadic occurrences of hazel and juniper. *Lonicera xylosteum* is common in a moist, centrally situated section of the area. In 1967/68 a dense grouping of aspens was cleared in the northern section of the area. Subsequently, both here and in a few other places, a dense growth of aspen suckers has appeared.

Unthinned oak-birch-hazel-wood with glades

This is the most extensive subarea, within which there exists a great deal of variation. The easterly section of the part located to the north of the northern road (see map, Fig. 1) is only sparsely overgrown. A number of the old hay-glades still lack tree and shrub layers, while others have been colonized by aspen and birch. The tree layer on the morainic hillocks is of varying density, from the abovementioned sparsely overgrown part to completely closed stands. The number of oak and birch trees is approximately the same but the basal area of oak is greater. Linden (*Tilia cordata*) occurs both as individuals and in dense clones. In the westerly section of the part which is located between the roads, there are numerous aspen trees. The shrub layer is dominated by hazel, which has developed into large, dense thickets especially on the edges of the old hay-glades. *Ribes alpinum* covers a slightly larger area than *Lonicera xylosteum*. Despite the large number of birches in the tree layer, regeneration is comparatively weak, except in the case of certain hay-glades in a stage of regrowth. The following summary by Brunner (op.cit.) concerning tree regeneration can be quoted (translation):

"In the clay-filled depressions, approximately 58% of all tree samplings are aspens, while birch and oak account for 16 and 13% respectively. In the case of the morainic hillocks, aspen dominates there too with just under 40%, followed by oak with 19%, linden with 16% and birch in fifth place with only 6%. Summarizing, it can be said that the major part of birch regeneration takes place in the clay-filled depressions, aspen regeneration is roughly the same in both the vegetation types, while the chief part of regeneration of other species, or in the case of spruce and linden all the regeneration, takes place on the morainic hillocks."

Thinned oak-birch-hazel-wood with glades

The result of the thinning operations was a more or less sparse tree layer dominated by birch and oak. Dense growths of hazel are located especially on the slopes of the hillocks. In or near the glades, hazel shrubs were cut back. The degree of cover of *Juniperus communis* is higher on the hillocks than in any of the other sections. After thinning, the glades have remained more or less treeless. However, aspen suckers are prevalent. One of the transects intersects a vegetation which "lies on the border between wetland vegetation and moist meadowland vegetation" (B.M.P. Larsson 1971a, p. 17).

Unthinned deciduous wood on esker

This subarea has the greatest basal area per area and the latter is distributed more evenly between the different tree species than on the morainic sections. There are also differences here between the different parts.

The northern sections are characterized by notable occurrences of tall aspens. Rowan is also numerous. Maple is numerous in the free-lying middle section of the esker. It is unusual to find such a rich occurrence of maple in the deciduous forest stands of Uppland. This is characteristic for the area. The low-shrub layer is prominent. *Lonicera xylosteum,* for example, has a cover twice as high on the unthinned esker as in the unthinned oak-birch-hazelwood. Oak and birch regeneration is poor while that of aspen, maple and linden is appreciably better. The two transect strips which land on the free-lying section of the esker also cross gravel pits and thus do not give an adequate picture of the tree and shrub vegetation.

Thinned deciduous wood on esker

Approximately 225 m of the southernmost section of the esker were included in the above-mentioned thinning in 1967/68. Only a short section of one of the 1971 transects intersected this ecosystem. The former and present composition of the tree layer can

Fig. 7. The voluminal distribution of tree stems measured either as parabolic volume ($0.5\ \pi\ r^2h$) or as the square of the diameter at breast height multiplied by the tree height (D^2h). The strip transect is divided into 25 m long sections and the volume in each section is added and expressed in m^3/ha. The Figs. are from Brunner 1972.

Fig. 8. The percentage distribution of cover in four shrub species, measured in line transects. The length of the line covered by a species was added within each sector and expressed as a percentage of the total length of the section line (25 m). The Figs. are from Brunner 1972.

be exemplified by the conditions in sampling area II:1. Along the lake shore grows, in the main, birch, predominantly *Betula pubescens,* and sporadic examples of alder (*Alnus glutinosa*). After the thinning, a dense thicket of aspen appeared both outside of, and within, sampling area II:1. The low-shrub layer is denser here than on the morainic hillocks and comprises for the most part *Lonicera xylosteum* and *Ribes alpinum. Daphne mezereum* and *Viburnum opulus* are also found, and, near the southern end of the esker, one also comes across *Rhamnus cathartica* and *Crataegus calycina.*

Spruce stand

On a bouldery section within the unthinned morainic area is to be found a spruce stand. Waldemarson & Larsson, S. (1970) pointed out that dwarf shrubs (*Vaccinium* spp.) were more common in this stand than in the deciduous wood sections. Sporadic occurrences of oak, birch and other species are to be found between the spruces. The shrub layer is poor.

Distribution of trees

The true stem volume is in general somewhat higher than the parabolic volume illustrated in the figures, see e.g. Whittaker & Woodwell (1968). The species differ from the point of view of the shape of the trunk, with the result that the relation between the volume index and the true volume differs for the different species. The volume index approximates the volume of a tree with one main stem or trunk, which not all individuals have.

Fig. 7 shows the great irregularity in volume or biomass distribution. The volume is greatest in the northern esker section, where a number of tall *Populus tremula* are to be found. If the bulk basic density is taken to be about 0.5, a trunk biomass of roughly 350 ton per ha is obtained in the case of the section where the volume index was highest. To the latter figure one should add the branch weight. The high volume-index value in a section in the southern part of the study area is due to a single oak which had a diameter at breast height of almost 1 m. The volume index is lowest in the birch-wooded pastureland and in the glades in the thinned section.

Oak and birch are relatively evenly distributed within the study area while aspen and other tree species are distributed in a more uneven way. The table below gives a percentage figure for the portion of the strip sections taken up by a certain species.

Acer platanoides	17 %
Betula spp.	47 %
Picea abies	16 %
Populus tremula	27 %
Quercus robur	41 %
Sorbus aucuparia	21 %
Tilia cordata	18 %

It has been stated earlier that the transects landed in an unfortunate way on the free-lying section of the esker, both of them intersecting gravel pits. The chief occurrences of maple and linden are to be found in this particular section. This, however, was not shown by the vegetation analyses taken from the transects.

The map, Fig. 1, and the description probably give the impression that the main factor in the distribution of the vegetation has been the variation in the soil material. The differing tree and shrub composition and density are, however, probably better regarded as due to the former land use and to the different times in the course of this century when hay-making and grazing ceased. A connection is evident between the latter and the distribution of the soil materials. The "free-lying middle part" of the esker was probably never grazed or at least abandoned as pasture at an earlier point in time than the till and clayey sections, on which haymaking preceded the use as wooded pasture (B.M.P. Larsson, in preparation).

Description of the sampling areas

The location of the three sampling areas, 50x50m in size, can be seen in Fig. 1. A full description of the vegetation, with lists of the species found in these three sampling areas has been prepared by Hans Persson (in press). They obviously do not include the entire range of vegetation to be found in Andersby ängsbackar. The densest sections of the study area, e.g. the uncleared deciduous forest on the esker, and on the other hand, the partly cleared mixed deciduous forest on the mosaic of till (morainic hillocks) and clayey soil are not represented. Also, the spruce stand is outside the sampling areas. These parts have been treated in a more cursory manner, e.g. by the transects traversing them.

Methods

The number of individuals in the tree layer belonging to each species was counted during the spring of 1968 and the diameter at breast height (1.3 m) of each trunk was measured. From the latter, it was possible to calculate the cross-sectional area at breast height, i.e. the basal area. The diameter of a certain number of trunks in sampling area III was not measured until the spring of 1969. The tree diameters were again measured on several occasions during the course of the study.

All examples of tree species with a diameter at breast height of over 5 cm were registered and mapped. The vertical crown spread of each tree was measured and mapped (in 1969) by grading from the trunk outwards to the periphery of the crown in four directions. The heights of the trees and the crown depths were measured with a Suunto hypsometer during 1969.

The trees of different species, which, prior to the investigation, had been felled in areas I and II:1, were also registered and the diameter at breast height, as well as other parameters, were measured in those cases where the trunk was recovered and identified. However, in II:1, the diameter was, in some cases, calculated from the tree stump, living trees being used for comparison, in order to estimate the breast-height diameter by extrapolation.

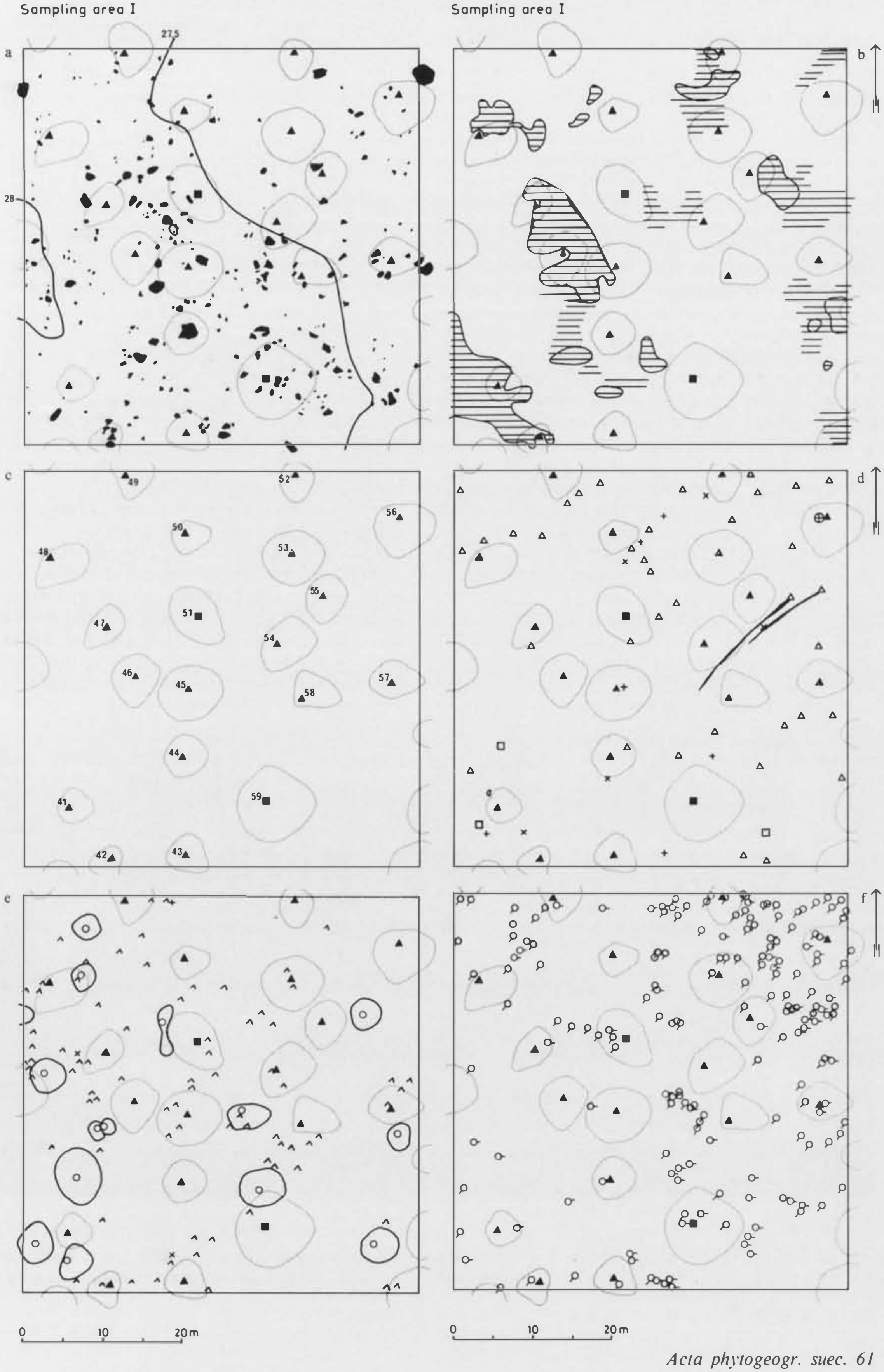
Stumps from previous felling operations were also plotted as well as fallen trees.

The crown projection of the hazel colonies was also plotted and the number of shoots in each bush was reckoned in the spring of 1969 and, in some of the colonies, also at later times. It was difficult and, in certain cases, even arbitrary to separate one hazel bush from the other.

Apart from the above, all other shrub species in sampling area I were plotted. During the springs of 1969 and 1971, the diameters of all tree species in sampling area III which had reached breast height but which had a diameter of less than 5 cm were measured.

The boulders have been plotted in all sampling areas. Height contours with an equidistance of 0.5 m over all the sampling areas have been obtained from a map drawn up from photographs taken from a low-flying aircraft.

Fig. 9. Map of sampling area I. *Betula* spp. ▲, *Quercus robur* ■.
a) Distribution of boulders with 0.5 m contours.
b) Distribution of open water (within unbroken lines) and waterlogged soil on April 12th, 1969.
c) Distribution of trees, with crown projections and tree numbers 1041-1059, cf. Table 6.
d) Distribution of stumps. *Betula* spp. △, *Picea abies* +, *Picea abies* old ⊕, *Pinus silvestris* old ×, *Quercus robur* old □, *Salix* sp. old ℚ, fallen *Betula* stem.
e) Distribution of *Corylus avellana* ○ (canopy projections within unbroken lines), *Juniperus communis* ∧, *Picea abies* + and *Pinus silvestris* × in the shrub layer. Spring 1969.
f) Distribution of *Lonicera xylosteum* ⌕ and *Ribes alpinum* ⊸.


Sampling area I
Sampling area I
a
b
27,5
28
c
d
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52
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50
48
53
55
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47
54
46
45
57
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42
43
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10
20m
0
10
20m

Sampling area I

The area is located in a rather even section with an overall difference of level of about 0.75 m (Fig. 9). The substratum in the lowest lying sections was composed of sediment, partly clay. Otherwise, the substratum consists almost entirely of till (cf. the map of the Quarternary deposits, Fig. 2 in Larsson, B.M.P. 1971b). The soil contains a large number of boulders, but the latter do not protrude above ground level to any great extent. During the spring thaw of 1969 and 1970, a shallow layer of water accumulated. On April 9th, 1969, approximately 70-80% of the sampling area was covered with snow. Fig. 9b shows the state of affairs on April 12th when small, isolated patches of snow were still to be observed. The lowest lying sections were only flooded in parts, since the land north of the sampling area is even more low-lying.

The level of the ground-water has not been measured. During soil sampling in the *Filipendula* stand in November 1968, after a rainy October, the sampling pit was filled with water to about 16 cm from the surface. During subsequent sampling, e.g. in October 1969, no ground water was found down to a depth of 30-40 cm.

The cartographic material collected and published by Bengt M.P. Larsson (1971a) shows that, in the year 1739, the sampling area was part of a larger area probably used for the purposes of shifting cultivation. This is all the more likely since, as mentioned, charcoal remains have been found. The 1877-78 map shows that the southwesterly section was part of an area which was termed enclosed pastureland, Larsson, B.M.P. 1971a, p. 20. The northwesterly section is classified as woodland and the easterly section, i.e. that located below the 27.5 m contour, as meadowland. The exactitude of the old maps is deemed by Larsson to be good (personal communication).

Table 6. Stand structure in sampling area I.

Tree no.	Diam br h cm	Tree height m	Crown depth m	Increase in basal area cm^2
B 1047	19.0	14.0	10.0	7
44	22.0	16.0	12.4	28
41	23.6	16.0	12.5	14
46	25.5	15.8	13.5	28
57	29.3	19.5	11.0	19
52	30.1	21.3	14.5	42
56	30.7	20.0	12.0	40
42	31.3	16.0	12.3	11
54	31.4	19.0	13.0	26
49	33.3	19.5	10.0	56
50	33.9	22.5	12.0	83
55	36.3	22.2	13.3	67
43	36.8	19.5	14.5	32
58	37.0	23.0	12.0	54
48	37.4	21.5	16.3	49
45	37.4	20.8	14.3	105
53	51.6	24.5	17.3	104
Q 1051	22.3	15.5	12.5	58
59	43.0	16.8	14.3	125

Explanations, see Table 7.

In Fig. 9d are inserted stumps and fallen trees. The oldest stumps were of pine and oak trees and this seems to suggest that the tree stand was, at an earlier point in time, of a different character, at least in part. The stumps of the two latter named species are especially resistant to rot. On the same map are to be found the stumps of trees which were felled during 1967-68.

Fig. 10. The thinned birch-wooded pastureland with occasional occurrences of other deciduous tree species and sparse *Corylus avellana, Juniperus communis* etc. The vegetation in the foreground is grazed. Note the higher field layer within the sampling area I, mostly *Calamagrostis arundinacea*. The litter baskets and areas employed for clipping of the field layer can also be observed.
Photo: Folke Hellström Oct. 23th, 1969.

The composition of the tree layer, both before and after the clearing operations, is to be found in Tables 6 and 9 and the distribution of the different diameter categories in Fig. 15. The total number of trunks and the basal area were low even prior to the clearing operations. The lower-lying sections were more densely populated than the higher-lying. After clearing, only a scanty tree layer consisting of birch and two oaks remained with a crown projection of just over 20%. The larger examples of birch tree were, in the main, *Betula verrucosa*. In some cases, it was difficult to specify exactly which particular *Betula* species a tree belonged to since it displayed both *verrucosa* and *pubescens* characteristics.

The distribution of the diameter categories prior to the clearing shows that only a small number of trees belonged to the lower diameter categories, i.e. less than 15 cm, and no tree belonged to the lowest category. Thus, it can be safely assumed that no regeneration had taken place. The clearing operations meant a further relative displacement into the higher diameter categories. The mean diameter before clearing was 23.6 cm and after 31.4 cm. Tree height prior to clearing was difficult to gauge. The height of the remaining trees varied from 14 to 25 m. The mean height was 19.5 m. The majority of the birch stems were free of branches in their lower parts and, thus, had a comparatively small crown depth. The crowns of the two oak trees began approximately 2 m above ground level.

The age estimates are summarized in Table 10. The age of the stumps of the felled birches was 70-80 years. It is probable that the remaining birches and the smaller oak are of the same age. The age of the stumps of the felled spruces was 31-36 years.

The following species of tree samplings were growing in the shrub or field layers: *Pinus, Picea, Acer, Betula, Quercus, Populus* (tillers from a felled aspen), *Salix caprea, Sorbus aucuparia, S. intermedia, Tilia*. Many of the small oaks had acquired a shrublike appearance, due to grazing by roe-deer.

The distribution of the few remaining hazel shrubs is to be seen in Fig. 9e. The distribution of other dominant shrubs can be seen in Figs. 9e and f. *Juniperus communis* and *Lonicera xylosteum* are mutually exclusive to a certain extent, with a greater density of *Lonicera* in the lower-lying sections covered with mull, where only a few examples of *Juniperus* are to be found. *Rosa majalis* was found in two areas measuring about 100 m^2 each. Other shrub species were *Daphne mezereum, Rosa dumalis, Rhamnus frangula, Salix cinerea, S. myrsinifolia, S. repens* and *Viburnum opulus*.

The most frequent graminids in the field layer were *Agrostis tenuis, Calamagrostis arundinacea, Deschampsia flexuosa, Luzula pilosa* and *Poa angustifolia*. During the spring, the field layer was dominated by *Anemone nemorosa*. Frequent herbaceous species were *Convallaria majalis, Fragaria vesca, Galium boreale, Geranium silvaticum, Lathyrus montanus, Trifolium medium, Veronica chamaedrys* and *Viola riviniana*. The moister north-easterly section diverged slightly from this pattern, *Filipendula ulmaria* and *Calamagrostis canescens* growing there in large numbers.

Sampling area II:1

This sampling area was located on the thinned section of the esker, with a distance of roughly 10 m to the arable land to the east. The highest point in this area was about 30 m above sea level and the lowest 26.5 m. The eastern side of the esker is steeper than the western, see Fig. 11.

Table 7. Stand structure in sampling area II:1.

Tree no.	Diam br h cm	Tree height m	Crown depth m	Increase in basal area cm^2
A 2090b	4.6	bent down		2
96	6.2	6.5	3.5	4
88	7.1	6.5	4.3	2
2108	7.8	8.3	4.0	3
2084	9.2	8.8	6.5	10
91	9.8	9.5	5.0	8
90a	10.1	bent down		6
2107	10.7	10.3	6.8	5
2071	11.3	12.2	6.2	16
78	12.4	12.5	7.3	22
41c	16.8	13.0	8.0	20
74	20.0	10.9	6.5	19
72	17.9	14.1	7.1	30
2105	20.1	13.5	8.0	16
2085	18.9	13.8	11.5	23
82	23.4	15.2	8.5	8
57b	24.1	18.0	6.0	52
39c	26.1	14.5	9.0	24
79	27.3	16.3	12.5	17
2110	27.6	17.3	7.5	52
2052b	29.4	17.0	11.5	30
93	29.3	16.8	11.6	43
56b	28.9	19.5	10.5	84
2106	29.7	16.5	9.5	41
2044c	30.4	17.5	12.0	48
56c	30.3	19.5	10.5	70
2104	31.8	16.5	10.5	25
100	32.5	24.0	20.0	37
B 2033b	22.6	20.0	15.0	116
Po2087	32.7	22.8	12.5	91
Q 2097	30.5	15.8	13.8	29
94	33.0	16.5	12.0	22
99	34.5	19.8	12.5	41
80	39.1	15.4	12.5	69
81	44.7	12.0	10.5	38
2112	46.1	17.0	14.0	57
2095	47.5	18.0	8.0	62
Sa2089	15.7	8.0	6.3	13
So2083	17.2	12.0	8.0	64
2103	19.1	14.5	9.0	29
109	23.9	15.8	6.5	21
T 2073	15.4	(6.4) broken		10
86	21.2	19.0	11.5	20
2111	22.3	15.5	9.5	22
102	27.0	17.5	10.0	19
2092	27.7	16.5	11.0	50
75	28.4	19.5	5.5	42
70	28.5	14.8	11.0	50
98	34.1	19.5	10.0	30
2101	37.9	16.5	11.0	34
2076	44.6	19.0	11.5	29
48b	41.7	21.0	12.0	77
77	44.5	19.4	10.1	46

Species: A = Acer platanoides, B = Betula pubescens or B. verrucosa, Pi = Picea abies, Po = Populus tremula, Q = Quercus robur, Sa = Salix caprea, So = Sorbus aucuparia, T = Tilia cordata.

Increase in basal area: sum of five years

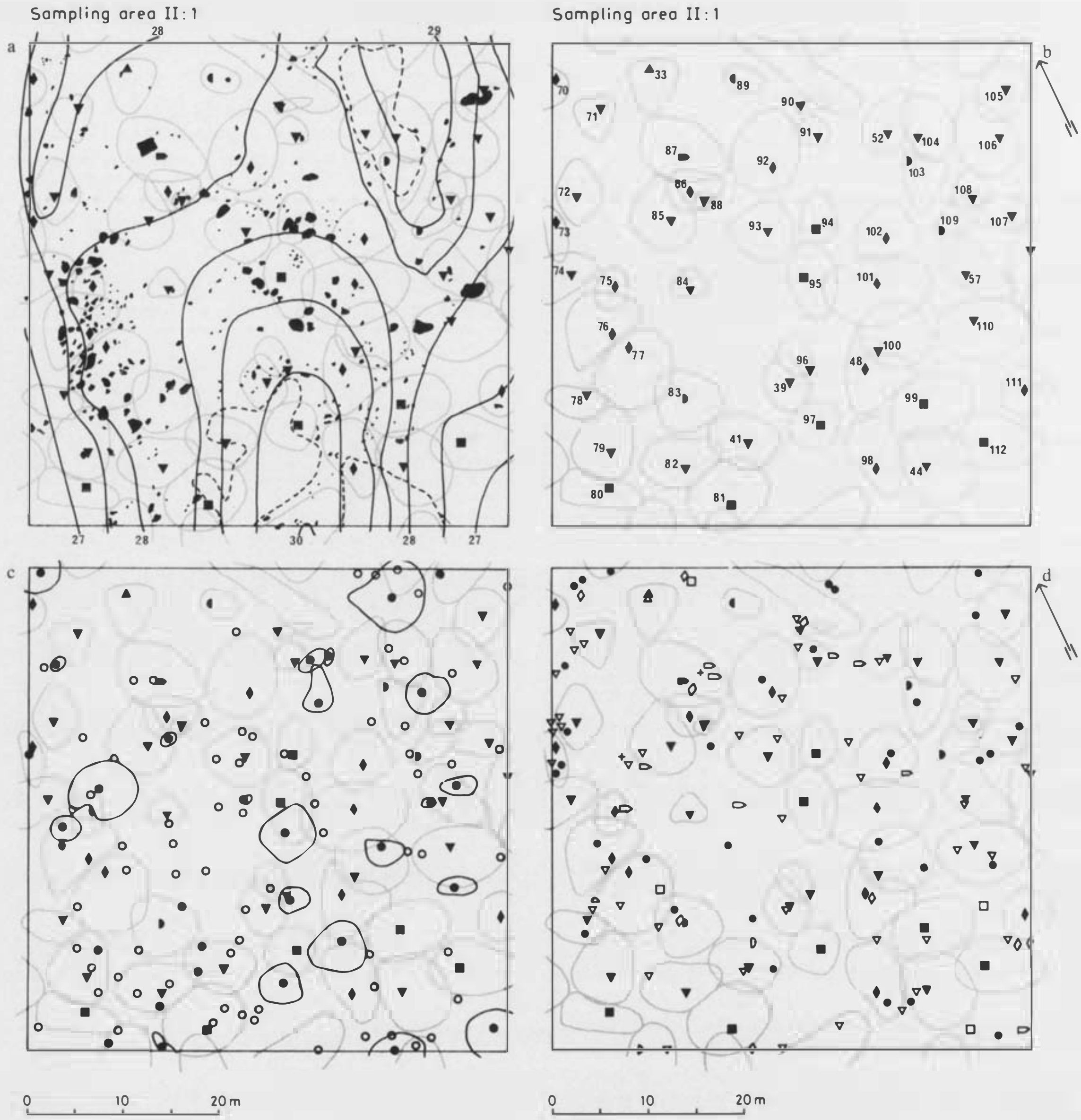


Fig. 11. Maps of sampling area II:1. *Acer platanoides* ▼, *Betula verrucosa* ▲, *Populus tremula* ▬, *Quercus robur* ■, *Salix caprea* ◖, *Sorbus aucuparia* ◗, *Tilia cordata* ♦.

a) Distribution of boulders and areas with only thin humus over the boulders (within broken lines). Unbroken lines are 0.5 m contours.

b) Distribution of trees with crown projections and tree numbers 2001-, cf. Table 7.

c) Distribution of *Corylus avellana* ● (canopy projections within unbroken lines) and *Corylus* stumps ○.

d) Distribution of tree stumps. *Acer platanoides* ▽, *Betula verrucosa* △, *Fraxinus excelsior* ⌓, *Picea abies* +, *Populus tremula* ▭, *Quercus robur* □, *Sorbus aucuparia* D, *Tilia cordata* ◊, old tree stumps, regardless of species ●.

Despite the presence of esker material, the soil is rich in boulders and several large boulders are pronounced features of the landscape. On the crest the fine soil material has been washed away. In a flat area in the northern section of this sampling area, the upper layer of soil is composed chiefly of sand. The level of the ground water was not investigated but is probably the same as that of the lake, i.e. between 24 and 25 m above sea level.

In the 1739 map, the esker section in which sampling area II:1 is situated is described as 'high, stony esker, on which oak, hazel and birch shrubs grow' (translated from Larsson, B.M.P. 1971a, Fig. 13). On the 1879 map, the esker is classified as woodland.

The composition of the tree layer before and after the

Fig. 12. The thinned sampling area II:1. The tree layer consists of *Acer platanoides, Quercus robur, Tilia cordata, Populus tremula* and *Betula verrucosa.* Note that few branches are located on a low level on the stems. The shrub layer with a dense stand of suckers of *Populus tremula.* The field layer in the spring is dominated by *Anemone nemorosa.*
Photo: Håkan Hytteborn May 11th, 1974.

clearing of 1967-68 is to be found in Tables 7 and 9 and the distribution of the diameter categories in Fig. 15. The sampling area differed from sampling area I both in its composition by species and its distribution of diameter categories. Prior to the thinning, the majority of trees were in the lowest categories, which points to a considerable amount of earlier regeneration, especially of linden and maple.

The basal area did not decrease too much after the clearing, since the largest specimens were left standing. To an even more obvious extent than in sampling area I, the clearing resulted in an artificial stratification of foliage, with a level completely free of foliage between the tree crowns and the hazels and the low shrub layer. Tree crowns covered approximately 56% of the area.

The clearing operations meant a decrease in the number of species and a change in the distribution of diameters so that the stand was characterized by a large number of heavier, thicker trunks. The mean diameter of the stand was 18.8 cm before clearing and 27.3 cm after clearing. Roughly one half of the remaining trunks were of *Acer*. However, counted as basal area, the difference between *Acer* and *Tilia* was small. *Quercus* had a somewhat lower basal area. The tree height varied from 6 to 24 m.

The age of some of the felled trunks is to be found in Table 10. The great age of the *Acer* individuals, the oldest being 177 years old, is of special note. According to Lagerberg (see Sjörs 1962), it is exceptional for maples to exceed an age of 150 years. The oldest maples, lindens, and certainly oaks too, belonged to an older generation than the aspens, birches and spruces.

During the years of investigation, an extremely dense stand of suckers of *Populus tremula* grew up from the roots of the felled aspens, and this stand dominated the shrub layer throughout, except on the crest. During the course of the first year, these suckers grew between 20 and 60 cm and, in the autumn of 1971, the tallest were approximately 2.5 m long.

Four years after the clearing, there were large numbers of young rowan plants, the majority less than 15 cm long, but several individuals had attained a height of 1 m. Tillers had sprouted from almost all the linden stumps the same being true of the maple stumps.

Oak regeneration was less noticeable, there being only a few 20-30 cm high plants. One or two ash saplings were also noticed.

Only 25 of the 99 hazel bushes originally present were left standing. The lower shrub layer was dominated by *Lonicera xylosteum* and *Ribes alpinum,* with examples of *Daphne mezereum, Viburnum opulus* and *Rhamnus cathartica.*

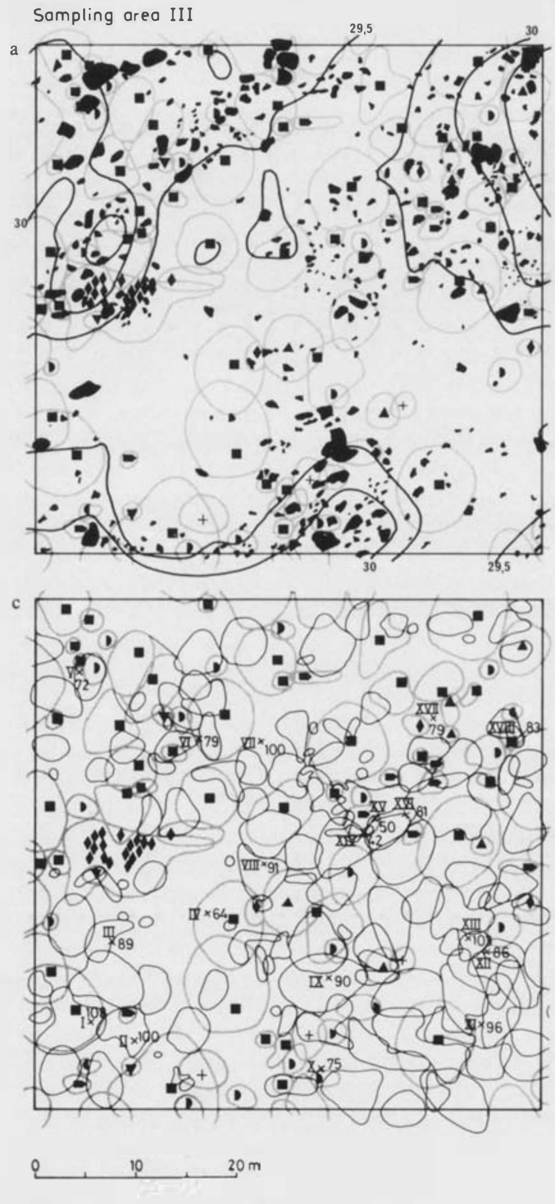
During the spring, the field layer was dominated by dense stands of *Anemone nemorosa* in admixture with *Cardamine bulbifera.* Other frequent species were *Milium effusum, Anemone hepatica, Fragaria vesca, Lathyrus vernus, Maianthemum bifolium, Oxalis acetosella, Paris quadrifolia, Pulmonaria officinalis, Veronica chamaedrys* and *Viola riviniana.*

Sampling area III

This sampling area is located in the unthinned forest on till and clayey soil. The terrain is undulating, with a height above sea level which varies from 29.5 to 31 m. The lower sections have a clay surface-layer with a few boulders projecting from the underlying till. A great deal of the surface consists of stony till, locally rich in boulders, see Fig. 13 and Fig. 2 in B.M.P. Larsson (1971b). According to B.M.P. Larsson (1971a and b), the sampling area is located in a part which, on the 1739 map, is termed 'Stony, sloping ground with oakwood, and birch, spruce and hazel shrubs' (translated from B.M.P. Larsson 1971a, Fig. 13). In the 1877-78 map, the area is referred to as woodland. Charcoal remains have been found in the soil and this, once again, suggests that the area was once utilized in shifting cultivation. A closely situated, still open, former hay-glade is characterized by an almost unbroken layer of charcoal, lying 10-15 cm below ground level. It is furthermore reasonable to assume that haymaking took place at least during certain years in the admittedly small, but, nevertheless, even, sediment-filled areas.

Thawing varies in its occurrence within the sampling area, mainly due to the undulating nature of the topography and the varying degrees of density in the tree and shrub layers. Consequently, on April 21st, 1969, at a time when both sampling areas I and II:1 were nearly free of snow, 50% of area III was covered with snow, and there was still an unbroken layer in the area's southern section, which slopes northwards, and in the depressions. Less extensive patches of snow persisted even into early May.

The level of the ground water was never measured. During the greater part of the vegetation period, it



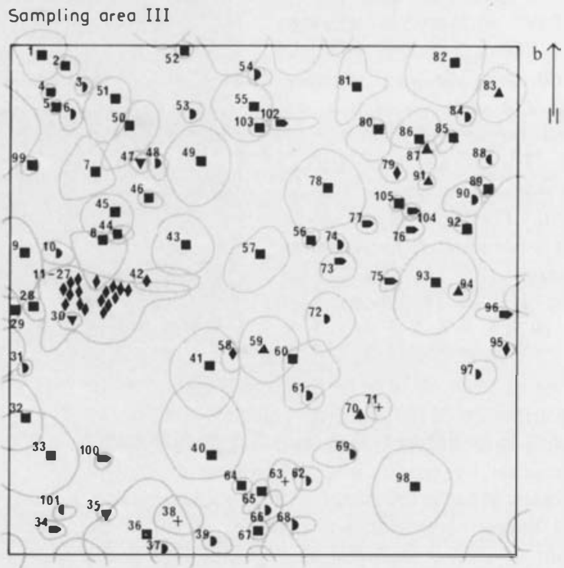


Fig. 13. Maps of sampling area III. *Acer platanoides* ▼, *Betula verrucosa* ▲, *Picea abies* +, *Populus tremula*, *Quercus robur* ■, *Salix caprea*, *Sorbus aucuparia*, *Tilia cordata* ♦.
a) Distribution of boulders and the 0.5 m contours.
b) Distribution of trees with crown projections and tree numbers 3001-3105, cf. Table 8.
c) Distribution of *Corylus avellana* , with canopy projections within unbroken lines.
Location of the rain funnels (I-XVIII) and the throughfall for each funnel in % of the precipitation in an open place during the periods.

