ISSN 0308-3675

MERLEWOOD RESEARCH AND DEVELOPMENT PAPER

Number 77

ANNUAL RINGS OF BIRCH (*Betula pubescens* ssp *tortuosa*) (Ledeb) (Nyman)), CLIMATE AND DEFOLIATION:

AN EXPLORATORY STUDY

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R & D 80/77

ABSTRACT

The suitability of mountain birch as a subject for tree ring analysis was explored in a study near Jänkäjärvi based on a small number of samples and published monthly summaries of climatic data. Examination of the distribution of annual wood formation along the stem, in the form of annual growth layer profiles, gave inconclusive results, but significant correlations were obtained between climatic variables and ring indices derived from horizontal ring-width sequences. Simple correlations were significant only with measures of temperature, of which maximum temperature was the most important. Highest correlations were with average maximum temperature of June and July of the year of ring formation and August of the previous year. Discussion of the results in relation to independent observations of birch growth in general, to defoliation and to the sub-arctic environment leads to the general conclusion that ring analysis could make a significant contribution to the study of birch - climate - defoliaton interactions, but relationships with climate and with defoliation require to be examined in more detail than in the present study.

1 INTRODUCTION

During the British Schools Exploring Society's Expedition to Finnish Lapland in 1976, the period 26th July to 16th August was devoted to a scientific programme, with the general theme of birch defoliation, which was carried out in a limited study area within one of the smaller regions severely defoliated in the 1965-1966 outbreak of *Oporinia autumnata* Bkh. The investigation reported here was part of the programme, which also included surveys of the topography, soil and vegetation, the area of birch severely damaged in 1965-1966, and its recovery after that defoliation.

The periodic widespread occurrence of severe defoliation of birch by larvae of *Oporinia autumnata* Bkh has long been recognised as a major factor in the ecology of the birch forests of the Scandinavian mountain chain. A summary of available reports of *Oporinia* outbreaks (Tenow, 1971) has shown that they have occurred at approximately ten-yearly intervals in some part or another of the mountains since at least 1862, outbreaks having been reported in northern Finland in 1898, 1906-1907, 1926-27, 1939 and 1949 ("only local attacks"), 1954-1955 and 1964-1966. The 1906-1907 outbreak was the only one not reported from Inari Lapland. The 1964-1966 outbreak was particularly severe and widespread and its extent in northern Finland has been described in detail by Kallio & Lehtonen (1973). An estimated 5 000 km^2 were severely damaged, of which an estimated 1 000 km^2 will be converted to open tundra as the dead trees decay and fall (Kallio & Lehtonen, 1975).

The phenomenon of decreased annual radial increments following defoliation of trees by lepidopterous larvae is well known (eg Mott *et al.*, 1957; Koerber *et al.*, 1970; Fletcher, 1974). The effect is not limited to the year in which the attack takes place and a reduction in ring width can be shown in subsequent years. Nuorteva (1963) attempted to relate subsequent annual ring widths of birch with the severe *Oporinia* defoliation recorded in 1927 and concluded that birch which had survived exhibited "low growth rates for more than five years subsequently". No particular growth cycles could be recognised in the ring-width patterns but it was remarked that "growth depressions of a similar magnitude, but probably due to other causes, are not unusual". The possible nature of these causes was not discussed, but birch forest in northern Finland is close to the climatic forest limit and is sensitive to climatic changes (Kallio & Lehtonen, 1975). Haukioja (1975) has presented evidence in support of his hypothesis that defoliation induces a chemical defence in birch, the induction of which is slower at lower temperatures, and it has been suggested that it is the combination of low temperatures and *Oporinia* defoliation which may reduce birch forest limits (Kallio & Lehtonen 1975).

The latest available review of the literature on tree rings and climate in northern Scandinavia (Mikola, 1962) and a current search of the English language literature have not produced any references to mountain birch (*Betula pubescens* ssp *tortuosa* (Ledeb) (Nyman)). Studies relevant to forest limit conditions in northern Finland appear to have been confined to Scots pine (*Pinus sylvestris* L.) and the temperature of the growing season has been indicated commonly as the main factor influencing growth. It was also observed that the effect on pine ring-width of growing-season temperature in the previous year became more apparent as the forest limit was approached. Ring width has been correlated with the mean temperature of July in particular, and the observation that birch diameter growth at Kevo in 1969-72 was most active from 20th June to 20th July on average (Wielgolaski & Kärenlampi, 1975) suggests that birch ring width may also correlate with measures of July temperature. It was concluded that the effect of deficient precipitation could be detected only in exceptionally dry summers on the driest sites and of excessive moisture only on wet peatlands in rainy summers. However, Kärenlampi (1972) suggested, on the basis of only seven years observations at Kevo, that "the temperature probably determines the general range within which the productivity (of Scots pine) varies but most of this variation seems to be influenced by water relations".

Although the importance of climate for birch growth in the subarctic has been recognised in general terms, the relationship does not seem to have been studied in detail. Annual ring widths of many tree species have often been used to investigate environmental effects on growth, particularly where the growth-limiting factors have been few in number (Fritts, 1976); tree growth is near its climatic limits in Lapland, and it can be expected that ring widths of birch are sensitive to annually-fluctuating environmental factors. First steps in investigating birch-climate-defoliation relationships should include identification of the climatic factor, or factors, limiting ring width and recognition of the effect of climate in a way which distinguishes times when defoliation may have been responsible for the production of narrow rings. The feasibility of this approach was tested in the present study.

2 METHODS AND MATERIALS

2.1 Study area

The study area was located at about 69°22'N, 28°00'E (Figure 1A), within one of the smaller and less intensively surveyed regions which were severely defoliated in the 1965-1966 *Oporinia* outbreak. It was bounded in the west by Jänkäjärvi and in the east by the limit of continuous pine forest, lying between grid references 536-540 E and 7697-7702 N. This area was selected for the scientific programme because there was a greater concentration of birch stems which had died as a result of the 1965-1966 outbreak than anywhere else in the immediate vicinity.

The Jänkäjärvenharju ridge is the main feature of the area (Figure 1B), elevation varying from 183 m above sea level at the lake in the southeast to 255 m at the highest point of Jänkäjärvenharju in the north. The topography is gently undulating and lies in a general southwest-northeast direction.

Soil survey of the area (Koppi, 1978) showed that the surface horizon of soils under birch was usually 2 to 3 cm thick, varying from 1 to 5 cm, and had an abrupt boundary with the eluvial bleached horizon which was generally about 2 to 3 cm thick, varying from intermittent to about 12 cm where tongueing occurred. Roots were more abundant in the surface horizon and were virtually restricted to the two thin upper horizons.

Vegetation survey (Oldham, 1977) showed that the ground flora was dominated by dwarf shrubs everywhere, and that the ground vegetation of birch forest varied only inasmuch as the relative abundance of the main species was different under different forest canopy conditions. Bigger trees and closed canopy woodland were associated with damper conditions whereas smaller trees and open canopy woodland were associated with well-drained, often dry and elevated areas. Under closed canopy woodland *Vaccinium vitis-idaea* and *V. myrtillus* were better developed, bryophytes were more numerous and *Deschampsia flexuosa, Linnaea borealis, Trientalis europaea, Vaccinium uliginosum* and *Nephroma arctica* occurred more often than under open canopy woodland, where *Empetrum hermaphroditum* was much the most significant species of the ground flora. The vegetation of forest which had been most damaged in 1965-1966 was more like that under open canopy woodland but *Deschampsia flexuosa* was more abundant.

Averages of temperature and precipitation at the southwestern end of Lake Inari were calculated for the period 1926-1975 (Table 1) from annual climatological summaries (Finnish Meteorological Institute, 1927-1976). Mean temperature was above 5°C from approximately 24th May until

20th September, as estimated from the course of average monthly mean temperatures. This is close to the estimated thermal growth period of 27th May to 17th September at Kevo, derived in the same way for the period 1962-1973 (Skartveit *et al.*, 1975), which was 15 days shorter at 200 m higher altitude. Assuming a similar lapse rate in the Inari region, the thermal growth period on the study area would have varied between approximately 117 and 110 days, depending on altitude.

