DENDROCLIMATOLOGY OF PINUS SYLVESTRIS L.
IN THE BRITISH ISLES.

by

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Abstract.

A study of the properties of tree-ring density and ring-width chronologies from five sites in the British Isles, two in Sweden and two sub-fossil sites in Northern Ireland is described. The technique of x-ray densitometry is used to measure density. It is shown that it is possible to use x-ray densitometry on well preserved sub-fossil pine. Chronologies have been constructed for parameters of earlywood and latewood widths, ring-width, maximum and minimum densities for all sites. The statistical properties of chronologies are related to the latitude and altitude of the sites. Sub-fossil chronologies behave differently to any of the living tree chronologies.

Response functions on monthly temperature and precipitation data are calculated for the five tree-ring parameters for the living tree chronologies. A principal component analysis involving 25 ring-width chronologies from northwestern Europe is used to examine the spatial relationship between British and European ring-width chronologies.

The continuous pattern of density variation across the annual ring is measured for trees from two scottish sites, at Glen Derry and Glen Affric from 1900 to 1979. A method of constructing and comparing annual density profiles by fitting cubic spline functions to the density data is described. This has enabled the effects of growing season climate on density to be examined. The importance of temperature in governing tree-ring density is demonstrated. The use of image analysis techniques to measure the continuous variation in cell dimensions across the annual ring is described. Variations in ring density are explained in terms of changes in wall thickness and lumen diameter.

A comprehensive literature review on the physiological mechanisms controlling the response of tree-ring width and density in P. sylvestris to climate is described. The physiological causes for the climate-growth response in earlywood and latewood widths and densities are summarised seperately. It has been possible to explain some of the results of the response function analysis and the density profile study in terms of physiological processes.

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Chapter 1. INTRODUCTION

A. PINUS SYLVESTRIS L. AS A SOURCE OF MATERIAL FOR DENDROCLIMATOLOGY.

The geographical distribution of Pinus sylvestris L. is the largest of any coniferous tree species in the world. It is present across the zone of cool temperate Boreal forest in the Northern Hemisphere, from Great Britain in western Europe across Eurasia to 130°E longitude in the USSR. The northernmost latitude is greatest in Norway where it grows at 70°20'N, although it rarely extends beyond the arctic circle in the USSR. The southernmost limit is less well defined. P. sylvestris occurs in islandlike localities in many parts of the mediterranean region and in the mountains of southeast Europe. Large stands grow at a latitude of 40°N in Turkey although small communities of P. sylvestris occur further south than this in Spain. The altitudinal limit varies according to the geographical position and the climatic conditions, for example in Spain it grows to 2100m, in the Swiss Alps 1800-1950m (Kienast 1985), 1200m in the Vosges (Tessier 1984) and 940m in northern Norway (Bialobok and Zelawski 1967). In Britain the altitidinal limit is 580m in the northern Pennines (White 1974) and 450m in the Cairngorm mountains in Scotland (Pears 1968).

The genetic variation is large, as is the range of climatic conditions under which the trees grow. P. sylvestris grows in the arctic tundra in the north and extends southwards into regions which experience a mediterranean climate. It occurs on many types of soils ranging from dry sands to peat soils. In mountains it attains considerable altitudes mostly on shallow soils or soils of low fertility. The genetic variation is considered by some workers to be clinal. There is a rich scale of variability with regard to morphological and physiological characteristics over its extensive range (Bialobok and Zelawski 1967).

P. sylvestris reached its maximum extent since the last ice age around 4000 years ago, during the so called altithermal phase in the Boreal era. This is indicated in Scotland by studies of buried pine stumps in peat bogs (Birks 1975) and pollen analysis (Bennet 1984). The height of the tree line at that time in Scotland is thought to have been at 750m a.s.l. (Pears 1968, 1970). The reasons for the pine decline are considered to be climatic and partly due to the contribution of human factors. Evidence of a warmer period 4-5000 years ago, when tree lines were 500m higher has been found in tree-ring studies on bristlecone pines (P. longaeva) from the White Mountains of California (LaMarche 1974). There is also evidence that a similar growth enhancement in natural vegetation over the past 100 years has occurred due to changing climate and perhaps an increase in atmospheric carbon dioxide levels (Graybill 1987).

In the United Kingdom most of the natural native pine forests have been felled in the past. Scots pine would naturally occur over a large area of Scotland upto about 400m a.s.l. depending on the exposure (wind is a major factor limiting the altitudinal tree line in parts of Scotland (Fraser and Gardiner 1967)). In the rest of the British Isles during the Boreal era P. sylvestris grew abundantly on the higher level peat soils, in the fenlands and on sandy coasts and hills. Forest clearance and grazing pressure played a major part in the destruction of the original native pine forests (Steven and Carlisle 1959). The remnants of the original pine forests are found in the more remote Scottish Glens, where they mostly constitute open grown stands of very old trees. There has generally been very little natural regeneration except where efforts have been made to encourage it (Bunce and Jeffers 1977).

The maximum lifespan of a scots pine is about 500 years (Steven and Carlisle 1959). The oldest trees found in Scotland are around 350 years old (Faulkner, in Bunce and Jeffers 1977). As is the case with P. longaeva, the oldest trees are found growing at the altitudinal limit of the species range (LaMarche, personal communication). Native scots pine forests occupy only a 25th of the total area of pine in Scotland, a total of 10,000 hectares mostly in open stands (Bunce and Jeffers 1977). Plantations of scots pine are rarely more than 100 years old, and these trees are often unsuitable for dendroclimatology having been grown in close stands and subjected to rigorous silvicultural regimes which are the primary influence on growth. Thus dendroclimatological work on P.sylvestris is concentrated in the native pine areas, which in general are the more remote high altitude sites.

The climatic factors limiting the range of P. sylvestris vary according to the location of the site. Temperature is known to be the primary factor delimiting the northern and altitudinal tree lines (Mikola 1962, Schweingruber et al. 1979). In dry areas the amount of rainfall is the primary factor affecting growth (Schweingruber et al 1979). The processes limiting the trees' range are also likely to be the most important factors limiting their performance at the extremities of the range. Examples of a dual response to climate across an ecological gradient are found in trees growing on several mountain ranges in western North America. Trees at the lower forest border are primarily influenced by the amount of precipitation, whereas trees at the upper treeline are affected by temperature. Forest interior trees are less responsive to climate. This has been found in bristlecone pines in the Snake Range in eastern Nevada (LaMarche 1974) and for *P. ponderosa* in the San Fransisco mountains in northern Arizona (Fritts et al. 1965). Scots pine trees from Scandinavia and Scotland have been shown to respond to differences in summer temperature (Mikola 1962, Hughes et al. 1984, Briffa et al. 1987). The spatial pattern of growth response in the annual increment in the alpine and sub-alpine regions of central Europe is more complex. There is a greater diversity of site types and local climate regimes. The situation here lends itself to spatial dendroecological studies (Schweingruber 1985, Kienast 1985) and multivariate analysis of the different sites (Tessier 1984).

The abundance of *P. sylvestris* in forests in northern Europe has implicated that this species should be chosen for dendroclimatological studies. *P. sylvestris* is the only native conifer tree in Britain and in parts of northern Europe it is the most common tree species (along with *Picea abies*). The wide range of site types which *P. sylvestris* grows on has meant that information about both temperature and rainfall can be obtained from dendroclimatological studies of trees from different areas. At the northern and altitudinal timberlines radial growth is primarily affected by temperature. On dry sites the amount of precipitation is the major factor influencing growth. Anatomically *P. sylvestris* is suitable for tree-ring studies, both density and ring-width can be recorded. Studies on living trees are however limited to the past 350 years. Pines have a relatively short lifespan compared to certain species of conifers in western North America which can live for over 2000 years.

B. RING-WIDTH AND DENSITY MEASUREMENT.

The principle of crossdating sequences of tree-rings to produce a chronology was developed in North America by Douglass in 1904 although as far back as the eighteenth century observations had been made in Europe by Linnaeus on the crossdateable nature of oak rings. Douglass worked on the climatically responsive *Pinus ponderosa Laws.* growing in the dry climate of Arizona. He developed the technique of crossdating and produced a 500 year *P. ponderosa* chronology from living trees and archaeological specimens. He introduced the concept of dendroclimatology and published work on the estimation of rainfall from tree growth (Huntingdon 1914). Subsequent work continued in the United States notably by Antevs, Schulman and Gittings. A central Laboratory of Tree-Ring Research was set up in Tucson in 1937.

In Europe dendrochronology was slower to become established because the climate growth relationships were more complex than in western North America and because the work was being carried out in fragmented locations (Echstein 1972). The main centres for dendrochronological studies were in Germany, Scandinavia and Russia. A review of dating methods was first published in Germany by Huber (1941). Early Scandinavian work is described by Hoeg (1956) in Norway and Mikola (1956) in Finland. A number of dendrochronological studies had been made in Scandinavia, mainly concerned with tree growth and environmental studies on P. sylvestris. Dendroclimatological work on conifers in Europe has been concerned with several other species, for example Larix decidua (Serre 1978), Pinus halapensis (Serre 1977) and various species of sub-alpine conifers (Schweingruber et al. 1978). The International Tree-Ring Data Bank now contains a large number of European chronologies (Hughes et al. 1982). Several long conifer chronologies now exist, constructed from living trees and specimens from archaeological sites. In southern Germany Abies alba Miller has been extended back to 820 A.D. (Becker et al. 1970), Picea abies Karst to 1250 (Weiser and Becker 1975). The longest reported Pinus sylvestris chronology is from northern Finland, extending back to 1181 A.D. (Siren 1961). Reliable measurements however only extend back to 1383 A.D. (Hughes et al. 1982, Hughes personal communication).

Anatomically P. sylvestris is more difficult to work with than some other species of conifers but with care it is possible to overcome most of the problems. The ring boundaries are well defined, false and missing rings do occur and care is needed in locating these. Compression wood is sometimes present on leaning trees, at least two radii are measured on trees to compensate for a certain amount of radial asymmetry in the growth pattern. The dendrochronological properties of various conifer species are described by Schweingruber (1980).

Initially, simple ring width measurements have been used in the study of conifers. Intra-annual density measurements employing the technique of x-ray densitometry have more recently been utilised and have proved to be very successful. The anatomical simplicity of conifer wood makes it especially suitable for densitometry. The method of x-ray densitometry in which an x-ray negative film of the wood is analysed optically on a densitometer was first developed by Polge (1970) in France and later adaptions have been made in other laboratories (Lenz et al. 1976, Parker and Henoch 1971, Milsom and Hughes 1978, Jacoby

1980). Time series of maximum and minimum densities may be produced and these can be related to climate. Densitometry has often enabled additional and more seasonally specific climatic information (on temperature and precipitation) to be obtained (Hughes et al. 1984). Strong relationships have been found for conifers between maximum density and late summer precipitation in France (Polge 1965) and late summer temperatures in northern Canada (Parker 1976), eastern North America (Conkey 1979), in the Himalayas (Hughes and Davies 1987), in the Swiss Alps (Schweingruber et al. 1978), in Scandinavia (Briffa et al. 1987) and in Scotland (Hughes 1987). Spring and early summer temperatures are also found to be correlated with maximum density in P. resinosa in Maine (Conkey 1986).

In Europe and eastern North America there is a more complex response of trees to climate than in the western United States. The lifespan of European tree species is shorter than many American species, although conifer tree-ring records in Europe have been extended using archeological material. Measurement of density parameters in addition to ring-width have been successful on conifers from these areas. Maximum density has been shown to be related to late summer and early spring temperatures in several European and eastern North American conifers. It would seem that a closer examination of tree-ring density could aid in our understanding of the climate-growth response.

C. OBJECTIVES.

Recent work on P. sylvestris in Scotland has indicated that summer temperatures can be reconstructed for a period prior to the existence of climate records from tree-rings using ring-width and maximum density data (Hughes et al. 1984, Hughes 1986). They demonstrated that tree-ring reconstructions of temperature data were stable in both the time and frequency domains. It has been possible to reconstruct Edinburgh temperature back to 1720 (prior to the existence of climate data records) using tree-ring data from a number of sites in Scotland. A similar reconstruction of late summer temperature for northern Europe has also been carried out using tree-ring data (both ring-width and density) from northern Fennoscandia back to 1700 (Briffa et al. 1987). Hughes (1986) finds that in Scotland, July and August temperatures are the most important climatic parameters affecting maximum density at all sites although the inland tree line sites were more responsive to temperature than the more oceanic west coast sites. Schweingruber et al. (1979) consider the properties of chronologies from a small number of British sites in a European context. A detailed examination of the dendroclimatological properties of P.sylvestris on a variety of British sites at different altitudes has not been made.

So far these climate reconstructions have been based on material from living trees. Given the strong climate-growth relationship and the potential of tree-rings to reconstruct climate faithfully in the time and frequency domains, it would seem feasible to use preserved timber from an earlier period to reconstruct climate back still further in time. There is a wealth of P.sylvestris material that has been preserved in peat bogs throughout Britain and Ireland (Birks 1975, Pilcher 1973). This material is termed bog pine or sub-fossil pine. Oak chronologies have been extended back 7272 years which include peat bog material from Ireland (Pilcher et al. 1984). It would seem possible that a similarly produced chronology constructed using P. sylvestris timber could provide a considerable amount of climatic information. An important consideration might be in the study of temperature at the time of the maximum pine growth and during its subsequent decline at the end of the boreal era (5000-3000 yrs. B.P.). It is considered that there could be analogies with the changing climatic patterns today which is thought could be a result of carbon dioxide build up in the atmosphere (Graybill 1987).

The major problem in the production of a bog pine chronology is to locate a sufficient number of overlapping, correctly dated specimens. In order to produce a replicated crossdated series from pine timbers a quantity of contemporaneous material must be found, crossdating of the ring series must also be possible due to some degree of common pattern. A 500-year floating chronology has been produced from pine in the Irish Midlands, radiocarbon dated 4000-3500 yrs B.P. (McNally and Doyle 1984). In this work chronologies based on maximum latewood density from bog pines found in Northern Ireland have been produced, the properties of these chronologies are examined. Investigation of bog pines from sites in Scotland have also been made in an attempt to produce a chronology from a higher altitude site. It is well established that at the higher altitude sites in Britain, a strong response of tree growth to temperature is found. Such a strong well tested relationship could be used in extrapolation to the distant past. The best source of information about temperature in the distant past for Scotland and northern Europe is thus likely to be obtained from bog pines from high altitudes in Scotland.

There are difficulties in locating suitable timber and dating of sub-fossil pine to construct a sub-fossil chronology. There is also the problem of the large temporal gap in the availability of P. sylvestris material after 3000 yr. B.P.. Between this time and 1383 A.D. (the earliest data of the longest reliable pine chronology, Hughes et al. 1982) no material from P. sylvestris has been found. Unlike oak, pine was not extensively used in archaeological construction and it is not naturally durable.

The nature of the climate-growth signal in P. sylvestris from sites in Britain other than in Scotland has not been fully studied. It has been necessary to carry out further investigation into the variability of the properties of the rings on several site types in order to be able to compare the growth of sub-fossil pines on lower level sites with the growth of modern trees (not necessarily growing on peat).

The statistical properties of density and ring-width chronologies from five selected sites in the British Isles and two in Scandinavia are examined. Five tree-ring variables (maximum and minimum densities, earlywood width, latewood width and ring-width) are analysed seperately. Recently developed statistical procedures for tree-ring analysis are used. A principal component analysis is used to compare the British chronologies with a set of ring-width chronologies from sites northwestern Europe. The climate-growth response is investigated using the standard procedure of 'response function' calculation. The climate-growth responses for the five tree-ring parameters listed above are computed seperately for the five British and two Swedish sites.

Not only is it important to consider the differences in the climate-growth response between sites, it is also necessary to focus on the nature and physiological causes for the climate-growth signal. Of special interest is the biological basis for the strong maximum density-temperature response in high altitude trees. An extensive literature survey has been undertaken. The findings on what is known of the physiological response of the annual increment to climate are considered in relation to statistical evidence. Literature relating primarily to Pinus sylvestris is surveyed. It is necessary to consider how climate affects cell production and tracheid dimensions (both wall thickness and lumen diameter) at different times in the growing season. The physiological causes for climate-growth responses in earlywood width, earlywood density, latewood width and latewood density are summarised seperately.