Fig. 14a. Tree crown stratum in sampling area III. The big trees are *Quercus robur,* richly branched even in the lower sections. The young stems in the photo are mostly of *Populus tremula.* In the background, some *Picea abies.*
Photo: Håkan Hytteborn May 11th, 1974.

Fig. 14b. The unthinned sampling area III with a dense layer of *Corylus avellana* and small *Populus tremula.* In the field layer, mostly *Anemone nemorosa.* The substrate in the foreground and background consists of till and, in the centre, of clay. Earlier, this part was probably a hay-glade and has no old trees. It is overgrown with *Corylus.*
Photo: Håkan Hytteborn May 11th, 1974.

Table 8. Stand structure in sampling area III.

Tree no.	Diam br h cm	Tree height m	Crown depth m	Increase in basal area cm^2
A 3030	6.1	6.7	5.2	-
35	6.2	6.4	4.0	11
47a	4.1	10.0	5.0	-
47b	5.0	10.0	5.0	-
47c	5.3	10.0	5.0	-
B 3087b	6.1	7.5	3.8	10
91	6.7	7.8	4.3	15
94	7.3	7.5	4.5	9
87a	12.6	10.8	7.3	45
70	15.0	13.3	10.3	74
83	25.0	16.3	11.3	35
59	35.0	23.3	17.0	52
Pi3071	7.6	6.0	5.5	-
38	15.8	11.5	10.8	68
63	22.4	18.0	17.0	129
Po3102	5.0	bent down		-
104	5.2	6.3	2.3	5
100	5.1	6.5	3.5	9
3096	6.3	7.5	5.8	10
34	6.6	8.8	5.8	16
77	8.1	10.5	7.3	16
76	8.5	11.3	6.3	11
75	8.9	10.0	6.3	20
73	16.1	15.5	11.3	58
Q 3009b	5.1	3.0	2.5	-
99	5.1	3.3	3.3	-
44	5.4	3.5	2.5	6
3103	5.4	5.0	4.0	-
105	5.3	6.3	2.3	-
3004	5.9	6.0	4.3	4
46	6.7	4.3	2.5	7
64	5.3	6.0	5.3	7
89	7.0	4.8	2.8	-
67	6.1	7.3	4.5	8
85	8.7	4.0	2.0	-
65b	6.2	7.5	5.7	7
52	6.5	7.0	5.0	8
05	6.6	7.5	6.0	5
56	7.2	7.5	4.0	7
92	7.4	8.0	5.0	-
29	7.4	7.5	6.3	12
28	8.5	7.8	7.0	8
65c	8.9	9.8	7.8	16
65a	9.1	10.8	8.8	12
02	15.0	10.5	9.3	26
80	18.0	11.5	8.5	17
32	21.1	11.0	8.0	40
08	19.7	13.3	11.5	38
86	21.1	13.5	11.0	-
50	20.8	14.5	11.0	38
07	21.6	13.5	10.3	37
60	23.1	(8)	(3)	48
81	25.6	11.8	9.8	-
49	26.3	13.0	11.0	34
43	26.1	14.8	12.8	59
45	26.4	15.0	11.3	58
41	25.3	16.5	14.8	58
55	27.9	14.0	11.0	65
51	27.8	14.6	12.1	41
01	29.6	14.0	11.0	37
09a	34.5	15.4	10.0	50
57	34.0	19.0	14.5	55
82	40.1	16.0	11.0	52
78	40.5	16.7	15.0	78
40	41.8	17.3	14.0	71
33	51.4	16.3	10.8	83
93	50.9	17.9	13.9	101
98	55.3	19.0	13.7	59
36	58.0	20.5	16.0	198
Sa3101	5.7	7.0	2.5	8
3088	5.7	7.0	5.0	16

Table 8. (contin.)

Tree no.	Diam br h cm	Tree height m	Crown depth m	Increase in basal area cm^2
So 3037	9.6	8.0	4.0	7
68	10.6	8.5	4.0	9
03	10.8	9.8	4.5	6
39	11.1	9.5	7.5	5
53	11.1	8.0	2.5	3
61	11.5	9.5	4.5	22
62	11.2	9.4	5.2	8
84	12.2	8.3	4.3	-
31	12.3	9.0	4.0	14
54	13.2	10.0	3.3	5
06	15.1	11.3	6.5	29
10	15.2	11.3	5.0	13
66	15.5	10.8	3.5	8
48	16.1	10.3	3.8	16
72	16.6	10.5	7.0	16
90	17.6	12.0	9.0	26
69	18.2	(7)	(3)	39
74	19.5	11.0	6.5	19
97	20.2	12.5	9.0	33
T 3095b	4.2	7.3	5.5	-
58b	5.5	6.3	5.3	6
16	6.3			3
95a	6.3	7.3	5.5	-
79	6.4	6.0	5.5	-
23	6.9	Tilia clone (no.11-		9
42	7.3	27 and 42 about 11m		4
11	8.0	high and crown depth		7
20	7.9	about 6 m)		3
21	8.2			8
15	8.6			6
24	9.3			10
22	9.8			11
26	9.8			22
58a	9.3	7.8	6.8	10
25	10.5			17
19	12.0			20
13	12.1			15
12	12.3			10
14	12.2			22
27	13.1			33
17	14.3			23
18	14.9			26

[1] No. 3069 - 3105 measured in May 1969.

Explanations, see Table 7.

Table 9. Stand structure in sampling areas I, II:1 and III, each 0.25 ha. In brackets are given the conditions before clearing.

Species	I		II:1		III	
	Number of stems >5 cm at br.h.	Basal area spring 1968 m^2	Number of stems >5 cm at br.h.	Basal area spring 1968 m^2	Number of stems >5 cm at br.h.	Basal area spring 1968 m^2
Acer platanoides			28(74)	1.04(1.86)	5	0.01
Betula spp.	17(52)	1.45(2.8)	1(2)	0.04(0.12)	7	0.19
Fraxinus excelsior			–(1)	–(0.001)		
Picea abies	– (5)	– (0.17)	–(2)	–(0.09)	3	0.06
Populus tremula			1(11)	0.08(1.17)	9	0.05
Quercus robur	2(2)	0.18(0.18)	7(11)	0.87(0.91)	45	2.28
Salix caprea			1(1)	0.02(0.02)	2	0.01
Sorbus aucuparia			3(5)	0.01(0.14)	19	0.31
Tilia cordata			12(21)	0.99(1.21)	23	0.17
Total	19(59)	1.64(3.2)	53(128)	3.04(ca. 5.4)	113	3.08
Total per ha	76(236)	6.54(12.7)	212(512)	12.19(ca. 21.5)	452	12.30
Projection of tree crowns	22 %		56 %		48 %	
Number of hazel stools	14		31		137	
Number of hazel shoots	345		240		1778	
Tree and hazel crown projection	29 %		62 %		77 %	

probably lies at quite a considerable depth, perhaps not much higher than the water level of the lake and esker, which is approximately 24-25 m above sea level. No superficial water was noticed, as was the case in sampling area I. On November 19th, 1969, a soil profile was dug just to the south of the area in sedimentary soil (at 29.5 m above sea level). No ground water was found down to a depth of 70 cm.

The crown projection of the tree layer amounts to only 50%. The above-mentioned clayey sections lack large trees and, on the till, there are gaps between the crowns of some of the trees. The basal area amounts to 12.3 m^2/ha. The basal area for the unthinned forest on till and clay as a whole is 19.5 m^2/ha. Because of the relatively low density of the trees, the crowns are well-developed with a large crown depth, except for rowan, which is usually 8-12 m high and has a crown depth of only 4-6(9) m. Thus, there is no distinctive stratification of the foliage, thanks to the large crown depths, the saplings and the numerous shrubs. The subdivision into tree and shrub layers is, for this reason, somewhat artificial. The highest tree in the area was a birch, measuring 23 m in height. The tallest oak was 21 m high.

The tree layer was dominated by oak which accounted for about 75% of the basal area. The oak population is, in parts, old and well-developed. The two largest trees had trunk diameters of 58 and 55 cm respectively. In a stony section of the area is to be found a clone of lindens with numerous, narrow trunks. *Betulae* and *Populus tremula* are less frequent in this sampling area than in the uncleared woodland on till and clay as a whole. The opposite applies to *Quercus robur, Sorbus aucuparia* and *Tilia cordata*. Other species are to be found listed in Tables 8 and 9. The composition by species of the tree layer is similar to that found in sampling area II:1 but the distribution by basal area, on the other hand, is different, as can be seen by comparison with Table 9. Only a few age estimates for this particular area are available. The largest oaks are probably as much as 200 years old, cf. *Quercus* 4/25, 3a/15 and 3a/13 in Table 10. The high stump age of the four small oaks, with breast-height diameter between 6.8 and 9.8 cm, are surprising and depend perhaps on earlier grazing by roe-deer.

Beneath the tree layer and the gaps therein grows an upper shrub layer which is, in parts, dense and composed of hazel, Fig. 13c. Hazel crowns cover approximately 50% of the total surface. Trees and hazel bushes together cover approximately 77%. The largest and densest hazel thickets grow either in, or on the edge of, former glades with clay as the dominant component in the substrate. Apart from hazel, aspen and oak saplings are most frequent in the shrub layer. In Table 11 are to be found estimates of the number and the basal area of the tree saplings from two different observation periods. All tree species regenerate. In the lower shrub layer are to be found smaller examples of all the species, except for *Picea abies*. Within this category can be included badly developed bushes of *Juniperus communis*, numerous *Lonicera xylosteum* and *Ribes alpinum* and some examples of *Daphne mezereum*. *Corylus, Quercus* and *Populus* regenerate in the clayey glades as well as on the till. Frequent species in the field layer are *Anemone hepatica, Calamagrostis arundinacea, Deschampsia flexuosa, Convallaria majalis* and *Rubus saxatilis*. More frequent in the above-mentioned clayey depressions are *Trifolium medium, Deschampsia caespitosa, Lathyrus montanus* and *Viola riviniana*.

Table 10. Tree-age determinations; unless otherwise stated, from the winter of 1967/68.

No	Species	Age y.	Comments[a]	Estimated or measured diam. at br.h. cm
1002	Betula	73	Stump height	17
1003	"	75	" "	18
1004	"	74	" "	19
1024	"	72+	" " +1.8 cm	15
1025	"	71	" "	20
1028	"	80+	" " +0.4 cm	25
1029	"	75	" "	21
1034	"	76	" "	29
1040	"	75	" "	26
1001	Picea abies	31	" "	15
1013	" "	36	" "	28
1016	"	35	" "	17
1018	" "	34	" "	18
2001	Populus tremula	59+	" " +9.5 cm	38
2027	" "	68+	" " +12 cm	40
2030	" "	55+	" " +8.5 cm	29
2011	Picea abies	92	" "	25
2019	Acer platanoides	143+	" " +8 cm	25
2021	" "	160+	" " +2.4 cm	22
2042	" "	105	" "	18
2052a	" "	177	" "	27
2057a	" "	102	" "	27
2059	" "	86	" "	19
2033a	Betula verrucosa	105	" "	33
2034	Quercus robur	57	" "	13
2040	Sorbus aucuparia	79	" "	18
2048a	Tilia cordata	131	" "	40
3046	Quercus robur	39+	" " 1971/72 +0.5 cm	6.8
3052	" "	45	" " " ±2 år	7.1
3065a	" "	43	" " " "	9.8
3092	" "	43	" " " "	7.8
A	Quercus robur	118	" " 1969/70	26
100	" "	108	" " "	29
3/48	" "	90	" " 1970/71	28
1/42	Betula verrucosa	70	" " "	43
1/85	Sorbus aucuparia	80	" " 1971/72	12
4/9	Quercus robur	99	breast height "	36
4/25	" "	196+	" " "	41
3a/15	" "	206+	" " " +4 cm	43
3a/13	" "	175+	" " " +4 cm	47
1051	" "	66+	" " " +2.5 cm	24

[a] If the pith was missed or the centre of the tree was rotten the remaining estimated diameter is given. Trees with No. 1000- are from sampling area I, 2000- from sampling area II:1, 3000- from sampling area III. Other trees except No A and 100 are from the transects.

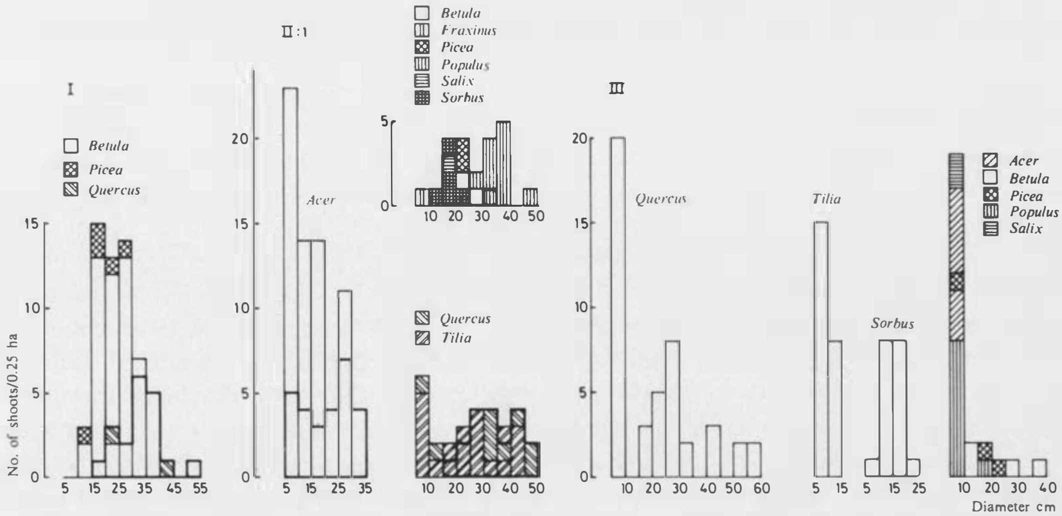


Fig. 15. **Diameter-class** distribution of trees at breast height. The columns represent the situation before the clearing. **The parts of the columns** with the bold lines show the situation after clearing.

Table 11. Basal area and number of tree saplings over 1.3 m in height but with <5 cm diameter at breast height in sampling area III.

Species	Spring 1969 dm²/ha	Spring 1969 No./samp. area	Spring 1971 dm²/ha	Spring 1971 No./samp. area	% increase in basal area, 2 years
Acer platanoides	5.60	31	7.65	40	27
Betula verrucosa	2.52	14	2.94	17	14
Picea abies	1.24	2	1.80	2	31
Populus tremula	24.92	140	28.79	161	13
Quercus robur	19.12	105	24.63	126	22
Sorbus aucuparia	7.16	87	8.06	99	13
Tilia cordata [a]	2.24	8	1.59	8	–

[a] One big *Tilia* was broken down.

Table 12. Measurement of throughfall in sampling area III during the autumn of 1971.

Period No.	Date	Incident rainfall, mm	Throughfall in percent of incident rainfall: minimum	mean	maximum
1.	16.8-27.8	1.1	0	57	131
2.	27.8-30.8	22.9	51	85	121
3.	30.8-3.9	21.1	42	79	115
4.	3.9-11.9	7.1	21	71	97
5.	11.9-17.9	6.9	26	82	119
6.	17.9-24.9	10.2	42	72	119
7.	4.10-16.10	24.4	47	86	107
1-7.	16.8-16.10	93.6	42	83	108

Measurements of interception in sampling area III

During the autumn of 1971 measurements of interception were performed in sampling area III. Eighteen one-litre plastic flasks were randomly distributed over the area (Fig. 13). The flasks were provided with funnels (19.7 cm in diameter). The edge of the funnels was about 25 cm above the soil surface. Two flasks with funnels of the same kind were placed on an open field about 240 m to the north of the sampling area. The measurements proceeded between Aug. 4th and Oct. 16th. The first rain was so heavy that all flasks were overfilled. For this reason, the measurements did not start before Aug. 16th. Unfortunately, an interruption in measurements had to be made between Sept. 24th and Oct. 4th.

On Oct. 16th, when the measurements were terminated, aspen, birch and hazel were nearly totally defoliated, but oak only partly, with autumn-coloured leaves. Only the throughfall, i.e. the water that has percolated through the crowns, was measured. The stem flow was not estimated.

In Table 12 the precipitation on the open field during the different periods is given. The two funnels on the open field recorded nearly exactly the same precipitation during all periods. In the same table the mean, maximum and minimum values of the throughfall as a percentage of the open-field values are included. On the map, Fig. 13, the measuring points are indicated and the mean values of the throughfall.

As an average for the whole period the throughfall was 83%. The greatest percentage of interception was measured during period 1, with low precipitation. During period 5, with only 6.9 mm rain, the interception was somewhat lower than during period 3, with three times as much precipitation. The interception was about the same during both period 2 and period 7, despite the fact that the leaves had partly fallen.

The distribution of the amount of the throughfall between the measuring points was different in the separate periods. Period 1, with little rain, had greater dispersion than the other periods. Period 2, 3 and 7 received about the same amounts. During periods 2 and 3, five and six flasks respectively received over 100% of the precipitation on the open field, but during the last period, 7, though it occurred during the leaf-fall period, only one flask trapped more rain than the flasks in the open field.

Great differences were found between the different measuring points. Two flasks, Nos. XIV and XV, constantly received, with one exception, less throughfall than the other flasks. They were situated below an aspen and a hazel bush respectively. Flask No. I received, during five out of seven periods, greater amounts than the flasks in the open field. During the last period, however, this flask got comparatively less precipitation. Other interceptions were more varying. For example, bottle No. XII received, during the different periods, between 23% and 117% of the precipitation in the open field.

If a measure of the whole interception of the tree and shrub layers is aimed at, the stem flow also has to be measured. Observations in the sampling area indicated that the stem flow was insignificant in all trees, except in aspens, which were small and few. The oak trees, whose basal area makes up about 75% of the total, had thick, fissured bark and the branches grew at great angles to the stems. Both attributes reduce stem flow.

According to White & Carlisle (1968) the stem flow, as measured in l per basal area, was greater in birch than in hazel, which, in its turn, had greater stem flow than oak. The stem flow in hazel was about three times greater than in oak. In a mixed deciduous thicket, with oak, ash, birch and hazel, the stemflow contributed to 9.9% of the total throughfall. Carlisle et al. (1967) measured the same relative value to 2.1% in an oak high forest.

The mentioned values for stem flow were received in closer stands than the stand at Andersby. The stem flow ought, for that reason, only to a small degree, possibly with the exclusion of the stem flow on hazel and aspen, to have an effect upon the interception in the study area.

More flasks were placed below crowns than corresponding to the relation between crown-covered and uncovered ground. The interception over the whole area probably was, for this reason, in addition to the stem flow, somewhat lower than 17%. In Andersby, much of the autumnal precipitation falls as drizzle, which is likely to give a comparatively greater proportion of interception. The winter precipitation is, during normal winters, prevailingly snow, which in a deciduous forest—in contrast to conditions in coniferous stands—probably diminishes the interception during the winter (cf. Geiger 1966, p. 37), though the actual throughfall in winter depends on the frequency of wind, thawing and insolation. About 20% of the precipitation falls as snow (Pershagen 1969, p. 49).

Carlisle et al. (op.cit.) estimated the interception during the whole year to 10.6% and White & Carlisle (op.cit.), during the foliated period, to 16.7% and, during the leafless period, to 12.1%.

During an autumnal interception study in an *Ulmus-Fraxinus* stand in Vårdsätra Naturpark (40 km SSW of Andersby), J. Cuttaree found a tendency towards a reduction in interception with a reduced amount of leaves (Cuttaree 1966). On Nov. 1st, when the trees were leafless, at a rain intensity of 2 mm/h, Cuttaree measured an interception of up to 23%. In this study, only the throughfall was measured and ash has at least higher stem flow than oak (White & Carlisle, op.cit.).

A detailed study of interception, throughfall and stem flow has been carried out by Bengt Nihlgård in South Sweden both in a beech stand and in a spruce stand (Nihlgård 1970). The precipitation during the years investigated amounted to about 1000 mm. In the beech stand, the stem flow was measured to as much as 11.4% of the precipitation in an open field. The corresponding value in the spruce stand was only 2.6%. The yearly throughfall in the beech stand amounted to 70.9% and, in the spruce stand, to 57.5%, and so, the estimated interception was 17.7% and 39.9%.

Beside the interception in the tree crowns, Carlisle et al. (op.cit.) also measured that portion of the precipitation caught by *Pteridium aquilinum*. During the course of four months, the fronds of *Pteridium* intercepted 12.7% of the throughfall which had bypassed the tree crowns. This was somewhat less than the amount intercepted by the oak crowns during the same period. Annual interception by *Pteridium* was 3.7%. In the glades, the cover of the field layer is higher than beneath the crowns (H. Persson, pers. com.) and the interception in the field layer is probably also higher in the glades, though it will not reach the interception value of the tree layer.

In a study of the water consumption in a spruce stand, Stålfelt (1944) measured the interception in the tree layer and in the bottom layer and the litter. The interception in the bottom layer and the litter beneath the crowns amounted during May-August to 18% and, during September-April, to 9%.

The amount of precipitation which reaches the ground and can be absorbed by the tree roots may thus be considerably lower than the measured throughfall through the tree and shrub layers.

Winter biomass, wood increment and bark production

Introduction

Research into forest production, carried out for forestry purposes generally aims at ascertaining the stem volume and the increase in the stem volume, starting with individual trees and proceeding to entire stands and area units. Because of the emphasis on merchantable timber, branch and twig increments have generally been overlooked. However, in more recent times, there has occurred an upsurge of interest in increment and production rates as a whole. Since scientists became interested in obtaining figures for the total net primary production of trees and shrubs, there came into consideration, apart from increment in branches and in other sections of the tree, that type of production which does not result in lasting biomass changes, but in the formation of litter, consumption by herbivores and insects etc. In attempting to transfer the latter into biomass terms, one comes across many problems. Different researchers' solutions to these problems are discussed in a few special cases.

If one strives to arrive at a picture of the net primary production, it is not sufficient to express growth in units of volume since several terms such as bark growth and litter-fall are more suitably expressed in units of dry weight. It is also necessary to use weight as a basis for comparison within an ecosystem with different species of trees and, in like manner, between different ecosystems where the (basic) wood density of the same species can vary. It is also possible to convert dry weight into units of energy, because the heat of combustion for various bulk materials varies comparatively little in woody species.

Kira & Shidei (1967) and Newbould (1967) cite two different ways of estimating net primary production. In the case of the first method, the biomass is estimated on two occasions and the production figure is obtained by adding the losses of plant material which occurred between the two periods to the difference in biomass, whether the latter be positive or negative. With the second method, the biomass is measured on one occasion only. Simultaneously, the increment during the last year or, for example, the last 5 years, is measured and calculated. This apparent increment together with that produced and measured as plant-material losses during the period in question accounts for the net primary production. The latter method has been implemented throughout the course of this study. One of the greatest difficulties with this method is to distinguish how much of the material in these losses was produced prior to the commencement of the period of measurement. This latter amount should, of course, in principle, not be counted.

The task was to estimate the weight of the different above-ground parts of single, selected trees which were representative of the different species and diameter categories. The most accurate estimate of the biomass is probably obtained if the tree in question is felled, and all its parts weighed, subsamples being taken and weighed again after oven-drying. During the course of this study, which was made in a future nature reserve, only a limited number of trees could be felled, viz. 4 large and 11 small ones. The volumes of the stems of all the other trees used as samples were estimated—see below—and the volume values were converted into biomass (dry weight) while branches were weighed directly with the help of sawn-off samples. All in all, 35 trees were investigated in this way apart from the 4 and 11 mentioned above.

The present increment measurements were concerned with the formation of stem and branch wood from 1967 until 1971, i.e. 5 years of growth, as well as the annual shoots which had been produced during 1971. The growth of bark was calculated but not measured.

Methods

Selection of sample trees

For the purpose of the investigation, the production of the ecosystems was of more importance than its total living mass, the biomass. Therefore the production aspect determined the selection of the trees to be used for sampling purposes. Trees within their respective sampling areas were subdivided into diameter categories, after which the percentage increase in their basal area was calculated. Trees with a median increment were selected as representative for each category. The trees sampled were distributed within the sampling areas in the following way: 6 in area I, 11 in are II:1, 21 in area III and the remaining 12 in connection with the transects studied by Brunner (1972).

Field and laboratory measurements

The following method was used on *standing trees*. The volume of the trunk was estimated by measuring the circumference at different heights along the trunk. The latter was thus divided into a number of imaginary "logs". At each point of measurement, one or more increment cores were bored. In the laboratory, these cores were used for measuring the width of the annual rings. The thickness of the bark was measured in situ in the field. In trees with several stems, the latter were measured one by one. The upper diameter of the imaginary top log could be measured only in exceptional cases and had to be extrapolated from the nearest diameters. Errors thus arising with regard to the total volume of the bole are of minor importance. An increment core was bored out from the middle point of the last "log".

The top of the tree was, in some cases, included among the branches and in others specially treated. The limit between the trunk and the top section was modified in each case to suit the shape of the particular tree in question. The trunks' end-diameters varied from 1 to 13 cm, with the majority lying between 5 and 10 cm. Trees were climbed, the branches counted and, if the need arose, divided into different size categories. Whenever branches were into different strata, the sample branches were taken from each stratum by subjective selection. In the case of unstratified sampling, branches were sawn off at regular intervals.

The sawn-off branches were weighed separately and their end-diameters were measured.

After weighing, the brances were sawn into sections at those points where the diameter (on bark) measured 1, 2, 3 . . . . cm. The thicker part of the branches were sawn up at intervals of 2 cm. Birch branches and hazel stems were sawn up at those points where the diameter measured 0.5, 1, 2, 3, ... cm. The length of these samples varied from a couple of centimeters to around 7 dm. Sections from all sample branches, or if the branches were stratified, from the samples within the respective stratum with the same end diameter, were weighed together.

Thereafter, as many as 7 samples from each diameter category were selected and weighed one by one, after which a disc was sawn out at the point of mean cross section, the corresponding diameter, D_m being calculated by means of the formula:

$$D_m = \sqrt{\frac{D_1^2 + D_2^2}{2}}$$

in which D_1 and D_2 refer to the end diameter.

This discs were then put into plastic bags. In the laboratory, the portion of bark was estimated as well as the dry matter of the bark and wood. The diameter of the wood in each disc was measured from 2 different directions; the diameter minus the last 5 annual rings was also measured.

Likewise, sample twigs were selected from the finest branches <1 cm (<0.5 cm in birch and hazel). The current shoots were pinched away, after which the remaining twig was treated in the same way as the other samples. The current shoots were taken to the laboratory, where the buds were separated from the shoots and the dry weight was estimated. This task was especially complicated in the case of *Quercus robur* where, in many cases, two generations of shoots had been formed. The shoot generations have been kept separate and, in cases of doubt, the number of annual rings was checked.

All attached dead material was weighed on its own. Subsamples were used for dry-weight estimates.

The weighing of branch sections and samples was carried out in the field using two balances, each with a different capacity. The more sensitive one had a capacity of 0.01 g to 2.5 kg. Discs, current-year shoots and buds were weighed in the laboratory.

The *felled trees* were weighed. The trunk was divided into a number of logs and a disc was sawn off each basal end and the top end of the uppermost log. These discs were taken to the laboratory in order to estimate the content of wood and bark as dry matter, as well as to measure the diameter and the increment in growth during the last 5 years. All branches were weighed, after which sample branches were taken which were treated as outlined above.

Calculation of biomass

Trunk. The volume of the trunk was calculated from the circumference measurements. Between each point of measurement, the trunk was assumed to have the shape of a truncated straight circular cone. This method gives slightly erroneous values when the trunk tapers unevenly, especially for the basal section, which tends to be over-estimated. For this reason measurements of the basal "log" were taken at a shorter distance from ground level. The measurement of the circumference gives a somewhat higher value of the basal area than the measurement of two diameters, since there is an approximation to the area of a circle, which is the greatest surface which can be inscribed within a given circumference. If the ratio between the longest and shortest diameter is 1.5, the formula for the surface area of an ellipse gives a value which is roughly 6 % lower.

Inclined linden trunks are usually almost oval in shape. Therefore, diameters of these trees were measured instead of circumferences. The diameter of the wood was calculated by subtracting the double thickness of bark from the trunk diameter. The volume of wood was then calculated in exactly the same way as the trunk volume. The difference between the volumes was assumed to represent the volume of bark. There were certain difficulties in measuring correctly the bark thickness on stems which had formed fissured bark. An average value has been used. As the circumference includes the maximum thickness of bark but the diameter of the wood is calculated assuming an average bark thickness, the figure arrived at for the volume of wood will be somewhat high, but, the volume of bark has been calculated more accurately.

Certain trunks were measured as late as the summer of 1972, but then that year's volume of wood was subtracted.

In order to convert volume into terms of dry weight, the basic density of the wood and bark were estimated. The volume values needed were obtained by measuring the amount of liquid displaced by samples of wood with and without bark. The samples were covered with a thin film of plastic. When calculating the biomasses, a mean value of these measurements was implemented.

The basic density varies not only between members of the same species but also within the same trunk. According to Peterson & Winquist (1960) in J. Fries (1964, pp. 152-154), there was no significant correlation between the variation in the basic density and the point in the tree at which the sample was taken. The basic density of birch wood was stated to lie between 0.48 and 0.53.

The basic density of the wood of deciduous trees, at least those with ring-porous wood, increases in relation to the width of the annual rings. Therefore, one can expect different densities within a trunk cross-section if, for example, growth during the last few years has increased. Likewise, an oak branch which is slow-growing and comprises almost only early-wood ought to have a different value from the trunk. The variations measured were not regularly distributed in any of the trunks of the species studied. Variations registered in the same tree and between different trees of the same species, in connection with the somewhat primitive experimental equipment, imply that the values employed are not very precise. However, their moderate precision is less important than their good representativeness, resulting in acceptable accuracy for the material and purposes of the present study.

Below can be found a comparison between density values in Mork (1966) and those obtained by the present author:

	Mork	Hytteborn
Acer platanoides	0.62	0.58
Betula spp.	0.61	0.54
Populus tremula	0.42	0.47
Quercus robur	0.67	0.64
Sorbus aucuparia	0.60	0.55
Tilia cordata	0.49	0.39

My values are lower than those arrived at by Mork, except in the case of aspen wood. The greatest difference is to be noted with regard to the density of linden wood, where the present author's value is very low.

Branches. The accurate categorization of branches into sections with determined end-diameters was carried out in order to enable the estimation of the increment in branches—see below. The fresh weight of the wood and bark of all the diameter categories was calculated using the branch discs which were transported to the laboratory. From the dry matter contents of wood and bark, the dry weight of both could be calculated and, finally, a figure could be arrived at which showed the total dry weight of the sample branches. By comparing the total number of branches on a tree or in the respective strata with the number of sample branches and the results obtained from the latter, the biomass of the branches could be calculated.

Finally, by adding together the trunk biomass and the branch biomass one obtains a figure for the tree's total wood and bark biomass.

Calculation of wood increment

The increment in the wood volume of the trunk was calculated by determining the increments for the final 5 years' period, i.e. 1967-71, from the wood diameter and the annual rings as measured in the increment core. The wood volume in the autumn of 1971 and the spring of 1967 was calculated and the difference between the 1971 and 1967 figures divided by 5 provided a figure for the average annual increment in trunk volume. The latter value was then multiplied by the above-mentioned basic density, giving the trunk's production of wood mass.

In the laboratory, the ratio between the annual mean increment in the cross-sectional area and the total cross-sectional area of each branch was calculated from the discs. If discs lacked five annual rings, a corresponding calculation was carried out for the outermost ring. Assuming that the ratio was representative for the entire section and that the density remains constant throughout the entire cross-section, the increment in wood was obtained by multiplying the ratio by the weight of the wood section.

When this had been achieved, a mean sample ratio between annual increment and biomass of wood was calculated for the particular diameter category. Taking into consideration the entire category's wood biomass, it was then possible to work out the wood increment of the category. The wood increment figures for the different categories were added, and by multiplying with the relationship between the number of branches on a tree and the number of sample branches, the wood increment of all the branches was reached. To this was added the biomass of the current year's shoots, but excluding buds, which were regarded as representing a future generation of shoots.

Calculation of bark production

In the biomass tables, it can be seen that the production of bark is of great importance, and in Table 16, it can also be seen that bark production can exceed wood production in the finer types of branches. The production of bark has not been measured but a method of calculation, in accordance with the literature quoted, has been used in order to give an approximation. The calculation rests on the quite uncertain assumption that the percentage of new growth for a piece of stem or branch is the same for wood biomass and bark biomass. The calculation does not give the increment in bark but is assumed to represent more fully the net production. This assumption probably leads to an underestimation of bark production in trees on which the bark remains fairly thin even on thick stems and branches (e.g. *Fagus, Picea,* thin-bark specimens of *Betula* and *Populus*). The bark biomass in each log and in each branch category has been multiplied by the above-mentioned ratio found for wood. Whittaker & Woodwell (1968, p. 5) applied this method to the trunks of trees and Duvigneaud et al. (1971, p. 43) to the branches.

Calculation of the stand's biomass and increment

Regressions are, nowadays, probably the most common method of converting the biomass or production of a number of individual trees or tree-parts into an expression of the entire stand's biomass and production—see e.g. Kira & Shidei (1967), Newbould (1967), Whittaker & Woodwell (1968), Bunce (1968). In Sweden, F. Andersson (1970b) and Nihlgård (1972) have employed a regression between the logarithm for diameter^2 · height and the logarithm for the biomass or production. Regressions of this type are often more or less linear, though, when diagrams are drawn on log-log paper, the linearity may be somewhat deceptive, as the deviations appear small due to the log-scales.

In the course of this study, the biomass of the stand has been calculated by multiplying the weight of the sample tree or tree-part by the ratio of the total basal area of the category to the basal area of the sample tree; while the increment of the stand has been worked out by multiplying the increment weight, as outlined above, by the ratio of the total increment in basal area to the increment in basal area of the sample tree.

Estimation of the shrub layer

From the description of the three sampling areas, it can be seen which species are quantitatively significant in the shrub layer. The biomass and production of hazel was measured in sampling areas I and III. In sampling area II:1, the suckers produced by the roots of felled aspens (*Populus tremula*) were measured. Sampling in area II:1 was carried out jointly by Hans Persson and the author on August 30th, 1971. The foliage on the suckers had not yet been shed. Sampling of *Corylus avellana* took place during the autumn of 1971 and the spring of 1972, when the shoots were defoliated.

The number of *Corylus* shoots was counted. The hazel shoots were treated in the same way as the branches, see the relevant section in the present work.

The number of aspen suckers was obtained from Hans Persson who had estimated these from analyses carried out on 121 1/4 m^2 plots randomly distributed in sampling area II:1. The figure arrived at was 3.27 shoots per m^2. 11 stems were selected from area I, 10 from area II:1 and 21 from area III.