Interpolation of existing data (Johannessen 1970) suggests that the midnight sun lasts from about 21st May to 25th July at the latitude of the study area. It follows that climatic conditions and plant growth are under the influence of continuous daylight until about the beginning of the third week in July, following which a day-night rythm soon becomes pronounced (Kallio, 1957b). Temperatures and precipitation are highest from June to August inclusive, with July the warmest and wettest month and August warmer and wetter than June.

The study area was a mosaic of zones with live stems and zones with dead stems, but transition from one area to another was usually gradual and bore no obvious relationship to topographical features. The wood of the dead stems was too rotten to be prepared for ring measurement and sampling had to be restricted to areas of live stems. Selection of sample plots was on a largely subjective basis but was restricted as much as possible to areas with similar ground vegetation and the plots were sited where canopy conditions seemed reasonably uniform within and immediately around each plot. A total of 12 sample plots were selected (Figure 1B).

2.2 Sampling and preparation of samples for ring-width measurement

Each plot measured 20 m x 20 m and the following observations were made on every tree: diameter at 1.3 m above ground of every living stem over 4 cm, number of living stems under 4 cm diameter, number of dead stems and the estimated height of the tallest stem. The average number of stems per tree was calculated and the tree nearest to the average selected for sampling unless all the stems were less than 4 cm diameter, in which case the next nearest tree was selected. Each stem of the selected tree was felled by cutting as close to its base as possible and cross-sections were cut from it at 30 cm intervals from the base to the highest distinguishable point on the stem. The northern side of the stem was marked before felling and this was indicated on each section as it was removed. Sampling was carried out over the period 5th-10th August 1976.

Compared to most other species, birch has a fine-grained, uniformly textured wood which, even in wood with wide annual rings, requires much preparation before the rings can be displayed. The annual rings of slowly-grown trees can only be measured under a high degree of magnification and an adequately smooth surface was achieved by polishing with a succession of increasingly fine abrasives, using simple equipment and easily obtainable materials. The sequence of operations was as follows:-

1. Disc sanding using an electric sander with the finest grade of metal disc to remove saw marks and generally level the surface of the sample.
2. Orbital sanding with medium (100 grit) sandpaper followed by fine (150 grit) sandpaper.
3. Hand smoothing with grade 00 (280/F grit) emergy cloth).
4. Moistening the sample surface with turpentine substitute and continuing smoothing with used emery cloth.
5. Polishing with Perspex Polish No. 1, using a soft cloth.
6. Wiping the sample with a soft cloth moistened with turpentine substitute to remove polish residues.

This was usually sufficient to produce a satisfactory surface for microscopic examination but, in a few cases, a further polish with Perspex Polish No. 2 was necessary to make the structural features completely distinguishable. The final stage in preparing the specimen for examination was to mark north-south and east-west lines on its surfaee

The specimens were viewed under a stereo-microscope with a magnification of x 100, fitted with an eyepiece micrometer which measured ring-width to the nearest .01 mm. Measurements were made from the centre of the pith outwards along four marked radii and the average width of each ring calculated.

Sometimes a tree may not form a complete ring on all portions of the stem. This occurs particularly towards the base of the stem, commonly in a year with unfavourable climate, but it can also be caused by defoliation. Identification of partial rings in a set of radii was made by the process of crossdating (Fritts, 1976) which includes matching of the ring width patterns of all four radii; recognising any lack of coincidence; inferring where rings may be absent; and testing the inference by re-examining the circumference of rings on either side of the inferred position. In specimens with completely missing rings, crossdating can identify their chronological place by comparing the synchrony between ring patterns of different specimens from the same stem, from other stems of the same tree, and from the stems of other trees.

2.3 Climatological data

Climatological data for the Lake Inari area were extracted from monthly summaries for 1926 to 1975 (Finnish Meteorological Institute, 1927-1976). No single station observed during the whole period and no observations were published for 1945-1948, 1950 and 1953, and for some of the months in 1944, 1949, 1951 and 1952. The Ivalo observations for 1948, 1950 and 1953 were included to make the data set as complete as possible. The differences in mean monthly maximum temperatures between the Inari and Ivalo observations for June, July and August during 1961 to 1965 averaged 0.9^{o}, 0.7^{o} and 0.9^{o}C respectively, ranging from 0.2^{o} to 1.9^{o} in June and August and from 0.2^{o} to 1.4^{o} in July, and it was concluded that the effect of applying mean values as correction factors to the Ivalo data would have a questionable effect. Table 2 summarises station details in relation to the study area, also indicated in Figure 1A, and availability of data. It also shows a distinct group of stations in operation from 1949 to 1975, with breaks in 1950 and 1953, at a distance of some 45 km from the study area and another distinct group from 1926 to 1944 at about 65 km distance.

Where available, the following monthly data were extracted for each year:-

1. Measures of temperature - mean monthly mean, mean monthly maximum and mean monthly minimum. To avoid confusion, mean is now defined as the mean of daily observations in a calendar month and average as the average of the means of the individual months in a period of two or more months.

2. Measures of precipitation - total precipitation, number of days with precipitation greater than .01 mm/day and number of days with precipitation greater than .10 mm/day. The two latter measures were included as indicators of rainfall distribution, which could be important in shallow, well-drained soils which dry quickly.
3. State of sky - number of overcast days and number of clear days. These were included as gross approximations to sunshine duration, which was not observed.

In addition, a rough estimate of the thermal sum was obtained for each year by subtracting 5°C from the mean temperature of every month with a mean temperature greater than 5°C and accumulating the result. This took some account of annual variation in the length of the thermal growth period by excluding months when their mean temperature did not exceed 5°C.

2.4 Methods of analysis

The widths of rings formed in the same year in different sections of the same stem were plotted horizontally against a common vertical axis, representing the height of the section on the stem, to produce a simplified profile of the growth layer produced in that year, equivalent to the type 1 sequence of Duff & Nolan (1953). In addition, ring widths were plotted vertically against a horizontal time axis, equivalent to Duff & Nolan's type 2 sequence, which is the more familiar way of displaying ring width.

No accounts of analysis of type 1 sequences by quantitative methods have been found, probably because their complicated geometry makes them more difficult subjects than type 2 sequences, but they have often been used in a qualitative way, as in the present study, to indicate changes in crown conditions (Larson, 1963).

For present purposes, the factors affecting ring widths in a type 2 sequence can be grouped into two categories. Namely, those which produce the regular, gradual change in ring widths which determines the basic shape of the sequence, chiefly those associated with stem ageing, and those which superimpose a random effect on the basic shape, chiefly annual fluctuations in climatic factors. Linear, quadratic and exponential curves were fitted by regression analysis to the part of each sequence which referred to the period 1926-1975 and each measured ring width was divided by the value predicted by the best regression of ring widths on time to produce a ring-width index with the time trend removed. An average ring index for each year was then calculated from all suitable sequences to produce a ring index sequence standardised for age (Fritts, 1976).

Simple correlation analysis of average ring indices and climatic data was used to identify the probable important factors and their most effective measure. Initially, correlations were examined for the month of July in the year of ring formation and in the previous year to test for the presence of lag effect. The analysis was continued for various combinations of monthly values in an attempt to define the time of year when the effect of climate was greatest.

3 RESULTS

The material available for ring measurements was 25 basal sections from 12 trees, and a further 32 sections from six stems of three of these trees. Only 14 of the 25 basal sections were old enough to include the whole period for which climatological observations were available and these 14 sections were from the stems of 9 trees. It was not always possible to distinguish the pith from the first annual ring, which, in any case, differed from subsequent rings in that it was not on a shoot which was present before ring growth began, and the first annual ring was disregarded in further considerations. In addition, the response of earlier rings to climate may be modified to such an extent by factors inherent in the tree that they too can be disregarded, according to Fritts (1976). Only those basal horizontal sequence of more than 60 rings were used to calculate average ring widths, amounting to 12 stems from 9 trees (Table 3). Increasing the sample size to 21 basal sections produced average ring indices for 1948 to 1976 which were nearly all in close agreement with those calculated from 12 samples (Table 4), the main exceptions being those for 1974, 1972, 1967 and 1956, whose values showed an increase of .24 and a decrease of .14, .23 and .13 respectively, but only two of the additional 9 samples were from additonal trees and any change in the indices must refer more to between-stem than between-tree variation. It would have been more appropriate to sample from more trees and less stems in the available time.