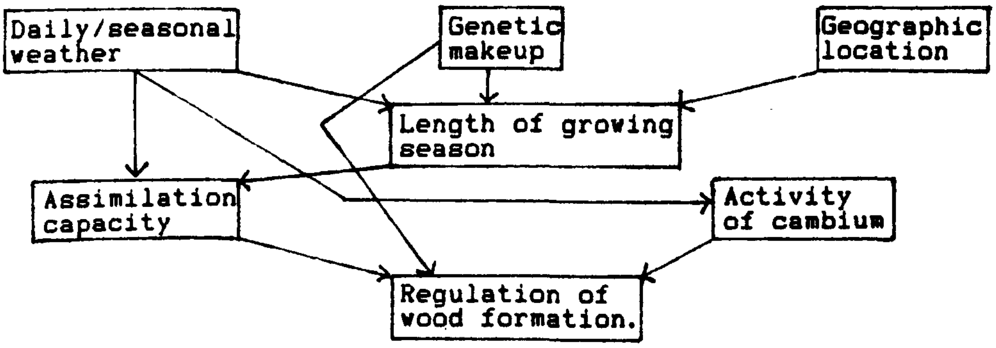
Information is needed about the variation in density across the whole ring and also the variation in cell dimensions through the course of the growing season. Only then is it possible to interpret the physiological and statistical evidence of climate-growth responses. In this work yearly density variation is examined by fitting cubic spline curves to the densitometric measurement to produce 'density profiles'. Climate data is related to yearly deviations from the mean density profiles. Variations in cell dimensions across the annual rings are measured on thin sections of wood. Analysis of cell dimensons is based on techniques developed in Germany. A preliminary trial using computer assisted image analysis is undertaken to investigate the possibility of quantitative analysis of variation in cell dimensions across the annual rings.

Chapter 2. PHYSIOLOGY OF THE CLIMATE-GROWTH RESPONSE.

A. INTRODUCTION.

There is considerable ecotypic variability in the morphological and physiological characteristics of *Pinus sylvestris L.* Some workers distinguish several climatic ecotypes, others consider that the variation is more or less continuos over the major part of its geographical range and thus the variation in properties is considered to be clinal (Bialobok and Zelawski 1967). Wright and Baldwin (1957) distinguish several European ecotypes for example; *Pinus sylvestris L. var. sylvestris* in Poland, Germany, Czechoslovakia and Hungary, *P. sylvestris var. lapponica Hart.* in northern Scandinavia and *P. sylvestris var. scotica Willd.* in Scotland. The results of physiological studies on scots pines from areas outside Scotland must be treated with some degree of caution when discussing the physiological characteristics of Scottish populations. Vaartaja (1959) demonstrated, in studies on pines at different elevations from England and Finland, that a hereditary photoperiodic response had undergone changes from one population to another, depending on the local photoclimate and environmental conditions. Thus distinct photoperiodic ecotypes can be distinguished.

The climate-growth response is regulated by the genetic makeup of the tree, its geographic location (which will affect the general climate pattern), and the seasonal and daily variations in the weather from year to year. It is the influence of yearly variations in climate on tree growth that is of interest to dendroclimatologists when attempting to reconstruct climate in the past from tree-rings. If a number of different sites are examined the genetic and geographic components must be considered. The following flow chart shows the relationships between these factors and the most important physiological processes regulating wood formation.

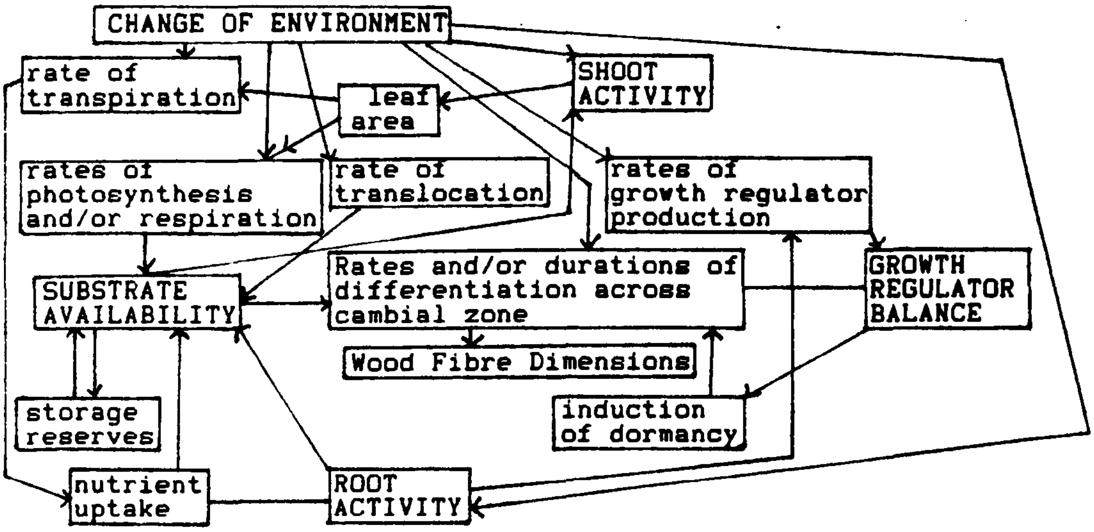


The following section contains part of an extensive review of the literature relating to the climate-growth response in conifers, with special attention to *Pinus sylvestris*. The topic is considered under three heading, these are; photosynthetic capacity of the tree, the intrinsic factors controlling growth and finally, external factors and how they might modify these processes. Many of the processes operating which were explained in relatively simple terms twenty or so years ago are now found to involve quite complicated mechanisms.

There is a confusing variety of experimental evidence as to the exact effect of many environmental factors on fibre dimensions. For example it has been shown that a reduction in daylength results in a decrease in wall thickness in P. radiata seedlings (Richardson 1964), but in similar experiments with larch an increase was found (Wodzicki 1964). Larson (1969) pointed out that only by considering the whole tree in relation to its total environment could such discrepancies be reconciled. A tree is a balanced self-regulating system, so the same conditions may have a different effect according to; the previous circumstances, the point in the growing season and other factors which may be operating simultaneously.

The following diagram shows a flow chart of some of the interacting processes affecting wood fibre dimensions (from Denne and Dodd 1981).

Figure 2.1



The picture is further complicated because a change in one environmental factor is often associated with a change in another; for example in the case of the relationship between the amount of precipitation (which affects the water balance of the tree) and number of hours of sunshine (affecting the rate of photosynthesis). Regular seasonal cycles of environmental conditions will interact with internal growth cycles including periodic shoot elongation, leaf expansion, apical activity, root growth and cycles of leaf ageing (Denne and Dodd 1981). The tree's response to changes in the environment will vary according to its physiological state and the time of year. The relative importance of the different pathways will change throughout the growing season.

B. PHOTOSYNTHETIC CAPACITY.

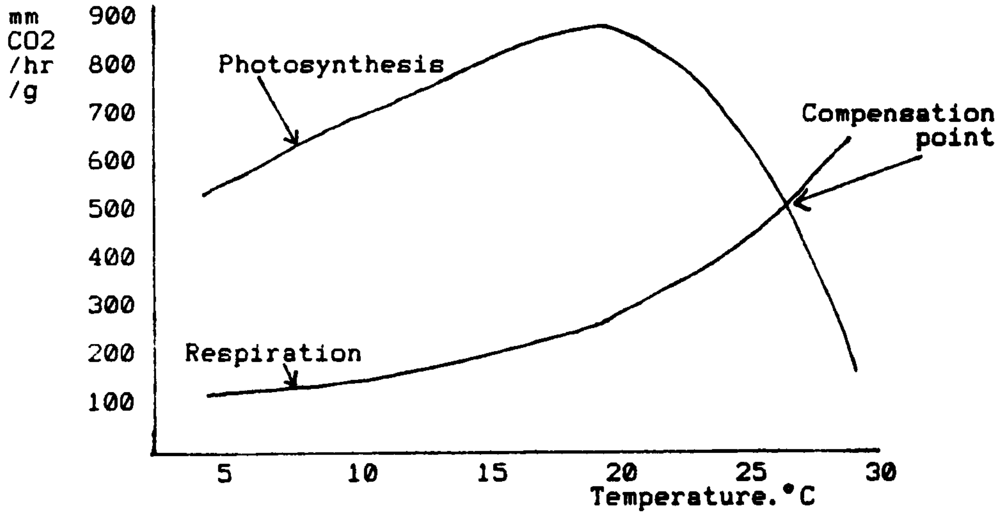
a) Foliage assimilation capacity.

The foliage assimilation capacity is affected by the length and number of needles and their physiological state, including age, time of year and health (Linder and Troeng 1980). Needle length in pines varies according to their genetic characteristics and the latitude and altitude at which the trees are growing. Trees growing further north and at higher altitudes have shorter needles (Steven and Carlisle 1959). Large differences in needle length can occur from year to year. Needle growth in pines can continue long after shoot elongation has ceased, unlike some other conifer species such as Abies (Worral 1980). Needle retention is usually four years in P. sylvestris, depending on the local environmental conditions. In situations of low nutrient availabilty, drought conditions or pollution the needle retention period is shortened (Bialobok and Zelawski 1967). In spring the second year needles are providing most of the carbohydrates whilst the new needles are initially a drain on the tree's reserves. Later in the growing season when the current year needles are mature they will be photosynthesising at a greater rate than they are respiring and thus take over as the main carbohydrate producers (Linder and Troeng 1980).

The photosynthetic capacity of the needles varies throughout the year, not only as a result of differences in the weather from season to season but also due to physiological changes within the needles themselves. During the winter the concentrations of the three needle pigments chlorophyll, carotene and xantophyll decrease. This is especially apparent in trees from the northern regions. In these northern pines the concentration of chlorophyll is lower in winter and higher in summer than in trees from central European provenances. The highest concentration of these pigments is found in spring immediately preceding bud initiation. Inactivation of chloroplasts also occurs during the winter, which will result in a decrease in photosynthetic capacity. Some photosynthesis occurs in the winter months after the cessation of wood formation at the end of the summer. It has been found that the artificial maintenance of high temperature (above 15°C) into the autumn can result in a maintenance of photosynthetic capacity and a temporary halting of the winter changes in needle pigments. Photosynthesis however does not generally occur at all beyond November in pines from northern Europe and this is thought to be due to low light intensity rather than low temperatures (Linder an Troeng 1980).

In the spring, under favourable conditions, the old assimilatory organs in scots pine begin to be active long before the initiation of bud development. This is dependent on the local climate conditions (Bialobok and Zelawski 1967, Philipson et al. 1971, Persson 1980). In Sweden, Linder and Troeng (1980) found that P. sylvestris was photosynthetically active from April to November, the season varied by about a month from year to year according to the prevailing weather. A considerable amount of carbohydrate may be synthesised in the autumn which is mostly translocated to the roots.

P. sylvestris is a light demanding species thus there is a large increase in photosynthesis with increasing light intensity (Tranquillini 1979). The compensation point is reached at a relatively high illumination compared with many other conifer species. Temperature is also an important factor governing the rate of photosynthesis in scots pine. The following diagram shows how photosynthesis and respiration are dependent on temperature at 10% natural illumination (Bialobok and Zelawski 1967). Maximum photosynthesis occurs at around 20°C, above this temperature respiration rate increases rapidly. At temperatures below -3°C no photosynthesis is found to occur.



The diurnal rate of photosynthesis is governed by a number of factors (the most important being conditions of light and temperature). A typical double peaked curve is found in photosynthetic rate throughout the day, maximum photosynthesis being in early morning (9a.m.) and in the afternoon (at about 2p.m.) with a drop in net photosynthesis and an increase in respiration around noon (Linder and Troeng 1980).* Polster and Fuchs (1963) in Germany found that net photosynthesis was positive in early March when temperatures were above freezing. Net daily photosynthesis increased as there was a general rise in temperature in spring. The typical double peak pattern did not occur until the

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* Scottish populations of P. sylvestris may behave somewhat differently to the Swedish population.

beginning of April when the maximum temperature rose above 10°C and the minimum temperature was above freezing.

Experiments on seedlings have shown the net assimilation of carbohydrate in the needles drops markedly in the spring during the stage of active shoot elongation (Neuwirth 1959, Barnett 1981). At this time the rate of respiration exceeds the rate of photosynthesis in the old needles. This is followed by a period of 'exhaustion' when both respiration and photosynthesis decline. After this, by the beginning of June, the rates of respiration and photosynthesis increase as the new needles take over as the primary assimilating organs. In a mature tree this exhaustion is less severe since utilisation of stored carbohydrate is possible, but a drop in net assimilation is still apparent (Tranquillini 1979). In Sweden, Linder and Troeng (1980) found that photosynthesis was often low during late spring and early summer in mature trees due to winter damage to the photosynthetic apparatus in the needles.

b) Length of growing season.

The growing season is considered as starting at the time the buds break in the leading shoots in the spring. It terminates when the cambium becomes inactive in the autumn. As described in the previous section, photosynthesis and other physiological processes can still occur outside this period. In terms of investigating the characteristics of the tree-ring itself and a possible direct response of growth to current weather conditions, it is important to determine the length of the growing season. A statistically determined climate-growth response can only be interpreted as a direct response if it occurs during the growing season.

The length of the growing season varies according to the geographic location, the prevailing weather conditions and the genetic characteristics of the tree. Genetic factors will affect how the tree responds to the environment (Lavender 1980). Genetic variation within a species is thought to be responsible for much of the geographic variation in bud-burst timing. Steiner (1979) examined the geographical patterns of bud bursting in several *Pinus* species including *P. sylvestris*. Strong geographical patterns were found in this timing. Multiple regressions of population means for each species against polynomial functions of latitude and longitude of origin accounted for 69 to 88 percent of the total variation. Scottish populations of *P. sylvestris* however flushed significantly earlier than others at the same latitude in Europe, apparently due to the maritime influence. The chance of a damaging late frost in spring is less in maritime regions, hence the trees are adapted to flush earlier. The geographic pattern of variation could be interpreted in terms of the combined effects of latitude and continentality of climate. Bud-burst in pines is believed to be primarily a response to rising temperature. At the northern timberline in Finland, *P.sylvestris* needs several days with temperatures above 12°C for active growth to commence (Mikola 1962). The temperature threshold for recommencement of growth in spring, as would be expected, is lower for populations native to habitats with cooler growing season temperatures.

In geographic terms, Steiner (1979) found that the timing seemed to correspond more closely to winter temperatures (January to March means) than to temperatures or incidence of frost at the time of bud-bursting. In *Pinus* species spring frost damage to the young shoot is rare, in contrast with many other conifers. There is known to be some ability to resist frost damage at the time of growth initiation, even at temperatures considerably below freezing. The fact that time of growth initiation corresponds better with winter temperatures than with conditions at the time of bud-bursting is thought to be because adaptive responses to winter temperatures are more important in controlling the processes leading up to bud-bursting (since pines may be photosynthetically active during the winter) than responses to temperatures in the spring when conditions are generally favourable.

The variation in weather from year to year can also be responsible for an annual variation in bud-burst timing at any one location. It would seem that, at a local level, the prevailing weather at the time of growth initiation may have an effect on the pattern of variation in the time of bud-bursting. This variation is found to be more apparent in southerly provenances of *P. sylvestris*. Lavender (1980) finds that prevailing temperature plays an important role in controlling bud-bursting in southerly provenances, with photoperiod also playing a part in trees from northern origins. On one site there can even be variation in the time of bud-breaking from tree to tree. Mikola (1962) found that for *Pinus sylvestris* and *Picea abies* at the northern timberline in Finland the dates of onset of bud activity differed by about a month from tree to tree. Denne (1979) found that time of bud-break varied within the crown of *Picea sitchensis*. It is thought that this may be associated with differences in chilling requirements for bud-break associated with variation in the duration of cambial activity in the previous growing season.

Bud-bursting in relation to commencement of cambial division at breast height varies according to tree vigour. Cell division at the base of the buds begins before bud-break and proceeds basipetally such that division at breast height will occur after bud-break (Denne 1979). Mikola (1962) found this initial cell division occurred 5-10 days before bud-break and cell division at breast height commenced 3-4 days after bud-break. The rate of basipetal growth initiation is much slower in suppressed trees. In severely suppressed specimens the annual ring may be non-existent at the base of the tree. Larson (1962) considers that an auxin or auxin-precursor emanating from the developing buds activates the cambium in a basipetal direction. Denne (1979) found in Picea sitchensis, that tracheid production began earliest at the tips of the branches below the main crown. In the main stem it began several internodes below the leader and progressed down the main stem. A delay of 5-10 days occurred before tracheid production commenced at breast height, depending on the light conditions. Tracheid production ceased throughout the tree in mid-September in dominant and co-dominant trees and in early August in supressed trees.