The aspen suckers, the majority of which were only four years old, were cut off at each bud-scale scar and sections with the same age were weighed together. An average value of the dry weight of each sucker and of each age section were estimated. The biomass was estimated by multiplying by the number of suckers per m^2. In order to calculate the increment, the mean weight of the 2-year-old section of a sucker was divided by 2, the 3-year-old by 3 and the 4-year-old by 4. The remaining sections were divided by the respective basal age. These figures plus the mean weight of the current shoots comprise the estimated production of wood and bark. Attached dead material amounted on an average to approximately 0.3 g/sucker. No other part of the losses of plant material was assessed.

Discussion of methods

For a description of several suitable methods see Newbould (1967). The following discussion follows the same outline as that in the section on methods.

The selection of suitable tree material was concentrated to choosing a tree with an average growth within a limited diameter category. Thus, there was a reduction in dispersion in the material. It is therefore possible that the calculation of increment is more accurate than would have been the case if the trees were sampled completely at random.

Motives for merely measuring the volume of trunks and not the weight are many and varied. First and foremost, it is a simpler and speedier method. Even when the weight of the trunks is being estimated, the trunk volume is often calculated since wood and bark have different bulk densities and often different water content—see Whittaker & Woodwell (1968). Because of the uncertainty in the estimation of basic densities, the errors were probably greater than if the stems had been weighed.

A check over how great the error may be is shown in Table 13a. Here are compared the dry weights of two felled oak trunks calculated in two different ways. By means of the first method, the fresh weight of the log was converted into dry weight using merely figures for dry material percentage while, using the second method, the wood and bark volumes of each log were calculated according to Smalian's formula and then converted to dry weight, using densities for conversion purposes. The differences between the two methods are acceptable.

A preliminary investigation showed errors over 100% in the estimation of branch biomass,

Table 13a. Comparison between actual weighing and the determination of weight by volume of two stems (wood and bark).

	Quercus A	*Quercus* 100
Fresh weight, kg	285	423
Dry weight, kg [a]	181	253
Volume, total dm^3	305	449
Volume, wood dm^3	254	379
Volume, bark dm^3	51	70
Estimated dry weight from volume, kg [b]	178	263
Differences, kg	– 3	+ 10

[a] % dry matter, in A 63%, in 100 60%

[b] Basic density, wood = 0.624; bark = 0.383 kg/dm^3

Table 13b. Comparison between different ways of estimating the branch biomass.

	Quercus A	*Quercus* 3/48
Total branch fresh weight, kg	115	107
Estimation by (kg):		
systematic sampling (deviation, %)	97 (−16%)	86 (−20%)
regression of basal diameter/ fresh weight (deviation, %)	138 (+ 20%)	113 (+6%)

when only systematic sampling was applied to branches with great differences in size. Therefore, as mentioned, when this occurred, the branches were stratified. Another way would be to establish a regression between the weight of the branches and their basal diameters, see Whittaker and others. A comparison of these two methods is to be found in Table 13b.

Systematic sampling gave, in both examples, lower values than the real, while just the reverse was true in the case of regression analysis. Nevertheless, it is impossible to determine which method is the most accurate from this comparison. In order to be able to use regressions, it would first be necessary to saw and weigh a sufficiently large number of branches, and to convert fresh weights into dry weights and to measure the basal diameter of the branches on the trees used in the sampling process.

Hughes (1971) estimated increment in the following way. He set up a regression between the diameter at breast height and the biomass of the tree. The diameter of the trees five years earlier was estimated from increment cores. Likewise, the bark thickness five years earlier was calculated. Subsequently it was possible to establish a relationship between the diameter at time t and at time t-5. The biomasses at the two points in time were calculated by using the above-mentioned regression. The biomass at time t minus the biomass at time t-5, gave the 5-year increment in growth. The same method of calculation was also used in the Meathop Wood studies, see Satchell (1971). It is, however, probable that the regression had altered during this period of five years. A dominant tree at time t was, in all probability, dominant also at time t-5, but attained the same weight as one of the thinner trees at time t, which may admittedly be a rather smothered tree. The largest uncertainty is probably due to the fact that the proportion of branches is usually greater in a dominant tree than it is in a smothered one of the same diameter. Furthermore, it is probable that thinning alters the appearance of the regression by causing diversiform growth patterns.

Measuring the production of the branch canopy by means of counting or measuring the annual rings is very time-consuming. Since trees in Andersby display a great deal of ramification and measurements of branch production are few in the literature, it was deemed essential to measure this production with a relatively great deal of care. Branch production is measured in a similar way in the studies at Virelles-Blaimont (see Duvigneaud et al. 1971; cf. also Satoo 1968).

Whittaker (1962, 1965), F. Andersson (1970b) and Nihlgård (1972) made use of a growth-increment factor, the weight of the branch in relation to its age. The growth-increment factor was obtained from a regression between the logarithm of the branch age and the logarithm of its weight. Whittaker (1965) investigated the precision of this method, as compared with annual ring analysis of branch sections, and found that the first method overestimated production in one case by 22% and, in another, by 6%.

Whittaker's method presupposes that the age of the branch can be ascertained with certainty. This was singularly difficult in the case of certain species, e.g. *Betula* and *Tilia*. Whenever the age of the branch can be estimated with speed and reliability, this method is certainly quicker than that used in this study. By using the method employed in this study, it was necessary to distinguish only the last five years of radial growth.

Van der Drift (1971) discovered in his study-areas that the width of the annual rings of *Quercus robur* varied within narrow limits of about 1 mm regardless of whether the annual rings were measured in the trunk or in the branches. A relationship was calculated between the growth increment of the trunk and two branch groups. With a knowledge of the trunk growth and the weights of the branch groups, the production of the branches could be determined. The width of the annual rings of oak-trees in Andersby does not vary in such a simple manner, mainly due to the variations in age and the effects of clearing and thinning.

The method used for calculating bark production was somewhat dubious, as already stated. The difficulties involved in measuring bark increment are many and have not been overcome, as yet, by any method. The bark peels off or is detached as flakes which are difficult to measure in the litter fall to any degree of satisfaction. Formation of annual rings is only exceptionally found and then, only discernible in the youngest phloem, but hardly in the corky layers (rhytidom). Growth in most barks takes place in two (or more) cambia, and some of the cells formed are, later, more or less resorbed. An anatomic determination of bark growth seems extremely difficult. However, the calculated values for bark, though possibly too low, are so high that the growth of bark must be taken into consideration when an estimation of net production is aimed at. This is all the more important with regard to the study of the distribution and circulation of minerals since bark, as a rule, has a higher ash content than wood (Srivastava 1964).

Whittaker & Woodwell (1968) name two other methods for calculating the production of bark. With one method, the dry weight of the bark is divided by the mean age of the log; with the other, used by both Whittaker (1962) and F. Andersson (1970b), the thickness of the bark is plotted against age. The curve thus obtained shows the net growth rate (in thickness) at different periods of time. In order to obtain the increase in volume, the increase in the circumference of the tree must also be measured. The first of the above-mentioned methods doubtless underestimates the production of bark (Whittaker & Woodwell 1968) while the other requires an estimation of age, which in itself can prove difficult for certain types of branches.

The annual bark production has been calculated for three sets of branches in two other ways. Firstly, the bark biomass of the branches sampled was divided by the age of the oldest branch. With the second, the biomass of each branch category was divided by the age of the category. A comparison of the results obtained by these two methods and the standard method outlined above is to be found in Table 14.

Table 14. Comparison between different ways of estimating bark production, see text, relative values.

	Quercus		*Betula*
	3093	5/21	2/10
Method used in this investigation	109	123	107
Each branch-class biomass/ class age	100	100	100
Branch biomass/oldest branch age	22	26	71

Though even the standard method used, as stated above, will very likely result in too low production figures for thin bark, it gave the highest estimate of bark production. If bark production is calculated by dividing by the age of the branches, the result that follows turns out to be a considerable underestimation. The estimated bark production of *Quercus* species tallies well with the results obtained by Duvigneaud et al. (1971).

Recently Staaf (1974) described a comparison he carried out on a *Fagus* tree between three methods of calculating branch production. This author compared the methods used by Duvigneaud et al. (1971), by Whittaker (1962) and by van der Drift (1971). The latter method—see above—gave a higher estimate than the other two. The lowest value resulted from Duvigneaud's method. This method resembles, as has already been pointed out, the one used in this study.

In order to determine which method is the most sound, as regards the measurement of branch growth, further studies are required. Notwithstanding, it is of interest to note that both Staaf (op.cit.) and Whittaker (1965) obtained a slightly higher value with the regression method than by analyzing the annual rings.

Baskerville (1965) has demonstrated in a thorough investigation of methods, used in the estimation of the biomass of a stand of balsam firs, divergences of between −50.2% and +47.8%, depending on which method of selection was used in the choosing of a sample tree. The tree with mean volume gave better results than the tree with mean basal area, mean diameter or mean height. The best estimate of the different tree parts was obtained if a stand table was employed.

Ovington et al. (1967) carried out an investigation into biomass methods in a *Pinus radiata* plantation in Australia. Three main methods were tested, namely (a) the unit area method, (b) the average tree method, (c) regression analysis. Method (a) was merely simulated and produced large percentage errors. Out in the field, one comes across the problem of measuring, in as accurate a way as possible, a volume distributed over a unit area. With regard to methods (b) and (c), Ovington states that "the best of the average tree and of the regression analysis methods gave comparable accuracies for the same intensity of sampling. These methods could also be applied in more diverse forests with a multiplicity of tree ages and species, provided the population was grouped appropriately for sampling". With method (b), a manifest improvement in accuracy was achieved if the weight of the sample tree was multiplied by the ratio of the total basal area to the basal area of the sample, and not by the number of trees. Even better results were obtained by combining basal area, the height of the tree, the crown depth and the diameter of the crown.

The reason why, in the present study, the basal area and the increment in basal area are the bases for the calculations, and not the multispecific regressions, is that the number of sampled individuals is small in relation to the multiplicity of species. A reasonable assumption was, also, that basal area increments are more closely related to total growth than the diameter or the square of the diameter multiplied by the height. The method presupposes that the ratio of the basal area increment of the category to that of a single tree is proportional to the ratio between volume increments, a supposition which applies strictly, only if the increment in height is the same for all the individuals within the category.

Bunce (1968) obtained different regressions for different deciduous species and also for the same species from different sites. The 95% confidence limits amounted to 30% in the upper end of the regressions, despite the number of samples being between 10 and 27. The combined species regression gave a lower confidence limites but the most valid prediction was provided with the regression for the separate species and sites.

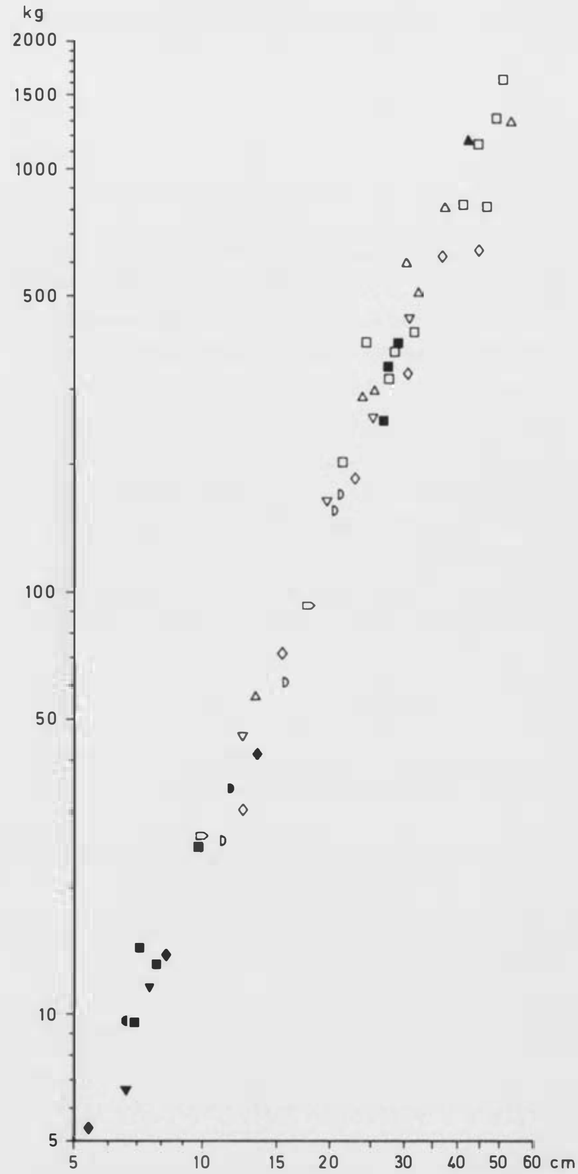


Fig. 16. Relationship between log biomass of tree (dry weight) and log diameter measured at breast height. *Acer* ▽, *Betula* △, *Populus* ⊃, *Quercus* □, *Salix* ◖, *Sorbus* D, *Tilia* ◇. Felled trees with filled symbols.

Results

Biomass of individual trees

The biomasses of the trees measured during the winter of 1971/72 are to be found plotted against the diameter at breast height in a logarithmic diagram, Fig. 16. Evidently, there is a relatively good linear correlation. This is usual with this type of regression and has been pointed out by a number of authors, among others Bunce (1968). Through the choice of log-log scales, the large differences which exist, especially between the larger individuals, appear less distinct. The dry weight of the tree samples varied from 5 to 1600 kg. The stoutest trees were *Quercus* and *Betula*.

The relationship between the diameter and the biomass is affected not only by the different basic densities of wood and bark of the different species but also by the variations in height and the variations in the portion consisting of branches. The relationship is easiest to observe in the case of middle-sized trees. The height increment and the proportion of branches is probably most variable in the largest trees and this could explain the poor relationship with the diameter. The height development of the smaller trees, on the other hand, varies because of the difference in competition from surrounding, dominant trees. When log D^2h was plotted against the logarithm of the biomass, there was a gentle upward swing in the lower section of the graph. A linear fitting produced a somewhat lower correlation coefficient than the above-mentioned relationship. The dispersion was great in the upper section of the graph. This indicates that the variation in the proportion of branches was greater than the variation in height. Linden trees, for reasons already pointed out, have lower biomasses than other species with the same diameters.

In Table 15 can be seen the distribution of the biomass in two felled oaktrees, which were hewn in the autumn of 1969. The amount of foliage on the tree which had all its leaves at the time of sampling amounted to 3.2%, a percentage which agrees with the state of affairs in sampling area III. Rodin & Bazilevich (1967) give 1.5-2 or 3% of the aboveground biomass and as much as 5% in young stands. Branch-wood and branch-bark biomass amounted to 26% in one tree and in the other to 28%. Wolfgang Brunner (1972) has estimated the biomass distribution and increment in two more felled trees.

Table 15. Biomass distribution of two felled *Quercus robur* (85°C).

	Quercus A		*Quercus* 100	
Age	118 years		108 years	
Diameter 1.3 m	26.4 cm		28.8 cm	
Height	13.55 m		17.55 m	
Biomass	*kg*	*%*	*kg*	*%*
Total above ground	262	100	353	100
Bole, total	181	69	254	72
Bole, wood	155	59	231	65
Bole, bark	26	10	23	7
Branches, wood and bark	73	28	92	26
Leaves	8.3	3.2	6.6[a]	1.9[a]
Dead branches[b]	6.6		3.9	

Days of sampling: QA: 9-12.9.1969; Q100: 9-10.10.1969[a]

[a] At the time of the latter sampling, some of the leaves had already fallen.

[b] Not included in biomass.

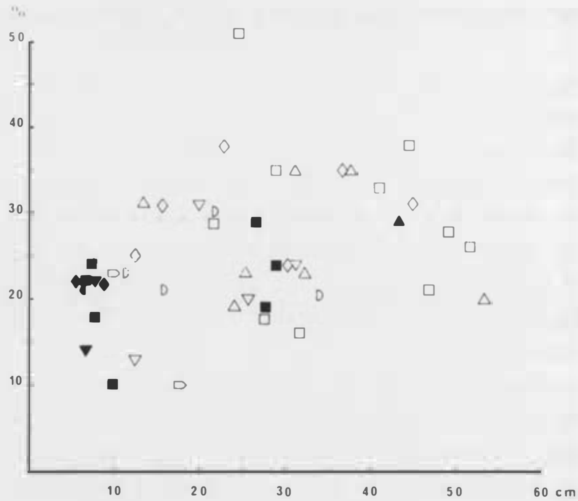
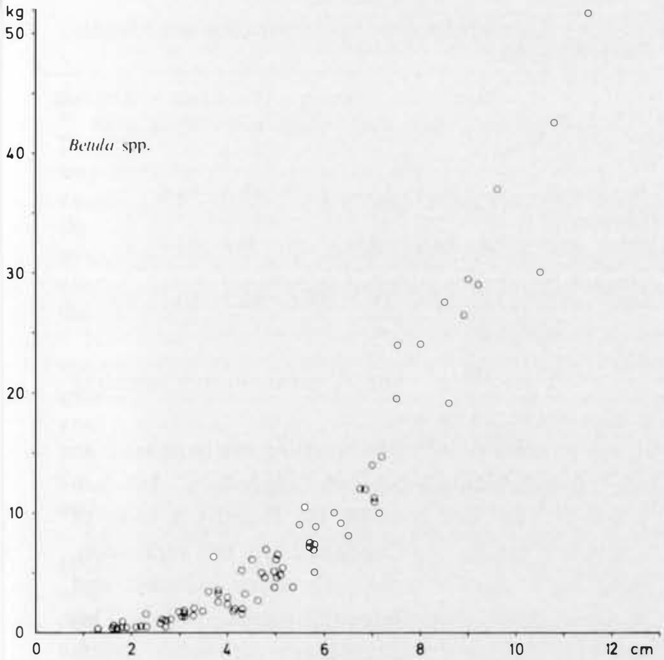


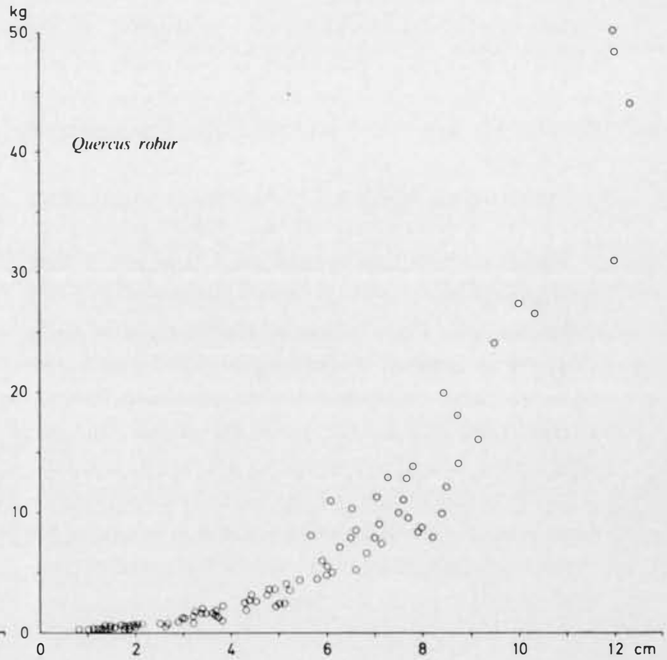
Fig. 17. Relationship between branch biomass as a percentage of tree total above-ground biomass (dry weight) and diameter at breast height. Explanations of symbols see Fig. 16.

The percentage of the branch biomass varied greatly—see Fig. 17. This was to be expected since the trees had grown in different densities. The two oaks, for example, in sampling area I had high percentages of branches, while the two oaks in sampling area II:1 had low ones. This difference can be directly explained by the fact that, prior to clearing, sampling area II:1 was rather dense with a basal area of something in the region of 22 m^2/ha, while sampling area I was relatively open even before the clearing operations. A very weak trend towards increased proportion of branches with increased diameter could possibly be obtained from the graph. The number of tree samples was so small that it was impossible to extrapolate any differences in the branch percentage of the different species.

The branch weight, in relationship to the branch diameter measured above the basal swell, is plotted in Fig. 18. Birch branches are somewhat heavier than oak branches with the same basal diameter. In order to be able to estimate the branch biomass by using this correlation, the different species must be treated separately. A comparatively linear relationship would probably be obtained if the material were presented logarithmically. However, then the dispersion would appear less distinctly.

In Table 16 is shown, by taking one example from each species, how the proportion of wood alters with the branch diameter. The proportion of wood is significantly higher in the trunks than in the branches





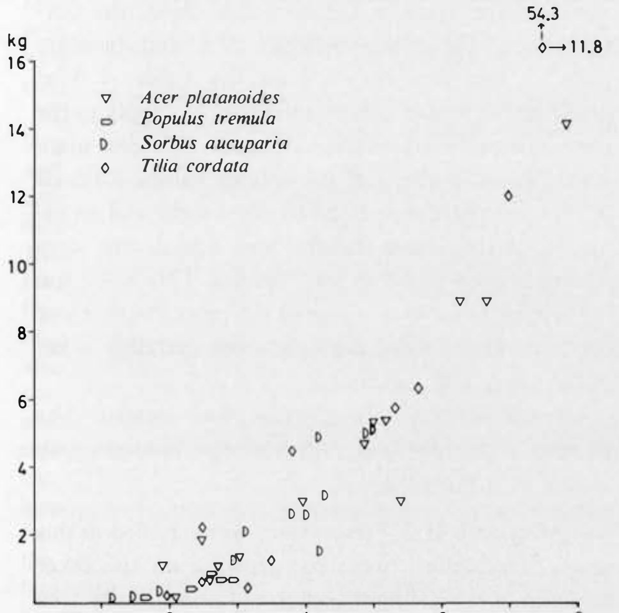


Fig. 18. Relationship between fresh branch weight and branch diameter, measured above the basal swell.

and also higher in thicker branches than thinner. In the lowest diameter category for linden branches, there is more bark than wood. In some cases, the same was observed in birch. Linden has a lower proportion of wood than other species in its branches and smaller trunks.

Biomass conditions in the sampling areas

The estimated biomass of the tree layer in the sampling areas is given in Tables 17-19. The

Table 16. Examples of wood percentage in five branches, divided into different size classes.

Diameter class (cm)	*Acer* 2106	*Betula* 1053	*Quercus* 3055	*Sorbus* 3097	*Tilia* 2/91
<0.5 0.5-1	61	60 54	62	56	39
1-2	63	68	54	70	46
2-3	64	65	63	61	49
3-4	68	79	65	67	53
4-5	82	81	72	67	57
5-6	73	78	74		60
6-7	77	81	75		60
7-8	76		75		
Total branches	68	71	66	63	53

measurements which had been performed of the shrub layer appear from Table 23. The biomass was low in all three sampling areas, depending on the low density, the low basal area and also the moderate tree height.

The relation between the biomasses in the three sampling areas (I; II:1; III) was 0.64; 0.85; 1.

Within the following sections, detailed critical statements are made on how the trees used for sampling differ from remaining trees within the same category as regards height, crown depth and crown diameter. The two latter-mentioned characteristics give an idea of the volume of the crown, but are, nonetheless, too approximate to provide an accurate estimate of the weight of the branches. The discussion illustrates the difficulties incumbent in taking the biomass or increment of individual trees as representative for the whole category.

Sampling area I. 4 birches and 2 oaks were measured in this area.

The sample tree in the smallest birch category had a somewhat smaller crown diameter than the other trees within this category despite the fact that it had two trunks from a height of 8.8 m above ground level.—Sample B1056 in the next category was also double-trunked from a height of 12 m upwards. The crown diameter was larger than the average. Both these samples were probably heavier than the average for the category. —B1055, with regard to the characteristics outlined, was a satisfactory average sample for the next category. Each of the other trees represents a separate category. —Birch B1053, from the point of view of size, was so different from the other large birches that it quite naturally called for a category of its own. At 15 m above ground level, it split to form three trunks.

The oak-trees, Q1051 and Q1059, were also so different in size and shape that they had to be taken separately.—The branch biomass of Q1051 was calculated to amount to 50%, which is probably an overestimate. —Q1059 had a secondary trunk which protruded from the side while the main trunk divided itself in three, 9.5 m above ground level. The tree had nine big branches and the volume of the trunk-like sections of two of these was measured.

Because of the above, the biomass figures for sampling area I are probably too high, even though the two double-stemmed trees do not exhibit a doubled biomass for the upper sections of the tree.

The biomass was estimated to about 49 ton/ha, see Table 17. About 87% consisted of *Betula*. The whole tree layer amounted to 96% of the above-ground biomass in the area. The percentage of

Table 17. Biomass of the tree layer in sampling area I, winter 1971, dry weight.

	Stem		Branch		Total tree		Attached
	ton/ ha	wood %	ton/ ha	wood %	ton/ ha	wood %	dead
Betula spp.	29.4	85.5	13.6	68.0	43.0	78.0	
Quercus robur	3.6	88.3	2.6	71.8	6.2	81.5	
Sum tree layer	33.0	85.8	16.2	68.6	49.2	80.1	0.4

branches was higher than in the two other sampling areas, about 34%.

An alternative way of estimating the biomass is to use the combined species regression between diameter and biomass, Fig. 16. Thereby a value of about 41 ton/ha was obtained. In the regression, only eight *Betula* individuals were included and seven of them were above the regression line. This points to the fact that a regression with solely *Betula* should have given a higher value. Also, the corresponding regression between D^2h and biomass gave for the same reason a too low value. A third possibility is to use volume tables. These apply to the stem volume above stump of trees with one main stem (Näslund 1948). If the volume values obtained in this way were converted to dry weight and an estimate of the stump weight was added, the stem weight arrived at about 24.7 ton/ha. This is 4.7 ton lower than the estimate given in the table. As many of the trees were forked the right value certainly is between these two estimates.

Of the bushes only *Corylus* was treated. The number of stems was 345 and the biomass estimated at 1.9 ton/ha.

Sampling area II:1. Eleven trees were studied in this area. In addition, two trees growing on the esker material in the northern section of the Andersby area were also measured. The following observations can be made concerning the sampling.

The maple, A2096, probably gave a correct representation of the weight of its category. —A2071 was slightly higher than the average for the category, but since the basal area was also larger than that of the average, there could hardly have arisen any overestimation of the weight of the category. —A2085's crown depth was considerably larger than the group average. This meant that the branch portion of this category, amounting on the sample tree to approximately 31%, was probably overestimated. —A3039c had the smallest crown diameter and was shortest in its category and therefore the biomass of the category was probably underestimated. —A2106 had a somewhat larger crown diameter than the category mean, while its crown depth and height were among the smallest in the category. Thus, the biomass of the category is probably lower than that calculated. —Summation of the maple colony shows that, in the cases of the two smallest categories, the biomass has been estimated correctly, in the middle category, the branch weight has been overestimated, and the biomass in the two largest categories have been underestimated, with the result that the sum total is somewhat low.

None of the three rowan trees in the sampling area was considered really suitable as a sample. The basal area increment varied between 24% and 5% during the five-year-period. So1/61 with a basal area increment of 14% was instead chosen as more suitable. The tree grew on esker material in the unthinned northern section. Its height and diameter lie within the category's variation.

Sample Q2097 in the smallest oak category had a somewhat larger crown depth than the other two and a crown diameter lying somewhere between those of the other two trees. —In the next category, sample Q2112 had a larger crown depth than the other trees. Oak-trees differ extremely with regard to shape. This contributed to the problems of choosing a sample tree the basal area and weight of which represented as closely as possible the oaks in the area.

The smallest linden T2111 probably underestimated the biomass of the category. —In the next category, the shape and growth of the trees varied so greatly that no tree was considered suitable for use as a sample. Results from measurements carried out on T2/91 were used instead. This tree grew on the esker material in the unthinned northern section of Andersby. T2/91 was double-stemmed from 9.7 m upwards and was in all probability heavier in relation to its basal area than the mean. Because of large amount of variation within this category, uncertainty is correspondingly large. —In the largest linden category, the crown diameter, crown depth and height of the sample tree all lie within the limits set by the variations within this category. The upper section of the trunk was not measured but estimated. —The wood density values used for linden are lower than those given by Mork (1966) and the lowest of all among the species investigated. The linden biomasses have, therefore, remained proportionately small. In Table 5a in F. Andersson (1970b), the slightly higher value of 0.43 for both *Sorbus aucuparia* and *Tilia cordata* was reported. By using the wood density quoted by Mork (op.cit.), the trunks would come to weigh about 26% more.

Within this sampling-area, there is one tree each of birch, aspen and sallow. Only the trunks of the birch and aspen have been measured. Because of difficulties encountered in measuring the upper section of the aspen trunk, its weight is more uncertain than that of other trunks. The sallow was not measured. The branches of the birch were poorly developed, consisting in the main of small branches and twigs and was estimated to amount to 50 kg. The branches of the aspen were estimated at 100 kg, thus making up for 20% of the tree's estimated biomass. The total weight of the sallow was estimated to amount to 70 kg.

Table 18. Biomass of the tree layer in sampling area II:1, winter 1971, dry weight.

	Stem		Branch		Total tree		Attached
	ton/ ha	wood %	ton/ ha	wood %	ton/ ha	wood %	dead
Acer platanoides	18.5	77.7	5.8	69.9	24.3	75.9	
Quercus robur	14.3	75.2	3.5	72.2	17.8	74.6	
Sorbus aucuparia	1.5	91.9	0.6	71.7	2.1	85.8	
Tilia cordata	12.1	81.3	5.1	53.8	17.2	73.1	
Other deciduous trees[a]	2.9		0.7		3.6		
Sum tree layer	49.3	79	15.7	65	65.0	75	1.3

[a] *Betula v., Populus, Salix caprea*

In this sampling area, most of the biomass of 65 ton/ha was shared between *Acer, Quercus* and *Tilia* with 37%, 27% and 26% respectively. The branch part was 24%. The percentage of bark was higher in this sampling area than in the two others, depending on high bark percentage in the branches of linden and oak. The alternative estimation with the combined regression between diameter and biomass gave, in this case, a considerably higher value, viz. about 75 ton/ha. This depended on the fact that the lindens were estimated at too high values and also, the oaks, since they had few branches in this particular area.

In the shrub layer, the biomass of the *Populus* suckers was measured. It amounted to 2.3 ton/ha. The few remaining *Corylus*-bushes and the biomass of the other bushes was not measured but as the *Corylus* stems were fewer than in area I and the weights of the other bushes probably were low the additional standing crop in the shrub layer amounted to about 2 ton/ha. The share of the shrub layer was then about 6% of the lignoses.

Sampling area III. The biomass calculations in this area are based on basal area estimates from the spring of 1971. It is hardly likely that the ratios between the total basal area of each category and that of the corresponding sample tree would differ after the 1971 increments have been included.

There were only five small maples in this area. The sample was the shortest of the five and, thus, the maple biomass is probably too low.

The birches were treated as one category in spite of the great differences in basal area and height. The two samples lie in the middle of the category with the result that the biomass was underestimated since one of the other trees is considerably higher than the samples.

The volume of the three spruces has been calculated using Näslund's equations for southern Sweden and converted to weight, to which was added an assessment of the weight of branches and needles, which comprised 20% of the total above-ground biomass (Näslund 1948). The weight of the stumps was also estimated and added to the figures.

No tree was selected to represent the smallest aspen category but the weight of the measured sallow was used instead, after correction for the aspen's lower wood density, using a value from Mork. The sample in the next aspen category was probably representtive of the class. —The largest aspen formed its own category.

Two equally large sallows grew in the area, one of which was felled and weighed.

The classification of oak-trees into categories was based on both diameter and height. This method of classification shows differences from classifying by diameter only with regard to the smaller categories. Samples from the four smallest categories were felled with the result that their weights are more accurate than those of the remainder. These trees were considered to be good representatives of their respective categories. —Sample Q3050 is taller than other individuals within the category. This could have given the category as a whole a somewhat high biomass. —In the next category, two samples were chosen, Q3045 and Q3055. Their crown diameters were a little smaller than that of the average. In all other respects, they are representative of the category average. Nevertheless, the branch weights calculated diverge considerably. Q3055 has grown up in a more open environment and thus had a number of large, thick branches. —The sample in the next category, Q3078, had a slightly larger crown depth than the average while its crown diameter was roughly equivalent to that of the average. The proportion of branches was calculated to as high as 33% and probably the weight of the category was overestimated. —The individual trees in the category with the largest and tallest trees are all dissimilar from the point of view of shape, being either many-stemmed or short-stemmed with a large number of thick branches. The tree selected had a continuous trunk with a crown diameter somewhat smaller than that of the mean.

The rowan sample tree in the smallest category was taller than the mean. —The individual used in next category gave an underestimate of the total biomass. —The sample in the next category grew in an open position and had developed a large crown depth. The proportion of branches calculated amounts to 34% of the tree's above-ground biomass. The biomass of the category may be slightly high.

The biomasses of the linden are based on four trees; two of these were felled. The sample from the smallest category T2/45 grew in a linden clone outside the sampling-area. Eighteen out of twenty-three lindens grew in a clone in the westerly section of the area. The sample trees were considered to represent the whole categories well.

The largest and tallest oak-trees are decisive with respect to the total above-ground biomass of the sampling-area. Over 50% of the calculated biomass is accounted for by the nine largest trees. It is a matter of some dissatisfaction that only two of these nine trees were studied.

As regards the other species, it may be stated that the biomasses of maple, birch and spruce were underestimated while that of rowan was overestimated. The weights of the remaining species were estimated more or less accurately.

The estimated tree biomass amounted to 76 ton/ha. The share of the oaks was 81%. None of the other tree species' biomass exceed 10%. The branches constituted 27%.

The biomass estimated using the regression amounted to 72 ton/ha, a slightly lower estimate than the above-mentioned. This estimation was based on the diameter 1970/71, but even with correction for one additional yearly increment the value was lower than the biomass given above. If the sample trees were treated as average trees in each category a somewhat higher value—76.4 ton/ha—would be obtained.

The sampling area differed from the others in that it had a well developed shrub layer mainly consisting of *Corylus avellana* bushes. Their standing crop was estimated at 6.5 ton/ha, more than any of the tree species except *Quercus*. Also many young tree stems grew in this area. A reasonable guess at the weight of this part of the shrub layer is 1 ton/ha. The percentage of the shrub layer within the total standing crop was then about 9%.

Table 19. Biomass of the tree layer in sampling area III, winter 1971, dry weight.

	Stem		Branch		Total tree		Attached
	ton/ ha	wood %	ton/ ha	wood %	ton/ ha	wood %	dead
Betula verrucosa	3.5	84.0	0.9	66.1	4.4	80.2	
Quercus robur	44.8	89.3	16.9	72.8	61.7	83.9	
Sorbus aucuparia	3.5	81.9	1.3	63.0	4.8	76.7	
Tilia cordata	1.6	65.0	0.7	52.8	2.3	60.9	
Other deciduous trees[a]	0.9	85.1	0.2	62.7	1.1	80.9	
Picea abies	1.2	93	0.3		1.5		
Sum tree layer	55.5	87.8	20.3	71.4	75.8	82.7	1.3

[a] *Acer, Populus, Salix caprea*

According to Axelsson et al. (1970b, Table 5) the biomass of the hazel was 9.5 ton/ha in the unthinned part of Andersby. This value was based on samplings carried out in sampling areas A and B. Area A was especially rich in large hazel stems.

Increment in sample trees

The above-ground increment of wood and bark measured in the sample trees is plotted against the diameter at breast height in a logarithmic graph to be found in Fig. 19, in the same manner as that for the biomass of the sample trees. In the case of bark, the calculated values are more of an approximation of the production which has taken place but, for the sake of simplicity, only the term increment will be used. There is a greater dispersion in this graph than in that for the biomass.