Type 1 ring sequences were constructed to give annual growth layer profiles for 6 stems from 3 trees. Their value was greatly limited by the lack of data from higher stem levels and it was considered that the time involved in constructing sequences for more stems would not be justified by the amount of additional information to be gained. Profiles in one stem from each of the 3 sample trees are shown in Figure 2, in which 12.1 refers to a vigorous stem with branches along its length, 4.1 refers to a stem which had grown slowly throughout its life and was free of branches in its lower part, and 9.1 refers to a stem which was intermediate in character. The pith plus the first ring could only have been in the leading shoot, therefore a sequence which includes them must represent the whole stem in that year, and incidentally provides an estimate of stem height at that time. Thus the dashed lines in Figure 3 subtend virtually complete profiles and, by comparison of highest pith height in the diagrams with stem height in the year of felling, the proportion of stem length represented by the 1976 profile was estimated to be 53% for 12.1, 43% for 4.1 and 82% for 9.1.

For trees in general, the width of the annual wood layer at different stem heights varies consistently wtih crown size and the distribution of branches along the stem, and is affected by environmental factors through their influence on crown activity (Kozlowski, 1971). Maximum ring width tends to be at a height associated with maximum leaf amount, ie near the base of the crown, and gradually moves upwards as the stem grows and lower branches become physiologically less efficient, whilst it tends to move lower in years with favourable growing conditions than in unfavourable years.

Most of the profiles from stem 12.1 and the earlier ones from stem 4.1 closely resemble those described from open-grown monocormic tree species with long crowns, while those later in the life of the oldest stem closely resemble profiles from close-grown monocormic trees (Farrar, 1961). The profiles from stem 9.1 give a general impression of insensitivity, with annual variation in shape appearing almost random but this could be because they under-represent stem length to a greater degree than the profiles from the other stems. It is not possible to detect any effect of annual variation in growing conditions on the height of maximum ring width in any of the diagrams with any degree of confidence, possibly because the sample interval of 30 cms was too wide.

Stems 4.1 and 9.1 were old enough to include all the *Oporinia* outbreak periods from 1898 onwards, but 12.1 only included those after 1909, hereafter referred to as the 1927, 1939, 1949, 1955 and 1965 outbreak periods.

Up to about 1931, the sequences in stem 12.1 suggest that development was towards a high crown but that some factor, which decreased wood production in the upper part of the stem only, then became effective until about 1944. A period of about 6 years ensured when the shapes of the sequences were similar to those in 1931 and 1932, and this was followed by a repeat of the 1932-44 pattern of development, culminating in 1954 and 1955 with no wood formation apparent in the upper parts.

After 1955, annual wood production was fairly evenly distributed along the profile and tended to increase up to 1961. Wood production appeared to be relatively high in 1964 and was very low in 1965 and 1966, after which the profiles soon assumed the earlier type with maximum ring widths towards the base of the stem. It is possible to speculate on these patterns in the growth layer profiles in terms of gradual fluctuations in the degree of annual defoliation, with maxima in 1944, 1954-1955 and 1965-1966. This would agree with the 10-year population cycle suggested for *Oporinia* (Tenow, 1972), and the latter 2 maxima agree with the last 2 major outbreaks; however, it is difficult to reconcile the first one with any of the reported outbreaks. Fluctuations in the areas of the annual wood layer profiles seem to follow a similar course in the other stems, but it is much less obvious. The results might have been more convincing if sampling had been extended to the tops of the stems, but the diffuse branching habit of most crowns made systematic sampling virtually impossible.

Average rates of radial growth in the horizontal sequences constructed from the 25 basal sections varied from .19 mm to .64 mm per annum (Table 3). Diameter of stem base bore little relation to stem age, for example 68 annual rings were counted in the widest section (12.1 - 87 mm) whereas the section with most rings (4.1 - 197 rings) measured 75 mm in diameter.

Horizontal sequences derived from one stem from each of the 12 sample plots (Figure 3), agree with Nuorteva's (1963) observations that ring widths were, in general, less than 0.6 mm and rarely exceeded 1.0 mm. They differ in that Nuorteva's diagrams show a ring width every year whereas Figure 3 shows years in most samples when ring widths were not measurable. Cross matching of his ring patterns appears to be good, as far as can be judged by eye, and it seems unlikely that incomplete rings would have escaped notice. Sampling by Nuorteva was probably carried out at a higher level on the stem than in the present study where zero measurements in basal sections mark years in which wood production did not extend all the way down the stem. These zero measurements often had the disadvantage of making cross matching difficult, but it was considered that this was more than offset by the advantage of greater sensitivity of the ring widths to annual variations in wood production.

Starting about the turn of the century an overall trend in growth may be discerned in the ring-width sequences, with values increasing until some time in the 1930's and 1940's after which they tended to decrease until the mid-1070's at the latest. This growth trend broadly coincides with the general trend in growing season temperatures in northern Finland this century (Mikola, 1971). Depressions in the general growth trend may have occurred in the 1950's and less obviously in the 1920's, but the narrow ring-widths in 1965 and 1966 are obvious. Average ring-widths and average ring indices for 1926-1975 show these trends more clearly (Figure 4).

It has been observed that severe damage by *Oporinia* seems to be associated with cool growing seasons prior to defoliation (Haukioja 1975) but comparison of average ring-widths and average ring indices with temperature (Figure 4) suggests that the narrow rings in these trees in the 1920's and the 1950's were more likely caused by climate than by severe defoliation in the 1927 and 1955 outbreak periods. Testing for relationships between ring indices and climatic factors produced statistically significant correlations only with measures of temperature. It seems that the other factors were not usually limiting for growth or their influence was so weak that it was masked by the effect of temperature. However, Kärenlampi (1972) showed that a strong positive correlation between the July temperatures at two places 300 kms apart in Finnish Lappland was accompanied by an extremely weak negative correlation between their precipitation amounts which suggests that the distances of the climatological stations from the study area, 45 to 80 kms could have had less effect on the relevance of the temperature data than on that of the precipitation data.

The highest correlations were with maximum temperature, followed by the thermal sum and monthly mean temperature; correlations with minimum temperature were usually not significant and never reached the 1% level of significance (Table 5). This agrees with Mikola (1962) who remarked that "where temperature is the growth-limiting factor the temperature aggregate or thermal sum (calculated on a daily basis) during the growing season is probably decisive, and therefore the maximum temperature may be more important than the mean temperature of a fixed period", with the added suggestion that even a simple estimate of the thermal sum, derived from mean temperatures, may be better than mean temperatures alone. An effect of maximum temperature on ring-width during the year of ring formation and a lag effect of temperature in the previous year are evident in the results and, in this respect, birch resembles Scots pine near its northern limit. Although the correlations were weak and differences between the values of the correlation coefficients small, the results also indicate that the current effect of maximum temperature was strongest in June and July and the lag effect in August, the latter having the highest correlation in Table 5. The method used to estimate thermal sums in the present study took some account of annual variation in the times that the thermal growth period started and ended, 24th May and 20th September on average, which could account for the highest correlations with the thermal sum being in the periods May to July of the current year and August to September of the previous.

It can be assumed that temperature affected ring-width by influencing the photosynthate production on which annual ring growth depended, and that the lag effect resulted from the use of food reserves accumulated from photosynthate production in the previous year. Obviously, the different temperature effects did not operate in the same way, but all the significant correlations were positive,which suggests that the two effects were additive. This additive effect is as approximated by calculating the average maximum temperature of all possible combinations of current and previous periods with correlation coefficients significant at the 1% level, and correlating ring indices with these averages. Table 6 shows that nearly all the correlations were significant at the 0.1% level, which would appear to confirm the above suggestion. The highest correlation coefficients indicated that the effect of maximum temperature was strongest in June-July plus August-September and June-August plus July-September. The average thermal growth period lasted until the end of the third week in September, an effect of temperature in September was shown by the thermal sum (Table 5), and a similar result for maximum temperatures can be considered reasonable. The first combination does not contradict the June-July plus August combination indicated by the results shown in Table 5 but the second combination, showing the end of the current effect in August and the beginning of the lag effect in July is less compatible.