The cessation of cambial growth in the autumn and the onset of dormancy are also found to vary from year to year. It is thought to be internally controlled by photoperiod, but environmental conditions may induce a premature cessation of cambial growth. The relative importance of photoperiodically induced and environmentally induced dormancy may depend on the latitude and the site conditions. Kramer (1964), investigating pines in North America found that an adequate water supply was necessary to prolong latewood production. Dormancy was often induced by a lack of moisture as early as mid-August. In years when the amount of water was not limiting, growth continued well into the autumn. Termination of cambial growth was then induced by low temperatures and photoperiod. At northern European locations, such as in Finland where Mikola (1962) carried out his studies, photoperiodically induced dormancy is likely to occur earlier in the year (due in part to genetic adaptions to shortening photoperiod in these regions). Photoperiod may thus be the critical factor in a greater proportion of the years. Latewood production also begins later at higher latitudes and elevations (Tranquillini 1979). The time at which the densest wood is laid down in the latewood is thus perhaps more consistent from year to year in northern regions. The best correlations between maximum density of the annual ring and late summer temperatures are found in trees from northern regions (Briffa et al.

1987).

More recent work has indicated the existence of other internal controlling factors. Denne (1974) suggests that the duration of cambial activity is possibly related to the duration of primordial production at the shoot apex. Lavender (1980) also introduces the possibility that low night temperature may be another of the interacting factors in the initiation of dormancy.

C. INTRINSIC GROWTH PROCESSES.

a) Inherent growth pattern.

Within the tree there is an inherent pattern of ring-width variation which is manifested both vertically and horizontally. Duff and Nolan (1953) conducted a detailed investigation of these trends in several species of Canadian conifers. Vertical ring-width sequences formed in a single year were measured with respect to the stem apex. The maximum diameter increment was found to occur just below the internode carrying the maximum foliage weight. Having investigated trees in various canopy positions and in the open, it was concluded that the intrinsic factors controlling ring-width were nutritional gradients in the tree axis and the distribution of foliage. Duff and Nolan considered that by examining the sequences of ring-widths of the same age at the time of ring formation, the effects of the intrinsic patterns could be eliminated, hence leaving the effect of the external factors only. This approach, although not entirely successful has subsequently proved useful in providing information about anatomical features of wood. LeBlanc et al. (1986) use this method to investigate historical growth patterns in red spruce, in northeastern United States. Using a sophisticated computer programming method developed by Fayle et al. (1983), they were able to determine the timing and pattern of growth decline in the spruce trees.

b) Earlywood-latewood definition.

The relative amounts of earlywood and latewood in each ring also changes vertically. Earlywood cells have a large diameter and thin walls whereas latewood cells are smaller and have thicker walls. Earlywood is therefore less dense than latewood. The boundary between the two layers may be defined at a predetermined density (measured for example by x-ray densitometry). A widely used definition of earlywood and latewood proposed by Mork in 1928,* defines the boundary in anatomical terms. Latewood consists of those tracheids which have a radial diameter less than twice the thickness of the common wall between two contiguous cells. This boundary may not however coincide

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* (Fritts 1976)

with the obvious line of radially flattened, thin walled cells produced at the beginning of the latewood, especially when the transition is drought induced. More recently Creber and Challoner (1984) used a more sophisticated technique which defines the boundary by cell diameter only. This method can be used to identify different types of earlywood-latewood transitions. The cumulative algebraic sums for each cell (starting from the beginning of the earlywood), of the deviations from the mean radial cell diameter are calculated. The maximum point on this curve is used to define the earlywood-latewood boundary. This in essence is defining the boundary as the point of maximum rate of change in cell diameter across the ring.

c) Latewood initiation.

Latewood production begins at the base of the tree and proceeds acropetally in most conifers. Thus the proportion of latewood in the ring is greatest at the stem base. Larson (1962) noted that the proportion of latewood was determined by age of the tree and distance from the crown. This implies that processes within the tree crown are operating to determine the time of latewood initiation. He considered that auxin produced in the needles diffuses basipetally down the stem, the concentration of auxin being the main factor controlling cell size.

Water availablility can influence the time of latewood initiation. Latewood is formed earlier in drought affected trees and earlier at breast height than in the lower crown. In irrigated trees the transition to latewood production takes place later and more or less simultaneously throughout the stem (Kramer 1964). Kramer investigated trees under simulated drought conditions and found that although the growth of irrigated trees was much greater than that of drought affected specimens, the percentage of latewood showed no consistent pattern of variation. The tracheids of drought trees were considerably more flattened in the radial direction. This cell flattening is thought to be regulated by auxin gradients (Wodzicki 1978). During mid-summer the tracheids of drought trees are alive and assimilating wall material whereas those of irrigated trees are maturing more quickly and functioning as water conductors. The production of drought induced radially flattened cells may be a reversible process depending on how early in the season it occurs. A subsequent wetter period after a drought in early summer will result in larger latewood cells being produced which are not necessarily radially flattened. These may in fact be large enough and have sufficiently thin walls to be considered as earlywood tracheids. This is the mechanism by which a 'false ring' is formed. None of the samples investigated in this study showed false rings.

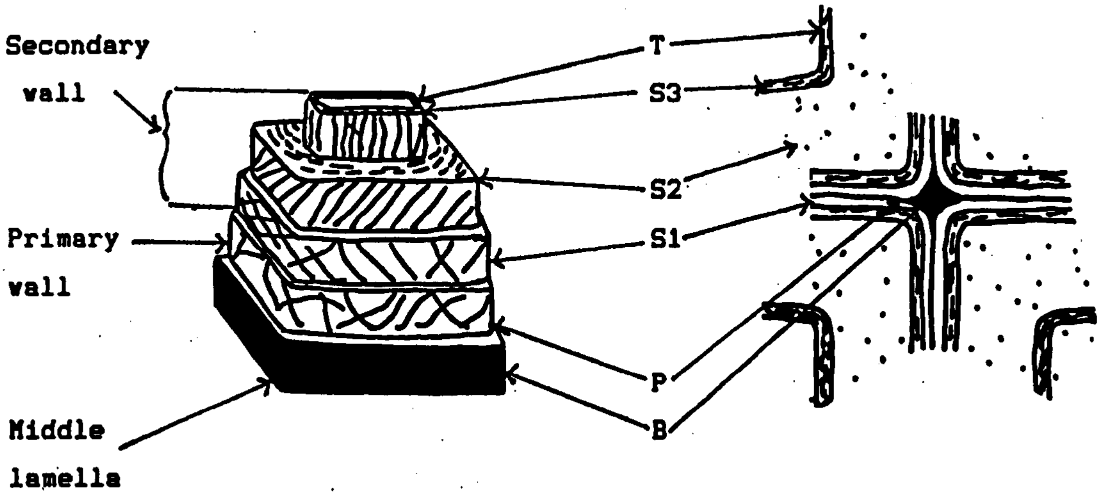
Larson (1964) found that thickening of the latewood wall preceded a decrease in cell diameter in *Pinus resinosa*. He considered that the metabolic changes in the new needles triggered changes throughout the tree. The current-year needles mature and begin to export carbohydrate at the time shoot elongation ceases. This increase in substrate availability was thought to be the cause for the increase in wall thickening in the latewood tracheids.

The duration of active needle elongation, bud activity, photosynthesis and respiration were investigated in *Pinus resinosa* to determine how they related to the time of latewood formation (Gordon and Larson 1968). It was possible to explain the changes in cell size in the stem in terms of needle activity and auxin gradients. The production of thick walled latewood tracheids in the upper stem was coincidental with the peak of photosynthetic activity in the new needles. Drought however can have a modifying effect on the pattern of latewood initiation throughout the tree (Kramer 1964). This was attributed to differences in auxin gradients in drought and irrigated trees.

Denne and Smith (1971) investigated the effect of daylength on seedlings of *Picea sitchensis* and *Pinus sylvestris*. They found evidence to suggest that tracheid wall thickness was related to the availability of substrates. The situation is however complicated by differences in the distribution of substrates throughout the tree as the season progressed and substrate availability changed. It was later concluded that the transition from earlywood to latewood was associated with changes in growth regulator balance which may be associated with the cessation of shoot extension or needle maturation (Denne and Dodd 1981). Wodzicki and Wodzicki (1980) determined that the gradual accumulation of the growth inhibitor abscisic acid was responsible for controlling latewood production in *P. sylvestris*. They considered that abscisic acid was responsible for regulating the processes which determine the rate of cell maturation.

d) The process of wood formation.

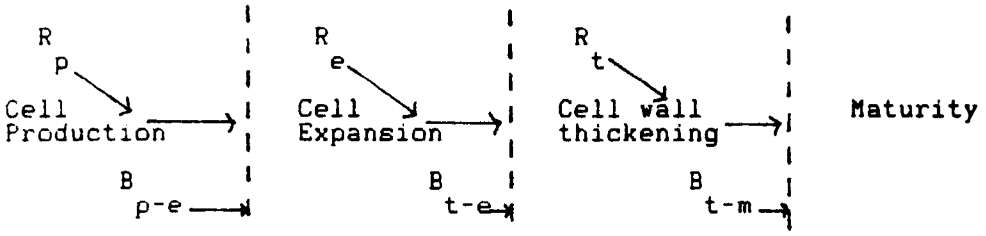
Tracheid cells constitute about 90% of the wood volume in pine, the remainder being ray cells, parenchyma and resin ducts. The development of a cambial derivative into a tracheid can take from as little as 15 days to as long as 60 days (Kremers 1964). Below is a diagram of the wall structure of a pine tracheid showing the different layers in the cell wall.



B - Middle lamella, P - Primary wall, S1 - external layer of secondary wall,
S2 - middle layer of s.w., S3 - internal layer of s.w., T - tertiary wall.
(From Tomaszewski 1967).

The process of cell formation first involves cell production. Cell division by mitosis occurs in the cambium. An initial mother cell divides to produce two new cells. Elongation and radial expansion of the new cells takes place, at this time the primary cell wall is plastic and has a high water content. A secondary cell wall is then laid down and no further expansion of the cells can occur. The secondary cell wall is composed mainly of cellulose. It consists of three distinct layers, S1, S2 and S3 differing in the proportions of cellulose and lignin and the arrangement of the cellulose microfibrils. Lignification of the cell walls is partly simultaneous with the cell wall thickening stage and continues after cellulose deposition has ceased. It has been shown that there is a diurnal rhythm in the deposition of the cell wall. Cellulose is mainly deposited in the afternoon whereas lignin is deposited at night (Necessany et al. 1965). At the final stage the cytoplasm in the cell dies and small quantities of mineral substances are deposited in the walls. The cell is then mature.

The rate of cell production and the durations and rates of the phases of cell differentiation affect the final cell dimensions and the numbers of cells produced. A diagramatic representation of the process of xylem cell differentiation is shown below.



R_i - Rate of process

B_{i-i} - Boundaries

The boundaries between the zones of cell production, cell expansion cell wall thickening and maturity are moving continually outwards. The width of each zone and the number of cells in each change during the growing season (Wodzicki 1971). The boundaries may move relative to each other and the rates of each process can change. The durations of cell expansion and wall thickening for each tracheid depends on the width of these zones. Measurements of the time taken for cambial derivatives to grow and differentiate have been made by Skene (1969) on Pinus radiata. The duration of expansion in earlywood cells was three weeks whereas in the latewood expansion took only one week. The zone of cell expansion was more restricted later in the season despite an increase in the number of expanding cells. The time taken for deposition of the cell wall increases as the season progresses (Skene 1972). Skene found that in earlywood, wall thickening took 3-4 weeks and 8-10 weeks for the latewood. This implies that the prevailing environmental conditions can have an effect on latewood cell development over a much longer period than for earlywood cells. Earlywood cells may be more succeptible to short term fluctuations in environmental factors.

Wodzicki (1971) measured the durations and daily rates of tracheid expansion and wall thickening throughout the growing season in adult trees of P. sylvestris in Poland. He found that seasonal changes in cell diameter were primarily caused by changes in the RATE of cell expansion. Seasonal changes in wall thickness were mostly dependant on changes in the DURATION of the wall thickening phase. Below is a diagramatic representation of the relative widths of the zones in the differentiating xylem of earlywood (EW) and latewood (LW). The numbers of cells counted in each zone are also shown (from Wodzicki 1971).

	P	E	T	M
EW	5	4	3	
LW	4	4	12	

P - Cell production, E - Expansion, T - wall thickening,
M - Maturity.

e) Factors controlling cell dimensions.

Wodzicki (1971) found that the rate of cell wall deposition for *P. sylvestris* increased from 0.1 µm/tracheid/day in May to a maximum of 0.3 in July and then a steady decrease ensued for the rest of the summer. Skene (1969, 1972) did not find such a marked decrease towards the end of the season in *P. radiata*. Using a correction factor for decrease in perimeter of the cell wall, as wall thickness increased, the rate was measured as 0.15 µm/day at its maximum with a much slower rate of decrease than Wodzicki had found.

Wodzicki (1971) found that both rates of cell expansion and wall thickening were affected by temperature. There was a highly significant correlation between mean daily rate of wall thickening and mean air temperature over the whole of the growing season although precipitation had no effect. Ford et al. (1978) found a significant correlation between daily solar radiation and the rate of cell production (Rp) in the earlywood of *Picea sitchensis*.

If the rate of production of cells increases and the cells are to remain the same size, there must be a decrease in the rate of cell expansion and an increase in the supply of photosynthate (Ford et al. 1978). The supply of carbohydrate might be expected to increase with daily solar radiation, but Ford et al. found no simple relationship between supply of photosynthate and the rate of cell wall thickening in the earlywood of sitka spruce. Wodzicki found that the relationship between rate of wall thickening and wall thickness varied throughout the season. Three phases could be distinguished. During the first phase, from the beginning of the season to July an increase in wall thickness was accompanied by an increase in the rate of wall thickening. In the second phase lasting until the middle of September, there was a negative correlation between rate of wall thickening and wall thickness but an extension in the DURATION of wall thickening. The final phase, lasting until the end of the growing season, showed a decrease in wall thickness corresponding to a decrease in the rate of wall thickening. Thus during the middle period (corresponding roughly to latewood formation) the increased carbohydrate supply corresponds with the extension of the zone of wall thickening.

Wodzicki (1978) considered how carbohydrate supply might affect the duration of the wall thickening phase. Tracheid maturation is terminated by autolysis of the cytoplasm and death of the cell. The rate of termination of the wall thickening phase was found to be related to the duration of wall thickening. The rate of termination is thought to be independent of carbohydrate supply, but this rate is important in governing the duration of the wall thickening phase.

f) The role of growth regulators.

Growth regulators (Indole Acetic Acid (IAA or auxin), Gibberellins, Abscisic acid and Cytokinins, plus other unknown and minor factors) synthesised in the shoot, leaves and cambium are important in the coordination of the cambial metabolism (Little 1980). It was originally thought that the concentrations of growth regulating substances directly controlled the rate of cell production and size of tracheid cells (Larson 1962). Several new theories have emerged considering growth regulators as unspecific factors controlling xylem differentiation. They must be present but changes in their concentration do not have a direct effect (Zajaczkowski 1973, Zajaczowski and Wodzicki 1978).

The level of IAA is found to increase markedly in the spring at the initiation of cambial activity. The basipetal initiation of cambial growth was thought at one time to be a result of the diffusion of auxin from the enlarging buds and shoot (Wodzicki and Wodzicki 1973). Auxin is also synthesised in the cambium for a limited time (Kramer 1964). The relationship of auxin to renewed cambial growth depends on the species, in some auxin is already present in the cambium before bud-break. In conifers, an auxin precursor is present in the cambium before the buds open. It is converted rapidly to auxin at the time of bud opening. There may be an interaction between auxin and carbohydrate in the control of tracheid dimensions. This is supported by observations made on the formation of compression wood (Larson 1969).

Zajaczkowski (1973) found that spring initiation of cambial activity in P. sylvestris was not correlated with a consistent concentration gradient of auxin. He determined that there was a complex relationship involving changes in cambial responsivity. The response to auxin seemed to be conditioned by some factor connected with the relative age of the cambium and changes in seasonal sensitivity in the cambium. Wodzicki (1980) proposed that auxin regulates the periclinal divisions in the cambium by a system of three dimensional waves of characteristic amplitude, frequency and wavelength.

Some authors believe that it is the changes in growth inhibitor concentration that are responsible for differences in the amount of cell wall thickening. Wodzicki and Wodzicki (1980) showed that the seasonal accumulation of abscisic acid affects phenomena associated with the autolytic breakdown of protoplasts. Abscisic acid has the effect of delaying autolysis of the cytoplasm resulting in an increase in the duration of the cell wall thickening phase in the latewood. This results in the formation of thick walled tracheids in the latewood. Little (1975) showed that internal water stress in Abies balsamea L. was a factor in increasing the level of the growth inhibitor abscisic acid. Thus the thicker walled tracheids associated with a drought induced false ring (or an early transition to latewood as a result of drought) may be formed as a result of the reaction to abscisic acid.

Some growth regulators are believed to originate wholly or partly in the roots. There is evidence that bud-break in Pseudotsuga menziesii is stimulated by gibberellins produced in the roots (Wareing 1980).

D. EXTERNAL FACTORS AFFECTING GROWTH.

a) Direct influences.