The highest increment was recorded in the case of a multi-branched oak growing in the cleared sampling area I. That of the largest oak in sampling area II:1 was only a quarter of the latter's. The oak-trees in II:1, during the period prior to clearing, had been growing under denser conditions with the result that the percentage of branches was low. The smaller oak in area I with a diameter of 24.4 cm had a higher increment than other individuals with the same diameter.

The largest linden growing in II:1 had a low increment. A linden with a diameter of approximately 13.5 cm and an increment of only 0.8 kg grew in a dense clone.

The second highest increment of all the individuals measured was recorded in the case of the birch which was studied by Wolfgang Brunner (1972). This particular tree grew in a fringe area of the woodland and was thus favoured to a certain extent. It had a higher increment than the largest birch in sampling area I, although the latter had a higher biomass.

Both the aspens had higher increments than individuals of other species with the same diameter.

In Fig. 20, the increment is plotted against the increment in basal area in a linear diagram. Since a three-dimensional quantity (increase in weight being

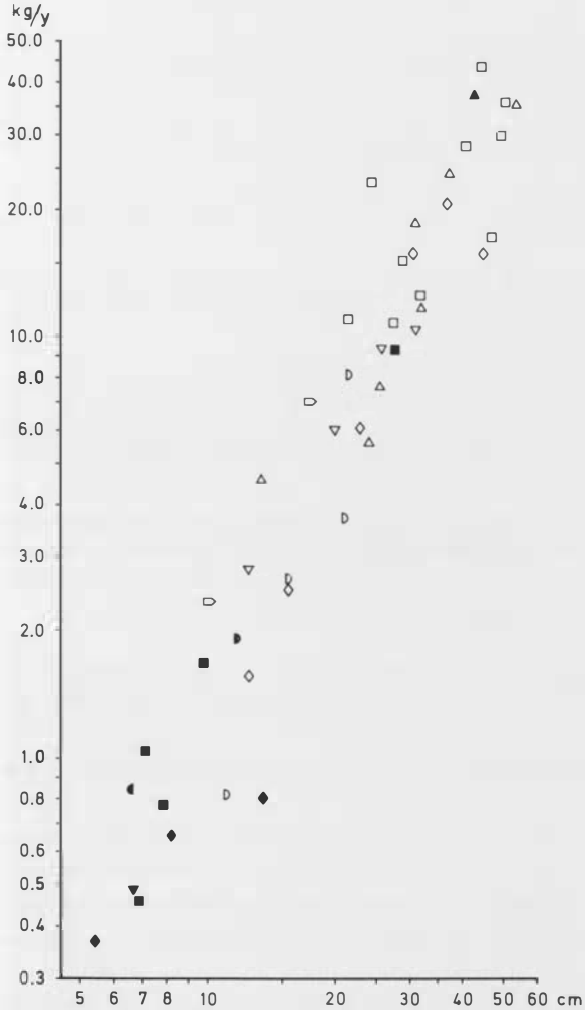


Fig. 19. Relationship between log wood increment and bark production (dry weight) and log diameter at breast height. Explanations of symbols see Fig. 16.

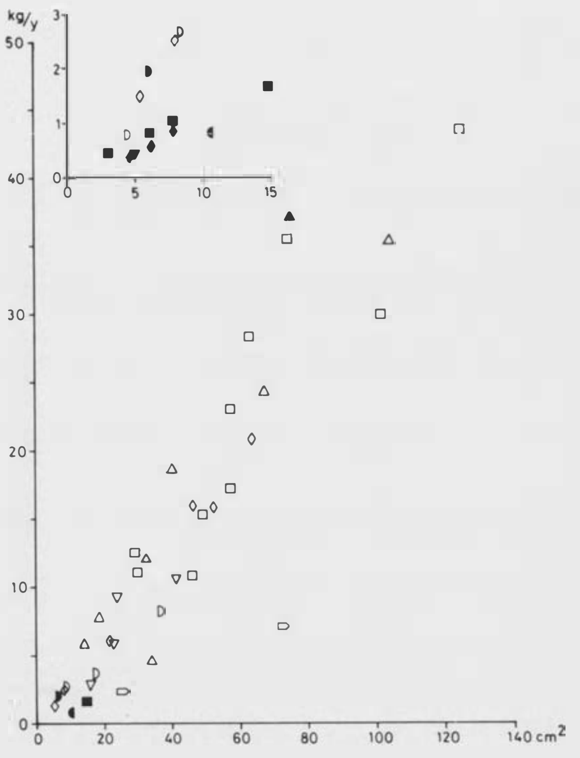
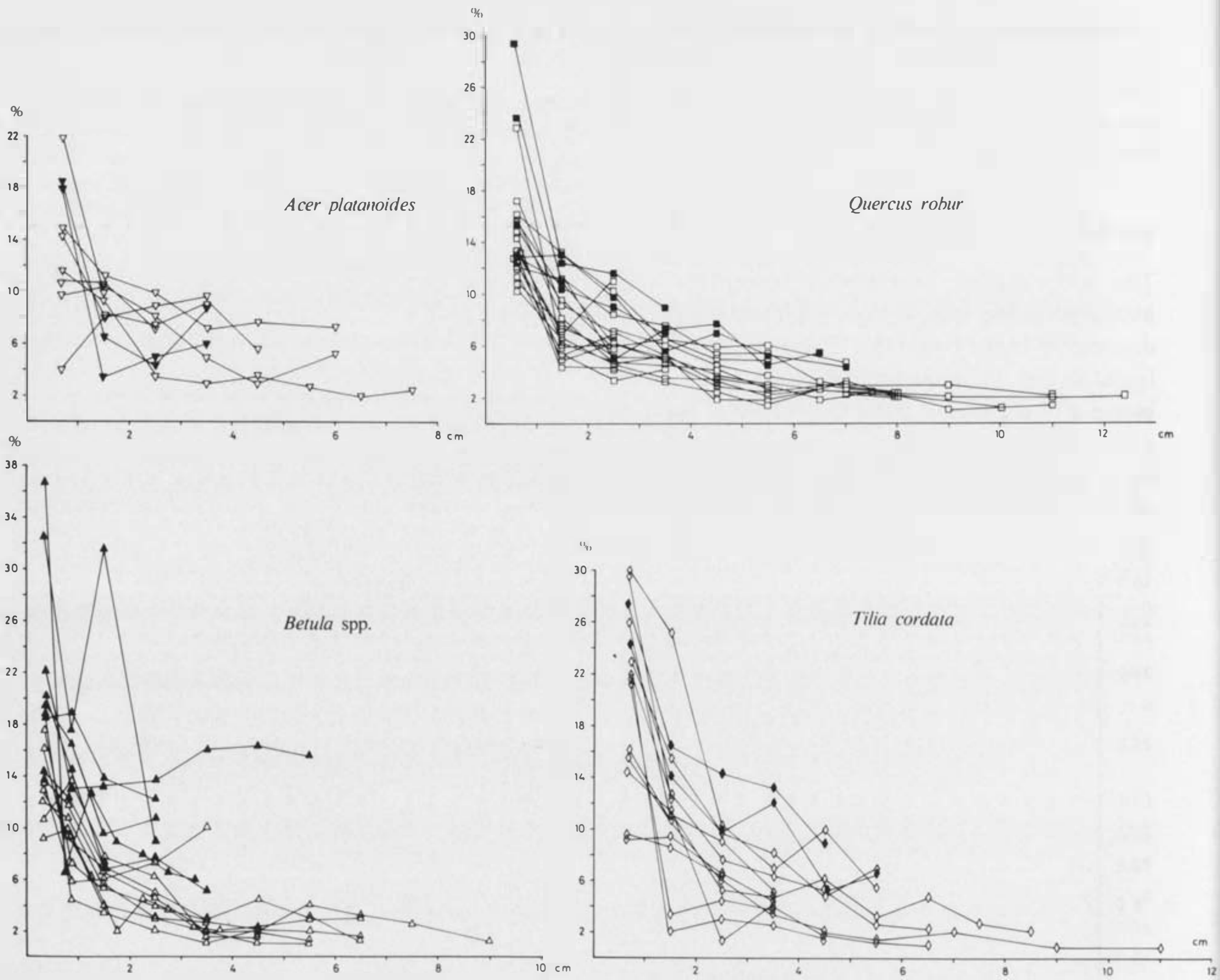


Fig. 20. Relationship between wood increment plus bark production (dry weight) and increment in basal area. Explanations of symbols see Fig. 16.



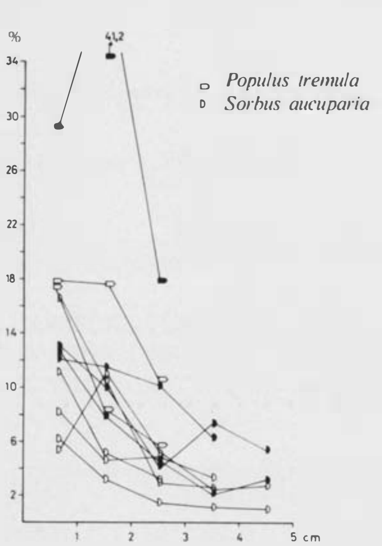


Fig. 21. Annual relative increment in branches (open symbols) and tops (increase in cross-sectional area as a percentage of total wood cross-section) in relation to diameter.

directly dependent on the volume increment) is plotted against a two-dimensional quantity (the increment in basal area) as abscissa in the graph, one would expect an upward skew in the dispersal of the points as long as there occurs an increment in height, branch length and ramification. On the other hand, when both the height and branch increments decrease, one should obtain even an S-shaped graph. The diagram displays a weak tendency of the latter type. The proportions of the increment accounted for by height and ramification apparently diminish among even medium-sized trees. Thus, the diagram gives a faithful reproduction of the state of affairs at the time of the investigations, with the prevailing distribution between dominant, co-dominant and suppressed trees of different ages and species but not of the increment rhythm of individual trees, which might have produced something completely different.

The percentage of the increment accounted for by branches varied from 35% to 80%, with a diverging, low value of 19% also recorded. The only conclusion possible to draw is that the smallest trees, i.e. those with a diameter at breast height less than 15 cm, had a somewhat lower proportion of their respective increments localized to the branches than the larger trees.

In Fig. 21, the relative wood increment at different branch diameters is illustrated. By relative wood increment is meant the cross-sectional area of wood yearly produced on an average during the years 1967-71, expressed as a percentage of the total area late in the year 1971. This ratio is plotted against the branch diameter (including bark). Each marking is a weighted mean value with consideration given to the weight of the branch section—see Methods. As regards the larger branch categories, this mean value is based on only one or a few samples. The branches of all the trees in the sampling programme plus the tops which were given special treatment are shown in the diagram and the increment figures from each tree connected. The irregularities in the connection lines are due to the fact that the number of samples in certain cases was small, with the result that single samples with an unduly high or low increment affected the appearance of these lines. This is of especial interest in the case of the tops, where the larger diameters had, in many cases, a higher increment than the smaller.

The dispersion recorded between the different branch systems was considerable. This is especially true of the smaller diameter categories. The five lowest values in the smallest diameter category in the *Tilia* diagram originated from the five smallest lindens, all of which grew in dense clones.

As a rule, tops had a higher increment percentage than branches. A birch top with a high relative increment value even in the larger diameter categories came from a tree with a diameter at breast height of 13.5 cm; the entire increment of the latter tree was high. In those cases where the branch system was divided into an upper and lower stratum, the upper had consistently higher relative increments than the lower.

Birch branches grew somewhat more slowly than oak, linden and maple branches. Comparisons between the fine branches of the different species was rendered more difficult since *Betula* branches were subdivided into one further category, that is one more than in the case of the other species.

The production of current year's shoots was calculated for one year only, viz. 1971. This is of importance since the length of the shoots varies from year to year. According, for example, to Romell (1925), the final length of spruce and pine shoots is partly determined by the character of the previous growth period, see also Kozlowski (1971). (An early drought period may also shorten the twigs, a later one only the needles in pine.) The current year's weather conditions, etc. according to Kozlowski (op.cit., vol. I, p. 324), have their greatest effect on the long shoots of species with long growing seasons, "which do not contain a fully preformed shoot in the winter bud (e.g. *Populus, Betula* . . . .)". Buds have not been included in the production figure totals since their increment was assumed to be zero, being registered as a part of the following year's growth and production. On the other hand, bud scales were, of course, included in the losses of plant material.

Increment in sampling areas

In Tables 20-22 are to be found figures for wood increment, bark production, and current growth in shoots, for the tree layer in the three sampling areas. The mode of calculation is given in the section on Methods.

The relationship between the increments in the three areas is 0.65: 0.88: 1 (I: II:1: III). This relationship was in almost complete agreement with the biomass relationship for the three sampling areas. The distribution between trunk and branches, however, differed, with a greater proportion of the increment assigned to the branch system than that accounted for in the biomass figures.

The bark production calculated was high and amounted to 24.8% in sampling area I, 27.8% in area II:1 and 20.8% in sampling area III.

In all the sampling areas, the increment was higher in the branch systems than in the trunks. It should be observed that even large, thick branches were included in the branch systems.

In sampling area I, the branch increment amounted to 67% of the total increment which was a surprisingly high percentage. The branch systems of two birches, in particular, had high increment figures but also the two oak trees had a higher branch increment than trunk increment. The part of the increment accounted for by wood was in the region of only 1 ton/ha. The increment of hazel shrubs was assessed to approximately 0.16 ton/ha, i.e. roughly 10% of the increment of woody species. The increment proportion of hazel is greater than its share of the biomass, due to the fact that turnover is higher in the hazel shrub layer than in the tree layer.

The increment in the tree layer in sampling area II:1 was estimated at approximately 2 ton/ha. Branch increment accounted for roughly 60%. Lindens, in particular, registered high increment figures in their branches. The increment of oak trees is about half of that of maples, despite the fact that their biomass is only 27% lower. The maple increment is spread over 4 times as many individuals. The increment in birch and aspen branches was not estimated, nor was *Salix*, with the result that the final figure given in Table 21 is somewhat low.

The above-ground increment of aspen tillers was high when compared with their low biomass. The length of the shoots varied from year to year, that of 1969 being longest in all but one case. The width of the annual rings also varied. Those of 1971 were so much narrower than those of other years in 8 out of 10 shoots, that the volume increment in the older sections of the shoots was lower in 1971 than during the previous years. Therefore, the calculated increment of 0.9 ton/ha for 1971 is too high. If the increment is calculated by dividing the sum of the weights of the old shoots by 4 and adding to the latter the weight of the current year's shoots, 713 kg/ha is obtained. This method of calculation probably underestimates the increment for 1971.

The increment of aspen tillers in their older sections amounted to roughly 60% as compared with the wood increment in the tree layer, while their amount of current year's shoots exceeded that of the tree layer. The aspen tillers were sampled together with their leaves and the weight of leaves was estimated at 580 kg/ha. Thus,.the net primary production of the aspen shoots during 1971 amounted to about 1.5 ton/ha.

The increment in the tree layer in sampling area III was estimated at just over 2.2 ton/ha. The portion of branches amounted to approximately 59%. Oak trees dominated the tree-layer increment with about 77% of the total increment of this sampling area's tree layer, i.e. somewhat lower than the percentage accounted for by their biomass. The bole-bark production and branch increment of spruce was not calculated, being almost negligible in this area.

The increment in hazel shrubs was estimated at 0.55 ton/ha, approximately 8.5% of the biomass, which is considerably higher than that registered for tree species in the same area. The same percentage was measured in the case of hazel shrubs in sampling area I.

The results were, to some extent, unexpected since a higher increment percentage was expected in the

Table 20. Estimated increment in wood and bark production in the tree layer in sampling area I, kg/ha, 85°C.

	Stems			Branches				Total
	total	wood	bark	total	wood	bark	current shoots	trees
Betula spp.	385	329	56	813	453	250	110	1198
Quercus robur	90	80	10	174	101	47	26	264
Sum tree layer	475	409	66	987	554	297	136	1462

Table 21. Estimated increment in wood and bark production in the tree layer in sampling area II:1, kg/ha, 85°C.

	Stems			Branches				Total
	total	wood	bark	total	wood	bark	current shoots	trees
Acer platanoides	340	255	85	455	291	138	26	795
Quercus robur	169	147	22	234	110	59	65	403
Sorbus aucuparia	47	43	4	41	23	11	7	88
Tilia cordata	180	147	33	412	163	181	68	592
Other species [a]	95	80	15					95 +
Sum tree layer	831	672	159	1142 +	587 +	389 +	166 +	1973 +

[a] *Betula* and *Populus*, the branches were not measured.

Table 22. Estimated increment in wood and bark production in the tree layer in sampling area III, kg/ha, 85°C.

	Stems			Branches				Total
	total	wood	bark	total	wood	bark	current shoots	trees
Betula verrucosa	75	64	11	70	43	20	7	145
Quercus robur	650	556	94	1063	575	240	248	1713
Sorbus aucuparia	62	51	11	100	54	33	13	162
Tilia cordata	38	25	13	59	24	25	10	97
Other species [a]	87	78	9 +	30 +	15 +	8 +	7 +	117 +
Sum tree layer	912	774	138 +	1322 +	711 +	326 +	285 +	2234 +

[a] *Acer, Picea abies* (only stem wood), *Populus, Salix caprea.*

cleared sampling area I, partly because of the decrease in competition and partly because the hazel shrubs in sampling area III were somewhat suppressed. (Samuelsson (1966), in his study area—Hässlen in southern Dalecarlia—estimated the mean annual increment percentage over the last 10 years at 13.3% in the case of hazel. The vigoruous *Corylus avellana* stand in the above-mentioned area was practically unshaded and had, apart from the field layer, only a few birch trees as competitors. F. Andersson (1970b) estimated the increment in hazels growing at Linnebjer in Scania at 8.45% of the biomass. In the latter area, hazel forms an understorey layer with oaks and lime trees in the upper storey.

Table 23a. Estimation of biomass (winter 1971/72) and net primary production of *Corylus avellana* in sampling areas I and III, kg/ha, 85°C.

	Biomass	Production
I, wood	1489	121
I, bark	388	38
I, current shoots	8	5
I, leaves [a]		26
I, sum	1885	190
III, wood	5287	400
III, bark	1161	124
III, current shoots	84	28
III, leaves [a]		433
III, sum	6532	985

[a] = litter leaves

Table 23b. Estimation of biomass and net primary production of *Populus tremula* (suckers) in sampling area II:1, 1971, kg/ha, 85°C.

	Biomass	Production
Wood and bark	2110	755
Current shoots	210	186
Leaves [a]	578	578
Sum	2898	1519

[a] Green leaves

During the dry summer of 1969, the hazel shoots showed clear signs of suffering from the drought. A large portion of their leaves were shed as early as August. The year after, it could be seen that the drought had killed shoots or sections of shoots. Hazel was the species in the entire area which evidently suffered most from drought conditions. This can also be seen in the width of the annual rings which, during the course of the last few years, except in the case of young shoots, were, in general, narrow.

Seasonal course of above-ground growth in woody species

Methods

The following species were measured:

Acer platanoides	*Tilia cordata*
Betula spp.	*Corylus avellana*
Populus tremula	*Lonicera xylosteum*
Quercus robur	*Ribes alpinum*

The change in the girth of the trunk and the growth of shoots and leaves were measured in the above tree species, while only the growth of shoots and leaves were measured in the case of the three shrubs. All individuals studied were growing either in, or close to, sampling area III. Measurements were carried out from 1969 until 1972. The measurements reported here include the changes in girth in 1970-72 and the leaf development in 1970 but not the shoot elongation except for *Picea*. The material representative of each species embraces only a small number of twigs and trunks. Shoots were chosen which could be measured from the ground. Thus, the measurements do not give a complete picture of the development of shoots and leaves. The girths can be found in Table 24.

Table 24. Girth of measured trees, 10.3.1974.

Species	No	Girth cm	Comments
Acer platanoides	a	61	
	b	31	double-stemmed
	c	55	
	d	54	
Betula verrucosa	a	63	
pubescens	b	28	double-stemmed
verrucosa	c	63	
verrucosa	d	48	
Picea abies	a	18	
	b	34	
	c	44	
Populus tremula	a	49	
	b	26	
	c	54	
Quercus robur	a	36	
	b	44	
	c	76	
	d	66	
	102	65	
Sorbus aucuparia	a	34	
	b	34	
	c	39	
Tilia cordata	a	38	
	b	25	
	c	39	
	d	40	

The shoots were measured from the previous year's bud scar to the base of the current year's terminal bud (when developed). Leaves were measured from the tip of the leaf to the petiole's junction with the blade of the leaf. Before the bud actually bursts, the bud scales of a number of species first grow somewhat. Within the bud grow the shoot and the leaves. During the first few days after leaf burst, the shoots and leaves are small and consequently difficult to measure. Measurements of both shoots and leaves were carried out with a ruler.

Changes in girth were measured at breast height with the help of a steel tape. One end of the tape was fixed to the tree by means of a nail. The tape was then stretched around the trunk with the aid of a constant weight. Before the tape was actually fixed, the bark was evened. The difference between two scratches was measured with a magnifying measuring glass to the nearest 0.05 mm. The measurements were all taken, when possible, before noon, to avoid, as much as possible, the diurnal changes.

The steel tape was manufactured of special steel (the same steel being used in measuring tapes) with a coefficient of expansion of $9.3 \cdot 10^{-6}$. This means that a tape of this type, measuring 40 cm, would expand 0.1 mm at a temperature difference of 25°C. This source of error might have affected measurement on some occasions during the summer and, almost certainly, during the winter. The errors were not corrected and, in practice, lack significance.

With the steel tape all changes in the girths are measured and not only the increment. Other causes of changes have been dealt with by a number of authors e.g. Romell (1925), Kozlowski & Winget (1964), Leikola (1969).

The differences in the water content in the stem is considered to be the cause of the long-known daily varition in the girth of stems (e.g. MacDougal 1929) with the smallest girth during the afternoon and the greatest before sunrise. The variation is not noticeable during days with high humidity.

The girth of the stem depends on both the speed with which water is supplied to the stem and the speed with which it is given off. The measurements at Andersby were performed during the mornings in varying weather, so they are not completely comparable.

At temperatures below zero, the diameter diminishes (cf. Winget & Kozlowski 1964, Leikola 1969). This is considered to depend mostly on a shrinkage located to the bark. Evidently, the wood also shrinks as frost cracks, which can be produced in frozen stems, reach into the wood (Lagerberg, see Sjörs 1962). The size of the shrinkage is, according to Winget & Kozlowski (op.cit.), "primarily a function of species and stem thickness" and "site and growth rate had little effect".

According to Ladefoged (1952, p. 17), the cells in the cambium often swell to double their size in spring before division starts. Romell (1925) and Fraser (1956, p. 782) stated that the first increase in the girth, measured with dendrometers, did not correspond to cell divisions. The effect of the root pressure occurring in certain species during the early spring is not clear.

Except for growth in phloem and xylem, the periderm may also increase in thickness, and, in addition, there may occur the formation of new periderm layers. The intensity of the formation of periderm varies from species to species. The periodicity of the phellogen is, on the whole, unknown (Srivastava

1964, p. 231). Nor is the course in growth of the phloem completely known (Srivastava, p. 219). The measurements of the increment are also complicated by the fact that older elements of the phloem can collapse.

Leaf and shoot growth

In Fig. 22 the growth in leaves of broad-leaved trees and bushes and the shoot growth in *Picea abies* during 1970 are given. The other years of measurements, 1969 and 1971, gave a similar picture except for a difference in the time factor, depending on the fact that the leafing started later in 1969 and earlier in 1971 than in 1970. Measurements of shoots of broad-leaved trees were carried out but omitted as they closely coincided with the development of the leaves. The cumulative growth curves are based on either leaf areas obtained from a regression between the length of the leaf lamina and the leaf area or simply by using the square of the leaf length. The square of the leaf length is related in a linear way to the leaf area (Inggårde 1969). The leaf area was calculated as a percentage of the final leaf area at the time when leaf growth ceased.

Leafing varied from individual to individual and from clone to clone and even within an individual. Big oaks and lindens started leafing before small ones. For this reason, it is difficult to obtain a quantitative picture of the course of the leaf growth.

As observations were not performed each day, the exact date of the sprouting is not known. Arnell (1923) gives the following order and average dates regarding Svealand during the years 1873-1917.

Betula spp.	May 15th
Sorbus aucuparia	„ 17th
Corylus avellana	„ 23rd
Acer platanoides	„ 23rd
Tilia cordata	„ 27th
Populus tremula	„ 28th
Quercus robur	„ 31st

The growth of shoots and leaves in all species, except *Betula*, was nearly completely terminated during June. *Betula* had, on the contrary, a rather considerable growth of new leaves on long shoots up to as late as July 25th. The leaves on short shoots were fully developed towards the middle of June during 1970 and 1971.

The growth of the leaf area in *Acer* and *Quercus* differed from the conditions in *Betula* and *Corylus*. The leaves in the latter two species grew out successively but in the former two species the number of leaves is predetermined in the bud, and the growth of the separate leaves was parallel. *Populus* and *Tilia* occupied an intermediary position with only a few late leaves. According to Axelsson et al. (1974a) a constant

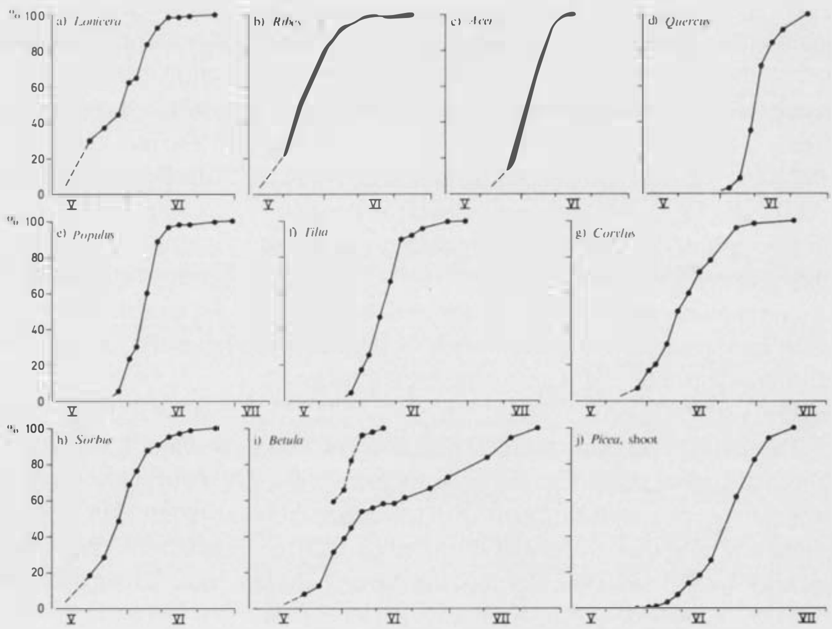


Fig. 22. Cumulative increase in leaf area during 1970 and cumulative growth in shoots of *Picea abies* during 1970. Each measuring indicated with a dot. Broken line: short shoot.

value of the dry weight per leaf area is obtained in *Corylus* when the leaf area is fully developed.

Bud-burst is considered to depend mainly on temperature (Fries, N. 1971) including that of the previous weeks.

Comparing the leaf growth and the simultaneous temperature, a co-variation was found. Thus, the growth rate was low during the first days in June, as, at the same time, both the night and day temperatures were low. Furthermore, a cold period occurred between June 10th and 15th. Most of the leaves and the shoots had, at that time, nearly attained their full length, but the species which still grew had a slow growth rate.

The measurements at Ultuna of the total irradiation showed that the irradiation was low during the same period as the temperature was. To what extent the varying growth rate depends on temperature and to what it depends on irradiation cannot be determined.

Diameter growth

The course of the increase in girth during 1970, 1971 and 1972 is evident from Fig. 23 (NB. the different scales). Unfortunately, the measurements started, in some cases, too late, due to faults in the steel tapes so that the first changes were not recorded (three *Quercus* individuals in 1970 and all *Picea* and *Quercus* in 1972). In 1972, a fault occurred in a steel tape on one of the birches but, nevertheless, it was possible to get good measurements. An obvious wrong measurement of the girth of one of the oaks has been corrected to the most probable value. Both these inadvertences have been noted with question-marks in the figure. One of the *Acer* trees was excluded during 1971 and a further stem during 1972 because of frost cracks. In 1972, the girth was measured on only a few occasions. If any short-term changes occurred, they were not registered.

During the early spring, occasional changes in girth were measured. For that reason, it is difficult to distinguish exactly when the first cell divisions occurred.

This started in May or the beginning of June. During the first days thereafter, the changes in girth were small. The start (at breast height) coincided in *Picea* and *Quercus* stems and occurred in 1971 between May 8th and 19th. Between the same points in time the increment in *Populus* and *Betula* stems started. However, the steep part of the curves began later in these two species than in the curves for the two first mentioned. The increment in the three *Acer* individuals started between May 23rd and June 12th, in the *Tilia* trees between June 2nd and 8th, and in one of the *Sorbus* stems (a), between May 26th and June 2nd; the start in the two others could not be defined.

The diameter growth starts at different times at different heights in a tree. According to Ladefoged (1952, p. 52), the cell divisions started at the bud base and spread in a basipetal direction (cf. Fraser 1958).

According to N. Fries (1973, p. 342), it seems now to be clear that growth hormones formed in the buds are spread at the swelling of the buds in the spring and that the hormones initiate the cell divisions in the cambium.

It is consequently not easy to correlate the time at which growth at breast height starts with the temperature of any particular period, nor with any sum of temperatures (cf. Leikola 1969, p. 64). However, in 1971, with a warm period in the middle of May followed by a cool period at the end of May, the "early" species started at an earlier date than in 1970, but the "late" species, on the other hand, started at about the same time both years. During 1970, the temperature rose without any long, uniform warm or cool periods.

Growth in girths started at breast height earlier than growth in shoots in *Picea* and *Quercus*. This is in accordance with Ladefoged (1952).

The main increase in girth occurred during June and July and during the first week in August. The growth curves for 1970 and especially for 1971 did not display an even trend. During certain periods, shrinkages in stems were even measured, see *Populus* 1971, *Quercus* 1970 and 1971, *Sorbus* 1970 and 1971 and *Tilia* 1971. The irregularities in the curves can be correlated with periods of low precipitation. During 1970, two drought periods occurred, viz. during June and the beginning of July and during August. In spite of the drought, the girths of most stems increased, showing that an increment occurred and that this exceeded the shrinkage of the stem.

A great increase in all species was measured between July 12th and 17th 1971. The first rain for half a month fell. It is probable that the increase in cell width had ceased temporarily during the periods of drought but had continued after precipitation had occurred. During August 1970, only 5 mm of precipitation fell, as compared with the normal amount of 62 mm. The first real rain fell on September 10th and, thereafter, on September 13th and 16th. In *Acer, Quercus* and some *Tilia* stems increases in girths were measured during September 1970. The greater girth on Sept. 30th, as compared with Sept. 9th, can be accounted for by the hypothesis that the stems, during August and the beginning of September had probably suffered from water stress because of a deficiency in water. A further indication of this is the single measurement performed on *Populus* on Sept. 16th, the girth of which had already reached the same value as on Sept. 30th.

The drought was most severe in 1969. All species (only two stems of each species that year), except *Tilia* stems, increased less that year than during the following years. The bore cores, however, showed that this was not the general state of affairs. Several of the bored *Quercus* stems had a thinner annual ring in 1970 than in 1969.

In most stems, the rapid increase ceased in July or in the beginning of August. At the end of July, 80% or more (up to 95%) of the increase was completed. Some stems continued increasing during the whole of August at a rather great rate, e.g. *Populus* c and *Picea* b in 1971 and 1972 and *Betula* c in all years. However, during the last part of August and thereafter, the girth, in most cases, increased only insignificantly. An increase was, however, recorded up until the beginning of October. The point at which the growth ceased was extremely difficult to ascertain with this method because of the gradual increase during the entire course of the autumn.

The growth curves indicate that the increment in *Picea* ceased in the middle or at the end of August, but in *Picea* a and c in 1972, in the beginning of September.

According to S.O. Andersson (1953), annual ring formation in *Picea* and *Pinus* ceased on average in the middle of August in the whole of Sweden. The actual point in time varied during 1941-1946 between August 11th and 24th. The mean temperature was then considerably higher than the temperature limit of +6°C which Langlet (1936) used for the vegetation period.

He measured, however, the increment on bore cores, but Žumer (1969, Fig. 6 and p. 13) found that phloem increased after the late-wood was completed.

Ladefoged (1952) stated that trees with a thin annual ring ceased wood formation at the end of July or the beginning of August. On the other hand, wood formation in trees with a broad annual ring continued until the end of August or beginning of September.

Leikola (1969), whose investigation area lay somewhat further to the north than Andersby ängsbackar, found that diameter growth in birch terminated at the end of July or the beginning of August, and in spruce and pine, in most individuals in the middle of August. Leikola obtained certain differences between the years in question.

Fraser (1956) registered diameter growth in seven deciduous tree species in Ontario during the period 1949-53. The diameter increment ceased all years and in all species at the end of July or during August. He made a special study of *Betula lutea* and stated that neither temperature nor soil moisture limited growth. Instead, Fraser stated, in accordance with numerous other authors, that the cessation of growth is regulated by the photoperiod, which acts through a growth hormone. However, Leikola (op.cit., p. 81) considered that neither the photoperiod nor any other theories (p. 80-81) could fully explain the cessation under Finnish climate conditions. Caution must be observed with comparisons with other areas, also the probable development of photoperiodic ecotypes (Håbjørg 1972) may be of importance.