The period of most active diameter growth of birch at Kevo ended on 20th July, on average, from 1969 to 1972 (Wielgolaski and Karenlampi 1975) when the mean July maximum temperature fell below its 1926-1975 average twice, by about 1^{o}C, and the mean August maximum once, by 0.5^{o}C, so that diameter growth in these months was not limited by unusually low temperatures. This supports the view that the period when the current effect of maximum temperature was strongest ended in July rather than in August, and the lag effect was strongest after July. Average maximum temperature as an estimate of a single effective temperature may have been too approximate to make a critical distinction.

The relationship between ring indices and temperature is shown in a form which allows discussion of the results down to the level of individual years (Figure 6). The indices with largest deviations from the calculated regression were for those rings formed in 1964, 1966, 1967 and 1975. The index for 1966 was negative and shows the greatest difference when summer temperature was somewhat above average (Figure 5). These conditions were not greatly different to those relevant to the 1969, 1962 and 1928 indices, which were all much bigger than the 1966 index, and the circumstances suggest that some factor other than temperature was operating. The rainfall regime was not extreme that year (Finnish Met. Inst. 1927-1976), but the area had been severely defoliated in the 1965 outbreak period, and the magnitude of the difference can be ascribed to the latter with a high degree of confidence.

The 1967 index had the next greatest difference, which was positive, but the difference in its value from that based on 21 samples (Table 4), indicates an inadequate number of samples as the cause.

In the case of the 1964 index, summer temperature was average but the previous autumn was one of the warmest of the period and probably terminated later in September than in most other years. In addition, the mean monthly temperature of May in 1963 was the highest in any year by 1.9^{o}C and its mean maximum was the highest by 6.6^{o}C. The growing season must have been unusually long and could have been particularly favourable for accumulation of net photosynthetic production in excess of that required for immediate use in growth and respiration.

The 1975 summer temperature was very low and the previous autumn temperature slightly below average, but comparable conditions prevailed for the 1968, 1929, and 1928 rings , the indices for which are grouped close to the regression line. In this case there is no justification for invoking a factor, such as length of growing season, which cannot be expressed by the data in their present form.

In 1976, the sample trees showed no external indications of having been severely defoliated in recent years; values for the 1967 average ring index and ring widths in all the diagrams suggest that recovery from the 1966 defoliation was satisfactory; and subsequent years did not indicate an obvious lag effect of that defoliation. Annual variation in ring widths may have been somewhat less after 1967 than before 1965 in many samples (Figure 3) and since these 12 samples included the oldest stems, senescence may have been a significant factor in conjunction with the cold 1975 summer. However, in the absence of any evidence to the contrary, much of the difference in the 1975 index from its predicted value must be ascribed to data error.

4. DISCUSSION

If the results of the statistical analysis reflect a true relationship between ring width and temperature in June and July of the current year and August or August and September of the previous, the different phases of the temperature effects should reflect different phases in the seasonal growth cycle of birch. Observations of seasonal differences in the mean dry weight of birch leaves at Kevo, in 1973 (Haukioja & Koponen 1975), and of the period of most active diameter growth, from 1969 to 1972 (Wielgolaski & Karenlampi 1975), give clear evidence of a first phase of active growth. None of the years were climatically extreme and generalisation can be made from the 2 sets of observations. Thus, bud burst occurred about the beginning of June, mean leaf dry weight attained its maximum in the latter half of July and decreased slightly during August, and leaves fell about the middle of September. There is a time lag between bud burst and initiation of cambial activity in the lower stem of diffuse porous species such as birch (Digby & Wareing, 1966); thus the period of most active diameter growth began about 3 weeks after bud burst and ended about the end of the third week in July, at approximately the same time as maximum mean leaf dry weight was attained. The duration of growth in birch is known to be controlled by photoperiod (eg Kallio & Makinen 1978) and Håbjørg (1972) has shown that the critical day length for the induction of terminal dormancy in birch seedlings, from a provenance some 30 kms northwest of Kevo, was between 20 and 24 hours. Such a value would account for the transition from the active growth phase occurring at the same time as the transition from continuous daylight to day-night conditions at Kevo.

An increasing proportion of the net photosynthetic production would become available for accumulation in storage tissues when its use in respiration and growth declined during the transition from the active growth phase. Food reserves seem to be particularly important for cambial growth of trees in the subarctic, as indicated by the lag effect of temperature in the previous year on birch ring width in the present study (Tables 5 and 6), and by the increasingly pronounced lag effect on ring width observed in Scots pine as the northern limit of pine forest is approached (Mikola 1962). It is generally concluded that cambial growth of trees in the temperate regions depends primarily on current net photosynthetic production and on reserve foods only to a limited extent at the beginning of the growing season (eg Kozlowski, 1971). However, the short sub-arctic growing season dictates that all growth must be completed within a more limited period and the time when cambial growth depends on food reserves must represent a larger proportion of the season. Furthermore, cambial and shoot growth of birch occur at the same time and there may be competition for restricted photosynthate supplies where net photosynthetic production is reduced in cool growing seasons. Because growing regions nearer the photosynthetic source generally attract more of the available supplies, the stem cambium must be at a disadvantage and must depend on food reserves which have already been heavily depleted in the initial stages of growth at the beginning of the season.

The objectives of the study have been achieved to the extent that a relationship between ring width and temperature has been identified clearly enought to recognise the effect of defoliation in the 1965 *Oporinia* outbreak with a reasonable degree of confidence, in the 1966 ring at least. However, the presence or absence of defoliation effects in other outbreak periods was not shown conclusively, possibly because the correlation with temperature was not strong enough to reveal years when the response of ring growth to temperature was disrupted significantly. The weakness of the correlation could have been caused by several potential sources of data error, such as inadequate sample size, the use of monthly temperature data from distant sites, and inaccuracy of the estimated effective temperature of the combined growth phases, but another environmental factor may have been operating. The evolution by mountain birch of a defence mechanism against leaf-eating insects (Haukioja & Niemela, 1979) suggests that insect defoliation over long periods could suppress the pattern of annual variation in ring widths, attributable to other environmental factors, as reported in *Quercus robur* in England (Varley, 1978) and *Eucalyptus* species in Australia (Morrow & LaMarche, 1978).

According to Rafes (1970), radial increment loss in trees is insignificant below 75% defoliation but loss following as little as 25% defoliation has been reported, according to Franklin (1970). Presumably the response to defoliation depends on the trees' vigour, and a low degree of defoliation may be appropriate for the mountain birch forests of the sub-arctic. *Oporinia* is by far the most important of several invertebrates which feed on birch leaves but nothing is known about annual fluctuations in their population densities over long periods (Haukioja & Koponen, 1975). About 4% of the birch foliage at Kevo was consumed by invertebrates in 1972 (Kallio, 1975) and 15% in 1973 (Haukioja & Koponen, 1975). *Oporinia* numbers were very low in both years and it is possible that they would not need to be much higher than those in the latent part of the population cycle for the defoliation level to have a significant effect on ring width.

In the period to which the results refer, birch forest in Inari Lapland was most extensively damaged in the 1927, 1955 and 1965 outbreak periods and local attacks occurred in 1939 and 1949. Although the reports were probably biassed towards the most obvious areas, they could be indicative of generally high *Oporinia* populations about these times, eg severe defoliation did not occur in population sampling plots in the 1965 outbreak at Abisko, Sweden, but populations in the plots reached a maximum that year (Tenow, 1972). *Oporinia* outbreaks at individual sites are considered to last for 2 to 4 years and it may not be entirely coincidental that the ring indices for 1927, 1938, 1948 and 1955 corresponded more or less with outbreak periods and had higher negative differences from their predicted values than most of the other indices associated with similar temperatures (Figure 6). In fact, if allowance is made for small sample size by reference to Table 4, all of the indices along the lower edge of the scatter of points about the regression line, except those for 1959 and 1975, correspond with reported outbreak periods. The low value of the 1975 index has been attributed to data error, which could have been responsible for the low value of the 1959 index also. However, by inference from the indices coincidental with outbreak periods, it could indicate severe defoliation which was local enough to escape notice. The interval since the 1955 outbreak period seems short compared to *Oporinia's* population cycle but is comparable to the interval between the 1949 and 1955 outbreaks; locally severe defoliation, especially in remoter areas, could have occurred more frequently than the reports indicate.