The cambium reacts to the environment primarily through the influence of the crown. The response is controlled by the action of growth regulators produced mainly in the foliar organs (Larson 1969). Direct influences on the cambium such as temperature and mechanical stress are also important (Worral 1980). The stresses on the cambium (for example those due to wind or the tree's own weight) affect cambial growth, allowing stem taper to be modified to suit the structural support requirements of the tree. Jacobs (1939) demonstrated that when trees were guyed so as to eliminate stresses due to swaying, stem taper and annual increment were markedly reduced. Brown (1964) also demonstrated in tissue culture, the importance of external pressure in regulating the differentiation of cambial cells to form tracheids. It is thought that izoelectric effects created by tension in the cellulose micelles may be partly responsible for regulating cambial cell development.

Experiments with 'temperature bridges' which enable direct heating of the cambium have shown that cambial activity is modified by temperature. Worral (1980) demonstrated that a threshold temperature of 2°C was necessary to induce cambial swelling in Pseudotsuga menziesii. He considered that the reaction of the cambium to temperature modified the response of the cambium to growth regulators.

The effects of temperature on the rates of cell expansion and cell wall thickening in Pinus sylvestris seedlings have been demonstrated by Denne (1971). Ford et al. (1978, 1987) also showed that the temperature of the cambium directly affected the rate of cambial cell division.

b) Photosynthetic capacity of the shoot.

The number of needles produced in the elongating shoot is determined in the previous autumn by the number of primordia laid down in the bud (Mikola 1962). The total leaf area is smaller after an unfavourable summer when cessation of growth may have been premature. The length of the needles in the new shoot will be determined by the growing conditions in the spring and the storage reserves available (Mikola 1962, Hari and Siren 1972). Needle length in P. sylvestris has been shown to be affected by drought, light intensity, latitude and temperature (Zelawski and Niwinski 1966). Pine needles have a seperate basal meristem and this allows them to elongate for an extended period if conditions are favourable. There can be considerable variation in the lengths of the needles from year to year (Bialobok and Zelawski 1967).

Boyer (1970) showed that the rate of shoot growth in Pinus taeda saplings was highly correlated with daily heat sums in the spring and indices of solar radiation. Total shoot growth was determined by the rate of elongation and not the length of the growth period, which was almost constant. Temperatures in the spring might be expected to have a similar affect on the rate of needle elongation and hence needle length.

In Picea sitchensis the production of latewood cells is associated with cessation of shoot elongation and the production of next year's terminal bud. In Pinus sylvestris and P. resinosa, it is the cessation of needle growth and not shoot elongation or terminal bud production that is associated with the transition to latewood (Larson 1964, Gordon and Larson 1968, Denne and Smith 1971). This may account for the observation made by Mikola (1962) that earlywood width in pine is more or less constant (the period of needle elongation varying little from year to year), whereas in spruce, earlywood width is more variable (shoot elongation in spruce being affected to a greater extent by the prevailing environmental conditions).

New needle maturity, which is the developmental stage at which the new needles begin to export carbohydrates (prior to or coincident with the cessation of shoot elongation), is associated with the production of thick walled latewood cells. The total area of the new needles will affect substrate production at the time of latewood formation. Linder and Lohammar (1981) measured the monthly photosynthetic production of different age classes of needles in 20-year-old scots pine. The current-year needles supplied 30% of the photosynthate mostly from July to September, second-year needles supplied 48% of the photosynthate, being the main producers from April to July. Third-year needles supplied a total of 19% of the photosynthate, the remaining 3% came from fourth-year needles. The photosynthetic efficiency of needles decreases with age (Linder and Lohammar 1981). Differences in the relative area of the current year needles will therefore have a greater effect on carbohydrate supply than for other age classes of needles. The importance of current-year needles in supplying carbohydrates to the latewood is thus evident. Climatic conditions during the spring will affect the latewood as a result of the effects on the development of the current-year shoot. Conditions during the spring will also (to a smaller extent) affect the supply of photosynthate during the following spring via the effect on the second-year needles.

Tranquillini (1979) found that in the more extreme climates at higher altitudes and latitudes there was a greater seasonal variation in the photosynthetic capacity of the needles. Damage to the photosynthetic apparatus in the second-year shoot by low winter temperatures may take upto three months to be repaired. Full photosynthetic efficieny in the older needles may not be attained until July (Linder and Troeng 1980).

c) Light intensity and substrate availability.

The properties *Pinus sylvestris* needles are found to differ according to whether they are grown in shade (shade needles) or full light conditions (sun needles). Shade needles are more efficient at low light intensities, whilst under good illumination photosynthesis is more intense in the sun-type foliage. *Pinus sylvestris* is a light demanding species and it responds very strongly to increased light intensity by raising the net photosynthetic rate (Hodges and Scott 1968). The intensity of illumination for light saturation and the photosynthetic efficiency are found to vary with needle age and are dependent on the conditions under which the plant has been growing (Bialobok and Zelawski 1967).

Changes in substrate availability as a result of differences in the amount of photosynthesis seem only to have a minor effect on tracheid cell dimensions in sitka spruce seedlings (Denne and Smith 1971, Smith 1974). Seedlings of *Picea sitchensis* were grown in high, medium and low light intensities, corresponding to open illumination in bright sunlight, moderate illumination and the light intensity on shade leaves (Smith 1974). After three months despite considerable differences in dry weight, the tracheid wall thickness did not vary significantly between treatments. There was a small increase in tracheid diameter with light intensity. The rate of tracheid production was not significantly different between medium and high light intensities, although at low light levels the rate decreased. At low light, variations in rate of total assimilation were compensated for by differences in the rate of tracheid production and tracheid diameter increment, resulting in cells of similar wall thickness in all cases. At higher light intensities in *Picea sitchensis* more substrate is diverted to branch and root production rather than to the main stem, this again offsets the effect of light intensity.

In 8-year-old sitka spruce, light intensity had a greater effect on the rate of tracheid wall thickening and cell production than in seedlings (Denne 1974). In first-year seedlings the main stem only accounts for approximately 5% of the plant weight and all parts of the stem are in close proximity to the functioning leaves. In older trees the stem may account for 50% of the plant weight. Photosynthate must be transported further and distributed to a greater amount of tissue. Thus the rates of tracheid wall thickening and cambial productivity in older trees are likely to be more sensitive to changes in light intensity (or substrate availability) than young trees (Smith 1974).

At low light intensities, changes in leaf assimilation efficiency occur at which can partially offset the effects of light intensity (Denne and Dodd 1981). In P. sylvestris these changes take place at lower light intensities than in more shade tolerant species (Smith 1974). Thus net assimilation in P. sylvestris may be more succeptible to changes in light intensity than species such as Abies and Picea sp.. Linder and Troeng (1980) found that photosynthesis in Pinus sylvestris in late autumn was limited by low light intensity rather than temperature.

Treatment with short days is shown to have a similar effect to low light intensities, and long days to high light intensities. Greater net assimilation is possible on long days. However rates of assimilation of carbohydrates are found to be greater for short day treatments than for long days because of suppression of photosynthesis on long days due to the accumulation of storage products in the leaves (Denne and Smith 1971).

At high light intensities there are changes in the distribution of assimilates. Smith (1974) showed that in Picea sitchensis seedlings, at high light intensities extra substrate is diverted to branch and root production rather than to the main stem.

Small changes in substrate availability due to daily fluctuations in solar radiation can be compensated for by changes in the distribution of assimilates. For example, a reduction in photoperiod may actually increase the amount of carbohydrate available to the cambium because of the removal of other growing sinks (such as terminal bud production). The concept of competing metabolic sinks can account for some of the observations on adaptation to changing environment and also for the fact that an increase in substrate availability does not necessarily result in an increase in wall thickness (Doley and Leyton 1968). During active elongation of the shoot in the spring, the ability of the cambium to compete for carbohydrates may be low. At the very beginning of the season there is competition for substrates between the cambium and the old needles. After maturation of the new needles the xylem is the primary sink, late in the season substrate is translocated to the roots and accumulates in the parenchyma and the new buds (Smith 1976).

Therefore during the main stage of latewood formation the cambium is the primary sink. In a mature tree the rate of wall thickening in the latewood may thus be affected by substrate availabilty. The adaptive mechanisms (such as changes in photosynthetic efficiency and redistribution of substrates) are unlikely to be important in governing the supply of substrates to the cambium. Ford et al. (1978) also consider that these adaptive mechanisms are unlikely to keep pace with changes in the environment in a mature forest.

Denne (1976) has shown that substrate availability in sitka spruce seedlings affects the rate of wall thickening although not its duration. An increase in the rate of cell production at the cambium is associated with increased daily solar radiation (Ford et al. 1978). Substrate availability is also increased at higher light intensities, hence a greater amount of wall thickening is possible. In mature trees this may result in an increase in wall thickness (and hence density) in the latewood since the cambium is the major metabolic sink. It is possible that there is a correspondingly greater increase in the rate of wall thickening than in the rate of cell production with increased solar radiation.

d) The effects of temperature.

The inherent pattern of changes in the rates and durations of cell production and differentiation through the course of the growing season have been considered earlier in this chapter.

The effects of daily weather conditions on the cell production in the cambium and tracheid differentiation have been investigated in *Picea sitchensis* saplings over a period of 15 days at the time of earlywood formation (Ford et al. 1978). They found that fluctuations in the rate of cell production were responsible for variations in tracheid wall thickness and cell diameter. Distinct groups of larger, thicker walled cells alternated with bands of smaller thinner cells. They suggested that this structure was a result of fluctuations in the environment which caused changes in the rate of cell production. The rates of cell production, cell expansion and wall thickening were correlated with the amount of daily solar radiation. Daily solar radiation had little effect on the duration of these processes in the short term. Larger diameter, thicker walled cells were thus associated with an increase in solar radiation.

Temperature has also been shown to affect the rate processes in *P. sylvestris* seedlings. An increase in temperature increased the rates of tracheid expansion and wall thickening but there was a consequent decrease in duration of these phases resulting in a small net affect on tracheid dimensions (Denne 1971). In mature trees Wodzicki (1971) found there was a positive correlation between mean daily temperature and rates of cell enlargement and wall thickening. There was no affect of temperature on the duration of the wall thickening phase but it did affect the rate of xylem cell production and the duration of radial enlargement.

The cell dimensions of earlywood tracheids are likely to be more responsive to short term fluctuations in the environment than latewood tracheids. Cells take about 6 weeks to develop in the earlywood and almost twice as long as this in the latewood. During earlywood formation shoot and needle growth are competitive metabolic sinks leaving the cambium more succeptible to changes in substrate availability. In sitka spruce earlywood, an increase in temperature causes an increase in the rates of cell production and enlargement. The duration of radial enlargement is not affected, thus larger earlywood cells are produced at higher temperatures (Ford et al. 1978). Richardson (1966) also found that a heating coil bridge applied to the stem of sitka spruce seedlings, caused an increase in tracheid diameter, but did not affect wall thickness. (This method would have no effect on substrate availabilty). In scots pine there is a consequent decrease in the duration of cell enlargement with an increase in the rate of enlargement (Wodzicki 1971). Temperature therefore will have less effect on cell diameter than in sitka spruce.

Changes in night temperature have been found in some cases to have a greater effect on tracheid dimensions than day temperature. Higher night temperatures cause a depletion of substrates by night respiration, although eventual substrate induced changes in photosynthetic efficiency would be expected to relieve this effect (Richardson 1964). High night temperatures were reported to result in an increase in lumen diameter, the effect on wall thickness however was variable (Richardson 1966). Tranquillini (1979) reports that at cooler temperatures there is an increased tendency for photosynthate to be transformed to sugar and starch rather than to cellulose. Tracheid growth (hence ring width and density) in trees growing at higher altitudes and latitudes is more succeptible to temperature fluctuations than in trees from warmer regions.

e) The effects of water deficit.

Internal water stress can affect cell dimensions either directly or indirectly (refer to diagram in section 2A). Water stress can directly affect cell expansion and wall thickening (Zahner 1968). It acts indirectly by limiting photosynthesis, transpiration and translocation, which in turn affect substrate availabilty and growth regulator balance (Denne and Dodd 1981). Doley and Leyton (1968) showed that cell expansion in the cambium of Fraxinus excelsior was very succeptible to water deficit. In conifers, cell expansion is greater in earlywood trachieds than latewood, the duration of expansion being about one week in the earlywood and three weeks in the latewood. Water deficit is likely to have the greatest effect on cell diameters in the earlywood. In Scotland, dry conditions are often most frequent in the spring and early summer (April to June).

Water deficit has been shown to affect the time of latewood initiation by the action of growth regulators (Kramer 1964). Premature dormancy may also be induced by drought in the Autumn (Whitmore and Zahner 1967). These observations suggest that water deficit has a greater effect on the total ring-width than on the density of the latewood. Water deficit is more likely to affect latewood cell dimensions via the indirect affects mentioned above. Kozlowski (1971) was unable to detect significant direct effects of precipitation on the rates and durations of expansion and wall thickening in the latewood of scots pine.

E. CONCLUSIONS.

Our knowledge of the physiology of wood formation is still inadequate and in many ways it is too incomplete to provide explanations for statistically derived relationships. The above review should however be of use in the identification of climate factors that are likely to affect growth rings.

Figures 2.2 - 2.5 summarise the findings from the above review. The processes operating to induce a climate-growth response in earlywood width, latewood width, earlywood density and latewood density are considered. The effects of meteorological data are considered since these are the only data usually available for statistical analysis.

Figure 2.2 shows the factors controlling earlywood width. Earlywood growth is closely associated with the duration of shoot elongation, which itself is controlled by growth regulators and is fairly constant in scots pine. A supply of stored reserves is important for earlywood growth since net assimilation may be negative at the time of shoot elongation. Prior autumn, winter and spring temperatures all affect stored reserves and substrate availability in the spring. Spring temperature and precipitation directly affect the durations and rates of cell production and cell expansion. Factors affecting wall thickening will also influence earlywood density (figure 2.3). Spring temperature will affect the rate of photosynthesis and hence substrate availability. The rates of wall thickening and cell production and expansion are directly influenced by spring temperature. Precipitation will influence density and width through the effect on cell expansion.

The factors controlling latewood width and density are shown in figures 2.4 and 2.5. Latewood width is affected by the duration of latewood cell production and the sizes of the cells. The sooner earlywood production commences the earlier latewood cell production will begin. An early transition to latewood production may be induced by drought in late spring. Growth regulators are important in controlling the time of latewood initiation. Warm temperatures in the autumn will allow cell production to continue into the autumn, although this may only have a minor effect on latewood width since these last few cells produced are usually small. (This has been seen on sections of P.sylvestris from Scotland). Summer precipitation and temperature will directly affect the rates of cell production and expansion in the latewood.

Latewood density (and hence the maximum density attained) will also be modified by the rate and duration of cell wall thickening. The production of thick walled cells requires a good supply of substrates to the cambium. The rate of photosynthesis will affect carbohydrate supply. Summer temperatures affect this directly, spring temperatures influence the current needle area (and it is the current needles which produce the majority of the assimilate during latewood production). Summer temperatures directly influence the rate of wall thickening. High temperatures at the end of the growing season will allow cell production and wall thickening to continue late into the autumn. Cells which were produced in late July will still be in the wall thickening stage in September, so a long growing season will allow these cells to be fully thickened. Thus autumn temperatures will affect latewood density.

Experiments on seedlings in controlled environments may be of limited use for the interpretation of growth of a whole tree. The artificial conditions imposed may cause an atypical growth response if the self-regulating mechanisms are overloaded. The effects of the environment on cambial growth are likely to be different on seedling than on mature trees since the cambium to foliage ratio may be four times as high in mature trees than in seedlings.

The response of the tree to daily changing weather conditions may be difficult to identify. The response is probably very complex and balanced by self regulating processes. The growth during the growing season may be more or less a continuum with a built in internal cycle of activity interacting with the external environment in a specific way. When environmental conditions become limiting short term fluctuations may become more important, in fact in mature trees the environment is likely to be more limiting than in juvenile trees, therefore a climate-growth response is more apparent.

There is a problem of measuring the environment around a forest tree. The forest itself will modify the conditions so that trees in a stand will have their own microclimate. The available meteorological data are usually for open conditions and are often collected some distance from the forest site. The frequency of the observations will affect the timescale of the climate-growth studies. The above review suggests that it may be necessary to identify certain threshold values of the climate parameters above or below which there is a limiting or promotion of growth. Various climate conditions may have a different effect according to the point in the growing season and seasonal changes in plant metabolism. For example it is often necessary to determine whether changes are photoperiodically induced (occurring at the same time each year) or perhaps related to accumulated environmental conditions. Cumulative climatic indices are likely to be useful in determining a climate-growth response. The internal balance of growth regulators will also modify the timing and magnitude of the environmental respones.