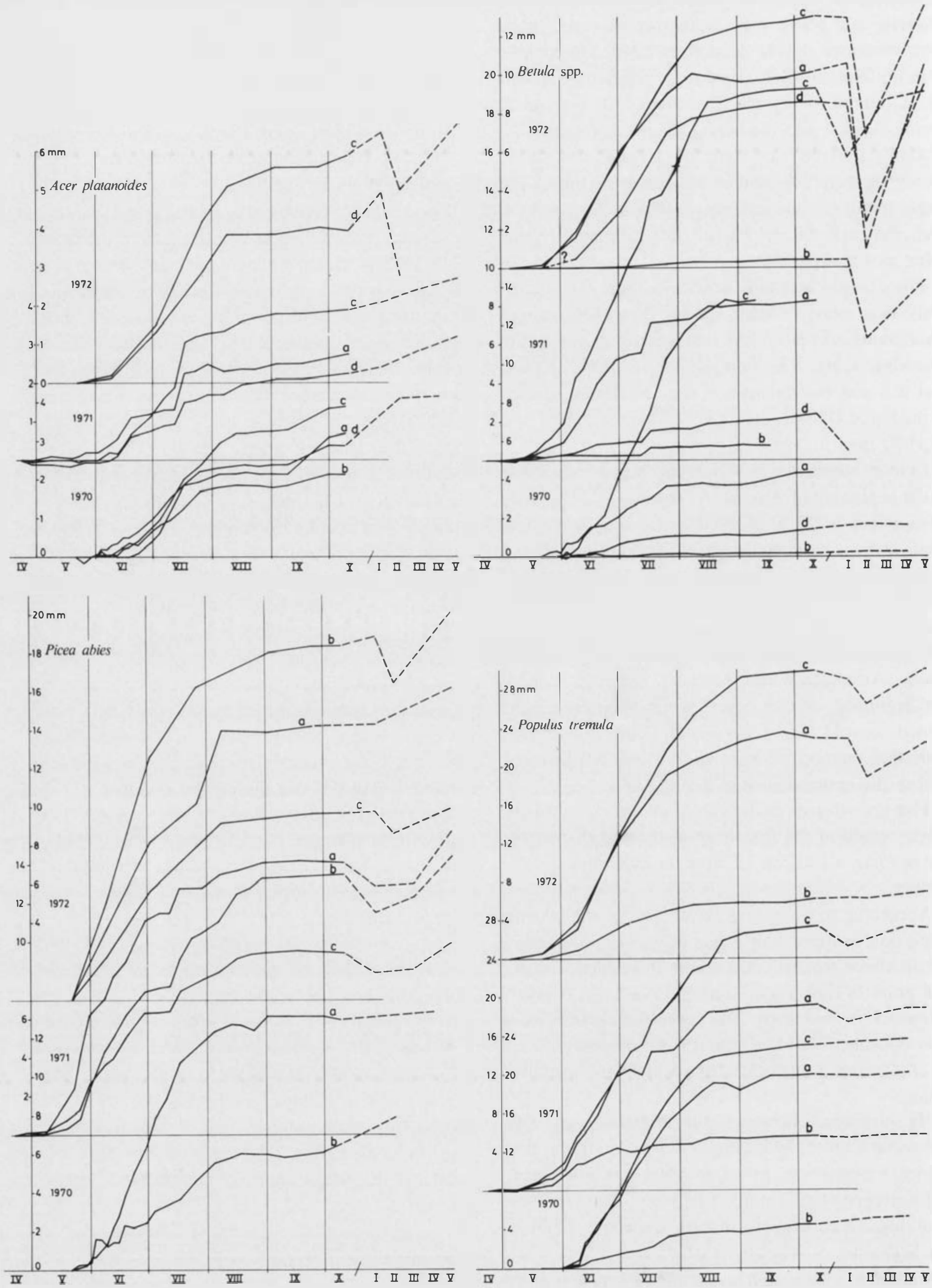
The large differences found in the cessation of diameter increase contradict the hypothesis that only the photoperiod is decisive. Stress with regard to, or competition for soil moisture and/or nutrients can modify the point in time at which increment ceases. Individuals with the greatest girth increase grew the greatest length of time during the autumn.

The results of the sporadic winter measurements appear from the right hand section of Fig. 17. Difficulties arose in the case of the winter measurements because of the development of ice between the bark and the steel tape.

The *Acer* individuals increased in girth all winters. During the course of the measurements in January 1972, the temperature was between −5°C and −10°C, in Jan. 1973 some degrees below zero, and in February 1973, about −10°C. With all other winter measurements, the temperature was above zero.

On the two coldest instances, the stems had shrunk, especially those of *Tilia, Sorbus* and *Betula*. The shrinkage in the *Tilia* stems in February 1973 exceeded the whole increase for the 1972 growth period.

During the leafless state, transpiration is low. Lundegårdh (1954, p. 91) discusses the sap flow and the positive sap pressure of birch. *Acer* is also well-


6 mm
Acer platanoides
1972
1971
1970
IV V VI VII VIII IX X I II III IV V
12 mm
Betula spp.
1972
1971
1970
IV V VI VII VIII IX X I II III IV V
20 mm
Picea abies
1972
1971
1970
IV V VI VII VIII IX X I II III IV V
28mm
Populus tremula
1972
1971
1970
IV V VI VII VIII IX X I II III IV V

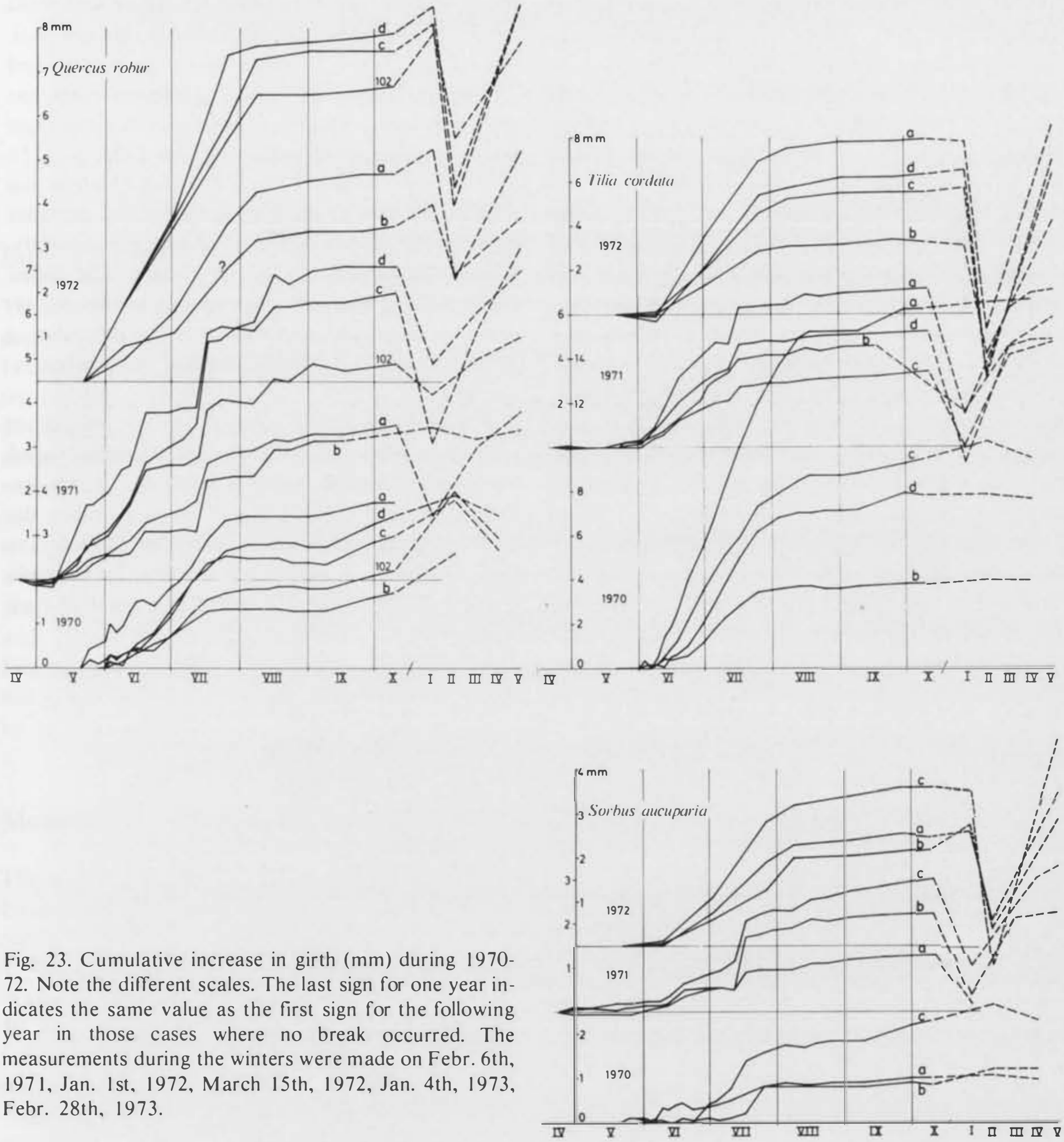


Fig. 23. Cumulative increase in girth (mm) during 1970-72. Note the different scales. The last sign for one year indicates the same value as the first sign for the following year in those cases where no break occurred. The measurements during the winters were made on Febr. 6th, 1971, Jan. 1st, 1972, March 15th, 1972, Jan. 4th, 1973, Febr. 28th, 1973.

known in this respect but was not investigated by Lundegårdh. *Acer platanoides* had sap flow at borings in the middle of April 1972. The early increase in the girths of *Acer* stems is possibly due to this. No investigation was carried out into, when sap pressure started during the spring or the winter. The birch stems did not show—despite the sap pressure—any obvious change in girth. The increase in oak stems, see February 1971 and January 1973, cannot be due to sap pressure since, according to Lundegårdh (op.cit.), oak does not display sap flow. On the other hand, the water content in oakwod and in lindenwood is higher during the winter than during the summer (Lundegårdh, op.cit.), and, probably, this increase occurs after leaf-fall; as regard oak during the middle of October at the earliest. *Tilia*, on the contrary, did not show any appreciable increase during the winter.

Because of the above-mentioned difficulties with the "tape" method in discerning the beginning and cessation of growth, no estimation of the length of the growth period is given. Especially difficult to explain with only "tape" measurements (even with more sensitive recording methods) are the permanent positive changes which occurred during the autumn and the winter. Taking successive increment cores has the disadvantage that the number of cells varies from point to point in the stems (Romell 1925, p. 115).

In all stems of *Acer, Picea, Populus, Quercus* and *Sorbus* and two of the four *Betula* stems, diameter growth was greatest during 1972 and, consequently, so was the increase in the basal area. The linden stems differed from all other species in that the increase was greater in 1970 or 1971 than during 1972. *Populus* and *Picea* stems had the greatest increment.

Variations in yearly increase between individuals were measured within the species. Increase varied even among equally sized individuals. In, for example, *Quercus* in 1971 and *Tilia* in all years, the growth curves separated as early as May or the beginning of June but, in other cases, for example *Quercus* in 1972, the curves did not separate until July.

Litter fall and leaf-area index

Introduction

Three separate investigations concerning the litter deposited in Andersby ängsbackar were carried out. In the three sampling areas (litter study 1) the leaf litter was determined during all three of the years 1968-70; however, during only the latter two of these three years, all types of litter from trees and shrubs were studied—see below: Methods. In 1969, in conjunction with the zoological team's investigations, a study of the quantity of hazel leaves (litter study 2) was carried out in four of the areas designated for zoological sampling, namely A-D. In connection with the latter, all kinds of leaf litter was collected. Finally, during the autumn of 1970, the sampling of leaf litter was extended to almost the entire Andersby woodland (litter study 3).

Methods

The methodological description outlined below concerns primarily Litter study 1 but refers to applicable sections of both Litter studies 2 and 3 also.

The litter sampling in areas I-III was carrried out in two ways. All litter, except branches longer than 40 cm, was collected in plastic baskets while the branches were retrieved from quadrats measuring 10 metres square.

The cross-sectional area of the basket apertures was 0.21 m^2 and the height of the baskets was 0.2 m. The baskets were placed at ground level so that the litter from the low shrub layer could also be trapped. Nevertheless, the litter fall from the latter layer was certainly underestimated. On the inside, the baskets were clothed in a terylene net with a mesh of approximately 1 mm^2. Openings in the bottom of the baskets permitted the effective draining of rainwater. In order to determine some litter material smaller than 1 mm^2, two of the baskets were further supplied with a densely woven fabric under the terylene netting. Carlisle et al. (1966) have reported that about 1.9% of the total litter fall was in the size category 0.2-0.6 mm. An appreciable part of the latter consisted of frass from caterpillars of the moth *Tortrix viridana*. Since the quantities of litter measuring less than 1 mm^2 were small, this material has been disregarded in this particular study.

The baskets had to be rather low in order to trap as much as possible of the litter fall. To test whether any leaves could be blown out of the baskets, some *Fagus* leaves, a species not growing in the study area, were left in two of the baskets and checked during the course of a year. On no occasion was any of the leaves blown away.

Each of the three sampling areas I-III and the four sampling areas A-D (used for zoological sampling) contained 15 such baskets, placed at random with the help of a co-ordinate system.

The arrangement in areas I-III took place at the end of July 1968. During the autumn of 1968, the baskets were emptied 4 times, during 1969, sixteen times and during 1970, thirteen times. The baskets were taken away in the spring of 1971. The annual litter fall was determined from one spring to the next. Throughout the leaf-fall period, i.e. during September and October, the baskets were emptied more frequently than during the summer. In times of rainy weather, the emptying process was repeated more often than during sunny periods. No emptying took place during the winter.

The material from the litter traps was taken in polythene bags to the laboratory, where it was dried at 36°C and then sorted. A subsample from each category was further dried to 85°C.

The material was sorted into the following categories:

Leaves (including needles) of roughly 18 different species, each of the species being taken separately

Reproductive organs such as catkins, flowers, nuts; male and female organs were sorted and separated into the respective species

Bud scales: these were not separated into species

Lichens
Mosses
Twigs
Miscellaneous material, such as bark and wood fragments, insect frass etc.

In 1968 and 1969, every collection was sorted separately but in the autumn of 1970 some of the collections were put together in order to reduce the amount of sorting. The material from each basket was taken separately in order to get an idea of the variation in weight between the different baskets.

The baskets were, of course, also open to birds and other animals, such as squirrels, and these might have had the opportunity to take nuts etc. as well as to soil the litter with their faeces. After careful examination, all droppings were removed from the baskets in order to prevent, as much as possible, any interference in the chemical analysis of the litter.

As regards the sampling of branches longer than 40 cm, this was done with the help of 5 quadrats located in each of the sampling areas and measuring 10 metres square. In July 1968, all branches longer than 40 cm were removed from these quadrats. Then, during the litter-sampling period, the freshly fallen branches were gathered and subsamples were dried and weighed. Thin branches, especially from *Betula*, were often difficult to find when the field layer had grown high and dense. The quadrats were picked clean once in 1968, twice in 1969 and three times in 1970.

The zoology team had stratified the Andersby ängsbackar into three strata (see Axelsson et al. 1970a). These three comprised the uncleared northern section, the southern birch-wooded pasture, and the interjacent partly cleared section with stands in close canopy and glade interstices. Sampling areas A-D were laid out at random within the respective strata, viz. two areas in each stratum. During stratification, all fringe sectors were excluded, with the result that the combined area covered only 16.2 hectares. This particular litter study was concerned with the northern stratum (areas A and B) and the interjacent stratum (areas C and D), see Fig. 1, and took the form of a comparison between the quantities of hazel leaves collected, partly green at the end of June and partly as litter. The comparison has been published (Axelsson et al. 1972). The collection of the litter, carried out by the present author, embraced, of course, all leaf litter (litter study 2).

During the autumn of 1970 (litter study 3), litter baskets were positioned along transects which covered the entire Andersby ängsbackar site, except for the free-lying esker section and some small morainic hillocks in the SW and the easternmost stripe, which was not cleared in 1967-68 because of different ownership. The baskets were placed at distances of 50 metres from each other. The distances between the transects varied in accordance with the heterogeneity of the topography, being 50 metres apart in the partly cleared wood with trees in close canopy alternating with glades, 100 metres apart in the more evenly thinned birch-wooded pasture and 200 metres apart in the uncleared woodland. Only leaves and needles were collected.

The leaf-area index is the quotient of the sum of one side of all the leaf laminae divided by the corresponding area of ground.

In order to estimate the leaf-area index, the leaves in the litter were counted, and leaves from subsamples taken from several collections were photocopied. The estimated mean leaf areas were multiplied by the number of leaves. Some values are taken from Inggårde (1969), who estimated the leaf-area index in 1968 by means of a regression between the leaf area and the square of the leaf length or the leaf length · leaf breadth (*Acer*). The regression for *Corylus* overestimated the leaf area with the result that a recalculation of this species area was made.

Litter study 1. Sampling areas I-III

Total litter

The results of the litter sampling in areas I, II:1 and III are found in Tables 25 a-d. As can be seen in Table 25a, there are sizable differences in the total litter fall between 1969 and 1970, i.e. the two years during which the total litter fall was investigated. In all three areas, the total in 1969 was greater than that in 1970, mainly due to differences in the fall of reproductive organs, twigs and branches.

The highest values, 3.5-4 ton/ha, were recorded in the uncleared area III and the lowest, 1.5-2 ton/ha, in the fairly strongly cleared area I.

Bray & Gorham (1964, p. 126) give 3.5 ton/ha as an average for the cool temperate zone, this being in fact a little lower than what was found to be the case in the uncleared area in Andersby. Rodin & Bazilevich (1967, p. 124) put forward a higher figure, viz.

5-7 ton/ha in the case of deciduous broad-leaved forests.

F. Andersson (1970b) estimated the total litter fall in a mixed oak-forest in Southern Sweden to a figure of 5.28 ton/ha while the values for the total litter fall arrived at by Nihlgård (1972) in the same province for a beech and a spruce forest were 5.70 ton/ha and 5.72 ton/ha respectively. Bonnevie-Svendsen & Gjems (1957) arrived at 2.50 and 3.13 ton/ha in the case of two beech forests in the Oslo region.

Leaf litter

The leaf litter comprised between 40 and 70% of the total litter, a percentage which is in accordance with the values given by Rodin & Bazilevich (op.cit., Table 32).

The highest leaf-litter values, 2-2.2 ton/ha, were recorded in the uncleared sampling area III, i.e. just over twice as much as in the partly cleared area I with 0.8-1 ton/ha.

In sampling area I, the leaf fall consisted of about 85-90% birch leaves. In area II:1, the leaf litter was more evenly shared by the species: *Acer* 33-40%, *Betula* 6-10%, *Populus* 7-13%, *Quercus* 13-18% and *Tilia* 17-18%. The leaf fall in area III was dominated by *Quercus* with 55-59%, but *Corylus* contributed sizably with about 21-22% and *Betula* with 7-9%.

Since small trees and many hazel stools in samp-

Table 25a. The mean dry weight of litter (g/m^2, 85°C) sampled in baskets and in quadrats in sampling areas I, II:1 and III with 95% confidence limits.

Sampling areas	Sample years	Leaves incl. needles	Reproductive organs	Bud scales, lichens, mosses, twigs, misc.	Total litter fall in the baskets	Branches >40 cm	Totals
I	1968	99.6 ± 14.4	–	–	–	–	
	1969	81.0 ± 11.6	74.1	35.4	190.5 ± 22.8	17.2 ± 12.5	207.7 ± 24.8
	1970	106.6 ± 15.5	13.0 ± 1.9	19.0 ± 6.5	138.6 ± 20.2	13.1 ± 5.1	151.7 ± 22.0
II:1	1968	166.4 ± 11.2	–	–	–	–	
	1969	182.5 ± 26.9	75.4	63.7	321.6 ± 56.0	61.7 ± 31.2	383.3 ± 58.2
	1970	195.7 ± 30.9	46.2 ± 8.5	51.2 ± 47.4	293.1 ± 61.6	12.3 ± 3.8	305.4 ± 61.8
III	1968	215.7 ± 23.4	–	–	–	–	
	1969	193.8 ± 24.4	37.0	70.0	300.8 ± 45.5	106.7 ± 75.5	407.5 ± 88.0
	1970	206.9 ± 10.2	22.3 ± 17.6	90.1 ± 30.2	319.3 ± 38.0	39.1 ± 24.8	358.4 ± 45.6

Table 25b. The mean dry weight of leaf litter (incl. needles) (g/m^2, 85°C) in sampling areas I, II:1 and III with 95% confidence limits.

	I			II:1			III		
	1968	1969	1970	1968	1969	1970	1968	1969	1970
Acer platanoides				64.80	63.79	65.02	1.11	3.78	3.50
Betula spp.[a]	90.14 ± 13.0	68.42 ± 9.5	97.18 ± 15.2	14.92	18.09	12.58	17.33	14.06	17.06
Corylus avellana	2.78	2.72	2.33	4.53	3.41	3.31	44.56 ± 16.6	42.62 ± 13.9	42.79 ± 13.5
Picea abies							8.92	10.45	8.38
Populus tremula	–	0.11	0.14	11.62	17.92	24.62	6.29	4.90	6.37
Quercus robur	5.24	7.75	5.01	28.95	24.47	34.79	125.43 ± 23.9	107.13 ± 17.7	116.54 ± 20.4
Sorbus aucuparia	0.18	0.20	0.29	5.52	11.01	10.08	8.94	6.80	8.85
Tilia cordata	0.43	0.65	0.41	28.11	33.46	33.71	1.13	2.64	1.67
Other leaves[b]	0.87	1.13	1.21	7.95	10.28	11.57	2.01	1.51	1.20
Totals	99.6 ± 14.4	81.0 ± 11.6	106.6 ± 15.5	166.4 ± 11.2	182.5 ± 26.9	195.7 ± 30.9	215.7 ± 23.4	193.8 ± 24.4	206.9 ± 10.2

[a] In area I: *B. pubescens* and *verrucosa;* in area II:1 and III: *B. verrucosa.*

[b] In area I: A.p., *Fraxinus excelsior, Juniperus communis, Lonicera xylosteum, Ribes alpinum;* in area II:1: *Alnus glutinosa,* F.e., L.x., R.a., *Salix caprea;* in area III: L.x., R.a., S.c.

ling area I and II:1 were cut down during the clearing in 1967/68, the share of leaves from the shrub layer in the leaf fall was smaller in these areas (4% in I and 7-9% in II:1) than in area III. In area II:1, the portion of leaves from this layer increased during the years of investigation. The share in sampling area III was difficult to calculate since the area has no distinct layers, but it must be more than the weight of the hazel leaves alone; the share of the total shrub layer is probably about 25%.

The variations during the three years were small. The litter-fall values for the three years have been tested by means of variance analysis. Significant differences existed between the litter fall in the three sampling areas, and the values in area I during 1969 and in area II:1 in 1968, deviated from those for the other two years. No significant differences between the years were obtained if the litter fall values in the three sampling areas were summated. This was partly due to the fact that litter fall increased during the course of the three years in sampling area II:1 but in sampling areas I and III, litter fall was lower in 1969 than in 1968 and 1970.

Certain common features with regard to the variation between the species during the three years were observed. Thus the birch leaf fall in areas I and III was lowest in 1969 while the rather high value for area II:1 during that same year could be ascribed to the fact that a birch outside the area, during the winter 1968/69, hung over some of the litter baskets and certainly contributed sizably to the birch leaf fall in 1969. Likewise, the oak leaf fall in areas II:1 and III was at its lowest in 1969. In sampling areas I and III, the leaf litter corresponded to a certain extent with the variations in birch and oak leaves respectively.

The rising values of the aspen leaf fall in area II:1 were due to the vigorous growth of suckers, although the leaf fall of the latter was probably underestimated. Among other important constituents of the leaf litter, both linden and rowan, found in area II:1, displayed lower values in 1968 than during the two following years. Maple in area II:1 and hazel in area III had roughly the same values throughout the three years.

The local distribution of the leaf litter inside areas I-III, on an average during the three years, can be seen in Fig. 24.

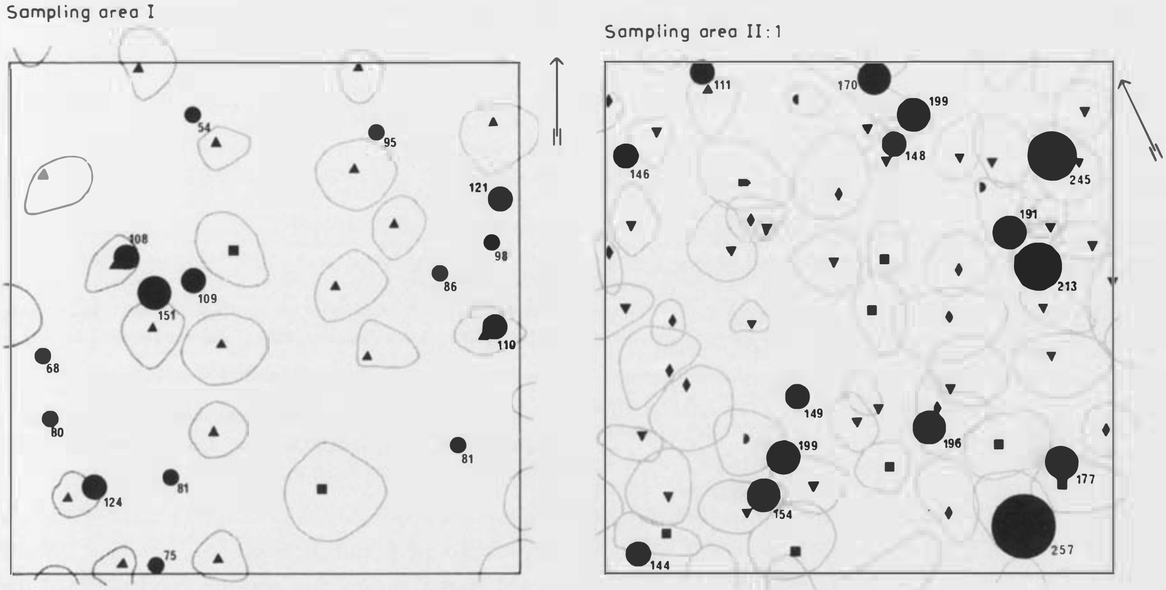
As was to be expected, the variation was greatest in area I where the tree layer is at its most open. The spot with the lowest leaf litter fall obtained only 36% of the value for the spot with the highest one. It was always the same litter basket which showed the lowest leaf litter fall. The same was true of the basket into which the litter fall was greatest. The distance from the nearest tree is not of absolute importance with regard to the amount of litter since the crowns of the trees, in many cases, begin at some height in sampling area I. Baskets which were positioned between individual tree crowns trapped an average of 86 g/m^2 while those located beneath the crowns and under their periphery caught 123 g/m^2. Thus, in area I, the variation from spot to spot was, by and large, the same during the three years. Rank correlation for the three years calculated in twos produced a high degree of unanimity in area I, r_s=0.85—0.89.

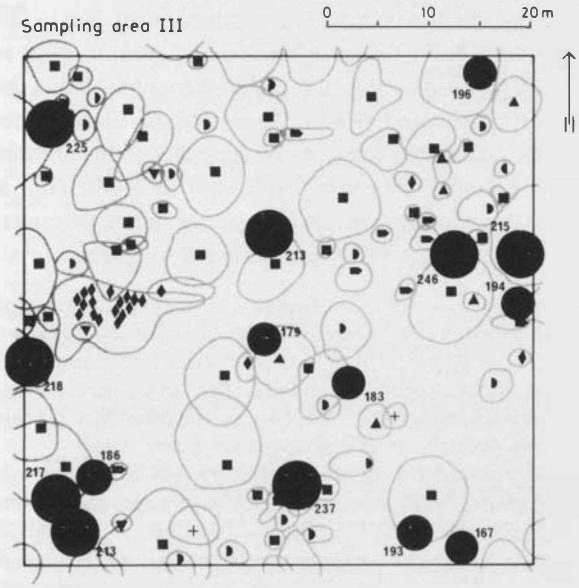
In area II:1, there was a high degree of positive correlation between the years 1969 and 1970, r_s =0.92, but this figure deteriorated when all three years were taken into account, r_s =0.61 and 0.65. Beneath the crowns, an average value of 196 g/m^2 was obtained with a corresponding 153 g/m^2 for sections located between trees. Two baskets placed under the periphery of crowns trapped 206 g/m^2. In area III, the correlation between the years 1968 and 1969 turned out to be negative, viz. $r_s = -0.02$, that between the years 1968 and 1970, r_s=0.13, and between 1969 and 1970, r_s=0.58.

The difference in the amount of litter collected in the three sampling areas may be slightly exaggerated due to the random distribution of the litter baskets. In area I, only 2 baskets happened to be positioned under canopy, 11 in the open and 2 under the periphery of a tree crown: this meant that 20% of the sampling baskets were covered and 80% not. The canopy cover in area I is 22%.

In area II, the corresponding figures were 7 baskets under canopy, 6 out in the open and 2 under peripheries, giving a percentage of 53% covered and 47% uncovered, whereas, in fact, canopy cover in area II:1 is 62%.

Finally, in area III, there were 12 baskets located beneath the tree and hazel canopy, 1 in the open and 2 under the edges of crowns, giving 87% covered and 13% uncovered. The canopy cover in actual fact is only 77% and thus, there is a distinct over-representation with regard to the litter baskets situated under canopy. However, there is little difference between the individual baskets in this area with the result that the figures recorded for litter are not influenced to too great an extent by this over-





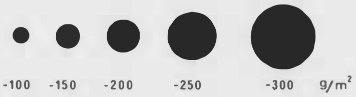


Fig. 24. Leaf litter-fall distribution sampled in baskets. Mean values 1968-70, g/m^2 (dry weight). Note that only the tree layers are mapped.

representation.

Compared with the average leaf-litter totals recorded for deciduous forests by Rodin & Bazilevich (1967) and for cool temperate forests by Bray & Gorham (1964), those arrived at in this study are somewhat lower. Bray & Gorham note 2.5 ton/ha (p. 126) in the case of leaf or needle fall and Rodin & Bazilevich (p. 127) report 3-4 ton/ha. In both works, it is pointed out that leaf fall decreases in more northerly latitudes. Andersby ängsbackar lie, as has already been indicated, in the northernmost part of the boreo-nemoral zone and, if this is taken into consideration, the values arrived at do not diverge from those expected.

There exists a great number of Nordic leaf-litter investigations, which have been carried out in both deciduous and coniferous forests. All investigations of mixed deciduous forests in southernmost Sweden—situated in the nemoral zone (Sjörs 1963)—show high litter values: Lindquist (1938), for instance, recorded an air-dried value of 2.9 ton/ha for a mixed deciduous forest dominated by oak, elm, ash and beech. For methodic reasons, this value might have been too low. F. Andersson (1970b) obtained an average spread over three years of 3.25 ton/ha in a mixed oak forest, while Nihlgård (1972), over the same length of time, recorded 3.57 ton/ha in a beech forest.

Julin (1948) has studied the litter of a former "park-meadow" overgrown by deciduous shrubs and trees, dominated by oak and situated in the province of Östergötland. The period in question for this investigation was the autumn of 1936 and the air-dried leaf litter amounted to approximately 3.2 ton/ha. The leaf-litter value in Julin's study is approximately 1 ton higher than the value from the uncleared area in Andersby and also somewhat higher than that from the elm-ash-forest at Vårdsätra mentioned below. In 1936, there were still to be found some rather small glades in Julin's area (1948, map 80), and the average for sites located in forest glades was somewhat lower than for those situated in areas with trees in close canopy (table 4), viz. 2.7 and 3.0 ton/ha respectively.

Bonnevie-Svendsen & Gjems (1957) measured the leaf fall in two beech forests in the Oslo region and obtained the figures 2.04 and 2.38 ton/ha during a two- and a three-year study period respectively. S.O. Andersson &

Enander (1948) studied a *Populus tremula* stand, with examples here and there of other species, reaching the value 1.81 ton/ha after only aspen leaves had been considered. In their publication, there is a reference to an unpublished work also carried out in an aspen stand where the values given for two different years are 1.91 and 1.95 ton/ha. Knudsen & Mauritz-Hansson (1939) recorded 1.77 ton /ha in a *Betula pubescens* stand. The above three investigations were carried out in the Stockholm region.

The Vårdsätra nature reserve near Uppsala, has a closed elm and ash forest with a basal area of 30 m^2/ha. Here the litter fall was measured during the autumn of 1971 using the same type of litter baskets as in Andersby. The leaf litter amounted to 273.3 g/m^2 (Hytteborn, unpub.).

Sjörs (1954) recorded 1.65 ton/ha in a birch stand with a tree canopy cover of only 45% in SW Dalecarlia. He also estimated the leaf-litter total in an area with a cover of 25% to about 0.88 ton/ha (air-dried). The birches in these stands stood well apart and their crowns were leafy almost down to the ground. This particular canopy cover of 25% coincides quite well with the actual state of conditions in sampling area I where the average value during the three years under investigation was only slightly higher, viz. 0.96 ton/ha.

In a closed birch forest with a dense regeneration of spruce in Norway, Mork (1942) estimated the leaf and needle fall to up to 1.27 ton/ha. Viro (1956), reporting on a four-year long investigation in Southern Finland, noted a mean value of 1.19 ton/ha. The two latter quoted values for birch are significantly lower than those of Knudsen & Mauritz-Hansson (1939, see above) and of Nordfors (1923) who gives 1.38 ton/ha in the case of a birch forest located as far north as Jämtland. Mork (op.cit.) has a very low value for a birch forest situated 800 metres above sea level, viz. 0.63 ton/ha.

Reproductive organs in the litter

The amount of litter produced from reproductive organs was surprisingly high and was significantly greater in 1969 than in 1970: see Table 25c. In sampling area I, where the reproductive organs were for the most part birch catkins, the respective figures were 35.8% and 8.6% of the total litter fall. In areas II:1 and III, the percentages for the two years differed much less, 19.5% and 15.1% in the case of area II:1 and 9.7% and 6.2% in that of area III, these figures being expressed as percentages of the total litter fall. The comparatively low litter fall of acorns and hazelnuts in area III is probably due to consumption of the latter by jays, nutcrackers and squirrels. Compared with the leaf litter fall, the litter from reproductive organs amounted to 91.4% and 12% in 1969 and 1970 in sampling area I. The corresponding figures for II:1 were 41.3 and 23.6% and for III

Table 25c. The mean dry weight of reproductive organs in litter (g/m^2, 85°C) in sampling areas I, II:1 and III.

	I		II:1		III	
	1969	1970	1969	1970	1969	1970
Acer platanoides			28.7	14.0		
Betula spp.	72.8	12.1	20.5	2.8	19.0	1.3
Corylus avellana					9.0	9.6
Picea abies					2.5	8.0
Quercus robur			4.2	2.7	5.3	2.5
Sorbus aucuparia			4.7	3.4		
Tilia cordata			15.0	19.6	0.2	0.6
Other species [a]	1.3	0.9	2.3	3.7	1.0	0.3
Totals	74.1	13.0	75.4	46.2	37.0	22.3

[a] In area I: A.p., C.a., *Lonicera xylosteum,* Q.r., S.a., T.c.; in area II:1: C.a., *Fraxinus excelsior,* L.x., *Populus tremula, Salix caprea;* in area III: A.p., L.x., P.t., S.c., S.a.

they were 19.1 and 10.8%.

Compared with other species, birch differed most during the two years. The production of maple flowers and fruits was roughly twice as great in 1969 as in 1970. Less sizable differences were recorded in the cases of oak and rowan. *Tilia cordata,* on the other hand, unlike the majority of species, produced more reproductive organs in 1970 than in 1969. *Tilia* is the only example of all the species under investigation that has a flowering period during July.

Various species of trees display a periodicity in flowering and fruit-setting. According to Kirchner et al. (1914 and 1911, pp. 245 & 110), *Betula* produces a larger amount of reproductive organs every third year, and *Quercus* every second to seventh year. *Corylus,* on the other hand, is said to produce an equal amount every year.

According to Lagerberg (1947, pp. 468 & 498), *Betula* and generally *Tilia* in most cases have a rich fruit-setting period every year while *Quercus* has these at intervals of five to seven years. Literature referred to in Grodzinski & Sawicka-Kapusta (1970) states that oak has a rich seed-crop every 3-8 years; maple and linden, on the other hand, exhibit this same phenomenon every or every other year. Jones (1959), in his description of *Quercus robur* and *Q. petraea,* writes that both these species "fruit with great irregularity" and that "heavy crops of seed. . . do not occur more frequently than once in 6 or 7 years". According to Hase (1964), a rich beechnut production occurs at intervals of 8-12 years'. Several authors cited in Matthews (1963, p. vii) point out that a year with particularly abundant flowering and fruit-setting affects the following year's production of reproductive organs and the current year's production of foliage and wood in a negative way, mainly because nutrients are used up which might otherwise have been suitable for the following year. In aspen, sallow and elm, which have separate inflorescence buds, a negative correlation obviously exists between number of inflorescences and number of leafy shoots of the same year.

From the above, it is obvious that different species flower and set fruit with different periodicities and therefore, a stand with many co-dominating species, as in area II:1, will provide a more even production of seeds. This may be an advantage to different consumers such as rodents and species of birds (cf. Grodzinski & Sawicka-Kapusta, op.cit.).