5 CONCLUSIONS

Annual growth layer profiles gave inconclusive results but they did indicate the extent of the layer in those years when ring growth did not take place near the base of the stem. When sampling is carried out for horizontal ring sequences only, it can be recommended that at least one extra section should be cut from a higher level as an aid to confirming partial wood layer formation.

Statistical analysis of horizontal ring width sequences and climatic factors identified a relationship between ring width and temperature clearly enough for the effect of defoliation in the 1965 *Oporinia* outbreak period to be recognised, at least in the 1966 ring, but the effect was not conclusively shown to be present or absent in previous outbreak periods. Regression of ring width indices on maximum temperatures showed that nearly all the indices with the highest negative differences from their predicted values were in years which corresponded closely with outbreak periods reported elsewhere in Inari Lapland. Defoliation heavy enough to significantly affect the response of ring growth to temperature may be sufficiently frequent to weaken correlations with temperature.

It is concluded that annual ring analysis of mountain birch can be of value in the study of birch-climate-defoliation interactions. Obvious improvements can be made in sampling methods to reduce data error, especially by increasing the number of sample trees, by selecting sample areas close to climatological stations and by correlating ring widths with daily climatic data. Relationships between ring width and defoliation could be investigated in short-term experiments, or in trees which have already been subjected to experimental defoliation, eg at Kevo (Kallio & Lehtonen, 1975). Since only a few of the outermost rings would be required, annual growth layer profiles could be obtained relatively quickly and used to estimate the effect of defoliation on total wood production as well as on ring width.

ACKNOWLEDGEMENTS

The author is indebted to the British Schools Exploring Society, for the invitation to participate in their 1976 expedition to Finnish Lapland, and to the Institute of Terrestrial Ecology, for granting leave of absence to make that participation possible and for the use of equipment and facilities. Professor P. Kallio, Professor of Botany at Turku University and Director of Kevo Subarctic Research Station, suggested the theme of the expedition's scientific programme and the region within which it could be carried out most profitably. Thanks are extended to Professor Kallio and his colleagues at Kevo for hospitality and useful discussions. The author is particularly grateful to D. M. Butterfield, T. J. Coburn, G. D. Fisher, R. W. Hotchkiss, D. M. Macleod, J. P. Pickard, C. J. Piper and C. W. Timms, who did the hard work during the expedition.

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TABLE 1. Averages of Monthly Temperature and Rainfall in the Lake Inari Area, 1926-1975

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Average Maximum Temperature (°C)	-8.5	-8.5	-3.6	1.5	7.5	14.6	18.2	15.6	9.6	2.3	-3.0	-6.3	3.3
Average Mean Temperature (°C)	-12.7	-12.8	-8.4	-2.8	3.5	10.0	13.4	11.3	6.1	-0.5	-5.9	-10.0	-0.7
Average Minimum Temperature (°C)	-18.0	-17.7	-14.2	-8.3	-0.9	5.5	8.8	7.0	2.6	-3.3	-9.6	-15.0	-5.3
Total Precipitation (mm)	19.2	15.7	15.5	20.4	26.8	47.4	67.2	66.6	44.8	32.2	27.3	23.1	406.2

TABLE 2. Climatological Stations nearest to the Study Area and Periods for which observations were published.

Station Name	Latitude	Longitude	Approx. distance from the study area (km)	Years with published observations*	Months without published observations
Toivoniemi	69°04'	27°05'	45	1959-66, 1969-75	
Vuopaja	69°04'	27°05'	45	1967-68	
Muddusniemi	69°04'	27°04'	45	1951-52, 1954-58	Jan-Mar. 1951 May 1952
Muddusjarvi	69°05'	27°06'	45	1949	
Riutula	68°57'	26°49'	65	1933-44	Jan-Feb. 1933
Enare	68°57'	26°49'	65	1928-32	Oct-Dec. 1932
Inari	68°57'	26°49'	65	1926-27	
Ivalo	68°39'	27°35'	80	1946-48, 1950,1953	

* None of these stations published observations in 1945

TABLE 3. Basal Sections: Wood Diameter, Ring Count and Average Radial Growth Rate

Sample Tree and Plot Number	Stem Number	Diameter (mm)	Number of Rings	Average Radial Growth Rate (mm/year)
1	1	48	88	.27
	2	40	82	.24
	3	10	19	.26
	4	11	11	.50
2	1	82	70	.59
	2	33	30	.55
3	1	34	41	.41
4	1	75	197	.19
	2	40	50	.40
	3	30	31	.48
5	1	81	79	.51
	2	65	77	.42
6	1	26	43	.30
	2	16	41	.20
7	1	30	50	.30
8	1	80	109	.37
	2	38	57	.33
9	1	75	84	.45
	2	35	36	.49
	3	32	36	.44
10	1	73	79	.46
	2	48	55	.44
11	1	61	122	.25
	2	68	112	.30
12	1	87	68	.64

TABLE 4. Average Ring-Width Indices of 12 Samples and 21 Samples

Year	Average Ring-Width Indices 12 Samples	21 Samples	Difference caused by Increase in Sample Size
1975	.32	.34	+ .02
1974	.69	.93	+ .24
1973	1.53	1.49	- .04
1972	1.69	1.55	- .14
1971	1.13	1.16	+ .03
1970	1.42	1.40	- .02
1969	.57	.59	+ .02
1968	.78	.72	- .06
1967	1.45	1.22	- .23
1966	.20	.22	+ .02
1965	.31	.30	- .01
1964	1.95	1.92	- .03
1963	.95	.95	0.0
1962	1.06	1.02	- .04
1961	1.28	1.28	0.0
1960	1.22	1.21	- .01
1959	.71	.80	+ .09
1958	.83	.91	+ .08
1957	.80	.85	+ .05
1956	1.36	1.23	- .13
1955	.49	.51	+ .02
1954	1.07	1.06	- .01
1953	.88	.84	- .04
1952	1.19	1.13	- .06
1951	.98	.92	- .06
1950	1.08	1.09	+ .01
1949	1.09	1.10	+ .01
1948	1.09	1.10	+ .01

TABLE 5. Simple Correlation Coefficients of Average Ring-Width Indices with Temperatures in Limited Periods

Period	Thermal Sum Current Year	Thermal Sum Previous Year	Monthly Mean Temperature Current Year	Monthly Mean Temperature Previous Year	Maximum Temperature Current Year	Maximum Temperature Previous Year	Minimum Temperature Current Year	Minimum Temperature Previous Year
			Mean		Mean		Mean	
May	-	-	NS	.30*	NS	.34*	NS	NS
June	-	-	.30*	NS	.30*	NS	NS	NS
July	-	-	.39*	NS	.43**	NS	.29*	NS
August	-	-	NS	.41**	NS	.49***	NS	NS
September	-	-	NS	NS	NS	NS	NS	NS
			Average		Average		Average	
May to June	.29*	NS	.31*	NS	NS	NS	NS	NS
May to July	.45**	NS	.43**	NS	.42**	.31*	NS	NS
May to August	.44**	.33*	.43**	.34*	.42**	.42**	NS	NS
May to September	.41**	.36*	.38*	.34*	.38*	.42**	NS	NS
June to July	.44**	NS	.44**	NS	.46**	NS	.35*	NS
June to August	.44**	NS	.44**	NS	.45**	.33*	.31*	NS
June to September	.42**	.31*	.40**	.29*	.41**	.35*	.31*	NS
July to August	.39*	.33*	.39*	.33*	.41**	.41**	NS	NS
July to September	.30*	.37*	.33*	.35*	.36*	.42**	NS	NS
August to September	NS	.42**	NS	.35*	NS	.41**	NS	NS

TABLE 6. Simple Correlation Coefficients of Average Ring-Width Indices with Average Maximum Temperatures of Combinations of periods in Two Consecutive Years.