In the following chapters certain hypotheses are made about the climate-growth response based on the statistical evidence and the physiological research outlined in this section. The physiological evidence has been used also in the interpretation of yearly density profiles. The above review suggests that it is necessary to investigate the relationship between wall thickness, lumen diameter and density and consider how each responds seperately to climatic conditions. A preliminary study of variation in cell dimensions across the ring is made using image analysis.

Figure 2.2 Factors controlling earlywood width in *Pinus sylvestris*.

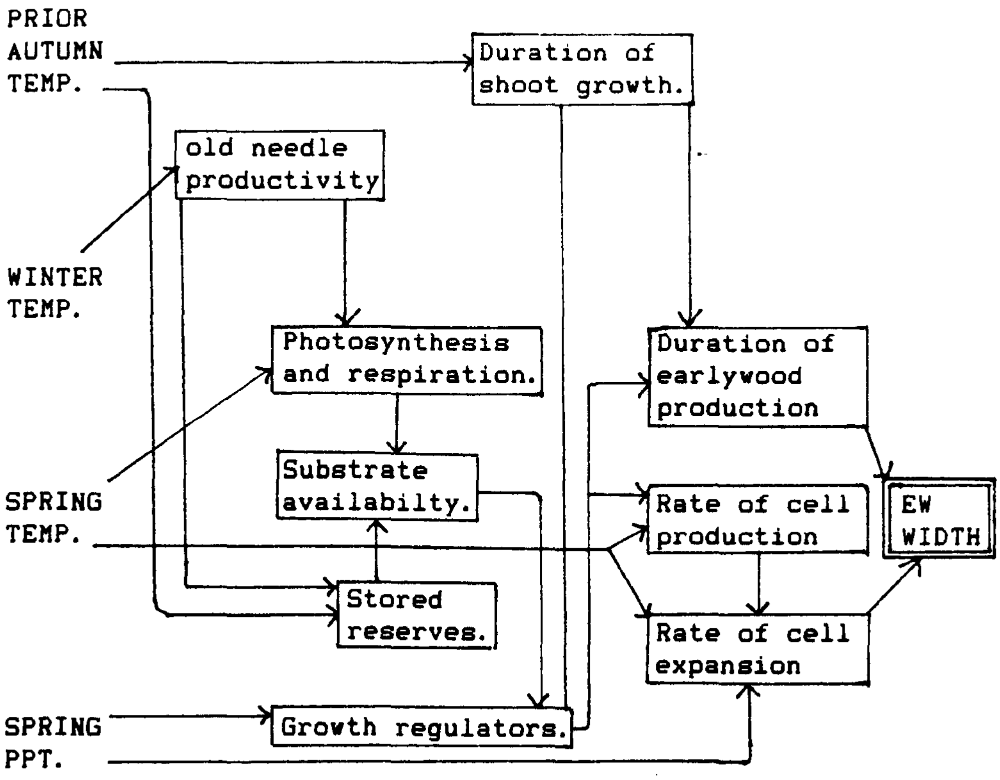


Figure 2.3 Factors controlling earlywood density in *Pinus sylvestris*

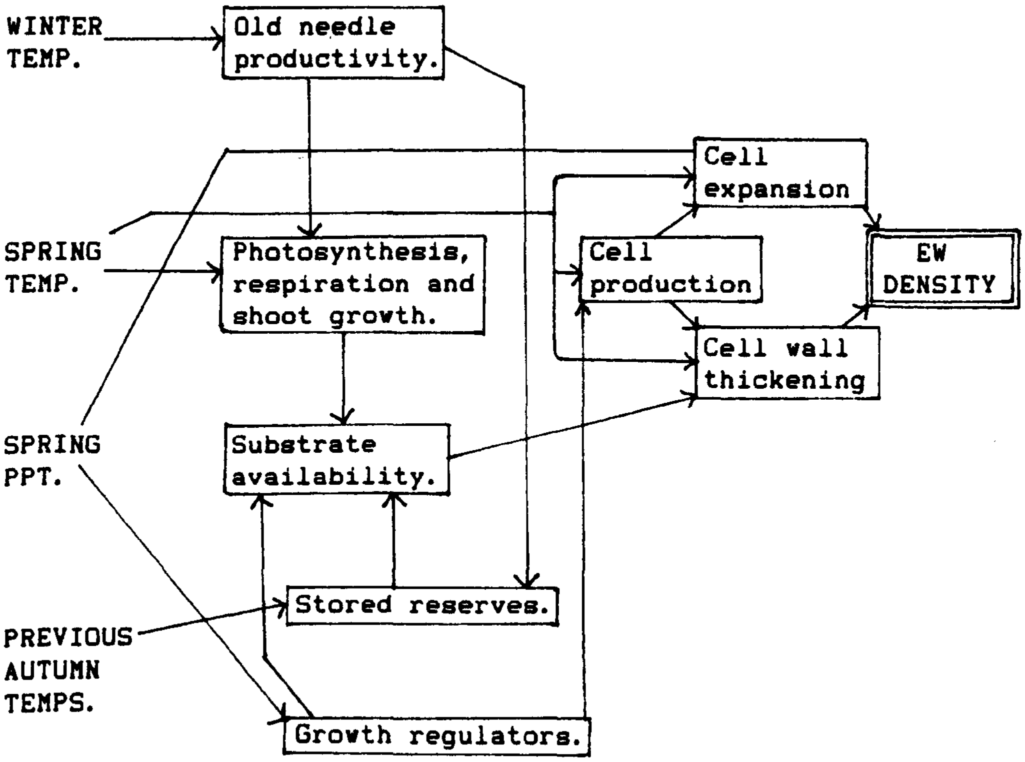


Figure 2.4 Factors controlling latewood width in *Pinus sylvestris*.

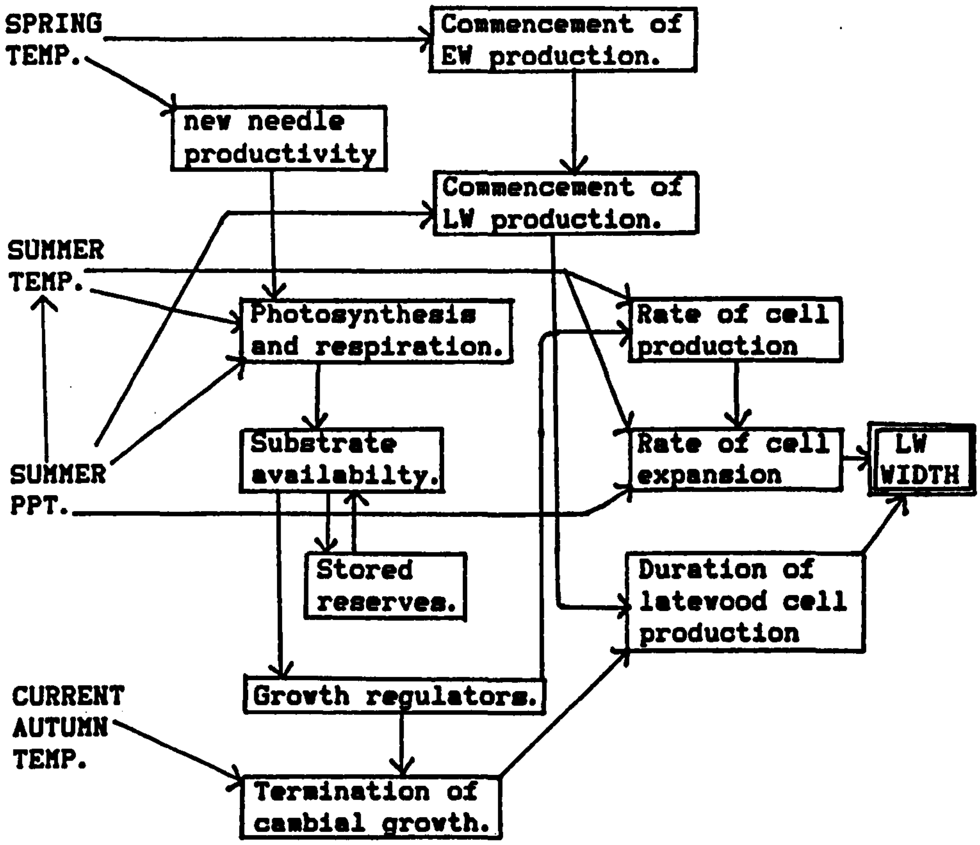
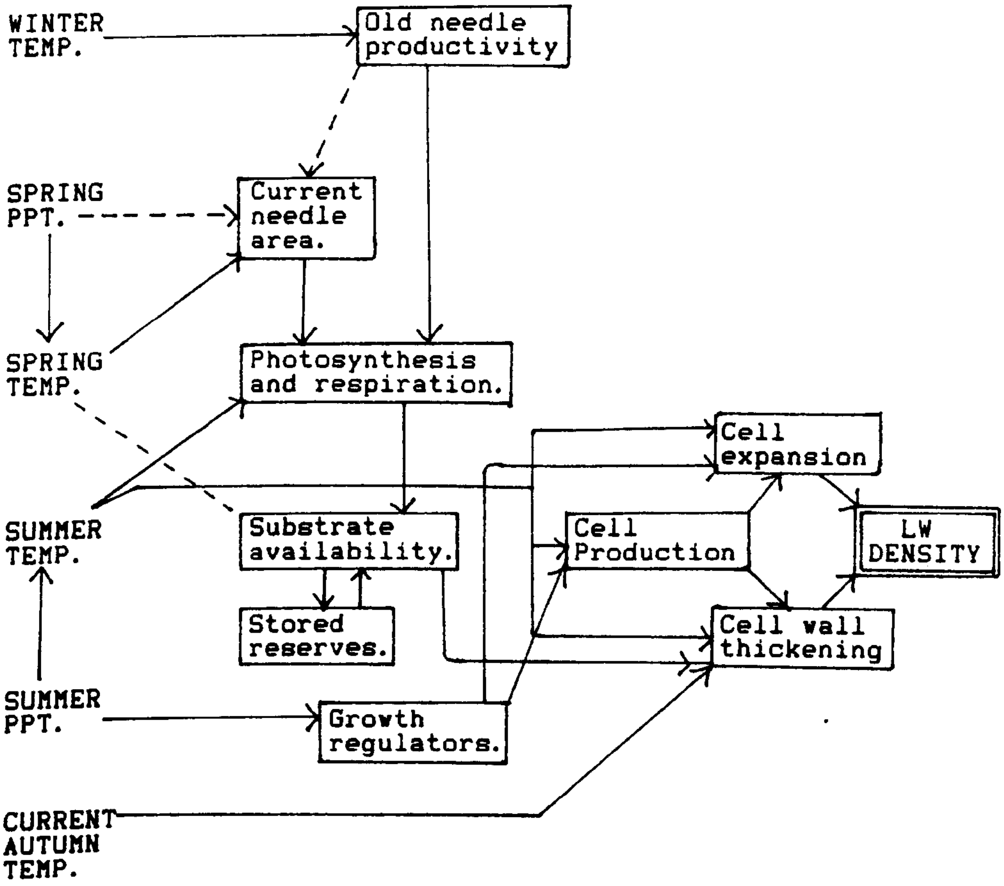


Figure 2.5

Factors controlling latewood density in *Pinus sylvestris*.



----- = minor factors.

Chapter 3. STATISTICAL PROPERTIES OF MODERN AND SUB-FOSSIL CHRONOLOGIES

A. INTRODUCTION.

In this chapter the statistical properties of chronologies from seven modern sites (five in the U.K. and two in Scandinavia) and two sub-fossil sites (in Northern Ireland) are examined. The procedures of sampling, ring-width measurement and crossdating are described here and densitometry is considered in detail in chapter 6. Five parameters of ring-width and density are considered for all chronologies; these are maximum density, minimum density, earlywood width, latewood width and ring-width. The technique of filtering the tree-ring series to produce an indexed chronology is discussed. The chronology statistics are then examined and the statistical quality of the chronologies is considered. It has been possible to compare the five density and ring-width parameters in terms of statistical quality of the chronologies. Comparisons are made between the modern chronologies from sites at different altitudes and locations. The properties of the sub-fossil chronologies are considered in relation to the modern chronologies.

The similarities between the modern chronologies have been examined by considering the correlations between sites. Principal component and correlation analyses using a further 21 P.sylvestris chronologies, mostly from Scandinavia have been undertaken to investigate spatial similarities between ring-width chronologies from northwest Europe.

The aims can be outlined as follows;

1) To consider the statistical quality of chronologies based on ring-width and density parameters.
2) To compare the properties of chronologies from different locations and altitudes.
3) To determine if the Irish sub-fossil chronologies resemble those from modern sites.
4) To consider the spatial relationships between modern chronologies in northwest Europe.

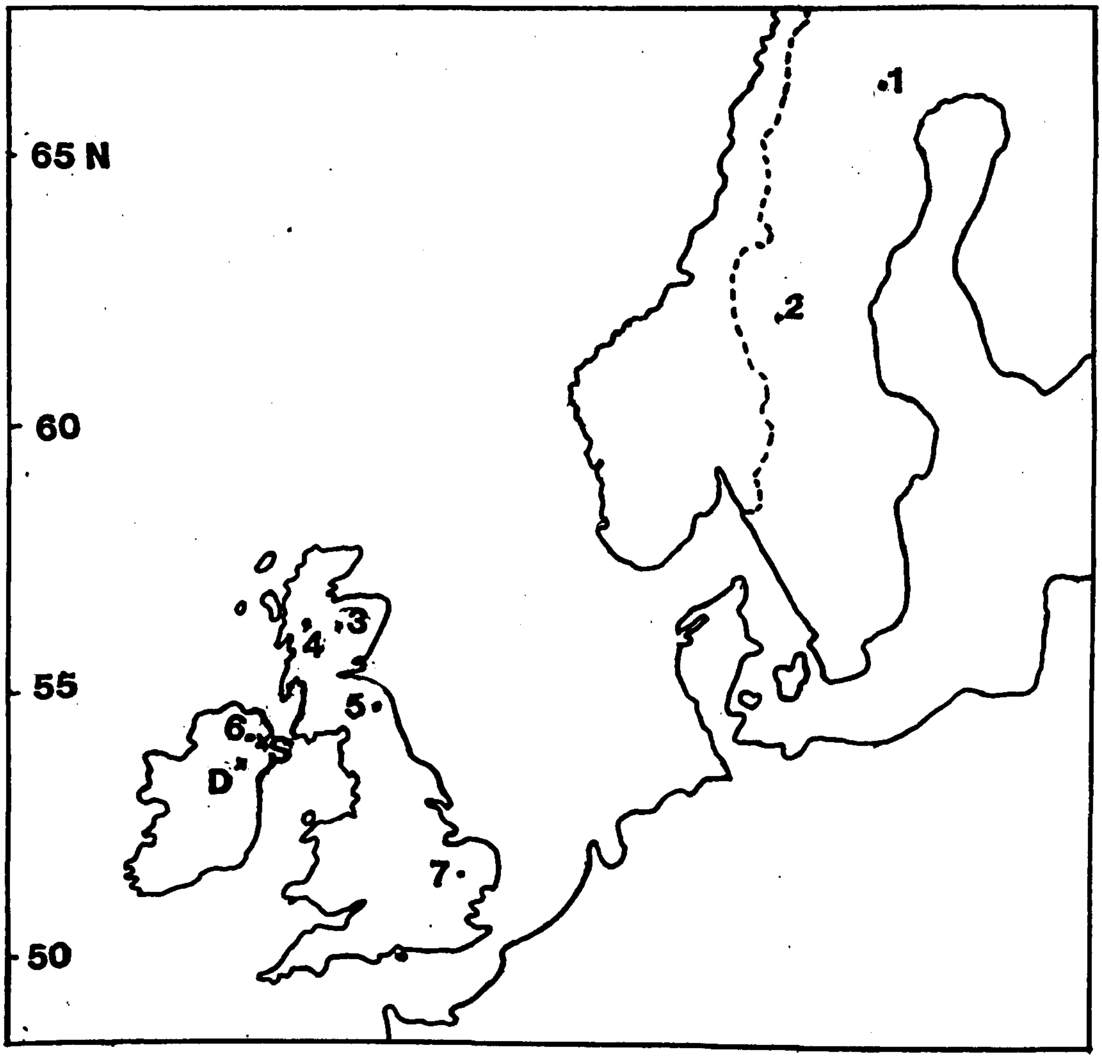
Map 3.1

Location of U.K. and Scandinavian sites.

1. Ö Frostsjoasen.
2. Muddus
3. Glen Derry
4. Glen Affric
5. Kielder
6. Randalsown
7. Chippenham fen

Sub-fossil sites.

S. Sluggan
D. Derrycrow


65 N
60
55
50
1
2
3
4
5
6
7
S
D

B. CHRONOLOGY CONSTRUCTION.

a) Site description.