Matthews (1963) has compiled data dealing with factors affecting the production of seed by forest trees, including both deciduous and coniferous species. This author states that the most important external factors affecting the initiation of inflorescence in the bud state seem to be temperature, light, water availability and nutrient conditions.

As regards temperature, a somewhat higher temperature may be required for the formation of inflorescence-bearing buds than for that of purely vegetative leaf-buds. Light and the length of day are considered to be two of the main factors.

Discussing the water factor, Matthews (op.cit.) gives the following generalization: "a reduction in water supply in summer is frequently associated with flower-bud formation, especially in *Fagus silvatica*", but he also remarks that "the opposite relations have under certain conditions been found".

As regards nutrient conditions, Matthews states that, as far as is known, a rich soil will give a higher production of reproductive organs than a poor one but then, on the other hand, too few species have been thoroughly studied. He adds that "there is no doubt that on many forest sites the application of fertilizers will stimulate flowering and seeding, but the results obtained so far are too variable to permit definite prescriptions". Matthews also writes that "it is widely recognized that isolated trees flower and seed more abundantly than trees in close canopy".

Matthews writes that wind-pollinated species ought to be less dependent on the weather during flowering owing to the great speed with which pollen dispersal takes place, as soon as conditions are favourable. Insect-pollinated species, on the other hand, demand weather which is suitable for the flying of the insects which will carry out the pollination. Matthews also maintains that "spells of warm, dry weather . . . favour the maturing of the fruit and seed" but states, at the same time, that a certain author, Lipposzy, had demonstrated that "adequate rainfall during the growing season is associated with good crops of acorns". A year of abundant flowering need not mean an abundant fruit-setting since ineffective pollination, unsuitable weather or consumption by different animal species can impede this.

During 1968, the weather during a large part of May was cold and rainy: however, during the last week of this month, it became warm and dry. June was one of the warmest experienced during the 20th century with an average monthly temperature of 16.7°C, as compared with a normal average value of about 14°C. The monthly rainfall was also lower than average. The first days of July continued extremely warm but then, there was a change to cold rainy weather (SMHI årsbok 50).

The monthly global radiation recorded about 40 kilometres SSW of Andersby was higher than average for June. Conditions of temperature were thus probably more than normally favourable to the formation of inflorescence-bearing buds. The irradiation reaching every tree was obviously increased because of the thinnings that had been carried out in sampling areas I and II:1. Besides the improved light-climate, this could also have had a propitious effect on the daytime temperature in the stand. On the other hand, the night temperature might have decreased somewhat compared with a close canopy stand. During the summer of 1968, there was less rainfall than usual, approximately 88%. Due to the thinning on the sites, there was a decrease in the competition for nutrients which must have been marked, even though the decomposition of roots, etc., had not as yet begun to release any large quantities of nutrients. The factors connected with the formation of inflorescence-bearing buds postulated by Matthews must have had a positive influence, especially in the cleared areas.

During 1969, the weather during the greater part of June was warm and, above all, dry. July and August were also warm. The weather during 1969 was thus also probably advantageous to the maturation of seed and fruit. No comparative data are to be found in Bray & Gorham (1964) and little if any, in Rodin & Bazilevich (1967). In most litter studies, unfortunately, the reproductive organs are not separated and are usually included in a category of "remaining litter" or in the leaf litter.

Ovington (1963) recorded a litter fall of seeds of 0.28 ton/ha in a birch forest in England. Ovington & Murray (1964) estimated a male catkin total of 0.03 ton/ha in an oak forest with an acorn total varying from 0 in 1961, 0.15 ton/ha in 1962 and 0.48 ton/ha in 1960.

Ovington (op.cit.), studying a *Populus tremuloides* stand in Minnesota, estimated the weight of the male aspen catkins to 0.54 ton/ha, just over 25% of the leaf litter.

According to Jones (1959), acorn production can reach as high a figure as 200 g/m^2 undried, corresponding to about 1 ton/ha dry weight.

Kubiček (1972) records a figure of 0.40 ton/ha for an oak-hornbeam-forest in Czechoslovakia; Carlisle et al. (1966), 0.20 ton/ha, and Sykes and Bunce (1970), between 0.10 and 0.25 ton/ha, the former for an oak-forest and the latter for a mixed deciduous forest in England. Duvigneaud et al. (1969) note a value of 0.41 ton/ha for an oak-hornbeam-forest, 0.27 ton/ha for a hornbeam-oak-forest and the same value for an oak-hazel-forest, all three located in Belgium.

The estimated production of reproductive organs in Andersby is surpassed only by the acorn production values in the above quoted cases and would probably be surpassed by the beechnut production during particularly favourable years. Of special note was the birch-catkin litter production in 1969, primarily in the open, birch-wooded pastureland, amounting to more than the birch leaf litter, cf. Tables 25b and c. The sorting and weighing procedures have been checked and the results confirmed. The amounts of both male and female catkins were greater in 1969 than in 1970. It must be taken into consideration that the biomass of the male catkins was in the main already obtained during the previous year. The weight of the male catkins in the litter fall during 1969 was 15.4 g/m^2 and of the female catkins, 55.7 g/m^2.

Bud scales, lichens, mosses, twigs, branches and miscellaneous

In all, these categories comprise between 20 and 45% of the total litter, see Table 25d. As regards dry weight, only twigs and branches amount to sizable quantities.

The total amount of bud scales in 1970 was greater in all three areas than in 1969. In area III, this difference was all the more striking, owing to the formation and development of lammas shoots in oak in 1970.

One of the greatest difficulties as regards litter investigations seems to be the estimation of the rather irregular fall of large branches and occasionally even trunks. An accurate determination of the latter would entail an extremely long and detailed series of measurements and observations. Taken together, the weight of the twigs and branches in 1969 was greater than in 1970. In area III, one single large branch in 1969 was the reason for the high value recorded for branches, see Table 25a. The figure for lichens is slightly underestimated because lichens on fallen branches were not separated and weighed by themselves but were taken together with the branches.

The category "miscellaneous" includes bark fragments. These were, of course, not sampled quantitatively because the fragments, for the most part, tend to fall close to the trunks. Pollen production should also be added if the true sum of the litter fall is being aimed at. This production, though small by weight, is comparatively great in oak and birch and perhaps hazel but almost negligible in other species, with the possible exceptions of *Tilia* and locally *Populus* or *Picea; Pinus* and *Ulmus* are too uncommon to be considered.

Table 25d. The mean dry weight of bud scales, twigs, lichens, mosses and miscellaneous materials (g/m^2, 85°C) in the litter in the sampling areas I, II:1 and III.

	I		II:1		III	
	1969	1970	1969	1970	1969	1970
Bud scales	4.7	5.3	7.4	9.0	5.1	9.4
Twigs	24.8	11.0	44.8	31.5	51.5	66.9
Lichens	1.7	1.4	3.1	2.2	4.9	4.9
Mosses	+	+	0.1	0.1	0.1	0.2
Miscellaneous	4.2	1.3	8.3	8.4	8.4	8.7

Litter study 2. Sampling areas A-D

In area A, the measured leaf fall varied from 285 to 75 g/m^2 and in B between 315 and 138 g/m^2, see Table 26. Both areas have open areas, which were earlier hayglades. The variations were greater in the more complex areas, C and D, ranging from 237 and 60 g/m^2 in C to 209 and 34 g/m^2 in D. The lowest values were recorded in the glades.

Two of the sampling areas have landed by chance on two of the 3-4 occurrences of elm in the area. Oak leaves dominated the litter in all the areas except for A, where the amount of hazel leaf litter was somewhat greater. Estimating from the litter, the following list of precedence was obtained for the uncleared section—oak, hazel, aspen, birch and maple. In the case of the interjacent section, the order was oak, birch and hazel. According to this estimation, the litter fall in 1969 in the uncleared section amounted, on an average, to 206 g/m^2, and in the partly cleared stands with surrounding glades, to 118 g/m^2. If the litter value of just over 81 g/m^2 in sampling area I, the birch-wooded pasture, in 1969 is accepted for the entire southern stratum, then the average total leaf litter fall in the combined stratified sections of Andersby amounts to 168 g/m^2 (standard error 10.4).

Table 26. Litter study 2. The mean dry weight of leaf litter in the sampling areas A and B (stratum I), C and D (stratum II), autumn 1969 (g/m^2, 85°C) with 95% confidence limits.

	A	B	Stratum I	C	D	Stratum II
Acer platanoides	30.9	6.5	18.7	0.2	1.9	1.0
Betula spp.	28.2	17.2	22.7	43.7	26.2	35.0
Corylus avellana	54.3	38.5	46.4	18.0	35.0	26.5
Populus tremula	14.0	45.9	29.9	+	0.3	0.2
Quercus robur	42.0	89.5	65.8	60.3	34.3	47.3
Sorbus aucuparia	9.2	6.7	8.0	0.4	0.5	0.4
Tilia cordata	1.5	12.4	7.0	4.6	1.4	3.0
Other species	10.9	4.6	7.8	1.6	7.0	4.3
Totals	191.0 ±34.9	221.3 ±30.7	206.3 ±31.4	128.8 ±28.7	106.6 ±30.2	117.7 ±23.8

Litter study 3. Transects

The results are shown in Table 27 and Fig. 25. Table 27 indicates the leaf fall per square metre within the various strata as well as mean values for the cleared wood with tree groupings and glades, the uncleared ground and, finally, the entire Andersby area. The low value obtained for the coniferous forest was due to the fact that the sampling took place during autumn and thus comprised merely one part of the annual needle fall.

In the birch-wooded pastureland only birch and oak leaves were collected in all the baskets. The high maple value depended principally on one single basket, the same being true for hazel. The total leaves varied from 65 to 165 g/m^2 in this section.

In the partly cleared morainic areas, excluding the birch-wooded pasture, oak, birch and hazel leaves accounted for 85% of the total litter. Birch and oak leaves were to be found in all baskets, hazel in all but two and rowan in all but four. The weight totals varied from 49 to 230 g/m^2.

The glades in this section were characterized by the low mean value of 53 g/m^2, varying from 34 to 70 g/m^2. In many cases, there are examples of isolated birches in the glades. This contributes to the fact that birch leaves account for the highest portion of the leaf types. Birch and oak leaves were to be found in all nine baskets, hazel and linden in seven. In one of the baskets about 50% of the total weight was made up of elm leaves.

No baskets were placed on the partly cleared esker, owing to a shortage of time, and sampling area II:1 was considered to be representative for this section. For the sake of comparison, the leaf litter fall in area II:1 has been reproduced in Table 27.

There was a great deal of variation in the leaf fall in the wood in close canopy on till and clay, the lowest value of 52 g/m^2 being recorded in the eastern section where the forest is rather open and resembles the birch-wooded pasture in appearance. The next value in line amounted to roughly 148 g/m^2, and the highest value of approximately 349 g/m^2 was measured beneath a solitary oak-tree, under which there grew some *Prunus padus* bushes. The next highest value amounted to 247 g/m^2. In this stratum oak leaves accounted for 36% of the total, birch leaves for 24% and hazel leaves for 15%: these three accounted for 75%, maple and linden contributing a further 7% and aspen roughly 8.5%. Birch, oak, hazel and rowan leaves were found in all 20 baskets, aspen in 18, maple in 14 and linden in 12. Ash leaves were collected in only one of these 20 baskets.

The uncleared section of the esker, of which only

Table 27. Litter study 3. The mean dry weight of leaf litter sampled in the different ecosystems during the autumn of 1970 (g/m^2, 85°C).

	1 Birch-wood thinned	2 Hillocks thinned	3 Glades	2 + 3	4[a] Esker thinned	5 Till and clay unthin.	6 Esker unthin.	7 Spruce-wood	5 + 6 + 7 unthin.	1 - 7 Andersby Total
Acer platanoides	16.1	3.7	0.6	2.3	62.3	8.0	43.8		17.2	15.8
Betula spp.	60.4	37.0	25.6	34.2	12.2	48.0	29.1	32.6	42.7	41.9
Corylus avellana	19.1	28.3	2.2	22.0	3.3	29.0	17.1	0.3	25.2	23.2
Populus tremula		3.9	0.7	3.2	24.0	17.0	60.7	0.5	28.1	20.3
Quercus robur	9.8	51.3	14.3	42.3	33.8	72.8	27.3	16.5	59.5	50.3
Sorbus aucuparia	0.3	1.0	0.5	0.8	10.1	4.8	16.7	1.2	7.9	5.8
Tilia cordata	0.5	8.0	3.8	7.0	33.5	5.8	15.6	18.9	8.7	8.3
Lonicera xylosteum + *Ribes alpinum*	2.2	0.9	0.1	0.7	6.0	0.6	2.4	+	1.1	1.2
Other deciduous species[b]	0.2	2.2	4.8	2.8	4.9	13.4	6.3	0.4	11.1	8.3
Needles[c]	+	0.2	+	0.1		0.1	+	22.5	0.6	0.5
Totals	108.6	136.5	52.6	115.4	189.9	199.5	219.0	92.9	202.2	175.6

[a] From Table 25b.

[b] *Alnus glutinosa* in 5 and 6; *Fraxinus excelsior* in 3, 4, 5 and 6; *Prunus padus* in 3, 5 and 6; *Rhamnus frangula* in 2; *Rosa majalis* in 3; *Salix caprea* in 2, 3, 4, 5 and 6; *S. cinerea* in 2 and 3; *Ulmus glabra* in 3; *Viburnum opulus* in 6.

[c] *Juniperus communis* in 1, 2, 3 and 5; *Picea abies* in 5 and 7; *Pinus silvestris* in 2 and 6.

<10 10 25 50 100 200 300 400 g/m²
Acer platanoides
Betula spp.
Corylus avellana
Populus tremula
Quercus robur
Tilia cordata

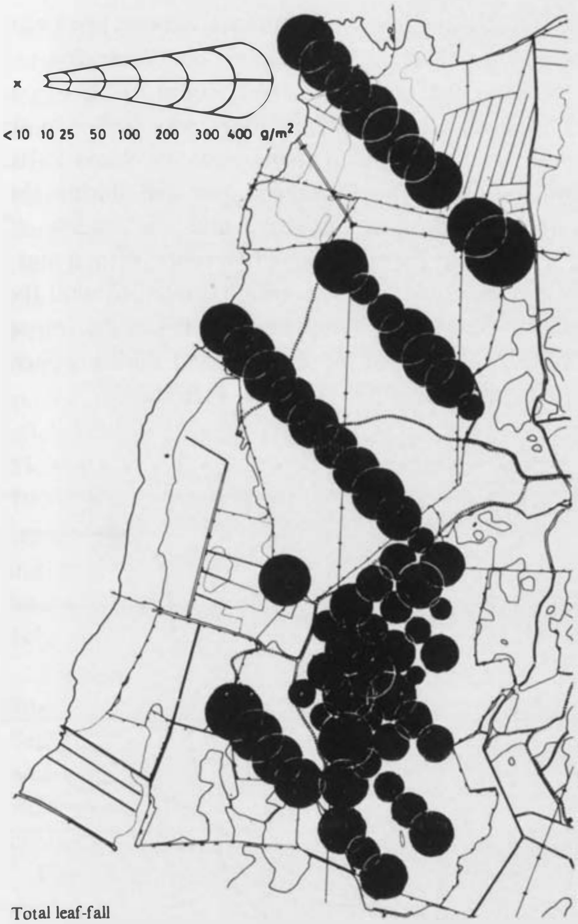


Fig. 25. Leaf litter fall sampled in baskets placed in transects during autumn 1970, g/m^2 (dry weight).

the adjoining part was studied, displays a smaller variation in the leaf fall, the latter lying between 167 and 258 g/m^2. The distribution by species, however, is different when compared with the uncleared wood on till and clay. Maple and linden leaves accounted for 27% of the total leaf litter fall, aspen for 28% while oak leaves formed a mere 12% of the total and birch 13%. Therefore only 34% of the leaf litter fall in this area was made up of oak, birch and hazel leaves (compare with above). The contribution from *Lonicera xylosteum* and *Ribes alpinum* was greater in this section than in the wood on morainic material. Maple, birch, oak, rowan and linden leaves were gathered in all 8 baskets, hazel and aspen in 7 and leaves of *Lonicera xylosteum* in 6.

Although rowan has an even distribution throughout the whole study area, it plays an insignificant part in most of the areas as regards leaf litter. In the two areas located on the esker, the total was 5% in the partly cleared sector and 7.6% in the uncleared section.

The uneven distribution of litter in an area characterized by both open, wooded meadowland and, in a few places, trees in close canopy, was investigated by Sjörs (1954), who employed a non-random sampling technique. His values ranged from 318 g/m^2 to as little as 1 g/m^2. Sjörs remarks that this distribution can vary from year to year, depending on the prevailing wind direction and, in the long run, the positioning of the trees and thus, the distribution of the litter on meadowland can be altered by felling and regeneration.

In the previous section, great divergences were also reported for Andersby. The lowest value obtained was 25 g/m^2 and the highest 346. An average of 53 g/m^2 was recorded for the glades, which were earlier used, for the most part, for haymaking. The location of the hay-glades in Andersby was conditioned by the topography, with the result that one can be certain that there has been no great redistribution of the glades nor of the groves of trees now in close canopy. The treeless glades, formerly often being larger, must in most cases have received an even lower litter-nutrient supply. However, it should be pointed out that some of these depressions were once inhabited by large oaks (B.M.P. Larsson, in preparation), which were probably rich in leaves.

The recorded distribution, being in baskets, takes no account of possible blowing around after the litter has fallen. This is said to occur only to a limited extent within deciduous stands except under extreme wind conditions, according to Sjörs (op.cit. p. 97). Thin, large leaves, like those of maple, have greater possibilities of shifting than smaller ones, like those of birch, according to Sjörs.

One of the factors which affects the humus content and the thickness of the humus layer is the amount of litter. Both of the above-named characteristics vary considerably. The vegetation in the clayey glades is different from that on the hillocks of till (see Larsson, B.M.P., 1971a and Persson, in press). However, there is a co-variation in several conditions, not only the litter and the geological substrate, but also the microclimate, the soil fauna and the human influence, with the result that it is impossible to associate differences in vegetation, decomposition and soil with differences in litter. Sjörs (op.cit.) could find no definite connection between the supply of leaves and the composition of the vegetation. On the other hand, the addition of leaf litter to the topsoil makes the latter more uniform and reduces the difference caused by the various inorganic substrates; in Andersby, the till, the clay and the esker gravel.

The annual pattern of the litter fall

The distribution of the accumulated total litter fall, coarse twigs and branches excepted, during the year 1969 is shown in Fig. 26a. In Figs. 26b, c and d is shown the fall pattern with respect to the three litter categories, i.e. leaves, reproductive organs and other litter, including bud scales, mosses, lichens, fine twigs etc. in the three sampling areas, see Table 25a.

During the entire snow-free period, there was a continuous litter fall. The pattern was similar in all three areas during both of the years 1969 and 1970, with a slight but unbroken litter fall during the summer and early autumn until the middle of September or the beginning of October: then, a maximum, due to defoliation, which continued until the end of October. Varying amounts fell in the course of the later half of the autumn and during winter, when twigs were for the most part shed.

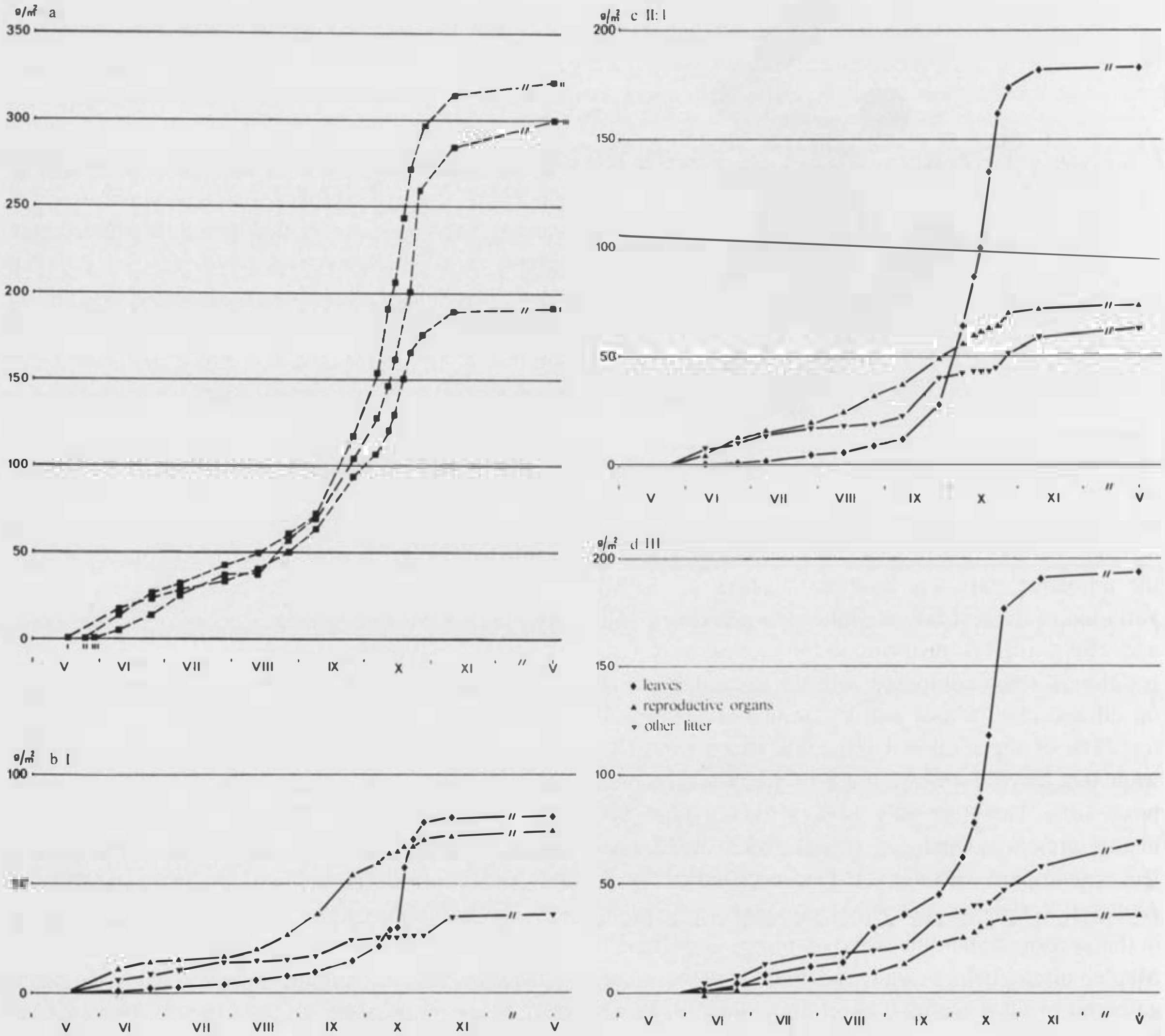


Fig. 26a. Accumulated total litter fall, except large branches in sampling areas I, II:1 and III during 1969 to spring 1970, g/m² (dry weight).
b-d. Accumulated litter fall divided into three fractions, leaf, reproductive organs and "others", sampled during 1969 to spring 1970 in I, II:1 and III, g/m² (dry weight).

Reproductive organs, shed during June, include the male catkins of birch and oak, and maple flowers etc. The flowers of linden-trees were shed during July and August. Scales and fruits of female birch-catkins were shed from August to October and also, in part, during the winter. The majority of fruits were shed during the autumn, but linden fruits, unshed during the autumn and early winter of 1970, remained on the trees until early January 1971 or even until February. Only a limited percentage of this part was trapped in the baskets since a large part was consumed by animals while it still hung on the trees or after it had fallen onto the snow-covered ground. Most of the linden-fruits collected in the spring of 1971 were split and their contents devoured. Bud scales shed in June (also in July 1970 in area III owing to the formation of lammas shoots). The lowest litter-fall totals were recorded during the months of July and August.

There was a clear connection between gales and litter fall, especially in the case of twigs. On September 22nd, during the last week of October, and on November 1st and 2nd, 1969, high winds were recorded, this also being evidenced by the increased fall of "other litter".

During all the years of the investigation, the main part of the leaves was shed in October. The earliest shedding of leaves, however, took place as early as June, i.e. not long after the burst into leaf. The causes of this were damage by the insect population, frost or periods of drought, or strong winds. A normal feature of hazel is the early shedding of dwarf leaves, and it is also normal that living twigs with green leaves become detached from oak-trees. The total amount of early shedding varied from species to species. The largest summer leaf falls are displayed by hazel, oak and birch, in that order. Since the outermost long-shoot leaves of birch and hazel are not fully developed until the end of July, it follows that the total amount of leaves collected from the trees was never growing on the trees at the same period of time.

During the very dry summer of 1969, unusually large amounts of leaves were shed in August, notably of birch, hazel and aspen. This applied to the entire area as regards hazel, but only to certain sections in the uncleared woodland as regards birch and aspen. Thus the cumulative curve for the total leaf litter fall in sampling area III showed a marked rise during August 1969. In the other sampling areas, the total figure for the leaf fall was not strikingly affected.

In contradistinction to the conditions prevailing in Andersby, Witkamp & van der Drift (1961, p. 298) found that the drought in 1959 delayed the leaf fall, especially in the case of *Betula verrucosa* and *Populus tremula*, other species studied being *Quercus robur* and *Alnus glutinosa*. In 1957 and 1958, on the other hand, quite large amounts of birch and aspen leaves fell during August and September.

Viro (1956, p. 42) found that in 1947, with its warm September, birch leaf-shedding was delayed until after November 1st but that in 1949, with its cool September, all birch leaves had been shed by this time; an average, taken over four years, showed that the maximum birch leaf fall took place in October.

Sykes & Bunce (1970, p. 329) carried out a three-year series of litter measurements in Meathop Wood in the English Lake District, a mixed deciduous forest consisting of *Quercus petraea* and *Q. robur*, *Fraxinus excelsior*, *Betula pubescens* and *verrucosa*, *Acer pseudoplatanus* and *Corylus avellana*. They stated that hazel leaves were retained 2-3 weeks longer in the autumn than the leaves of other species. The maximum leaf-shedding here took place as late as in November. However, conditions in this oceanic climate are hardly comparable with those in Andersby, where both birch and oak shed their leaves at a later date than hazel.

In the Dutch oakwood investigated by Witkamp & van der Drift (1961), the leaves of *Quercus robur* were shed in November. Julin (1948) said that in his area, in Östergötland, leaf fall had terminated by November 6th. Lindquist (1938) gave about the same date for Dalby Söderskog in Scania. Carlisle et al. (1966), state October for a wood located in the Lake District in England.

The unusually late leaf fall near Uppsala in 1974 was probably related to the exceptionally low number of frosty nights (only two until early November).

Witkamp & van der Drift (op.cit.) and Sykes & Bunce (op.cit.) have pointed out that the sequence of the litter fall has a specific influence on the structural composition of the litter layer. However, in this study, the difference is not so marked as in the above-quoted cases.

Below and in Fig. 27 are given further details concerning the pattern of the leaf litter fall, with regard to the common trees and shrubs. Unless otherwise stated, the notes are based on observations carried out in sampling areas I-III.

The curves in Fig. 27 were constructed from separate, cumulative curves for each individual species and each year, 1968-70, in each one of the sampling areas I-III. The average date for each 10% increase was calculated from these separate curves. However, certain omissions had to be made owing to a few extreme aberrations, such as *Corylus*,

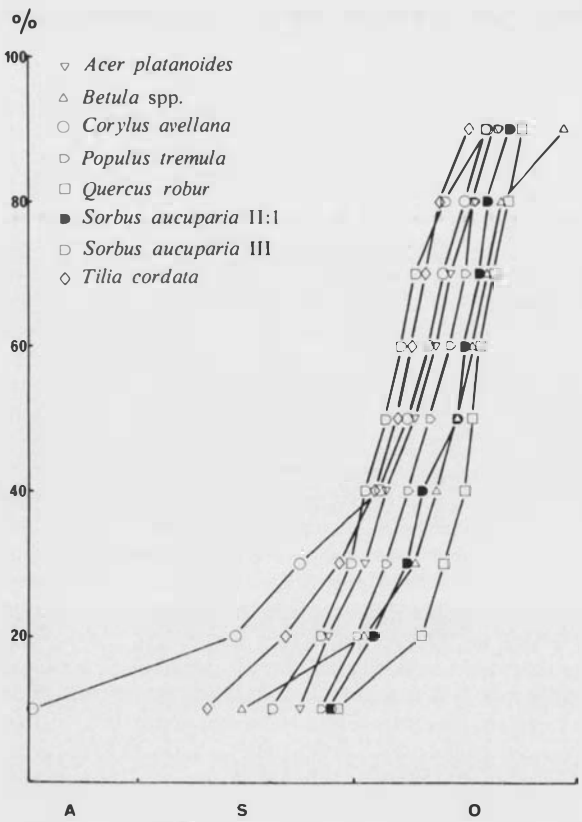


Fig. 27. Cumulative leaf litter fall for each species, calculated on a percentage basis, average for the years 1968-70, with omissions of extreme aberrations due to drought.

Betula and *Populus* in area III in 1969 and the figures obtained late in 1968 when there were too great intervals between the collections.

Members of the same species often shed leaves at different times. In sampling area III, for example, several of the oak-trees had approximately 80-90% of their leaves still attached on the 7th of October 1973; three individual trees, on the other hand had only 10-20% of their leaves still attached.

Acer platanoides. Roughly 10% of the leaf litter fall of maple took place before autumn commenced. The autumnal leaf fall began in the last week of September and ended about October 20th. The 50 percent mark was reached between the 6th and 11th of October during the three years in question. The mean date for the commencement of maple defoliation in Uppland, according to Arnell (1923), for the period 1873-1917, was September 27th.

Betula pubescens and verrucosa. With the single exception already mentioned (area III, 1969), birch leaf fall had a uniform pattern. A slight but continuous leaf-shedding occurred from the beginning of June with an increase in 1969 and 1970 in September and the first days of October, when 20-30% of the leaves (dry weight) had fallen. Subsequently, a vigorous defoliation took place, terminating in the last week of October. 50% of the birch leaves were shed by mid-October, 11th to 17th, in all the areas. Taken together, the two species of birch have a more lengthy leaf-fall duration than other deciduous trees which were investigated. Members of the species *pubescens* shed their leaves at an earlier stage of the autumn than members of the *verrucosa* species.

In sampling area I, on October 7th, 1973, it was observed that *Betula pubescens* had 0-10% of their leaves still attached, one tree having as much as 40% attached, while examples of *Betula verrucosa* had 40-80% of their leaves left, except for a single tree with only 5%.

The rather exceptional leaf fall in area III in 1969, between August 12th and 26th, affected no less than 25% of the total birch leaf fall but similar conditions were not observed, neither in areas I and II:1 nor in the zoological sampling areas A, B, C and D at this particular time. During the late summer and autumn of 1969, other trees visibly affected by the drought were observed, mainly in the uncleared woodland section. In one part of the latter, both birches and hazel coppices were almost completely defoliated by early September. Arnell (op.cit.) states September 29th as the beginning of birch leaf fall, this being an average for the period he investigated.

Corylus avellana. The leaf fall of hazel during the three years was not uniform but, in all cases, larger quantities fell prior to the commencement of the autumnal leaf-fall period than in the case of other species. In area I, no less than 10% of the total had been shed by the early part of June 1969 but, in contrast, in area II:1, the same percentage had not been shed until late July 1970. All areas, including the four areas of the zoological team, A, B, C and D, displayed the increased leaf fall in August 1969.

Between 15 and 50% of the leaves were shed as early as October 1st; the 50% value was attained between October 1st and 15th. Arnell (op.cit.) gave October 8th as the mean date when hazel leaves began to fall, slightly later than that noted for Andersby.

Picea abies. Spruce needles were collected in a few baskets only in area III. The needles were shed fairly evenly during all three years, but in 1969, an increase was observed in September and from late October onwards. About 28% fell during the winter, this figure being calculated from the total obtained for the period May 28th, 1969 to May 6th, 1970. During 1970, however, more than 50% fell between May 6th and July 21st, and as little as 9% during the following winter.

Populus tremula. Except, as mentioned, in area III in 1969, less than 10% of the aspen leaf litter was shed before the autumnal leaf fall, which commenced in late September or early October. After October 22nd, only scattered leaves were to be found remaining on the trees. The period was shorter than for any other species. In area II:1, the leaf fall started somewhat earlier in 1969 and

1970 than in other areas. This might have been due to shedding at an earlier date by the numerous saplings.

Arnell (op.cit.) stated that the aspen leaf fall began on October 1st.

Quercus robur. It is normal for the oak to cast twigs with green leaves during the summer. This, in area III in 1969, amounted to as much as 10% of the total quantity of oak leaves collected. Of all the oak leaves shed during the summer of 1970 in area III, the majority were damaged, blackish brown in colour and often fragmented.

The autumnal leaf fall began in the second week of October and 50% of the total leaf litter had fallen by October 12th-20th. The leaf fall occurred a little later in 1969 than in 1970. Few leaves remained on the trees after the end of October.

According to Arnell (op.cit.) oak leaf fall commenced on October 11th.

Sorbus aucuparia. Few leaves fell during the summer. The autumnal leaf fall began during the last two weeks of September, as a rule, but every years it started somewhat earlier in area III, with the result that the 50 percent mark was attained 8-13 days earlier in this area than in area II:1.

During the litter collections in 1970 with the transect method, rowan leaves were gathered both in the partly cleared and uncleared woodland on till, and in the uncleared woodland on the esker. The pattern of the leaf litter fall in area II:1 (esker, partly cleared wood) was similar to that in the uncleared woodland on the esker but was later if compared with area III (till, uncleared) and the entire uncleared woodland on till. Partly cleared woodland on till had a delayed leaf litter fall. It is known from literature cited by Bray & Gorham (1964, p. 138) that shade-leaves tend to be detached earlier but evidently other reasons may also play a part. The leaf litter fall ended during the last week of October.

According to Arnell (op.cit.), the leaf fall of rowan starts on an average on October 2nd.

Tilia cordata. Only insignificant quantities of leaves fell during June and July, but in 1969 and 1970, there was a gradual increase in late August and September. It is difficult to give an exact date for the beginning of the autumnal leaf fall during these two particular years. In 1968, 70-80% fell during the last week of September and the first of October. In 1969 and 1970, the leaf fall was more protracted than in 1968 and the final phase terminated later. Between October 2nd and 9th, 50% of the leaves were shed and the leaf litter fall was at an end in the third week of October.

Arnell (op.cit.) gave October 7th as the starting date.

The difference between the earliest and latest species was only about 12 days, if a comparison is made as to when 50% of the leaflitter has been shed. *Sorbus* in area III and *Tilia* were the earliest, followed by *Corylus, Acer, Populus, Sorbus* in area II:1, *Betula* and finally *Quercus*. The start of the leaf fall were in all cases earlier than the dates given by Arnell (1923).

A comparison between the different litter studies

The three different litter studies had different aims but also present three individual methods for estimating litter fall.

The three sampling areas, I, II:1 and III, had been laid out subjectively and the study included all litter. Sampling areas A-D were chosen at random and, because of technical reasons, the placing involved only two areas in each stratum, with the result that the statistical significance is low.