Current Year Period / Previous Year Period	June-July	June-August	May-July	May-August	July	June-September	July-August	May-September
Average Maximum Temperature								
August	.60	.59	.55	.54	.59	.54	.57	
August-September	.61	.60	.57	.56	.57	.57	.57	
July-September	.59	.61	.60	.59	.53	.57	.56	
July-August	.58	.59	.58	.58	.53	.54	.55	
May-August	.55	.56	.56	.58	.48**	.53	.50	
May-September	.55	.57	.57	.58	.48**	.54	.51	
Thermal Sum								
August-September	.58	.57	.59	.57	.52	.52		.53
Average Mean Temperature								
August	.54	.52	.52	.51		.48**		

All correlation coefficients were significant at the 0.1% level except where indicated

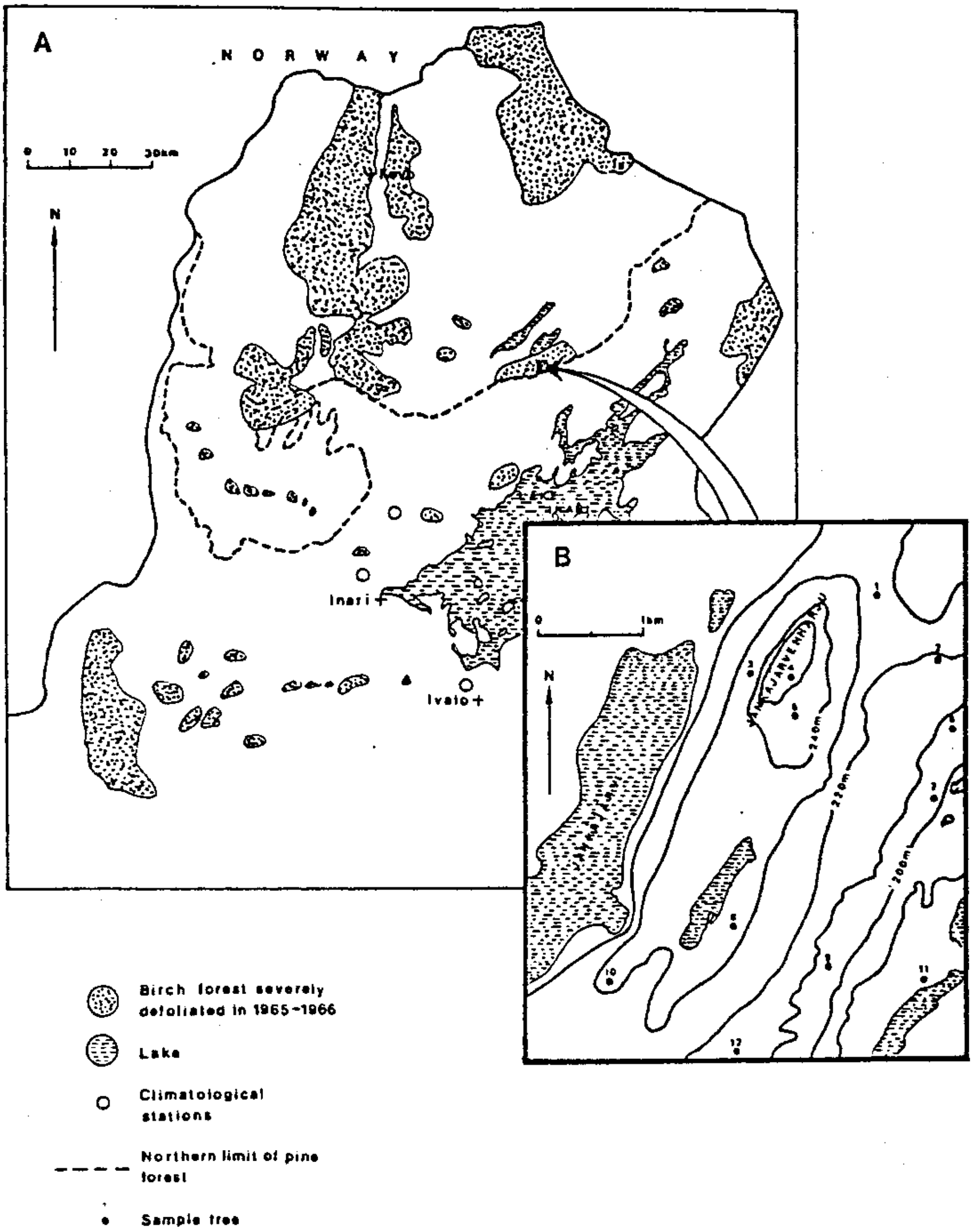


Figure 1. Map A: Location of the study area in relation to the distribution of birch forest severely defoliated in the 1965-1966 *Oporinia* outbreak in northern Finland (Kallio and Lehtonen, 1973).

Map B: Topography of the study area and the location of sample trees.

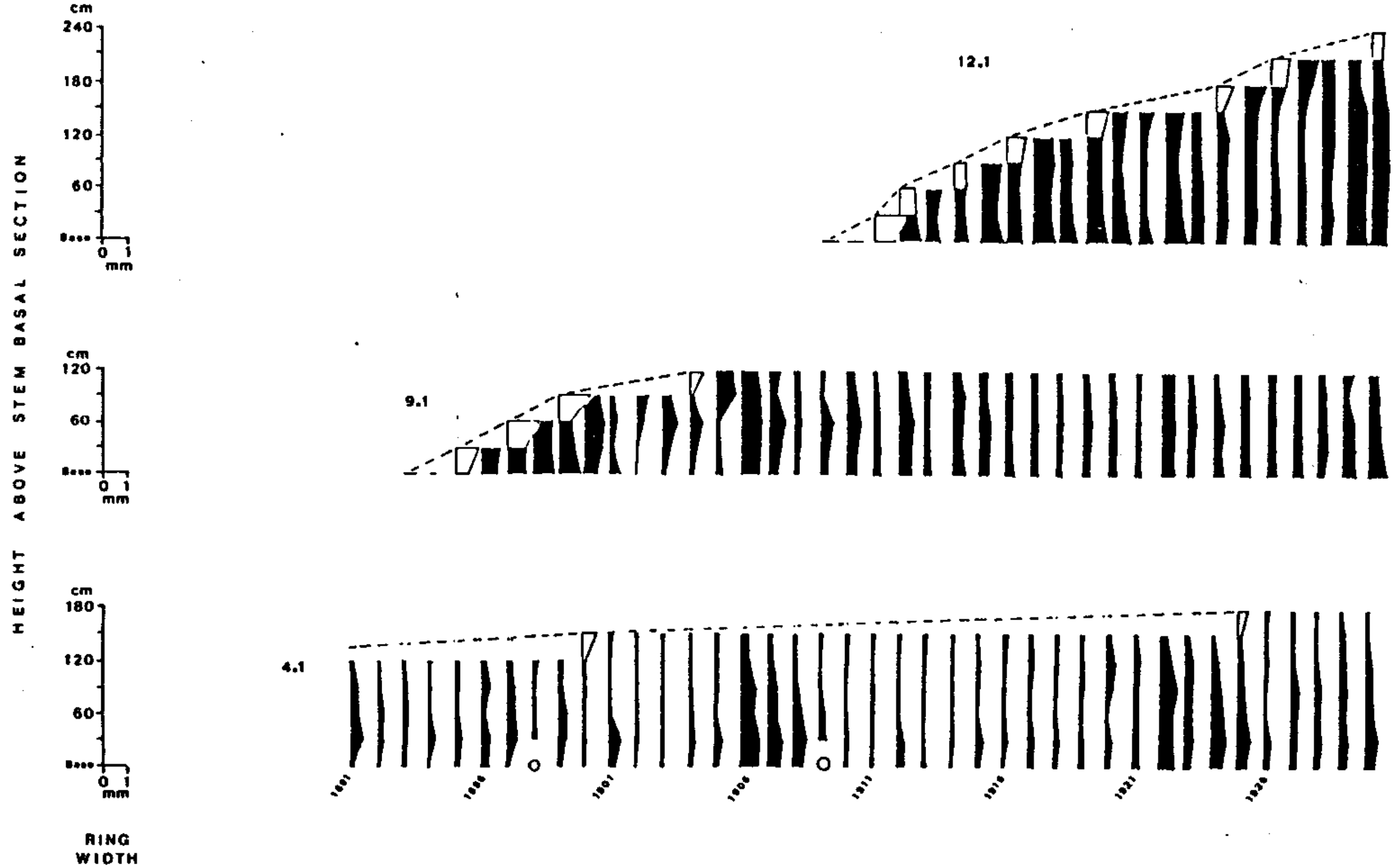


Figure 2. Annual growth layer profiles in three stems.