Map 3.1 shows the location of both the modern and sub-fossil sites described in this chapter. Full site descriptions are given in Appendix 1.

Chapter 5 gives details of the collection and occurrence of sub-fossil material. The two subfossil chronologies described are both from Northern Ireland. A modern site at Randalstown in Northern Ireland was chosen as a peat site at a low altitude (50m a.s.l.), with growing conditions which could be analogous to those existing at the time of growth on the sub-fossil sites. There are no living P.sylvestris trees on the raised bogs at Sluggan or Derrycrow. Indeed, scots pines growing on peat in this area are rare. The location at Randalstown was far from ideal. The trees were up to 150 years old, they had all been subjected to periods of considerable growth stress and disturbance, such that there were sections of very narrow rings and compression wood was present in most of the trees.

The site in Scotland at Glen Derry was chosen to represent the altitudinal limit of the range of P.sylvestris (390-550m a.s.l.). The effect of climate (notably temperature) on growth here is likely to be marked although the climatic factors affecting growth in these conditions may be different from those operating at lower altitudes (Fritts 1976). Glen Affric, the other Scottish site, was chosen as a slightly lower altitude (180-450m a.s.l.), more maritime location (being closer to the west coast), where climate is expected to be slightly less limiting to growth. Chandler and Gregory (1976) demonstrate that the degree of continentality increases markedly as one progresses from the west coast of Scotland to the Grampian mountains. Continentality is calculated from the Continentality Index devised by Conrad (1946) which is based on annual temperature range and latitude. The trees here are growing more vigorously than those at Glen Derry. Previous work on P.sylvestris in Scotland (Hughes 1986) has examined the climate growth response in P. sylvestris on eight sites ranging from high altitude treeline sites analagous to Glen Derry to maritime locations on the West coast. Glen Affric represents an intermediate between these two extremes. On both sites the trees have been selected from remnants of the native pine forests, described by Steven and Carlisle (1959). The trees are growing on impoverished, peaty soils where sub-fossil pine remnants are also to be found. The altitudinal limit of the sub-fossil trees however was higher than the present treeline (Pears 1968).

Chippenham fen is a low altitude peat site in eastern England (15m a.s.l.). There are ecological differences in the nature of a fenland peat site compared with upland peat. Chippenham fen has undergone several changes in water level in the past 50 years due to different drainage schemes, although the exact history of these changes is not known. It was of interest to consider how the growth characteristics and the climate-growth response of these trees compared with those of trees from the low level peat bog site at Randalstown in Northern Ireland. Kielder Castle is located in a central position relative to the other British sites at a moderate altitude (200m a.s.l.).

Two Scandinavian sites have been selected to allow results from the British chronologies to be considered in a European context. Ring-width data from a large number of Scandinavian sites is available. These two sites were chosen because density data was also available. They represent latitudinal and altitudinal limits of the range of P. sylvestris. Muddus is situated in northern Sweden near to the northern limit of P.sylvestris (latitude 66°51 N, 450m a.s.l.). O Frostsjoasen is in central Sweden (latitude 62°19 N) at an altitude of 800m a.s.l. Both sites are at high altitudes relative to their latitudes.

b) Sampling.

A standard procedure was adopted for collecting sample material. Collection of cores was carried out by the author at Glen Affric, Glen Derry and Randalstown. Similar procedures were adopted for sampling at the remaining sites. The trees are selected as a representative sample of the dominant trees at each site where this is possible, avoiding obvious damage due to lightning, fire and other sources. In the European situation, it is generally accepted that only trees of the same social status should be grouped into a site chronology (Schweingruber 1986).

Fifteen trees from each site were selected. At Randalstown all the healthy, standing trees were cored, the limited area of the stand eliminated the possibility of tree selection. In the Scottish woodlands large diameter, dominant trees from the less dense parts of the stand were chosen. Two cores were taken from each tree with a 5mm increment borer, preferably from opposite sides of the tree. When coring at least two cores are taken from each tree. It is advisable to take more than one core to increase the chances of reaching the pith and finding an undistorted radius. A minimum number of cores is taken to avoid unnecessary risk to the health of tree. It is also more profitable in terms of producing the longest, and most robust chronology to take two cores from a good number of trees rather than three from fewer trees (Schweingruber 1986). The cores are taken at breast height (1.3m), to minimise individual tree variability, and parallel to the line of the slope to avoid compression wood (see plate 3.1). On valuable trees or where there is a risk of infection, the holes are filled with Arbrex pruning compound and plugged with short lengths of dowel. The cores are removed and placed in labelled corrugated cardboard containers. This absorbs some of the moisture and resin but does not allow the cores to dry out completely or the resin to set hard. Information recorded at each site included: date, latitude and longitude, height above sea level, collector's name, species and number of trees and cores, broad category of ground vegetaton type, soil type, stand density, degree of slope and aspect.

c) Ring-width measurement.

The initial cross-dating of cores and stumps is based on ring-width measurement. Sample preparation involves sanding and polishing the surface of the section so that the cell structure is visible and the rings can be seen clearly. On cross sections a belt sander is used, with progressively finer sandpaper. The final surface is achieved by rubbing with brown paper. With increment cores, sanding of the radial surface is carried out by hand with fine sandpaper, to avoid the risk of breaking the delicate material. Cores are usually mounted on wooden blocks for ring-width measuring (with the transverse surface uppermost). When density is to be measured later, the cores will need to be mounted at right angles to this, with the longitudinal side at the top, hence in this case ring-width measurement is done on unmounted cores. To avoid unnecessary mistakes, the wood is marked with a dot on every tenth ring before ring-width measurement.

The ring-width measuring system uses a Bannister incremental measuring machine connected directly to an Apple IIe microcomputer (plate 3.2). The wood is placed on a table moved by a hand-driven precision screw. This is linked to an optical shaft encoder whose digital output is converted to a record of lateral movement accurate to 0.01mm. This in turn is connected to the Apple IIe computer. The wood is viewed through a binocular microscope and held in place with the ring boundaries perpendicular to the line of movement of the table. The start of the first ring is aligned with the eyepiece cross hairs and the table is moved along by a hand operated screw to the beginning of the next ring. The computer is then given the appropriate instruction to record a ring and the digital signal from the encoder is recorded. The procedure is repeated for each ring. In all cases one proceeds from the pith to the bark. The appropriate software is available to store, edit and manipulate the tree ring data.

Three or more radii are measured on cross-sections of sub-fossil pine, to help deal with the within tree variation in ring width due to the influence of root butresses extending up the stem. It is generally possible to choose the three radii where there is the least distortion in growth. Both cores are measured if there are 2 from each tree.

d) <u>Initial crossdating procedure.</u>

Once cores or radii have been measured, plots of the ring-width data are printed out. Plate 3.3 shows the relationship between the wood structure and the graphical computer plots. After confirmation of crossdating between cores from the same tree (by graphical and statistical methods) the means of the two or three radii from each tree are calculated, as a simple unstandardised average of the values for each year. Crossdating of the trees is based partly on visual comparison of the graphs. By superimposing the plots on a light table, any obvious false or missing rings can be identified at this early stage. A crossdating programme based on the programme CROS written by Baillie and Pilcher (1973) is used as a basis for statistical crossdating. The programme calculates the correlation coefficient (r) at each position of overlap between two tree-ring series (yi.. and xi..).

The correlation coefficient (r) is defined as;

$$r = \frac{\sum^{n} x_i y_i - N\bar{x}\bar{y}}{(x_i^2 - N\bar{x}^2)(y_i^2 - N\bar{y}^2)^{1/2}} \qquad 3....1$$

This coefficient takes into account the yearly variation in ring width but not the length of overlap. Student 't' values can be calculated from r.

$$t = \frac{r(N-2)^{1/2}}{(1-r^2)^{1/2}} \qquad 3....2$$

Where N is the number of years of overlap between the two series. Values of 't' can be obtained from tables to test for significance. Litton (unpublished data) has run simulated crossdatings on 30,000 replications to determine the significance of ring-width 't' values.

The 't' values which might occur by chance with the probabilities shown are given below for series with different lengths of overlap.

Table 3.1.

T-value at given minimum number of years overlap.			Probability of t occuring by chance at given overlap.
150	100	50	
3.6	4.0	4.1	0.01
4.3	4.5	4.8	0.001
4.9	5.0	5.2	0.0001

Computer crossdating is performed between the individual tree series from each site. The programme CROS (Baillie and Pilcher 1973) has been used in this study. Any 't' values above 3.5 are printed on the computer screen along with the period of overlap. Significant crossdating is determined by reference to the above table at the given period of overlap. The positions of overlap on significantly crossdated trees are compared, to look for any inconsistencies in the matching. A group of three or more trees which mutually cross match is then made into a 'working master chronology', by taking the mean for each year of the overlapping series. This will enhance any crossdateable (probably climatic) signal in the data and will usually give significant 't' values for comparisons between any other contemporaneous trees on the same site. Once all potentially matching trees have been identified and any inconsistencies eliminated, a site mean master chronology is constructed.

Before a 'working master chronology' or a site mean is produced, the individual series are standardised. The aim of this is to remove long term trends in the data such as those related to the age of the tree. Indexing then converts the data to a series with a mean of one. Each data set is therefore given the same weight during averaging. The programme used here fits a straight line through each ring-width series to standardise the data. Further discussion of standardisation procedures is given in section C of this chapter. In subsequent work a more sophisticated indexing procedure is adopted. The crossdated ring-width series produced here are used for dating and checking the densitometry data (which includes ring-width measurements).

e) <u>Densitometry and data preparation.</u>

Density measurement is carried out by the method of x-ray densitometry on thin sections cut from mounted cores. The procedure is described in detail in chapter 6, part B. Density measurement from x-ray negatives records the maximum density (MXD), minimum density (MIN), earlywood width (EW) and latewood width (LW) for each ring (total ring-width (RW) can be calculated). There is inevitably some loss of material in the process of preparation of the wood for densitometric measurement. The wood is apt to break up on cutting, very narrow rings or poor quality wood (such as compression wood) cannot be used. Densitometry readings are recorded directly onto computer disc with the four readings for each ring stored as 4 columns in the file. Dating of the densitometry data is done by matching the ring-width measurements from densitometry with the original crossdated ring-width series obtained from measurements on the incremental measuring machine. In this way any missing rings or anomalies in the densitometry data can be identified. Further checking may be carried out by crossdating the series using the MXD values (on some sites MXD gives consistently higher values for correlation between trees than does RW).

The dated densitometry data are transferred from Apple disc to a mainframe DEC20 computer using a special transfer program. Using the Fortran program PREP, the files containing four columns of data are read into five separate files, one for each parameter (MXD, MIN, EW, LW and RW), the data are thus arranged in labelled decades with one decade per line, in the standard TUCSON format (Campbell and Drew 1973).

Plate 3.1

Sampling at Glen Affric

Plate 3.2

Ring-width measuring system.

- A. Apple II computer.
- B. Digital display unit.
- C. Binocular microscope.
- D. Wood specimen.
- E. Moving stage.
- F. Operating handle.

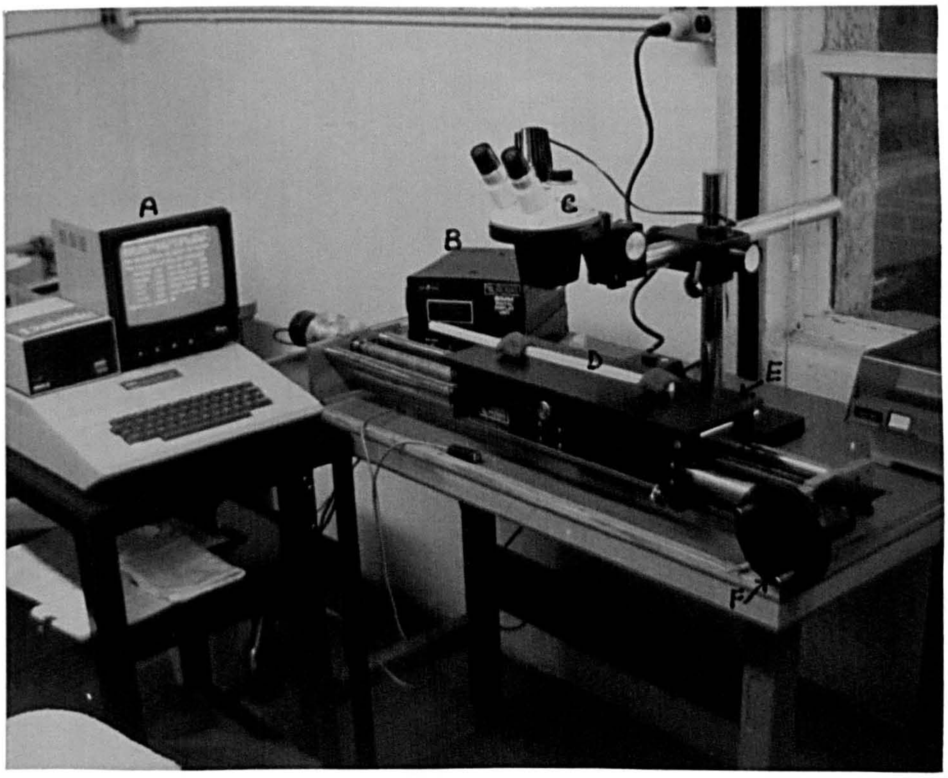
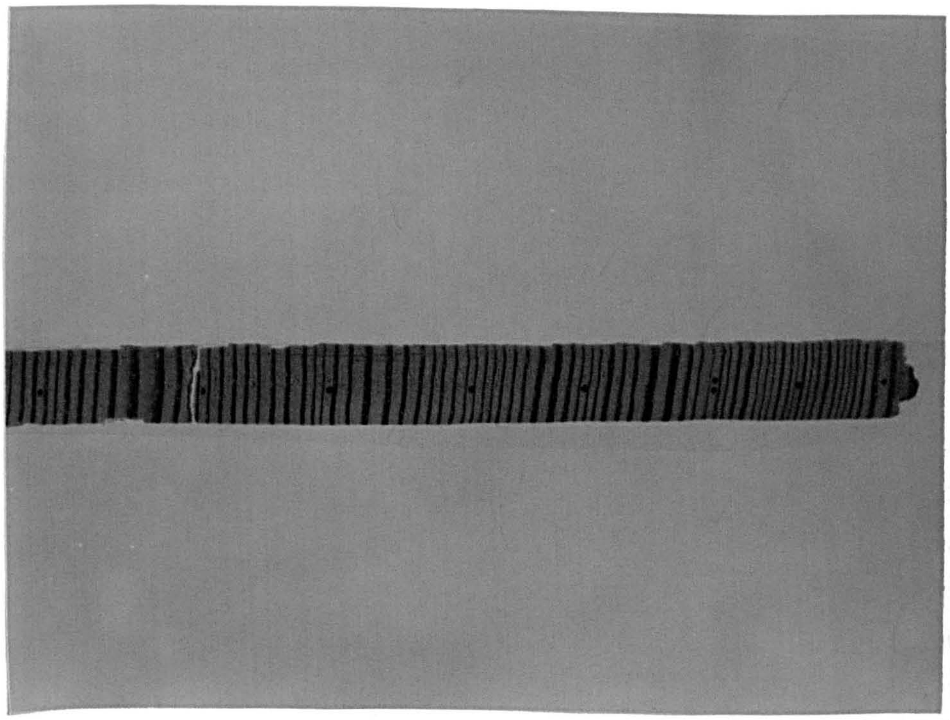
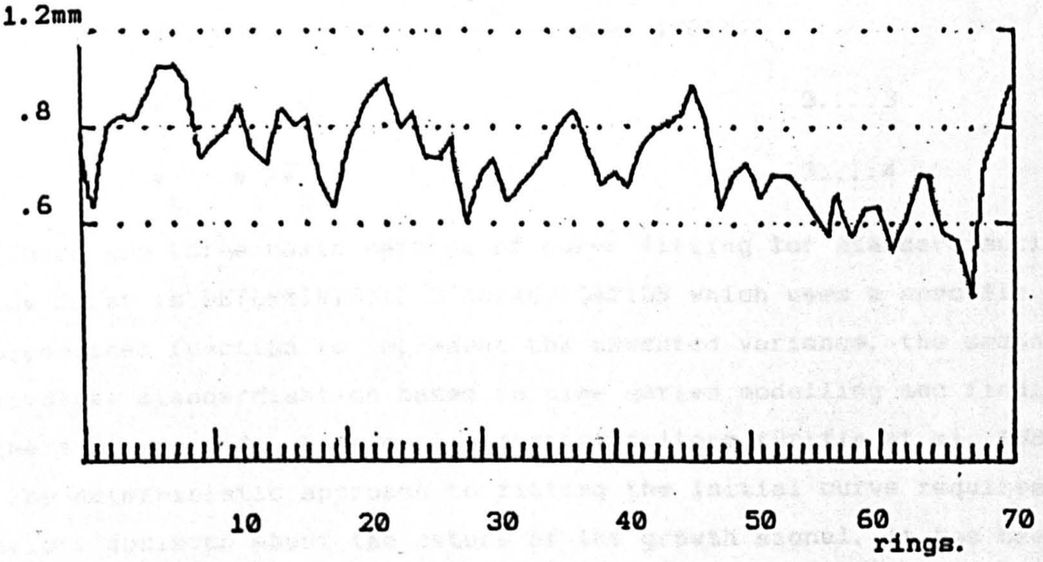

A
B
C
D
E
F

Plate 3.3

Illustration of ring-width measurement. Wood sample and ring-width plot.