The third study, which utilized transects over the entire Andersby area, constituted a systematic, non-random sampling, the statistical significance of which was probably good for the larger part of Andersby but, unfortunately, this varied since cer-

Table 28. Comparison between three methods of leaf-litter estimation. Further explanation, see text.

Till and clay, unthinned

	line transects	stratum I, A + B	sampling area III	
Collection year	1970	1969	1969	1970
Number of baskets	20	30	15	15
Leaf litter, g/m²	200	206	194	207
% *Betula* spp.	24.1	11.0	7.1	8.4
% *Corylus avellana*	14.5	22.5	21.4	20.4
% *Populus tremula*	8.5	14.5	2.3	3.0
% *Quercus robur*	36.5	31.9	54.2	55.7
% Other species	16.4	20.1	15.0	12.5

Till hillocks & clayey depressions, partly cleared

	line transects	stratum II, C + D
Collection year	1970	1969
Number of baskets	28	30
Leaf litter, g/m²	115	118
% *Betula* spp.	29.6	29.7
% *Corylus avellana*	19.1	22.5
% *Quercus robur*	36.7	40.2
% Other species	14.6	7.6

Thinned birch-wooded pastureland

	line transects	sampling area I
Collection year	1970	1970
Number of baskets	6	15
Leaf litter, g/m²	107	107
% *Betula* spp.	55.6	91.3
% Other species	44.4	8.7

tain strata were better represented than others. The study was performed in order to find out how the sampling areas differed from the situation as a whole and to obtain the variation in the whole study area. Possible comparisons are to be found in Table 28, where the percentages of the more important leaf types are also given.

Studies 2 and 3 were carried out during different years but the three-year study, no. 1 in areas I and III, showed that significant differences between years occurred only in the birch-wooded pastureland, in which method 2 was not employed. In this case, a comparison between methods 1 and 3 can be based on the measurements taken during the same year.

The mean values for the total leaf fall are almost exactly the same in all the comparisons. In litter study 3, since the sampling was not done at random, no variance was calculated; nevertheless, the differences between the methods with regard to the total leaf fall were obviously not significant. On the other hand, some of the species display certain differences depending on which sampling procedure was employed.

Assuming that sampling carried out throughout entire ecosystems gives a fairly adequate representation of the leaf litter with regard to evenly distributed species, the following remarks can be made.

In areas A and B, method 2, uncleared woodland, the share taken by hazel and aspen is higher than the average for the stratum while that of oak and, to an even greater extent, birch, is lower, compared with results obtained with method 3.

Sampling area III, method 1, is characterized by a higher than average percentage of oak and hazel leaves while that of birch leaves is far lower, only 1/3 of the value obtained with the transects, method 3.

Both the methods used in estimating the leaf fall in the partly cleared hillocks of till and the clay depressions showed roughly the same kinds of results; this even applies to the proportions of the litter borne by the different species. A modest excess in weight for hazel and oak in sampling areas C and D is hardly of any real significance. With the transect sampling method, the leaf litter of a greater number of species was trapped and this includes even some carr species which are not represented in the other sampling areas.

A comparison in the case of the birch-wooded pasture would be of limited value since only 6 baskets were used in the transect sampling method (see above Litter study 3).

The differences between the proportions and percentages of *Betula* are striking.

Concerning the average litter fall in the whole of Andersby ängsbackar, the litter study 2 gave a slightly lower value than litter study 3, 168 g/m^2 and 176 g/m^2, respectively. However, the sections richest in leaves, viz. those located on the esker, were not included in study 2 and only in parts in the transect study, method 3. The reason for the diverging results on a species level is, of course, that the tree and bush species are not evenly spread over the area but are aggregated; for instance, *Populus tremula* and *Tilia cordata* grow in clones. The size of the sampling areas, 50 x 50 meter, was obviously large enough to level the unevenness in the total leaf-fall distribution both in the thinned birch-wooded pasture and the partly cleared till hillocks with clay depressions.

The conclusion from the different litter samplings is that it is an advantage to stratify the investigation area. The distribution between glades and groves can serve as a primary basis for stratification or, in an area with sparsely growing trees, the distribution between ground covered by tree crowns and open ground. The next basis could be the distribution of the main species share of the crown cover.

In Fig. 28 are the different values from the leaf litter studies in Andersby set against the basal area of the trees. A flaw in the diagram is the fact that only the trees' basal area has been taken into con-

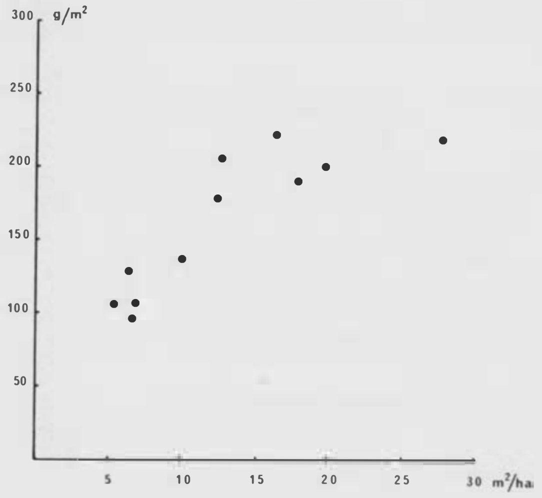


Fig. 28. Relationship between leaf litter fall (dry weight) and basal area in the different sampling areas and parts of Andersby ängsbackar.

sideration while that of the shrub and coppice layers, particularly of hazel, has not. The given values of basal areas in areas III, A, B and D are, for this reason, underestimated. The diagram suggests that the leaf-total increases with relation to the basal area up to around 15 m^2/ha and then remains at 200-220 g/m^2, irrespective of basal area.

Thus, litterfall can hardly be estimated from the basal area. When a stand is full-grown, the amount of leaves does not increase, but the basal area of the individual trees continues to increase. The total basal area of the stand will also increase but only until that point in time when the trees start to die back or fall, cf. Rochow (1974, p. 82). Bonnevie-Svendsen & Gjems (1957, Fig. 1), however, obtained a positive correlation between litter fall and basal area. Their material included both coniferous stands and deciduos stands with great differences in basal area.

Leaf-area index

The results of measurements carried out in sampling areas I-III are given in Table 29. The variations between the years in all the sampling areas were relatively high, viz. 1.4-1.8 in area I, 3.1-3.8 in area II:1 and 4.0-5.4 in area III. These values, of course, do not include the leaves of the field layer, the total leaf-area index being considerably higher. No results are, however, available for the leaf-area index of the field layer but it is obviously higher in area I than in area II:1 and III, thus reducing the great differences between the areas.

The leaf-area index values given were calculated from litter. According to Vanseveren (1969), the area of a litter leaf is approximately 10% less than the area of a corresponding leaf in a fresh state. Kubiček (1971), in a study of *Quercus petraea*, measured the regression between the leaf area and the product of leaf length and leaf breadth, partly with dry leaves and partly with green. He obtained two separate regressions. In order to obtain the area that the foliage had during the summer, it is necessary to adjust the index.

The leaf mass collected in the form of litter has, however, never been on the trees at the same time, since the leaf litter fall begins as early as the month of June, i.e. prior to the complete foliation of the total leaf mass.

This must be taken into special consideration, when dealing with species which have an early partial defoliation, e.g. *Corylus*, and species which have a long period of shoot production, e.g. *Corylus* and *Betula*.

The variations in sampling area I were in accordance with the variations in the foliage of birch. In 1969, the average leaf was smaller than in 1968 and 1970 and the amount of leaves was also smaller, Table 30, all of which contributed to a reduction in the leaf-area index. The leaf-litter values for birch varied in the same way.

The partly cleared sampling area, II:1, had in 1968 a leaf-area index which was 2.3 units lower than that of sampling area III, but the leaf-area index showed the same increasing trend as the leaf litter. Of special note were the increases in the leaf-area index of aspen.

After the clearing an unnatural structure with a leaf-free layer between the foliage of the tree layer

Table 29. Leaf-area index of the tree and shrub layers, m^2/m^2 in sampling areas I, II:1 and III.

	I			II:1			III		
	1968	1969	1970	1968	1969	1970	1968	1969	1970
Acer platanoides				1.08	1.19	1.10			
Betula spp.[a]	1.47	1.09	1.50	0.23	0.39	0.19	0.37	0.28	0.27
Corylus avellana							1.70	1.56	1.51
Populus tremula				0.17	0.40	0.62			
Quercus robur				0.54	0.48	0.57	2.91	2.45	1.76
Tilia cordata				0.64	0.64	0.74			
Other species[b]	0.22	0.32	0.26	0.39	0.56	0.53	0.43	0.46	0.43
Totals	1.7	1.4	1.8	3.1	3.7	3.8	5.4	4.8	4.0

[a]In area I: *B. verrucosa* and *pubescens*, in II:1 and III: *B. verr.*

[b]In area I: A.p., C.a., *Fraxinus excelsior, Lonicera xylosteum, Populus tremula*, Q.r., *Ribes alpinum, Sorbus aucuparia*, T.c.; in area II:1: *Alnus glutinosa*, C.a., F.e., L.x., R.a., *Salix caprea*, S.a.; in area III: A.p., L.x., P.t., R.a., S.c., S.a., T.c.

Table 30. Number of leaves/m² of the most important species in sampling areas I, II:1 and III during 1968, 1969 and 1970.

	I			II:1			III		
	1968	1969	1970	1968	1969	1970	1968	1969	1970
Acer platanoides				266	292	289			
Betula spp.	2190	2000	2170	403	587	307	434	437	335
Corylus avellana							775	705	693
Populus tremula				77	202	404			
Quercus robur				320	306	346	1540	1230	1900 [b]
Sorbus aucuparia [a]				202	465	453	407	366	409
Tilia cordata				283	424	522			

[a] Leaflets [b] 310 leaves from lammas shoots

and that of the lower shrub and field layers was obtained. This space was quickly filled by *Populus tremula* suckers. The leaf-area index of *Populus* is probably underestimated since not all the shrub-layer leaves were trapped to an appropriate extent in the litter baskets. In 1971, a sample was taken of 10 aspen suckers with their foliage still intact. An approximate estimate of the leaf-area index from this sample gives a value of 1.4 m²/m² in the case of *Populus*. Thus, one arrives at an estimated leaf-area index of roughly 4.5 for 1971, under the assumption that the leaf-area index of the trees is the same for 1971 as for 1970 (2.8 m²/m²), and that one includes an additional 0.3 units for the shrub layer. Thus, it can be stated that the leaf-area index had increased from 3.1 to 4.5 in the space of 4 years.

Contrary to findings in sampling area II:1, a decreasing leaf-area index was registered during all three years in sampling area III. This applied to the two dominant broad-leaved species, viz. *Corylus avellana* and *Quercus robur*. The decrease in the leaf-area index of *Corylus* was due in the main to a slight reduction of the number of leaves, while the average leaf size showed only small variations during the three years. The drought of 1969 killed off a number of stems and this probably contributed to the reduction in the leaf number in 1970. The amount of oak leaves in 1968 was greater than that in 1969 and this explains the fall in the leaf-area index for these two particular years. In 1970, the oak leaves were damaged and lammas shoots developed. The total number of oak leaves was thus higher, approximately 1900 per m², as compared with 1540 per m² in 1968 and 1230 per m² in 1969. It was possible to distinguish the leaves formed on the lammas shoots in the litter. The number was 310 per m². The total number of first shoot-generation leaves consequently coincided well with the number registered in 1968. A mere 140 per m² were in an undamaged state. The damages present on the leaves were due to different factors. A rather small number of leaves which had not developed fully fell at an early point during the growing season and these were dark or black in colour, probably the result of low temperatures. A comparatively large number had been damaged by insects and other animals. The chief part of the leaves were misshapen and dentate. In 1968 and 1969, the average leaf area was 18.9 and 20.0 cm² respectively. In 1970, the damaged leaves had an average area of 8.25 cm², the undamaged ones of 24.3 cm² and those from lammas shoots, 13.8 cm². The leaf-area index sank to 60% of that of 1968. The weight of the oak-leaf litter, on the other hand, did not diminish to any appreciable degree, see Table 25. The leaf-area index proportion of the shrub layer in sampling area III is difficult to estimate to any degree of certainty since the vegetation had no distinct layers and since the same species were to be found both as trees and as saplings. However, the leaf-area index of the shrub layer amounted to at least 1.7 units, possibly to 2 units, in which case the leaf-area index of the tree layer would be 3.7-3.4 units.

Carlisle et al. (1966, p. 70) have produced a compilation of leaf-area indices of tree species, based, for the most part, on information gathered by the Hungarian, Járó. Apart from two values of 8.44 and 7.48 recorded in beech forests, the highest values lie between 6 and 7. Carlisle et al. (op.cit.) arrived at a value of 4.75-5.47. Their particular study area was a *Quercus petraea* forest with *Deschampsia flexuosa* and *Pteridium aquilinum* in the field layer. During one particular year, an extensive attack by *Tortrix viridana* reduced the leaf-area index to 3.98.

Vanseveren (1969) quotes leaf-area indices of between 5.23 and 6.30 from studies carried out in 5 Belgian broad-leaved forests, dominated by one or more of the following species: *Quercus robur* and *petraea, Fagus silvatica, Carpinus betulus* and *Corylus avellana.*

Kubiček (1972) estimated the leaf-area index in his study area to 5.18; the tree layer there was composed primarily of *Carpinus betulus*, *Quercus petraea* and *Quercus cerris*.

The variations in the leaf-area index throughout the years of study are greater than the variations in the weight of the leaf litter, cf. Table 25. The value recorded for sampling area III in 1968 is comparable with the above-quoted values, without coming as high as the highest ones. This is natural enough since the sampling area contains several glades.

Chemical analyses of living material and litter

Samples of litter were taken for chemical analyses in connection with the general litter sampling carried out in 1970. The different categories of litter were taken when their particular maxima had been reached during the season.

Litter sampling was undertaken at intervals of one week. This was done in order to reduce, to as great an extent as possible, the amount of leaching. It is, however, impossible to prevent leaching completely, especially on rainy days. Nykvist has demonstrated that newly fallen leaves of *Fraxinus excelsior, Betula verrucosa, Alnus glutinosa, Fagus silvatica* and *Quercus robur* lose about 52, 33, 25, 17 and 15% of their respective inorganic contents during a single day's leaching at a temperature of 25°C (Nykvist 1959, 1961 and 1962). Nykvist's reports show that the size of this source of error is dependent on the timing of the cropping of the litter and also on the species. The leaching of potassium is by far the greatest.

Green-leaf sampling took place between July 28th and August 1st. Twigs were taken from different individuals of the same species and from different parts of the crown.

Completely whole, normal-sized leaves were taken from the litter and living material. The leaves were dried at 37°C for 24 hours. The area of the leaves, except for the *Corylus* leaves, was estimated. The analyses were carried out using whole leaves in order to enable the possibility of calculating the contents per unit area. The area of other litter material was of course not estimated.

The material was then digested in 20 ml concentrated HNO_3 + $HClO_4$ (4:1) nearly to dryness, following Johnson & Ulrich (1960, p. 32 et seq.). The remains were dissolved in 0.1 M HCl and the analyses were made with an atomic absorption spectrophotometer (Mg, Mn, Ca) and a flame photometer (K, Na). When analyzing Ca, $LaCl_3$ was added in order to mask phosphate.

Nitrogen content was analyzed according to Jackson (1958, p. 183 et seq.) with 0.5 g material.

In Fig. 29 the contents of the analyzed nutrients in green leaves and in litter leaves are plotted in diagrams. The contents are given both as a percentage of the dry weight and per leaf area. The green leaves and the litter leaves from the same area are connected in the diagram. In connection with the litter fall the weight of the leaves decreases, which may lead to an apparent but not real increase in the content of a nutrient, if calculated on a weight basis. By calculating on an area basis, this source of error disappears. The area of a litter leaf is considered to be about 10% less than the corresponding area of a green leaf, see above. For this reason, if no transport or leaching occurs, the content in a litter leaf calculated on an area basis ought to be a little higher than in a green leaf.

The contents of potassium were considerably higher in the green leaves than in the litter leaves, regardless of the method of calculation. The contents of magnesium were, except in *Acer* and *Tilia* leaves, insignificantly higher in litter leaves than in the green leaves, when calculated on an area basis. This difference, on the whole, could have depended on the reduction in area. The content of magnesium in the two samples of *Tilia* leaves, particularly in the litter leaves, were varying and the result is not very reliable. The measurements of the area were performed on dry wrinkled leaves, which causes an uncertainty, especially concerning the *Acer* leaves. The contents of magnesium calculated on dry weight were higher in all litter leaves except the *Tilia* leaves. The three remaining elements analyzed, manganese, sodium and calcium, all had higher contents in the litter leaves than in the green leaves calculated both on an area basis or on dry weight. The connection lines in the diagram run more or less parallel, indicating that the contents diminished or increased in a similar way in leaves of all species.

The results agree with the conclusions in Rodin & Bazilevich (1967, p. 134). They also noticed that the

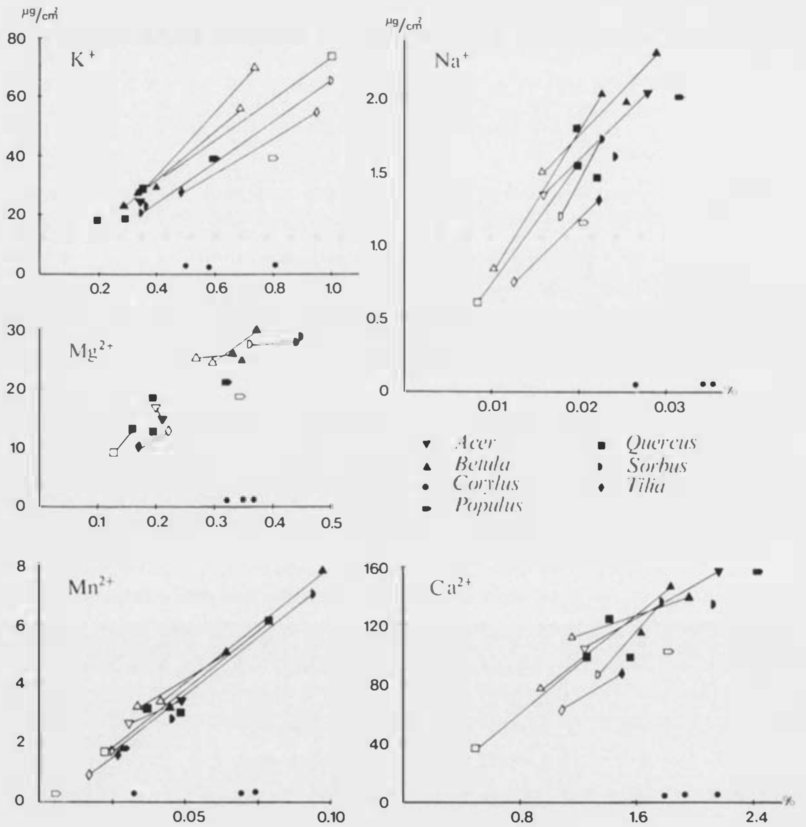


Fig. 29. Contents of potassium, magnesium, manganese, sodium and calcium in per cent dry weight (abscissa) and μg/cm² leaf area (ordinate). Green leaves (open symbols) and litter leaves (filled symbols) of the same species and from the same sampling area connected with a line. The area of the *Corylus* leaves was not estimated. The % content in *Corylus* litter leaves is given in the lower part of the diagram.

contents of magnesium did not show a regular pattern.

The low contents of potassium in the litter leaves depended on both leaching and translocation. Depending on which methods were used in calculating the contents in the green leaves of the different species, varying orders of precedence were obtained, see Fig. 29.

The contents of magnesium were higher in *Sorbus, Betula, Populus* and *Corylus* leaves than in *Acer, Tilia* and *Quercus* leaves. Low contents of manganese were measured in *Populus* and *Tilia* leaves and the highest in *Betula* leaves. The litter leaves showed great variations in the content of manganese with higher contents in *Betula, Sorbus, Corylus* and *Quercus* leaves from sampling area III than in corresponding leaves from sampling areas I and II:1. The lowest content were obtained in leaves from sampling area II:1. Sjörs (1954) also recorded great variations in *Betula* litter leaves (0.60-0.25 %). As Mn (II) is oxidized in circumneutral or alkaline soils, and plants take up manganese as Mn (II), the high pH in sampling area II:1 is probably the reason for the lower content in leaves from this area.

Table 31. Nitrogen and sum of calcium, manganese, magnesium, potassium and sodium (ΣMe) as percentage of litter dry weight, green leaves and *Betula* ♀-catkin.

		Litter leaves		Green leaves	
		ΣMe	N	ΣMe	N
Acer	II:1	2.77	1.10 0.62	2.45	
Betula p.	I	2.49	0.66	2.21	2.13
Betula v.	II:1	2.42	0.76		
Betula v.	III	2.60		1.99	2.79
Corylus	I	3.43			
Corylus	II:1	2.65			
Corylus	III	2.89	1.24		
Populus	II:1	3.40	0.87		
Populus	III			2.96	
Quercus	I	2.08			
Quercus	II:1	1.85	0.89		
Quercus	III	1.87	0.86	1.67	
Sorbus	II:1	2.90	0.78		
Sorbus	III	2.61		2.73	
Tilia	II:1	2.19	1.47	2.28	
Betula ♀-catkin	I		1.39		

Table 32. Per cent dry weight of potassium, magnesium, manganese, sodium and calcium in fresh non-leafy litter, sampled during 1970.

Category	Samp. area	Date	K	Mg	Mn	Na	Ca	Sum
Betula ♂-catkin	I	15.6	0.47	0.18	0.03	0.02	1.09	1.79
Betula ♀-catkin	I	19.9	0.50	0.15	0.02	0.01	0.68	1.36
Betula ♀-catkin	II:1	19.9	0.67	0.13	0.01	0.01	0.62	1.44
Acer schizocarp	II:1	22.10	1.42	0.16	0.02	0.01	0.83	2.44
Populus catkin	II:1	4.7	0.91	0.26	0.01	0.03	1.74	2.95
Tilia fruit	II:1	22.11	0.39	0.16	0.02	0.03	1.14	1.74
Corylus ♂-catkin	III	3.6	0.40	0.13	0.03	0.01	0.77	1.34
Quercus ♂-catkin	III	3.6	0.49	0.22	0.09	0.02	1.36	2.18
Lichens	I	18.8	0.30	0.08	0.01	0.01	0.50	0.90
Lichens	II:1	22.11	0.44	0.09	0.01	0.01	0.74	1.29
Lichens	III	22.11	0.39	0.07	0.02	0.01	0.80	1.29
Lichens	III	22.11	0.36	0.06	0.01	0.01	0.48	0.92
Bud scales	I	3.6	0.09	0.07	0.01	0.01	0.60	0.78
Bud scales	II:1	3&15.6	0.57	0.20	0.02	0.02	1.32	2.13
Bud scales	III	21.7	0.18	0.15	0.06	0.02	1.14	1.55

The contents of calcium in the litter were high. According to Mork (1942, p. 355) and C.O. Tamm (1951) the contents of calcium vary with the supply of calcium in the substrate, cf. Hesselman 1926, Lindquist 1938, Sjörs 1954, Viro 1956 and Samuelsson 1966. Higher contents of calcium have been measured in *Quercus* and *Corylus* leaves from Dalby (Scania) where the subsoil is rich in lime (Hesselman, op.cit., Lindquist, op.cit.).

The total contents of the analyzed mineral elements are summarized in Table 31. The following order is obtained when arranging the litter leaves after falling percentage contents as calculated on dry weight: *Populus, Sorbus, Acer, Betula, Tilia* and *Quercus*. Because of the varying results in the *Corylus* leaves, their placing remains uncertain. All leaves, except *Tilia*, had higher total contents in litter leaves than in green leaves.

The contents of nitrogen, Table 31, in the litter leaves of *Betula* were lower than stated in all abovementioned works. However, the contents in green leaves of *Betula* were within the limits given by C.O. Tamm (1956, Table XI). The contents in *Quercus* and *Corylus* leaves were also lower than as stated by Hesselman (1926), Lindquist (1938) and Nykvist (1962). The published values concerning the contents in *Populus* and *Sorbus* leaves are both higher and lower. Of all species, *Tilia* and *Corylus* had the highest contents of nitrogen in the litter leaves.

Mineral nutrients found in reproductive organs, in lichens and in bud scales are tabulated in Table 32. The concentration of potassium in the reproductive organs were higher than in the leaves; the schizocarps of *Acer* had an especially high potassium content. The magnesium content, on the contrary, was lower than in the leaves, except for *Quercus*.

The female catkins of *Betula* were considerably richer in nitrogen than the litter leaves. The supply of nitrogen to the ground varied considerably between 1969 and 1970 depending on the high production of catkins in the year 1969. The mentioned periodicity in the production of reproductive organs may partly depend on the fact that the trees had to accumulate nutrients during the course of several years in order to produce a great quantity of reproductive organs. In sampling area I, the ground was supplied during 1969 with more than double the quantity of nitrogen than in the year 1970. The concentration of mineral nutrients was, on the contrary, higher in leaves than in catkins.

Of all analyzed categories, lichens—unfortunately not determined to species before digestion—were poorest in nutrients. Great differences were measured in the mineral nutrient contents of the bud scales. The bud scales from sampling area I came, in the main, from *Betula*, in area II:1, in the main, from *Acer* and *Tilia* and in sampling area III, in the main, from *Quercus*. The bud scales from sampling area II:1 were especially rich in potassium.

Substrate

Methods

Introductory studies into the humus layer were carried out in sampling areas I-III. Nine separate samples were taken from each sampling area. These were systematically distributed over the area. Each sample consisted of two part-samples of defined volume (206.3 cm^3) and one general sample. Furthermore, a sample was taken in the spruce stand and a few samples were also taken along transects stretching from a clayey depression up to the crest of a hillock, one transect in the cleared area and one in the uncleared. Soil profiles were dug in all three soil materials, till, clay and esker material, to illustrate some of the properties of the soil. The three profiles were dug in the unthinned part of Andersby. The soil samples were transported to the laboratory and stored in a frozen state.

The chemical analyses were carried out on fresh samples which were first sieved through 2 mm mesh. All the estimates are based on this fine earth. In order to calculate the bulk density of fine earth, the volume of the gravel and stones was subtracted from the total volume of the sample.

The nitrogen content was estimated by means of the macro-Kjeldahl method according to Jackson (1958) from 4-5 g of soil, dried at 105°C.

The humus content was measured on dried samples as the loss on ignition at a temperature of approximately 550°C. No correction was made out for water losses from humus samples containing clay.

pH was measured in water extracts and in 0.01 M $CaCl_2$. The extracts were prepared according to Knutsson in Malmström (1949), Sjörs (1961).

The pH was measured electrometrically with separate glass and reference electrodes (Beckman Expandomatic), after the mixture had been shaken for 2 hours and filtered. The measurements were taken after the pH had stabilized. According to Peech (1965), pH measured in $CaCl_2$ is roughly 0.5 units lower than that measured in water extract.

Exchangeable metallic cations and hydrogen ions were estimated by the method used by Tyler et al. (1971). The water contents of the fresh samples were determined. 25 g of fresh soil were rotated in a polythene flask together with 150 ml 1 M NH_4Ac (pH adjusted to 7) for 2 hours. The particulate material was then filtered off. 100 ml of the extract were evaporated to dryness and reheated with concentrated HNO_3 and $HClO_4$. The sample was dissolved by adding HCl. Na^+ and K^+ were estimated with an EEL flame photometer and Mg^{2+} and Ca^{2+} by means of complexometric titration (Schwarzenbach & Flaschka 1965). Disturbances arose in connection with the titration of six of the samples from sampling area III. Nonetheless, satisfactory values were obtained. The contents of Mg^{2+} and Ca^{2+} in the samples from the profile were determined by atomic absorption.

The concentration of exchangeable hydrogen ions was obtained by measuring the pH of the above-mentioned NH_4Ac-extract, after which the concentration of H^+ ions was read off a pH curve which was obtained by adding small amounts of 0.1 M HCl to the 1 M NH_4Ac (pH=7) which was used during the extraction process (Brown 1943).

The degree of neutralization (Sjörs 1954, p. 73; 1961, p. 14) or percentage base saturation was arrived at by dividing the sum of Na^+, K^+, Ca^{2+} and Mg^{2+} equivalents by the cation exchange capacity, determined as the sum of H^+, Na^+, K^+, Mg^{2+} and Ca^{2+} equivalents.

Description of the humus layer and the soil profiles

The humus layer had developed into types, which resemble the descriptions and definitions of moder, mullish moder and mull, in Kubiëna (1953, pp. 45 et seq.). The litter layer was sharply separated and distinguished from the humus layer.

The aggregates were small but distinct in sampling area II:1. The humus contained numerous weathered white mineral grains. It was 5-10(13) cm thick. The same type of aggregation occurred in sampling area I's low-lying sections. However, the substratum was composed of clay, so only a small number of visible mineral grains occurred. In other samples taken from sampling area I, the aggregates were bound together by the roots of grasses and were less distinct, the humus containing recognizable remains of plants. In sampling area III, the humus was composed of loose aggregates on sediment. On the till, the humus had developed from types with distinct aggregates held together by roots to types with indistinct aggregation and a content of plant remains. The latter kind, however, was not a mor. Two samples located between boulders displayed this transitional stage, one of them covered with a layer of leaves.

The profiles are reproduced in Fig. 32. In the till profile was found a weakly developed eluvial horizon under the humus layer, but this was not the case in the clay and esker profiles. The different horizons in the clay profile probably resulted during the formation of the deposite rather than as a consequence of the soil development.

According to tradition in Sweden, the soil profile in the till is classified as a mull-podzol and the two other profiles as brown earths (O. Tamm 1930). O. Tamm made a distinction between climatic and aclimatic brown earths. Only the southeastern parts of Sweden belong to the region of climatic brown earths. The aclimatic brown earths depend on a vegetation with particularly favourable properties, or on a special hydrology such as surface/subsurface water flow, or on base-rich soil material. In Andersby ängsbackar, the vegetation and the soil material, with its original lime content, tend towards the development of brown earth.

Linnermark (1960) introduced the term podzoloid for intermediary forms between podzols and brown earths. He included in podzoloids, mull-podzols, mor-brown earths, etc. Linnermark maintained that dynamic soils could develop towards either brown earths or podzols. The podzoloids were distinguished from both podzols and brown earths by several, differing criteria: by an F-layer without or nearly without an A_2-horizon or by a mull over an A_2-horizon, by patchiness or by a marble-like appearance in both the A_2 and the B horizons or by diffuse outlines of the horizons. The till profile is, according to Linnermark, a podzoloid.

On the map produced by FAO (1965) of the soils of Europe, the part of Sweden to which Andersby belongs was indicated as having grey-brown podzolic soils and podzolized soils.

The characteristic of grey-brown podzolic soils (parabraunerde) is that a horizon with a high clay content is formed by downward transport and that an A_2-horizon is missing (Troedsson & Nykvist 1973). A clay horizon can, however, be developed for several reasons. It is uncertain whether the above mentioned brown earth profiles could be classified better as a grey-brown podzolic soil.

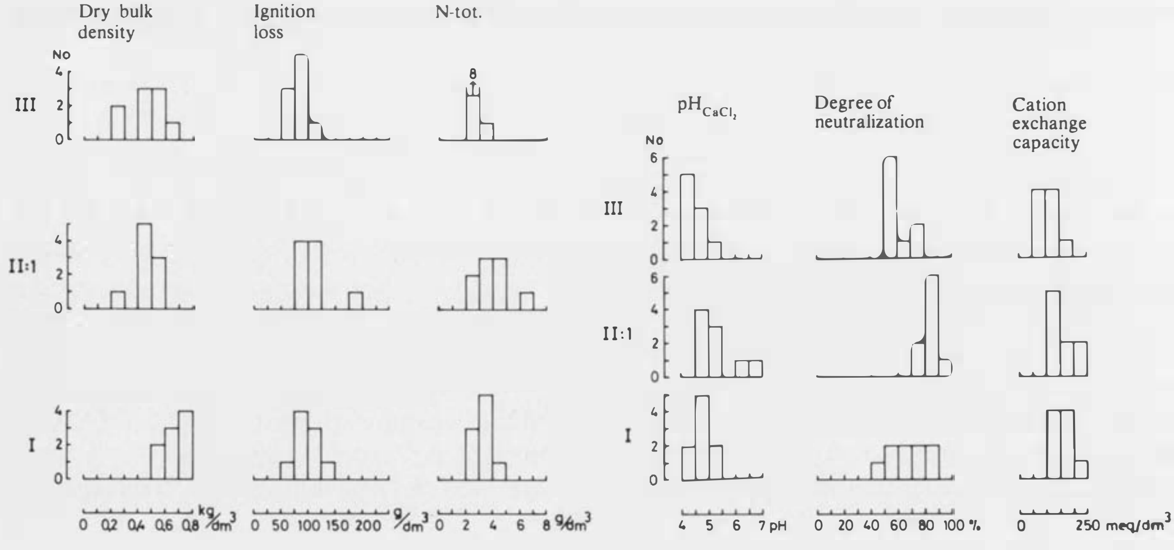
Nykvist (1968) pointed out the similarities between the soils we call brown earths and the Russian soils whose designation is often translated as sod-podzolic soils. Nykvist divided podzols and sod-podzolic soils into four types, podzols, strong, medium and weak sod-podzolic soils. The till profile corresponds to the medium sod-podzolic soil. According to Nykvist (pp. 425-426), the international trend is not to use the original brown earth concept according to Ramann. The classification is now changing and a new international system with new terms is being accepted. In the book by Troedsson & Nykvist (1973), it has not yet been adopted.

Analyses of the humus layer

Bulk density and humus content

The dry bulk density of the fine earth (Fig. 30) shows the greatest variation in sampling area III, where two of the samples had a lower density than the others. One particular value from sampling area II:1 was also significantly lower. Sjörs (1961) and F. Andersson (1970a) have demonstrated that one obtains a negative correlation if one plots the dry bulk density of the humus layer against loss on ignition expressed as percentage weight. The three above-mentioned samples had some of the highest ignition losses.

The bulk densities were higher and the humus content, expressed as percentage ignition loss, was lower in sampling area I. The highest loss on ignition registered in sampling area I was measured in samples which contained clay. However, this difference was too large to be solely dependent on



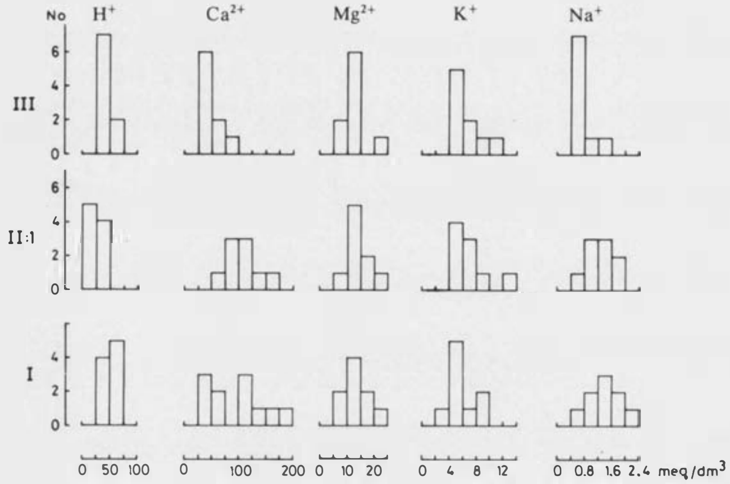


Fig. 30. Properties of the humus layer in the three sampling areas I, II:1 and III.

the clay content. Expressed as percentage of dry weight the losses on ignition were in area I 9.6-26.3, in area II:1 13.7-32.9 (47.1) and in area III 10.7-36.4.