The numbers identify the stems, e.g. 4.1 refers to stem number 1 of sample tree number 4 (Table 3). The unshaded portion at the top of a profile represents pith plus the wood produced by cambium formed in the year indicated at the bottom of the Figure, and the shaded portion represents wood produced by older parts of the same cambium. A circle indicates no wood production at that position on the stem. Dashed lines represent estimated annual growth in height, since the first growth ring can only be produced in a leading shoot.

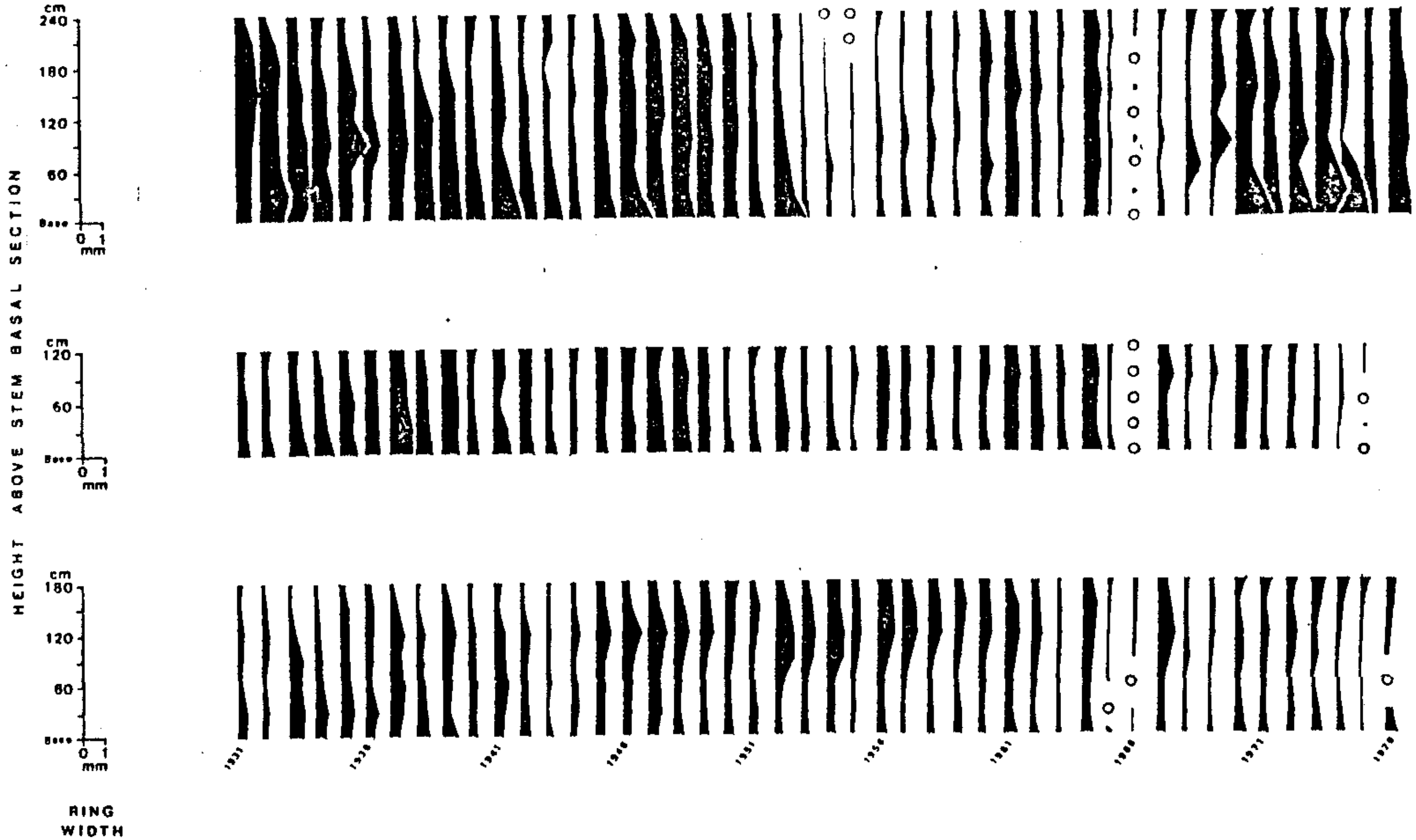
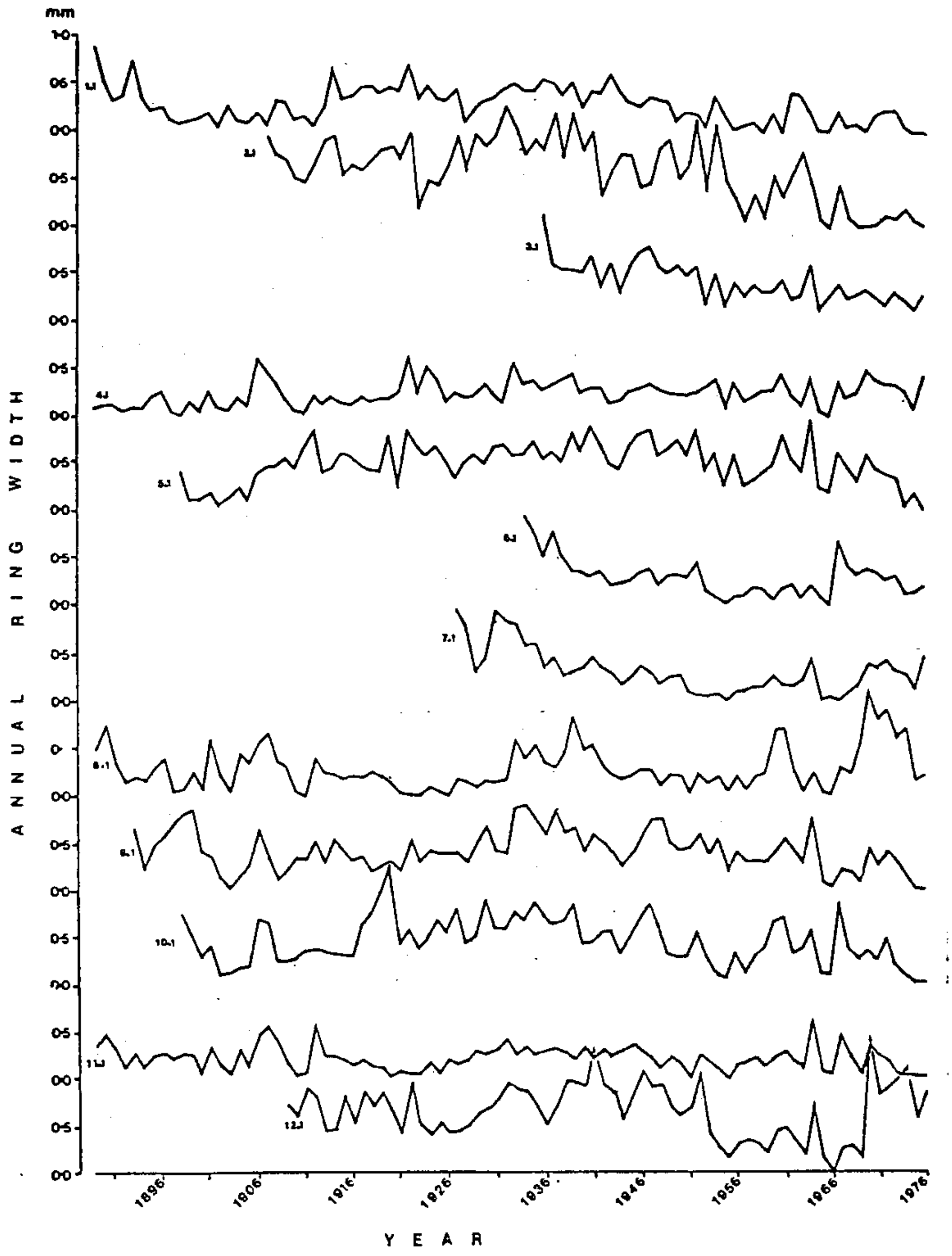


Figure 2. (Continued)



<u>Figure 3.</u> Annual ring widths measured on the basal section of one stem from each sample tree.