Tree Q382, Derrycrow.




1.2mm
.8
.6
10
20
30
40
50
60
70
rings.

C. PROPERTIES OF INDEXED SERIES.

a) Indexing Methods.

The program FSTAND developed at University of East Anglia by K.R. Briffa has been used in the analysis of the crossdated series and the subsequent production of mean indexed chronologies. The individual tree series are standardised by means of a digital filtering technique employing Gaussian filters. A full description of the development of the program is given in Briffa (1984), and it is discussed further in Briffa et al. (1986b).

STANDARDISATION of tree-ring series is necessary in order to enhance the desired part of the variance of the data (in this case the climatic information). The 'signal' is defined as the part of the variance associated with climate. All other parts of the variance are determined to be 'noise'. In this case noise is associated with growth influences such as those due to ageing, pollution, long-term cycles caused by water table fluctuations and competition factors affecting individual trees. Standardisation to produce an indexed chronology takes place in two stages; firstly a mathematical function is fitted to the data to remove the unwanted part of the variance, then the tree-ring series are normalised to ensure that the mean and variance of the individual series are comparable. To produce a homoscedastic series (one in which the variance is constant along the length of the series) from density data it is usually sufficient to subtract the fitted value from the raw value (equation 3....3). With ring-width measurements, variability is usually greater in wider rings therefore to produce a homoscedastic series the quotient of the raw and the fitted value must be taken (equation 3....4), (Briffa 198~~0~~4, Braeker 1981).

$$w_t = w_t - \bar{w}_t \qquad 3....3$$

$$w_t = w_t / \bar{w}_t \qquad 3....4$$

There are three basic methods of curve fitting for standardisation. The first is DETERMINISTIC STANDARDISATION which uses a specific predefined function to represent the unwanted variance, the second involves standardisation based on time series modelling and finally there are methods which employ digital filters (Briffa et al. 1986b).

The deterministic approach to fitting the initial curve requires an a priori decision about the nature of the growth signal. It has been used successfully in the program INDEXA which fits a negative exponential to the data (Fritts et al. 1969) and in later versions, with the option of fitting an orthogonal polynomial. Braeker (1981) examines the age-trends in earlywood width, latewood width, ring-width and maximum and minimum densities seperately. He found that negative exponential curves gave good approximations to the age-trends for the width parameters. Trends in density parameters could usually be approximated by straight lines, except on extreme sites (such as xerothermic and alpine sites) where maximum density is correlated with latewood width and shows a similar negative exponential trend. There are several disadvantages of the deterministic method. Using a mathematical function may be unnecessarily restrictive in that the curve may not be truly representative of the unwanted variance pattern. Medium frequency noise may be removed in some parts of the series but retained in others. The degree of fit at any one point on the curve may be influenced by data far removed from it.

TIME SERIES MODELLING overcomes many of these problems by using an autoregressive and/or moving average process. There is some physiological justification for this method since the lag effects of the internal physiological factors controlling growth are relatively short term (Briffa 1984). It is however difficult to separate the internal physiological causes of autoregression from the low frequency variation due to external influences on the whole stand. The time series coefficients also tend to be unstable in time. Time series or ARMA models are described by Cook (1986), Guiot (1987) and Meko (1981).

DIGITAL FILTERING methods provide a still more flexible approach. A time series is characterised by the amount of the total variance attributed to different frequency bands; its variance spectrum. Different parts of the spectrum of the ring-width or density series may be attributed to different causal factors. The filters can be designed to remove different parts of the variabilty from the tree-ring series according to their spectral characteristics. Digital filters have been used in several instances in the standardisation of coniferous trees (Parker 1971, Hughes et al. 1978 for oaks, Parker et al. 1981, Blasing et al. 1983). The characteristics of a filtered series are generally consistent and there is good control of the nature of the series produced. The disadvantage however is that it is often difficult to determine whether climatic information is being removed on filtering.

The program FSTAND uses the method of digital time series filtering. The individual tree ring series are standardised using a Gaussian filter, this is a set of weights applied to each term in the time series in the form of a moving average. The GAUSSIAN FILTER is a mathematically described frequency response function with a particular wavelength or period. The filter can be controlled to remove specific frequencies of variation in the time series. Further discussion on filters is given in Mitchell et al. (1966) and Briffa (1984).

The filter used in this work is chosen to remove a total of 25 percent of the variance of the series. The amplitude of the filter period is chosen in such a way as to remove as much of the non-climatic variation as possible without a significant loss of climatic information. When the mean correlation coefficient (r) between filtered series is computed for different filter amplitudes, it is found that the correlation between series generally increases with decreasing filter length at the higher altitude sites (table 3.2).

Table 3.2

Effect of using different filter lengths in standardisation on the mean correlation between trees.

	MXD			RW		
FILTER LENGTH	10	30	50	10	30	50
UFR	51	50	49	48	39	37
MUD	49	47	47	35	31	29
DER	46	43	41	21	23	20
AFF	41	36	30	27	23	22
KIE	43	41	39	15	18	23

Values are for r x 100. (Lengths of series are given in table 3.5).

The correlation between trees is improved as the filter length is shortened, due to the removal of non-climatic variation (such as age trends) in the individual trees. If too short a filter length is used, short and medium wavelength climatic information may be lost. There is also the danger that arbitary non-existent trends may be imposed on the data at too short a filter length. Briffa (1984) examines the variance spectra of several species including P. sylvestris and uses a filter length of 30 years with Quercus sp. from the Forest of Dean, and a 60-year filter for P. sylvestris ring-widths and densities from Finland and Norway. Briffa et al. (1987) again use a 60-year filter when reconstructing summer temperatures in northern Fennoscandinavia from P. sylvestris ring-width data. These data have a common period of 270 years and the growth characteristics of these trees differ from those of the more diverse oceanic and moderate altitude sites in Britain. Examination of the effect of filter length on the correlation coefficient between trees for the British and Scandinavian sites used in this analysis would suggest that a 30-year filter length is more applicable. The relatively short lengths of the tree-ring series (100 to 215 years of common overlap) does not allow long wavelength filters to be used (Briffa 1984). The 30-year filter permits the removal of medium term non-climatic variation due to factors such as water table fluctuations and the effects of competition and release on individual trees. The 30-year Gaussian filter is used on all variables. Where there are high correlations between the tree-ring variables as with this data, it is suggested that similar filters ought to be used on all variables (Braeker 1981).

The proportion of the variance of different period lengths in the data series removed by standardisation with the 30-year Gaussian filter is shown below. Most of the variance with a period greater than 60 years is removed, a decreasing amount of the shorter wavelength variation is removed.

Table 3.3

Period Band (Years)	Variance removed (%)
1-10	0
11-20	2.0
21-30	23.0
31-40	47.6
41-50	64.0
51-60	74.0
61-70	81.0
71-80	84.6
81-90	88.4
91-100	90.3
101-120	92.2

The effect of filtering is seen in the plots of raw and filtered series in figure 3.1.

Standardised tree-ring series are produced from the individual cores either by taking the quotient or by subtracting the raw value from the fitted value. The choice of method is dependant on the characteristics of the tree ring series. In the case of ring-width series the variance tends to be greater when the rings are wide, hence it is preferable to divide the raw value by the value on the fitted curve. Density data tend to be homoscedastic, hence it is better to subtract the raw from the fitted value. The program was run for each of the parameters using both methods and the mean correlation between trees was examined. Although the differences were not great (in the order of 2.0 to 5.0%) it was found that best results were obtained using subtraction for maximum and minimum densities and by taking tha quotient for the ring-width parameters. Each series is then given an equal weighting by being normalised to a mean of 1000 and a standard deviation of 200 units. The individual indexed series are then simply averaged to produce a site master chronology.

Table 3.4 gives the statistics from the correlation analysis for nine sites from Britain and Scandinavia (including the two Irish sub-fossil sites), using five parameters of tree ring measurement (MXD, MIN, EW, LW and RW). The correlation coefficient (r) is calculated as in equation 3....1,. The mean correlation coefficient ($\bar{r}$) of the comparisons between all series is given. The significance of $\bar{r}$ is dependant on the periods of overlap of the individual series. The mean significance has been computed here from the significances of the individual correlations between series.

FSTAND conducts a correlation analysis between the individual indexed series, giving the correlation coefficients, t-values and their significance between series, both for the maximum individual overlaps between trees and the maximum common period of overlap. An analysis of the master chronology yields values for mean sensitivity and autocorrelations for lags of 1 to 4 years, as well as checks on standard error and skewness.

The significance of the correlation coefficient indicates the strength of the common signal between indexed series and can be used to indicate the potential amount of climatic information in the mean chronology. If only one parameter was being considered, non-significant crossdating between series might suggest that there were missing rings or that the trees were not contemporaneous. In this case the positions of overlap have been confirmed by at least one parameter. Mean chronologies have been produced for all parameters at each site.

The results of the correlation analysis (table 3.4) indicate that MXD gives highly significant correlation between trees on the two Scottish sites, the moderate altitude site at Kielder and the Scandinavian sites. Moderate to high correlation is obtained between the Irish sub-fossil trees. No significant correlation is obtained from the low altitude sites at Randalstown and Chippenham for MXD. RW gives high correlations for the sub-fossil and modern Scandinavian trees, but more moderate correlations at the other sites, with Kielder yielding the least significant RW correlation. LW gives a more significant correlation than EW for the Scottish and the low altitude sites, but the converse is true for the Scandinavian sites. In only two cases is there any significant correlation using MIN, that is for Derrycrow (sub-fossil), and O Frostsjoasen (Scandinavian).

Together with the correlation coefficient, both the number of cores and their overlap periods are important for assessing the potential usefulness of data sets.

b) Statistical quality of chronologies.

The success of standardisation can only be judged in terms of what is known or the assumptions made, about the actual population signal. The climatic signal that we are searching for is termed the 'expected' signal as opposed to the assumed expression of this signal obtained from the chronology, the 'observed' signal. If the observed signal is assumed to be a faithful representation of the expected signal then the signal to noise ratio (SNR) could be used to assess the strength of the climate signal (Cropper, in Hughes et al. 1982).

Thus;

$$SNR = N\bar{r} / (1-\bar{r}) \qquad 3....5$$

Where $\bar{r}$ is the mean correlation between all pairs of cores, calculated on the basis of the maximum period of overlap between any two cores. N is the number of cores.

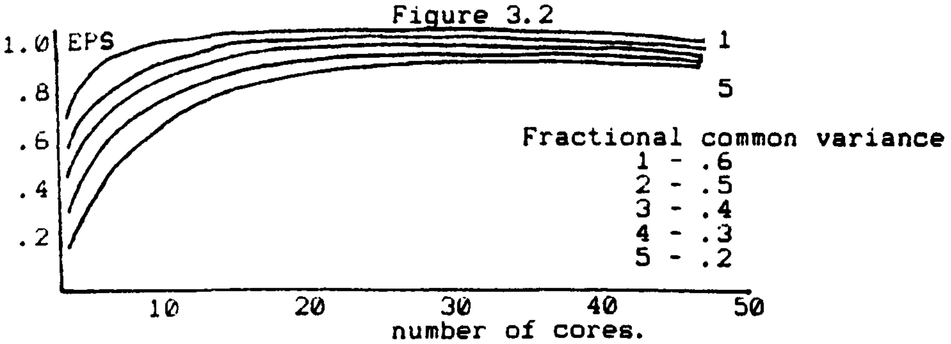
The statistical quality of a mean chronology can also be defined in terms of the Expressed Population Signal (EPS). This describes the fraction of the 'observed' chronology variance that is expressed in a chronology containing n samples. This is given by

$$EPS(n) = n\bar{r} / (1 + (n-1)\bar{r}) \qquad 3....6$$

(Briffa 1984, Wigley et al. 1984b).

The value of n is not constant throughout the time series since the cores do not all overlap entirely. EPS rises asymptotically towards 1 as n tends to infinity. When the mean correlation between series (r) is low, a large number of cores are needed to produce an improvement in EPS. Figure 3.2 (below) shows how EPS varies with the number of cores, for different amounts of common variance between cores, assuming one core per tree. The actual value of EPS is affected by the number of cores, the amount of common variance between cores and the filter length chosen.

Figure 3.2



The EPS plotted against number of cores (one/tree) for several values of fractional common variance. (After Briffa 1984).

A similar statistic which quantifies how well a part of a chronology containing only n series reflects the signal expressed by the part of the chronology containing all (N) series is the Subsample Signal Strength (SSS), (Wigley et al. 1984). This statistic is useful for assessing the quality of the early part of a chronology, which may only contain a few cores. It is defined as

$$SSS = \frac{n(1 + (N-1)\bar{r})}{N(1 + (n-1)\bar{r})} \qquad 3....7$$

FSTAND gives both EPS and SSS for values of n from 1 to 30.

The statistical quality of a chronology can thus be assessed in terms of the number of cores needed (using EPS) or the period where adequate samples are present (using SSS). What is acceptable in terms of an adequate 'observed' signal (EPS) will depend on how the data is to be utilised. Briffa (1984) considers how EPS is related to other statistics of chronology quality previously used to determine chronology acceptability (such as signal to noise ratio). An EPS of .85 is suggested if climatic reconstruction is to be carried out, as this is equivalent to a 50-60% common variance in the chronology. The greater the number of cores the larger the EPS and the greater the percentage of common variance. It may be necessary therefore to obtain more cores from a site if EPS values are too low.

Table 3.4 gives EPS values for the chronologies for each variable at each site. The expected EPS if ten trees had been used (EPS10) is also given along with the number of trees that would be needed to give an EPS of .85. The highest values for EPS10 are for MXD at Kielder and O Frostsjoasen, MXD also gives the most favourable results at Glen Derry and Muddus. LW is generally better than EW, with a very marked difference at Glen Affric, the exceptions here being Kielder, Muddus and Derrycrow where EW is marginally better than LW. The common population signal on the low level sites (Randalstown, Chippenham, Sluggan and Derrycrow) is stronger in the RW than the MXD series. O Frostsjoasen produces the most reliable figures for MIN, but even here an extra three trees would be needed to yield a chronology suitable for climatic reconstruction using the criterion of an EPS of .85.

The effects on the mean chronology of standardising the individual series with different filters can be monitored by examining the EPS values. Where EPS is low in unfiltered chronologies, filtering is found to improve the EPS considerably, although it has a smaller effect when EPS is initially high (Briffa 1984). Tests on the effect on the EPS of using different filter lengths have been carried out by Briffa (1984), testing chronologies from ten oak sites in southern England. Five of the chronologies exhibited increased statistical signal as the filter length was decreased, (indicating a high amount of low frequency variation), the remainder showed a peak in signal (as measured by EPS) at around a 30-year filter length. The conclusion was that a 30-year filter length is the most reasonable choice in this situation.

The success of standardisation using the Gaussian filter may depend on the characteristics of the frequency distribution of the population signal. EPS and SSS can confidently be used to assess the strength of the higher frequency signals in the chronology, but the strength of low frequency signals is harder to estimate (Briffa et al. 1987). This is because the variances of the individual r values tend to be higher for low frequency signals. In this study the high frequency, direct climatic response is considered since the series are too short to reliably represent low frequency responses. High frequency responses may be due to the direct response of the tree to climate (physiological study predicts a lag of not more than four year). Low frequency responses may for example be due to long term climatic trends, the effects of pollution and changes in the site conditions.

The effect on EPS of using 10-, 30- and 50-year filters has been examined for all nine sites for both RW and MXD chronologies (figure 3.3). The EPS values show a small decrease with increasing filter length, except for the two sub-fossil sites where EPS increases. This would suggest that there is a large amount of low frequency variation in the sub-fossil chronologies. As filter length is increased, less of the low frequency information is removed. The series are not of sufficient length for information on low frequency variation to be valid. These data confirm the choice of a 30-year filter length for both ring-width and density parameters. The anomalous case of the sub-fossil chronologies indicates that they exhibit quite a different frequency pattern to the modern chronologies. This may be due to the fact that the trees are strongly influenced by low and medium frequency (30-100 year cycles), which may be due to fluctuations in the water table. This is supported by evidence from the wood structure and information about the growing conditions derived from other site factors (this is further discussed in chapter 5).