Both the densities and the losses on ignition lay within the variations measured by Sjörs in samples which the latter classified as forest mull and related types of humus (1961, Table 2, p. 46). The weights of roots and gravel, which have not been included in the density of the fine earth, were in no case of such proportions as to affect the results.

Nitrogen

If measured as a percentage of the loss on ignition, nitrogen contents varied rather moderately. The variation in sampling area I was from 2.9 to 3.8%, in sampling area II:1 from 2.9 to 4.2%, and in sampling area III from 2.9 to 3.5%. Sjörs (1961) gives values of 2.4 to 4.0% for forest mull and related types of humus and goes as high as 4.7% in the case of mull from grasslands and other open sites. If the nitrogen content is expressed in g/dm^3 fine earth, see Fig. 30, somewhat greater variations will be obtained, because the humus content per unit volume varies and almost all the nitrogen is probably organic in nature. If the nitrogen content is expressed as a percentage by weight of the dry sample, high nitrogen contents are obtained in samples which have low bulk densities and/or high humus contents. Therefore, nitrogen contents given in this way say nothing about the humus quality with regard to nitrogen content, and are unsuitable as a basis for, e.g., ecological ordination.

According to Sjörs (1961), the nitrogen content in mor rarely amounts to more than 2.4% of the loss on ignition. The two samples from sampling area III with a humus type, which was less mull-like, had nitrogen contents of 3.1 and 2.9% of the loss on ignition respectively. Disregarding the manner in which the nitrogen content is given, the mean value of the latter was higher in sampling area II:1 than in the other two sampling areas.

pH

The pH values in all areas are high, and especially so in the case of sampling area II:1. The differences between pH values from water extracts and $CaCl_2$ extracts varied from 0.8 to 2 pH units and increased with pH up to pH 7 in water extract, cf. Black (1968, Fig. 5.9). In Fig. 30 are to be found only pH estimates in $CaCl_2$.

Two pH values in sampling area II:1 were considerably higher than those of the other samples. The median value of the $CaCl_2$ extracts was nearly the same in sampling areas I and III, viz. 4.5 and 4.4 respectively, and somewhat higher in sampling area II:1, viz. 5.0.

Exchangeable cations

Variations in the exchange capacity were greatest in sampling area I, lying between 112 and 242 meq/dm^3. The highest exchange capacities were recorded in the case of the samples taken on the sediment, which were rich in humus. Samples from area II:1 had almost the same mean value as those from area I. Samples with the highest exchange capacity were those which also had the richest humus content and vice versa. Sampling area III had a lower exchange capacity in the majority of the samples taken than the other two areas. The sample with the highest exchange capacity (approximately 150 meq/dm^3) also had the highest humus content. The mean values for sampling areas I, II:1 and III were 152, 146 and 102 meq/dm^3 respectively.

In Fig. 31 the exchange capacity per dm^3 has been plotted against the humus content per dm^3. A distinctly positive correlation was obtained, cf. Gorham (1953).

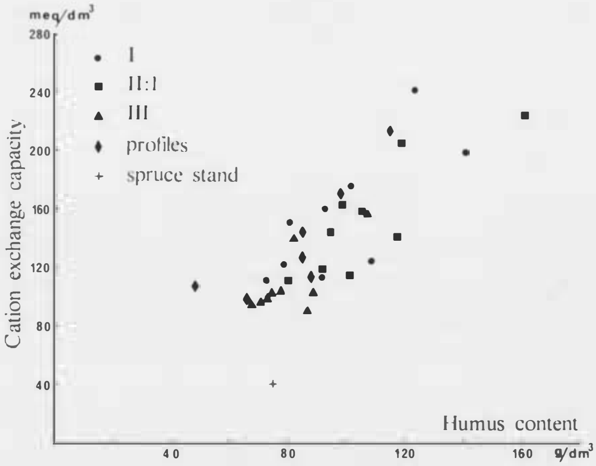


Fig. 31. Cation exchange capacity with relation to humus content (as ignition loss).

Two samples diverge from the imaginary regression line. The mor sample from the spruce stand had a lower exchange capacity in relation to its humus content than the other humus samples. This is in accordance with Sjörs (1961, p. 19). One of the samples from the transects had a very low humus content but, in spite of that, a normal exchange capacity. The results are possibly erroneous since the humus type did not differ from that in other samples. Sjörs gives values of 67 to 273 meq/dm^3 for forest mull, the lowest value coming from a mull which was on the borderline to being a mor. The values recorded by Sjörs (1961) and Gorham (1953) were obtained by a different method, which with low pH values give higher values for the exchangeable metallic cations, F. Andersson (1970a, p. 156).

The degree of neutralization (percentage base saturation) in sampling area II:1 was high and varied from 82 to 90%. Samples from area I varied considerably, from 46 to 88%. Four of the samples had a degree of neutralization higher than 70%. In sampling area III, the degree of neutralization lay between 50 and 76%, six samples having values between 50 and 60% and the other 3 higher. Samples with the highest degree of neutralization also had the highest Ca^{2+} content.

The dominant, exchangeable, metallic ion was the Ca^{2+} ion. The samples varied most in sampling area I where values of between 21 and 84 mmol/dm^3 were obtained. The samples from area III did not vary to such a great extent and also had low Ca content values—a mean value of approximately 17 mmol/dm^3. The exchangeable Ca content in sampling area II:1 varied from 33 to 81 mmol/dm^3. Sjörs (1961, Table 2) gives variations of between 12 and 240 meq/dm^3 for forest mull and related types of humus. During the course of this study, 25 g of earth were used with 150 ml of extractant, the amount of earth being probably somewhat too great to obtain a complete exchange in samples which contained a high quantity of minerals. Consequently, the Ca^{2+} values given for these samples may be somewhat low since the calcium ion is bound more tenaciously than the other common metallic ions. On the other hand, it is not deemed suitable to utilize NH_4Ac extract in the presence of $CaCO_3$ since the extractant dissolves lime, with the result that one obtains an overestimate of the exchangeable Ca^{2+} ions. No fragments of limestone were observed in the humus layer, neither was there any effervescence when HCl was added.

With respect to the three remaining metallic cations which were analyzed, viz. Mg^{2+}, K^+ and Na^+, no directly observable differences were noticed between the three sampling areas, except that the Na^+ content in sampling area III was somewhat lower than that in the other two areas. The Mg^{2+} and K^+ contents, in mmol/dm^3, were of approximately the same size.

Sjörs (op.cit.) gives a variation of between 2 and 10 mmol/dm^3 for the Mg^{2+} content in forest mull, 0.9 to 9.5 mmol/dm^3 for the K^+ content and 0.3 to 2.1 for the Na^+ content.

The content of exchangeable hydrogen ions was greater in sampling areas I and III than in sampling area II:1. Estimated in meq/dm^3, the content of exchangeable hydrogen ions was greater than that of exchangeable Ca^{2+} ions in 3 samples from sampling area I and 6 from III. In sampling area II:1, the hydrogen ion content was nowhere greater than the Ca^{2+} content.

Analyses of the profiles

The humus content in the humus layer of the profile in the esker material was high, Fig. 32, being on the upper limit of the variation in sampling area II:1. The losses on ignition of the mineral part of the clay profile have been corrected according to Ekström (1927).

In the profiles in the till and the esker material, the highest concentrations of exchangeable mineral elements and the highest exchange capacities lay in

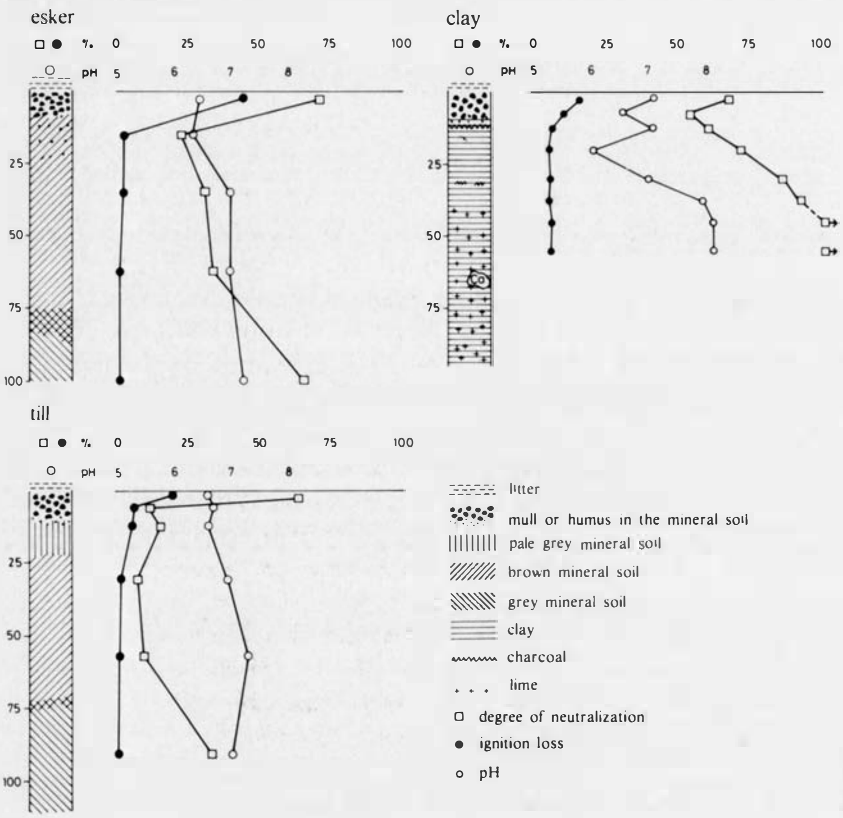


Fig. 32. Description of soil profiles in till, clay and esker material.

Table 33. Dry bulk density of the fine earth, the total nitrogen and exchangeable cation content in different horizons in three soil profiles.

	Depth cm	Dry [a] bulk density g/dm^3	N-tot % of air dry sample	Exchangeable cation meq/dm^3 H	K	Na	Mg	Ca	Sum metallic cation
Till	0-4	353	0.60	32.5	2.7	1.2	9.9	41.4	55.1
	5-7	319	0.15	29.1	0.5	0.3	1.3	1.6	3.8
	7-19	229	0.12	15.4	0.3	0.1	0.8	1.5	2.7
	19-43	455	0.02	12.3	0.1	0.1	0.4	0.4	1.0
	43-71	490	0.02	8.4	0.1	0.1	0.4	0.3	0.9
	71-110	596	0.01	3.9	0.1	0.1	0.6	1.2	2.0
Clay	0-5	659	0.55	64.5	3.8	2.0	14.1	113.3	133.3
	5-10	807	0.31	83.9	2.4	4.2	10.6	83.9	101.0
	10-15	1117		87.9	2.0	2.3	9.2	121.9	135.4
	15-25	1316	0.09	83.0	1.4	3.3	14.8	189.7	209.1
	25-35	1291	0.08	47.7	1.7	4.9	11.6	280.0	298.3
	35-40	1161		28.5	2.1	6.5	10.2	321.9	340.6
	40-50	1313	0.05	–	1.4	7.8	5.2	406.9	421.3
	50-60	1258	0.04	–	1.6	5.8	8.6	367.5	383.5
Esker material	0-5	218	1.39	35.9	3.7	1.1	12.6	69.6	86.9
	5-25	306	0.10	14.1	0.2	0.1	0.8	3.4	4.4
	25-50	252	0.05	9.4	0.2	0.2	1.1	3.0	4.4
	50-75	401	0.04	10.2	0.2	0.1	1.5	3.7	5.4
	100	276	0.03	3.0	0.2	0.8	1.0	3.7	5.7

[a] Only fine earth.

the humus layer, Table 33. In the clay profile, the concentration of exchangeable K^+-ions was higher in the humus layer than in the mineral soil but the opposite was true for the other cations analyzed.

The humus layers in the profiles in esker material and in till were more neutralized than the underlying mineral soils. The degree of neutralization increased towards the bottom of the profiles. The till profile was, however, not deep enough to reach the upper limit of material which probably contained lime, as is the case with till in other areas of Northern Uppland (K. Moreborg & T. Ingmar, pers.com.). In the clay profile the degree of neutralization had a minimum value in the lower part of the humus layer and the top of the mineral soils. The deeper mineral soils were overneutralized due to their lime content.

Summary and discussion

The qualities of the humus layer within the three sampling areas are within the variations described for mull by Sjörs (a few of his cases could better be termed moder, pers.com.). In the majority of respects, sampling area III had poorer qualities than the other two areas, e.g. a lower calcium content, a lower nitrogen content, a lower exchange capacity and a lower degree of neutralization. Variation was greatest in sampling area I, where the samples taken on the sediment had higher contents of nitrogen and humus per unit volume and, in three cases, higher calcium contents than the humus which had been produced on till. A similar difference was not to be found in sampling area III. This is perhaps a consequence of better water supply in the lower lying sampling area I (cf. F. Andersson 1970a, pp. 165-166). Sampling area II:1 had higher mean values than the other two areas in the case of nitrogen and calcium contents as well as the degree of neutralization; it also had a lower hydrogen ion content. However, the differences between the three sampling areas are not highly significant, since the variations between samples within each area were so great.

Samples taken from the transects showed no clear trends. The concentration of metallic cations, the degrees of neutralization, etc., fall within the limits already described. The sample from the spruce stand had a low loss on ignition for a case of mor, but the degree of neutralization and the metallic cation content were distinctly lower than in the other samples analyzed.

Compared with the soil conditions outlined for the plant communities *Flexuosetum* and *Hypochoeridetum* in park-meadows in southern Dalecarlia by Sjörs (1954), for an *Oxalis* community in an oak-hazel forest in Scania by F. Andersson (1970a), and for three beech forests in Scania by Nihlgård (1971), the nutrient content in the mull at Andersby is high. This applies to both nitrogen and minerals. The calcium values are especially high and also the potassium values are high. The high potassium values could partly depend on the fact that the percolating autumnal seepage takes up fairly large quantities of potassium, the potassium in the litter being easily leached (Troedsson & Nykvist 1973, p. 87) and transported down into the humus layer. Also the plants, at the time of sampling, had ceased to take up nutrients (a condition of significant magnitude only for potassium). The degree of neutralization in sampling area I is of roughly the same order as that registered by Sjörs in *Hypochoeridetum* which is somewhat similar floristically (cf. Hans Persson, in press). In all three sampling areas, the degree of neutralization is considerably higher than that registered by F. Andersson (op.cit.) and by Nihlgård (op.cit.). However, in an analysis of a *Geum rivale* community located in moister sections, F. Andersson obtained roughly the same values as those obtained at Andersby. Wallin (1973) has produced values for metallic cations and for the degree of neutralization from deciduous woods in Västergötland. Even in a limestone area they were somewhat lower than those recorded at Andersby. His values were in the latter case from an *Oxalis* community in a mixed *Quercus robur* - *Corylus* forest. Wallin also analysed a mull in a *Quercus petraea* - *Corylus avellana* forest in an area which was not alkaline. Both the degree of neutralization and the quantities of metallic cations were, in this case, significantly lower than those at Andersby.

An accumulation of nutrients occurred in the humus layer due to the high content of colloids. A leaching process is indistinct in the clay profile but obvious from the description of the other two profiles. This process is partly counteracted by the activity of earthworms. The soil structure at Andersby ängsbackar is apparently influenced by earthworms. According to Axelsson et al. (pers. com.), six lumbricid species have been found in the area, *Allolobophora caliginosa* Sav., *A. rosea* Sav., *Dendrobaena octaedra* Sav., *D. rubida* Sav., *Lumbricus rubellus* Hoff. and *L. terrestris* L. The most abundant species are *A. caliginosa* and *A. rosea* while *L. terrestris* is fairly scarce. The total abundance of earthworms is about 150-250 per m^2 (Axelsson et al. in prep.). The two *Allolobophora* species are fairly deep-burrowing and have been found at a depth of 50-60 cm during the cold season. These species, together with *L. rubellus*, seem to be responsible for most of the mixing of soil material at Andersby, since *L. terrestris* has a very low abundance, and the *Dendrobaena* species are restricted to the surface layers. Besides the physical interaction, the earthworms influence the chemical conditions. For example, Salisbury (1924) found that the faeces of earthworms had a pH closer to 7 than the surrounding humus, both in acid and alkaline soils.

Conclusions

In the previous sections, the increment and the litter fall in the three sampling areas I-III have been treated and summarized in Tables 20-22 and 25.

Increment

The figures for increment are very low. This depended partly on the low density and partly on the low basal area; but also the weather during the five-years period, with low summer precipitation combined with occasional high temperatures, was probably of significance. The increment measurements with dendrometers showed that the trees were, in fact, exposed to soil water deficiency. The map in Atlas över Sverige of the humidity index during the vegetation-period indicates that, even under average conditions this period is comparatively dry. This applies in particular to its earlier part, which is also the period during which the growth process is most active.

Increment (sum of wood increment and estimated bark production) was greater in branches than in stems in all sampling areas and in most of the sample trees. F. Andersson (1970b) recorded the same condition from measurements on *Quercus robur, Tilia cordata* and *Sorbus aucuparia* and also Nihlgård (1972) on *Fagus silvatica* in South Sweden. Whittaker & Woodwell (1968) and Whittaker et al. (1974) obtained the same results for a number of American deciduous trees, *Quercus alba, Q. coccinea, Acer saccharum, Betula lutea* and *Fagus grandifolia.* In these publications, the surface area of stems and branches is also given. The surface area of the branches was between 12 and 4 times greater than the surface area of the stem.

New phloem must probably be formed each year. Some trees may live with very little or even no new xylem being formed in the stem certain years. Sjörs (pers. com.) has measured annual rings of only 0.16 mm as an average for 50 years in a still-living, roughly 400 years old pine, growing in a mire. Literature in Kozlowski (1971, vol. II, p. 64), which, however, only concerns coniferous trees, described cases where the annual ring development completely failed in the lower part of the stem. One observation on a *Corylus* stem in Andersby showed the same phenomenon.

Kozlowski (1971, vol. II, p. 18) stated that, in some species it is observed that "the annual xylem increment is influenced more by environmental stress than is the phloem increment". During years with bad growth conditions, this probably leads to proportionally less growth in the stem as opposed to the branches than during years with good growth conditions. This should be more pronounced in trees in which the branches have a great total surface area, unless the tree, for other reasons, is superior in its competition for soil water, light and nutrients.

The growth in leaf area and shoot length had, in most species, ceased during June. The greater part of the diameter growth occurred during June and July (80% or more). It was, in the main, terminated during August but certain changes took place at a later point in time. Variations in total diameter growth were measured for the years in question. During drought periods, the increase in diameter ceased or the diameter diminished. Increment was greatest in most stems during 1972, though not in *Tilia* stems. All in all, total above-ground growth was by far greatest in June.

Beside increment measurable as external changes, material is also deposited in the cell walls at secondary wall formation and lignification. Žumer (1969) showed that this process in birch was at an end about 2 weeks after the cambium had ceased to divide. According to Koch (1972), lignin accounts for 25-30% of coniferous wood but only 15-25% of most hardwoods. Because basic density is determined on fully lignified wood, the secondary cell-wall development influences only that point in time when cessation of growth occur but not the final results themselves.

According to Kozlowski (1971, vol. II, p. 42), the change of a sapwood cell into a heartwood cell means a weight increase. The development of tylosis in the vessels of oak wood is an example of this.

A part of the material photosynthetized after the above-ground increment has ceased is probably used for below-ground growth. According to Kozlowski (vol. II, p. 229), root diameter increment in the temperate zone starts later and continues often for a longer time than stem increment. Ovington & Murray (1968) measured the length increment of birch roots. They found that the increment, in the main, was limited to the period May-August. Insignificant increment could, however, occur up to as late as December.

The storage of reserve nutrients and the translocations from and to the leaves are also a part of the annual growth cycle.

Growth is defined as the difference in weight between two points in time, see Methods. With the simple methods used in this investigation, it is not possible to give a complete picture of the growth rhythm, even if the number of measuring units were increased. The changes in weight depend on a number of processes, some of which do not result in measurable external changes in volume. However, this will hardly influence the values for total annual production to any significant extent.

The greatest uncertainty lies in the estimation of the increment in each category from the sample tree belonging to the category. As is evident from Fig. 20, the relationship between total increment and basal area increment was not highly significant. This depends presumably partly on the different conditions of competition, which result in different proportions being assigned to branches and trunk. The individual trees have different bulk basic densities and different growth rates. If a high accuracy is required for each sampling area in a production study of an area with a complexity corresponding to that of Andersby ängsbackar, the increment in all big trees ought to be measured. But sampling areas are not always fully representative. Thus, sampling area III had, as already mentioned, a lower basal area than the average in the unthinned parts and the increment was probably also lower than the average.

Each step in the sampling process—from sample to sample tree, from sample tree to tree category, combining the categories to a sum comprising the stand in a sampling area, and from sampling area to total area of investigation, involved statistical and other errors. To keep the errors down to minimum it was necessary to check the relevance of the data within each of these steps. In this way, attention was focused on the representativeness of each stage of the categorization.

Losses of plant material

Sjörs (1971) summarized the following categories of plant-material losses: primary consumption, consumption by parasites and mycorrhizal fungi, exudation, the detachment of root hairs and cells from root-caps, the disjunction of bark-flakes etc., leaching by rain, mortality suffered by branches and roots, the loss of bud scales, of reproductive organs including pollen, and of leaves or needles. Some plants also give off volatile organic compounds. Subterranean increment and some of the categories of losses just mentioned were not included in the present study.

The total litter fall varied between 1.5 ton/ha and 4.1 ton/ha in the different parts and between the years.

The leaf litter amounted to between 40% and 70% of the total litter fall. Between 7% and 30% of the leaf (dry weight) had fallen before the autumnal fall started, somewhat smaller amounts in 1968 than in the course of the two following years. The autumnal leaf fall proceeded at about the same time during the three years.

During 1969, *Betula, Corylus* and *Populus* suffered from drought, with partial death of twigs and leaves and partial early defoliation. Rather small differences between the patterns in the autumnal leaf fall of the different species were established, see Fig. 27.

Great differences were measured between the leaf falls in the glades, in the tree groupings and in the thinned birch-wooded pasture. Though some parts of the reproductive organs were underestimated, because of consumption by jays and nutcrackers, nevertheless a surprisingly great part of the litter consisted of reproductive organs. This was true particularly in 1969.

The three different sampling methods gave results of the same magnitude with regard to the total leaf fall but differed in the shares accounted for by the different species.

When branch production is measured the part which is formed but later falls off during the period of measurement will be neglected. On the other hand, it is in theory not quite correct to include all branches found in the litter fall as part of the production. This would be permissible only if a steady state prevailed between branch death and branch fall, but this is hardly likely. However, it can be assumed that the branch fall increases with the age of the tree to a maximum, which will occur at a somewhat later date than when the forest has become closed (cf. Rodin & Bazilevich 1967, pp. 125-126), depending on the fact that branches will remain on the trees some time after they have died. Different species vary considerably with respect to branch death and branch fall (Millington & Chaney 1973). Coarse branches, of course, usually remain for a longer time than fine twigs of the same tree.

The unthinned area III is closed in certain parts, but, on the whole, the crowns cover only 50% of the ground. The trees are not evenly spread but clustered. Most of the oaks have branches left on a low level but the other species show stronger self-pruning. Branch fall will probably increase when the tree layer becomes more closed. This will occur, however, at different times in different parts of the area. Compared with the state of affairs in an even-aged, homogeneous stand, yearly branch fall will be lower during the years of maximum shedding of branches, but on the other hand, a rather high shedding will be maintained during a greater number of years. From the measurements of the biomass in sampling area III in the spring of 1972, the amount of attached dead was estimated at about 1.3 ton/ha. This estimation is, however, uncertain because of the difficulties of transferring the individual values over to apply to the whole stand (cf. Ovington et al. 1967). The value is an underestimation since it is based on only the dead parts of the sawn-down, living branches, and because completely dead branches were not included in the sampling. The value for attached dead, thus measured, in sampling areas I and III is of the same size as the measured yearly branch fall; in area II:1 it is greater (see further below). In the thinned stands, the release caused by the cutting can possibly have increased the shedding of already dead branches in the first year or two, because of the fact that the exposure to wind had increased. On the other hand, the light also increased, and as reduced light is the most important factor in self-pruning, thinning is likely to have resulted in a reduced branch death. The branch fall in 1970 in the unthinned sampling area III was about twice as great as in the thinned sampling area II:1. The summer drought of 1969, followed by several gales during the autumn, probably raised the branch fall that year. The high value in sampling area III for that year depended, however, on only one very big branch. The branch fall values given in Table 34 regarding sampling area III are comparable with values given by Duvigneaud et al. (1971) of 1.4 to 2.5 ton/ha and by Satchell (1971) of 1.4 ton/ha.

According to Satchell et al. (1971), the decomposition of branches before they fall to the ground is so great that the production will be underestimated if this fact is disregarded.

In the data given in Table 34 on the primary production, shedding of pollen, leaching by rain and losses by consumption are lacking. Satchell (1971) stated that leaching amounted to 311 kg/ha in Meathop wood. This wood has greater basal area and leaf weight and also precipitation is higher due to which the value reported is surely higher than leaching in Andersby ängsbackar.

Primary consumption in Andersby, apart from grazing by cattle, which were kept out of the sampling areas by fences, is effectuated by roe-deer (which are able to jump the fences), hares, squirrels, small rodents (no excessive populations during the years of investigation, but both earlier and later), various seed-eating birds beside the above-mentioned species, and insects (see below). Snails are not important as primary consumers. Moose are only temporary visitors.

It is evident that many of the consumers live, at least partly, on plant material which, from a botanist's point of view, is litter rather than biomass, e.g. fruits which are already shed.

In Axelsson et al. (1974b), a study is reported on the consumption of *Corylus avellana* leaves by *Phytodecta pallidus* larvae. The field-studies were performed in Andersby ängsbackar, where *Phytodecta pallidus* was the greatest consumer of hazel leaves at the time of investigation (Axelsson et al. 1973). According to this study, *Phytodecta* larvae consumed only 0.42-0.06% of the hazel leaves during 1971. As the biomass of the *Phytodecta* population was about as great as the biomass of all other leaf consumers put together, the total consumption was estimated to about 1% of the weight of the hazel leaves. About 47% of the consumption by larvae became egesta and excreta. In the present study these have probably been collected in the litter baskets and are then included in the litter fraction "miscellaneous". As this part was not added to the production figures, the hazel leaf values ought instead to be increased by a factor of about 1%. In Axelsson et al. (1973), it is also stated that numerous pupae of *Tortrix viridana* were found, having probably fallen from the oak crowns. The population of *Operophthera* spp. was small during the investigation years and the total consumption of oak, birch and hazel leaves fell under 1% of the standing crop (Axelsson et al., to be published).

Annual production in the field layer

Hans Persson has kindly communicated that the production of the field layer in sampling area I amounted to about 1428 kg/ha. The corresponding value in sampling area II:1 was 1092 kg/ha and in III, 701 kg/ha. The production was calculated from two harvestings during each vegetation period during 1968-1970 and the highest biomasses found for each species were added to form a yearly production. Nevertheless, this method may give underestimated values for the majority of species. A mean value for the three years was calculated. For further discussions relating to the production in the field layer, see Persson (in press).

Annual above-ground production and turnover

Minimum values of the yearly above-ground production are reported in Table 34 as the sum of the increment and the losses of one-year-old plant material. As a matter of principle, only that part of the older twigs and branches in the litter fall which was produced during the years 1967-71 should be included, but this was a nearly impossible task because of the difficulties in deciding when a fallen twig has died. The estimation of attached dead was not suitable, as mentioned above, as a bases for the calculation of the mean time lag before the shedding of a branch in this fraction, because it was measured only once and this was furthermore later in time than the values for the branch fall. The amount of attached dead branches was of the same size as the branch fall in sampling area I and III, but nearly twice that amount in sampling area II:1. This indicates that dead branches remained on trees somewhat longer in sampling area II:1 than in the other two areas.

The yearly above-ground turnover, including increment, can be calculated with a greater accuracy. This was about the same in sampling area II:1 and III. In spite of high turnover in the field layer, the birch-wooded pastureland did not reach the same value as the two more closed sampling areas.

Ovington (1962, p. 128) discusses the prerequisites for adequate comparisons between different ecosystem. This author proposed the use of

Table 34. Estimated net primary production in tree and shrub layers and estimated above-ground turnover including increment in sampling areas I, II:1 and III, kg/ha·year (85°C). Field-layer values are taken from H. Persson (in press).

		Increment 1	Leaves[a] 2	Reproductive organs 3	Bud scales 4	Fallen twigs and branches 5	Field layer 6	Sum of 1-4	Sum of 1-6
Years of sampling		1967-71	-68-70	-69-70	-69-70	-69-70	-68-70		
I	Tree layer	1462	919	432					
	Shrub layer	164	38	4					
	Total	1626	957	436	50	331	1428	3069	4828
	% of turnover	33.7	19.8	9.0	1.0	6.9	29.6		100
II:1	Tree layer	1973 +	1661	595					
	Shrub layer	941	629	13					
	Total	2914 +	2290	608	82	752	1092	5894	7738
	% of turnover	33.7	29.6	7.9	1.1	9.7	14.1		100
III	Tree layer	2234 +	1614	204					
	Shrub layer	552	440	93					
	Total	2786 +	2054	297	73	1321	701	5210	7232
	% of turnover	38.5	28.4	4.1	1.0	18.3	9.7		100

[a] In area I and III, only litter leaves; in area II:1, litter leaves and green leaves of *Populus*, see Table 23.

the highest value for the yearly production during the whole lifespan of a stand, or the highest mean production. Both values have advantages and disadvantages; e.g., the highest production is maintained only during a low number of years. Another proposed basis for comparison is the yearly turnover of organic material in a steady state when increment is the same as losses of earlier formed plant material. Such a steady state will however hardly be persistent since increment in old stands diminishes while losses still remain constant. Moreover, such stands are exceptional in the Nemoral or Boreonemoral zones.

In the case of Andersby, a comparison is also hampered by the fact that the birches in sampling area I are fairly even-aged but trees in the other two areas are of extremely varying ages. Production is namely conditioned by age (Ovington 1962, Rodin & Bazilevich 1967). So little time has passed since thinning that a steady state has had no chance to develop.

The comparison results in the statement that, in this case, net primary production and turnover are lowest in the open pastureland. Ovington et al. (1963) compared the production in an oakwood, a "savanna" and a "prairie" in central Minnesota. They found that production dropped from about 8.2 ton/ha in the oakwood and about 5.3 ton/ha in the "savanna" to about 1 ton/ha (an exceptionally low figure) in the treeless "prairie". The authors drew the conclusion that the trees and the bushes were the most productive in the community "as the zone of photosynthetic activity became more complete and extended higher above the earth's surface."

The total figures in Andersby are low compared with values from other oak-mixed deciduous forests. Duvigneaud et al. (1971) have compiled biomass and production values from a number of European oak or mixed deciduous forests. The above-ground production amounted in these to between 9.8 and 14.7 ton/ha. F. Andersson (1970b) reported 13.3 ton/ha in a Scanian oak-linden-hazel wood. The biomass and the density in these forests were higher than in the sampling areas in Andersby. They are also situated more to the south and have a longer growth period.

Stake (1967) recorded production in Lake Dannemora and found 7.8 ton/ha in the part of the lake in which *Phragmites communis, Scirpus lacustris,* etc. grow; this is about the same value as the turnover in sampling area II:1.

In Table 35 are given turnover (columns 1-6 from Table 34) as a percentage of the biomass. The "percentage turnover" was greatest in sampling area II:1, of course, due to the high increment in the aspen suckers.

Table 35. Sum of increment and litter fall (column 1-6 in Table 34) as percentage of the biomass.

	I	II:1	III
"Percentage turnover"	9.5	11.5	8.8

In all sampling areas, losses in plant material were greater than increments. If the field layer is also included in the losses, this trend is still more marked. Of the sum of the non-increment turnover and the increment, the latter fraction accounted for between 30 and 40 %. As already mentioned, over 50% of the increment was deposited in the branches. This condition prevails even when one considers the increment in wood alone—bark increment was not actually measured, but was entered as an estimation of the production. From a forester's point of view, the low percentage increment located in stemwood must be regarded as un-economical.

Nihlgård (1972) compared the production in a beech forest with the production in a planted spruce forest and found thereby that production was greater in the beech forest than in the spruce forest, but the production of stemwood was near double as great in the spruce as in the beech forest. The calculations that Sjörs (1971) performed on material from Samuelsson (1966), in which a comparison was made between a spruce forest and a former "park meadow" overgrown with hazel, did not show any higher yearly non-increment turnover in the spruce forest. The production of stemwood was, however, considerably higher in the spruce forest than in the park meadow.

Ovington (1956) found in planted forests in Great Britain that coniferous stands had higher productivity than deciduous ones. Ovington supposed that this depended partly on the fact that the coniferous trees "utilized a site to a greater extent since their roots penetrate a considerable soil volume and a great weight of photosynthetic material is carried throughout the whole year". The estimation was, however, based on mean increment and not on yearly production. Ovington's conclusion is probably less valid in more northern latitudes.

The comparatively high increment in the branches in the three investigated sampling areas must not necessarily lead to a high branch biomass but may result in higher branch fall and thereby, a higher turnover, with regard to the branches, than in stands where the stem increment is higher than the branch increment. There is, however, in the literature hardly any evidence that branch fall is higher in deciduous forests, probably due to the fact that the fall of big branches occurs irregularly both in space and time (even though, especially in even-aged stands, it is age-dependent) and, in addition, no sufficiently long periods of measurements exist.

Reproduction

The greater stemwood-producing efficiency of *Picea abies*, is on a short term basis counteracted by the fact that deciduous trees can establish a closed stand in a natural way considerably faster than spruce, by seeds but, above all, through vegetative regeneration. In all sampling areas, the saplings and young trees consist nearly exclusively of deciduous species. In the two thinned stands, the distance to cone-bearing conifers is so great that dispersal of seeds to these stands was probably small, but in sampling area III, with cone-bearing spruces in the vicinity, very little spruce regeneration occurs. In sampling area I the young stems consists, above all, of oak and rowan, partly developing from stump shoots, and also of aspen suckers. Birch, linden and maple have also regenerated. In sampling area II:I, most of the saplings were made up of aspen suckers.

All remaining lindens, seven of the maples, two of the rowans, the sallow and two of the oaks had developed basal shoots. Many shoots had grown from the stumps. In sampling area III, young oak and aspen were most frequent, but all tree species regenerated.

Earlier, some parts of Andersby were invaded by spruce forest, or, at least, partly colonized by spruce trees (B.M.P. Larsson unpublished). This tendency is not evident at present, nor was the spruce ever able to compete successfully in the closed deciduous stand on the esker. The cutting out of all spruce in the partly cleared southern parts of Andersby will, for a long time, render these parts unsuitable for a study of reproduction that includes spruce as a competitor.

Instead of a natural regeneration of the forest, a directed management as a reserve, natural as well as cultural, will now take over, long after the cessation of the ancient rural economy. One of the problems of such a management will be to check the excessive reproduction by deciduous saplings, above all suckers of aspen. This strong regeneration shows that the potential productivity of the area is almost certainly much greater than the results arrived at in the present investigation.

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