The stems are numbered in the same way as in Figure 2 and Table 3.

(NB. 197, 109 and 112 rings were counted in 4.1, 8.1 and 11.1 respectively, but only 89 have been shown in order to make the diagram a convenient size).

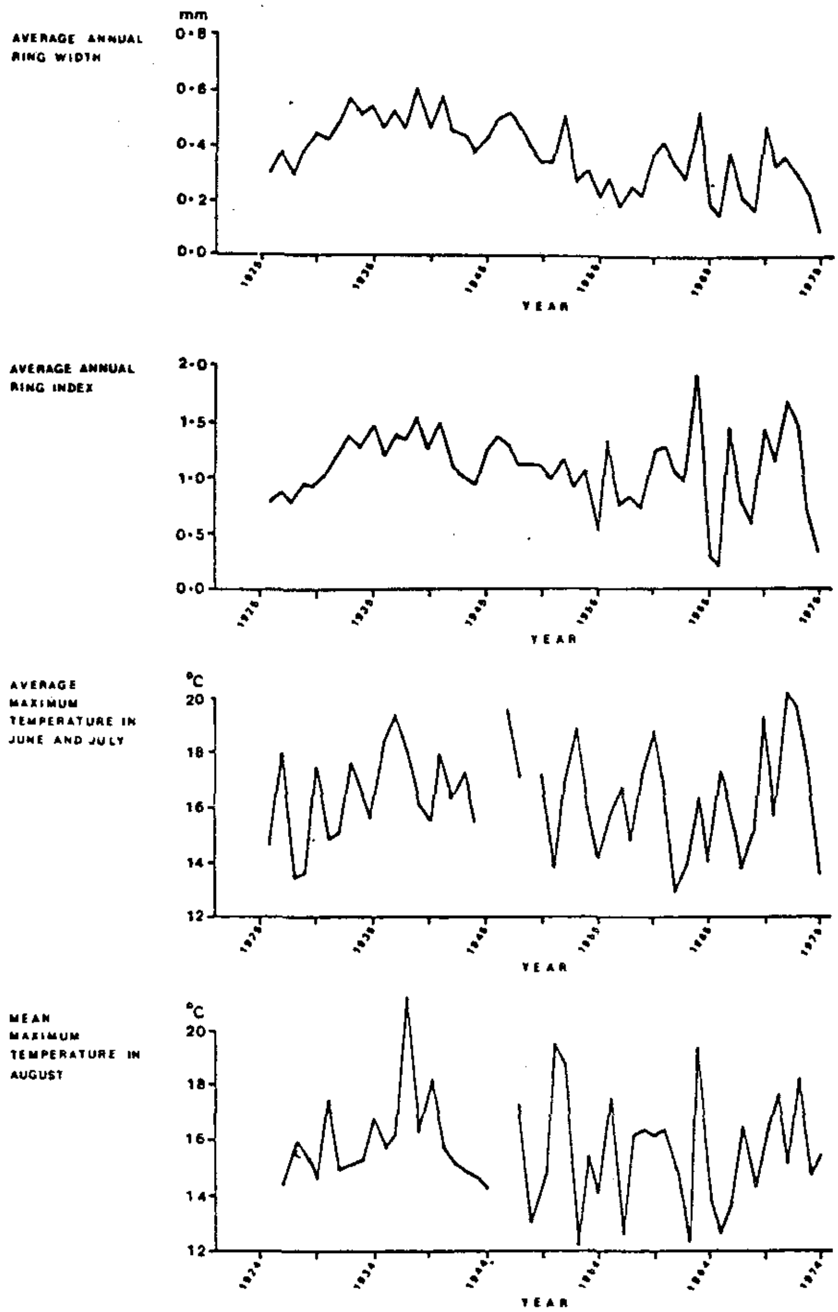


Figure 4. Average annual ring widths (1926-1975) calculated from the basal horizontal sequences in 12 stems from the study area (Table 3. 1.1, 1.2, 2.1, 4.1, 5.1, 5.2, 8.1, 9.1 10.1, 11.1, 11.2, 12.1), average annual ring indices derived from the same 12 sequences, and maximum temperatures observed at stations near Lake Inari (Figure 1, Table 2).

The terms average and mean, as applied to temperature data, are defined on page 9.

NB. The time scale of the bottom diagram has been displaced one year to facilitate comparison with current years in the other diagrams.

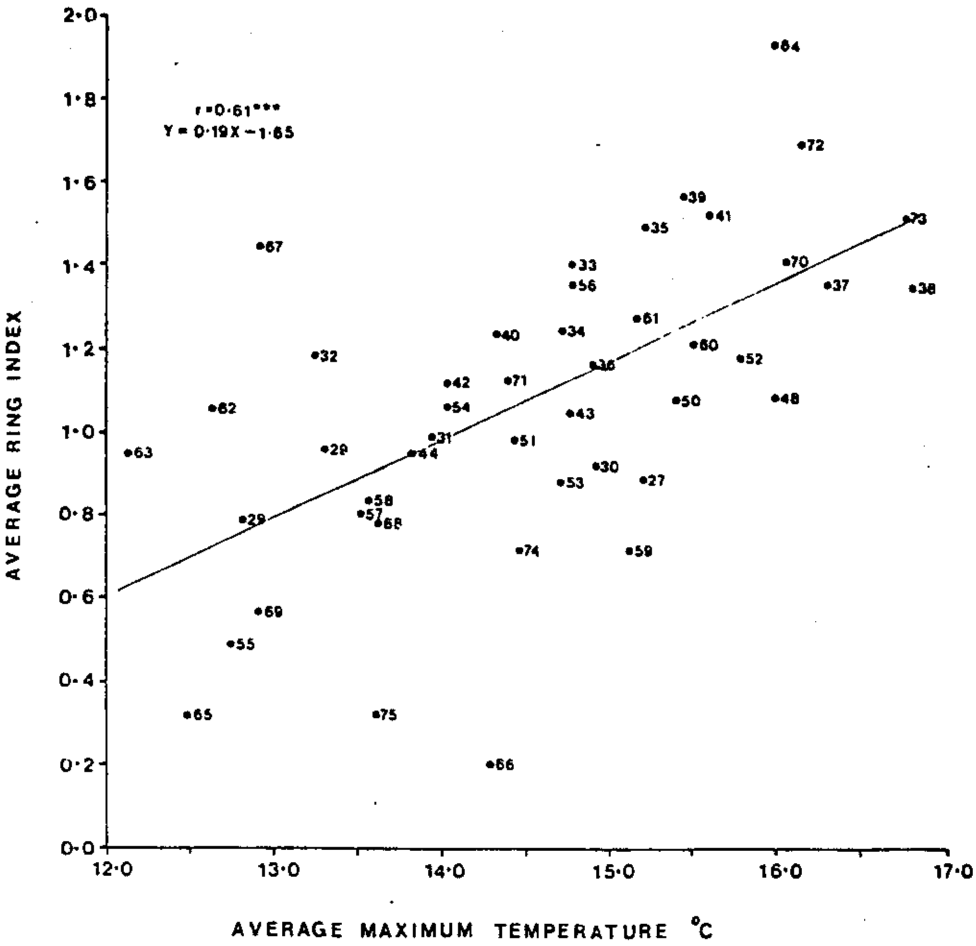


Figure 5. Correlation between average annual ring index and the average maximum temperature of June-July (in the year of ring formation), and August (in the previous year).