These parameters EPS and SSS only relate to the statistical quality of the chronology. They do not assess the amount of regional climate information contained within it. Assessing chronology quality by means of the EPS may in fact be preferable to using a direct comparison between climate variables and chronology variance since the exact pattern of the climate response is unlikely to be truly represented by crude climate data. Conversely, other site specific and non-climatic agencies may also be contributing to the common variation in the tree-ring series.

c) Chronology statistics.

The properties of indexed chronologies can be summarised using several standard statistics. Detailed discussion of statistical properties of chronologies and the calculation and interpretation of chronology statistics is given in Fritts (1976).

Table 3.5 summarises the chronology statistics obtained from the FSTAND program for the five tree-ring parameters, on all 9 sites.

MEAN SENSITIVITY was originally used by Douglass (1936) where it was found to be particularly useful for examining the potential signal in drought sensitive Pinus ponderosa. It measures the relative difference in value of the tree ring index from one year to the next. It ranges from zero where there is no difference, to 2.0 when a zero is always next to a non-zero value. Low values indicate complacent tree-ring series, higher values may indicate a strong common signal. The average mean sensitivity is calculated as follows;

$$ms_x = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right| \qquad 3....8$$

where x_t and x_{t+1} are adjacent ring indices.

The values of mean sensitivity in table 3.5 are for filtered series of the individual trees. The figures are computed from the mean of all values from the trees included in the final chronology. Mean sensitivities have previously been calcuated for seven P.sylvestris chronologies in Scotland (Hughes 1987). In the unstandardised series these range from 0.12 to 0.16 for ring-width chronologies and 0.03 to 0.08 for maximum density chronologies. Because mean sensitivity only assesses the high frequency portion of the variation it is affected by the method of standardisation. Using a 30-year Gaussian filter on the MXD data from Kielder, mean sensitivity is increased from an average of .10 in the raw data to .24 in the filtered series. A similar effect is found in all the modern MXD chronologies apart from Randalstown. In the RW series there is a slight decrease in mean sensitivity on filtering. There is a small decrease in mean sensitivity when individual filtered series are averaged to give a mean chronology, thus it will be to some extent dependant on the number of trees included in the mean. Mean sensitivity will be affected in part by the autocorrelation between one year and the next.

MXD is the parameter with the highest mean sensitivity after filtering, and thus perhaps the most suitable for climatic reconstruction. LW is likewise more sensitive than EW or RW. Mean sensitivity of the individual series does not indicate how reliable a chronology is, since it is only considering the nature of the variation in the data, which could correspond to asynchronous fluctuations which do not crossdate. Mean sensitivity can provide an assessment of data quality for dendroclimatology since it provides a measure of the high frequency variation. It should be used in conjunction with other statistics.

The SERIAL CORRELATION describes the amount of lag effect in growth from one year to the next. The statistic is computed by calculating the correlation coefficient (r) between one year's growth and the next (or next +1 etc., equation 3....1). A value close to zero indicates a small lag effect. The autocorrelation coefficient depend on the length of the chronology (the value of N in equation 3....1). The values in table 3.5 give serial correlations of filtered chronologies for a lag of one year. The serial correlation in MXD is generally low except for the sub-fossil chronologies and for Randalstown. LW is less strongly autocorrelated than either EW or RW, although it exhibits a stronger autocorrelation than MXD, except at Chippenham and for the sub-fossil sites.

Correlations between the five variables have been performed for each site. The results are shown in table 3.6 and illustrated diagrammatically in figure 3.4. In all cases there are highly significant correlations between RW and EW and beteeen RW and LW. MXD is most strongly correlated with LW at all sites. RW and EW are the most highly correlated pair of variables followed by RW and LW then MXD and LW. EW is correlated to a lesser extent with LW (and only with .1 sig. for Glen Affric) and is only sometimes related to MXD. A negative correlation between MXD and EW for Kielder suggests that EW may be behaving differently here than at the other sites. At Glen Affric MIN is highly correlated with all variables, at Derrycrow, Randalstown and Chippenham there is a positive correlation between MIN and LW, whilst at O Frostsjoasen, Muddus and Sluggan there is a negative correlation between EW and MIN.

These interrelationships agree with results obtained from nine moderate and high altitude sites (600-2400m) in the Alps for five conifer species, Picea abies, Abies alba, Larix decidua, Pinus cembra and P. sylvestris (Schweingruber et al. 1979). On all sites RW and EW were most strongly related, RW and LW to a lesser extent. MXD and LW are significantly correlated, being most strongly related on the dry sites. No interrelationships were found between MIN and other variables.

Table 3.4

Correlation statistics for comparisons between individual tree series at each site, given in programme FSTAND.

		MXD	MIN	EW	LW	RW
Muddus.						
N(n)	12(12)					
mean r		.468	.096	.295	.232	.311
sig. r		.001	ns	.001	.01	.001
EPS		.913	.561	.834	.783	.844
EPS10		.898	.516	.807	.751	.818
EPS(.85)		7	>30	14	19	13
O Frost.						
N(n)	14(16)					
r		.505	.259	.405	.288	.395
sig. r		.001	.01	.001	.01	.001
EPS		.935	.830	.905	.850	.902
EPS10		.911	.777	.872	.802	.867
EPS(.85)		6	17	9	14	9
Glen Derry.						
N(n)	12(20)					
r		.430	.087	.169	.309	.230
sig. r		.001	ns	.1	.002	.02
EPS		.905	.532	.709	.843	.789
EPS10		.888	.487	.622	.799	.585
EPS(.85)		8	>30	21	11	17
Glen Affric.						
N(n)	8(10)					
r		.360	.093	.156	.393	.232
sig.r		.001	ns	.1	.001	.02
EPS		.818	.451	.597	.838	.707
EPS10		.849	.507	.657	.866	.751
EPS(.85)		11	>30	29	9	20
Kielder.						
N(n)	8(8)					
r		.408	.057	.186	.175	.176
sig.r		.001	ns	.1	.1	.1
EPS		.892	.327	.696	.680	.681
EPS10		.912	.378	.733	.719	.720
EPS(.85)		5	>30	19	22	22

Table 3.4 cont.

Randalstown.

N(n)	5(6)					
r		.079	.003	.177	.218	.216
sig. r		ns	ns	.1	.05	.05
EPS		.301	.014	.518	.582	.580
EPS10		.456	.051	.714	.736	.734
EPS(.85)		>30	>30	24	21	21

Chippenham.

N(n)	5(7)					
r		.083	.041	.138	.208	.291
sig. r		ns	ns	ns	.05	.01
EPS		.311	.176	.444	.568	.774
EPS10		.446	.300	.523	.725	.804
EPS(.85)		>30	>30	>30	21	14

SUB-FOSSIL

Sluggan.

N(n)	5(5)					
r		.282	.046	.301	.354	.395
sig. r		.002	ns	.001	.001	.001
EPS		.470	.195	.683	.733	.765
EPS10		.798	.551	.811	.846	.867
EPS(.85)		16	>30	14	11	9

Derrycrow.

N(n)	5(5)					
r		.180	.182	.542	.334	.470
sig. r		.05	.05	.001	.001	.001
EPS		.522	.526	.856	.715	.816
EPS10		.633	.650	.908	.832	.898
EPS(.85)		18	25	5	11	7

Where MXD = maximum density, MIN = minimum density, EW = earlywood width,
LW = latewood width, RW = ring width. N = number of trees, n = total number of cores. EPS = expressed population signal, EPS10 = EPS for 10 trees, ESP(.85) = number of cores needed for an ESP of .85.
r = mean correlation coefficient between series and its significance level (sig.r).
Programme uses the maximum individual overlaps between trees (over the periods listed in table 3.5).

Table 3.5 Chronology statistics from programme FSTAND.

	MXD	MIN	EW	LW	RW
MUDDUS 1610-1983.					
Mean sens.	.22	.25	.16	.18	.15
Serial corr.	.03	-.02	.48	.13	.48
Mean value (mm)					.99
O FROST 1580-1983.					
Mean sens.	.23	.22	.20	.22	.19
Serial corr.	.01	.04	.27	.11	.31
Mean value (mm)					1.03
GLEN DERRY 1721-1983.					
Mean sens.	.23	.19	.17	.21	.18
Serial corr.	-.04	-.08	.36	.08	.37
Mean value (mm)					1.19
GLEN AFFRIC 1750-1983.					
Mean sens.	.21	.21	.18	.21	.17
Serial corr.	.05	-.02	.37	.06	.45
Mean value (mm)					1.25
KIELDER 1860-1981.					
Mean sens.	.22	.24	.18	.19	.15
Serial corr.	-.13	-.17	.32	.30	.55
Mean value (mm)					1.27
RANDALSTOWN 1823-1983.					
Mean sens.	.17	.16	.17	.19	.14
Serial corr.	.28	-.06	.42	.27	.45
Mean value (mm)					1.39
CHIPPENHAM 1814-1978.					
Mean sens.	.22	.19	.17	.22	.19
Serial corr.	.14	.09	.29	-.02	.29
Mean value (mm)					1.51
		SUB-FOSSIL			
SLUGGAN 245 years. 6615+/-95 B.P.					
Mean sens.	.19	.21	.16	.18	.14
Serial corr.	.31	-.03	.40	.16	.61
Mean value (mm)					1.15
DERRYCROW 188 years. 4630+/-60 B.P.					
Mean sens.	.15	.19	.12	.18	.13
Serial corr.	.51	.13	.63	.25	.56
Mean value (mm)					1.12

Table 3.6.

Correlations between variables.

	OFR	MUD	DER	AFF	KIE	RAN	CHI	SLU	DCR	MEAN
MXD										
x										
MIN	ns	ns	ns	44	ns	42	34	ns	ns	ns
EW	34	ns	ns	ns	ns	27	ns	21	ns	ns
LW	74	60	57	56	39	52	35	52	38	52
RW	56	40	39	44	ns	ns	24	48	31	33
MIN										
x										
EW	-55	-45	ns	85	ns	ns	ns	-21	ns	ns
LW	ns	ns	34	67	ns	23	27	ns	ns	ns
RW	-46	-40	ns	98	ns	ns	ns	-21	ns	ns
EW										
x										
LW	29	30	29	22	21	50	34	24	33	31
RW	93	87	90	84	85	75	70	80	80	83
LW										
x										
RW	61	55	65	65	64	71	71	56	70	64
MEAN	23	19	35	58	16	36	30	24	25	29

Significance; 32 = .01, 21 = .1 (table 3.1, eqn. 3....3).
Values are for r x 100, on 100 years of overlap (1879-1978).

Table 3.7. Correlation coefficients for crossdating between sites.

	OFR	MUD	DER	AFF	KIE	RAN	CHI
MXD							
OFR		***	***	***	***	*	**
MUD	.695		***	**	ns	ns	ns
DER	.381	.283		***	***	*	***
AFF	.375	.231	.806		***	**	***
KIE	.278	.136	.677	.664		***	***
RAN	.149	.094	.174	.184	.259		***
CHI	.179	.113	.387	.355	.344	.247	
Average correlation = .334.							
MIN							
OFR		***	**	*	ns	ns	ns
MUD	.394		ns	ns	ns	ns	
DER	.217	.089		ns	**	ns	ns
AFF	0	.089	.010		ns	ns	ns
KIE	.114	.007	.229	0		***	ns
RAN	.025	0	0	0	.304		ns
CHI	0	0	.051	0	0	.096	
Average correlation = .040.							
EW							
OFR		***	**	**	ns	ns	ns
MUD	.377		ns	ns	ns	ns	ns
DER	.217	.119		***	*	ns	ns
AFF	.184	.086	.470		***	*	ns
KIE	.031	.081	.173	.320		ns	ns
RAN	.021	.125	0	.157	.103		ns
CHI	0	.039	0	0	.035	.101	
Average correlation = .120							
LW							
OFR		***	*	ns	**	ns	ns
MUD	.447		ns	ns	ns	ns	ns
DER	.149	.005		***	***	**	***
AFF	.126	.009	.760		***	***	**
KIE	.222	.122	.346	.424		ns	***
RAN	.086	.017	.215	.359	.112		***
CHI	.129	.115	.276	.231	.439	.239	
Average correlation = .230.							
RW							
OFR		***	**	*	ns	ns	ns
MUD	.392		ns	ns	ns	ns	ns
DER	.185	.002		***	**	ns	*
AFF	.167	.059	.605		***	***	ns
KIE	.108	.084	.227	.341		ns	**
RAN	.023	.117	.111	.268	.132		*
CHI	.057	.086	.153	.070	.180	.172	
Average correlation = .170							

Significance; *** = .01, ** = .05, * = .10

Values are for the maximum common period of 118 years, 1860-1977.

Figure 3.1

Plot of raw and filtered tree-ring series.

Tree 52N Glen Derry. 1800-1899.
o - unfiltered ring-width series.
● - series filtered using 30-year Gaussian filter.

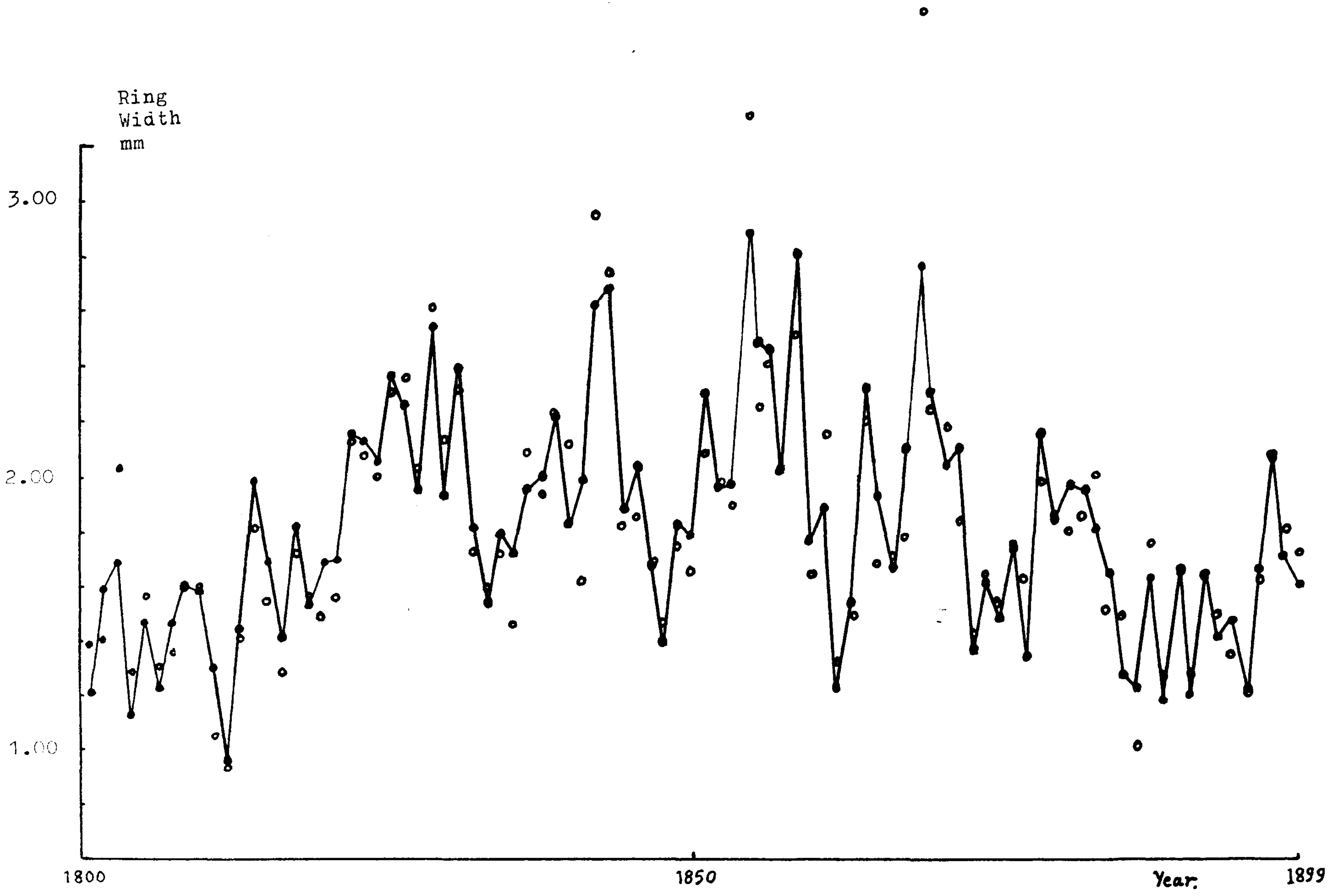

Ring
Width
mm
3.00
2.00
1.00
1800
1850
Year.
1899

Figure 3.3

Relationship of EPS to filter length.

Filter length in years. EPS - Expected climate signal.

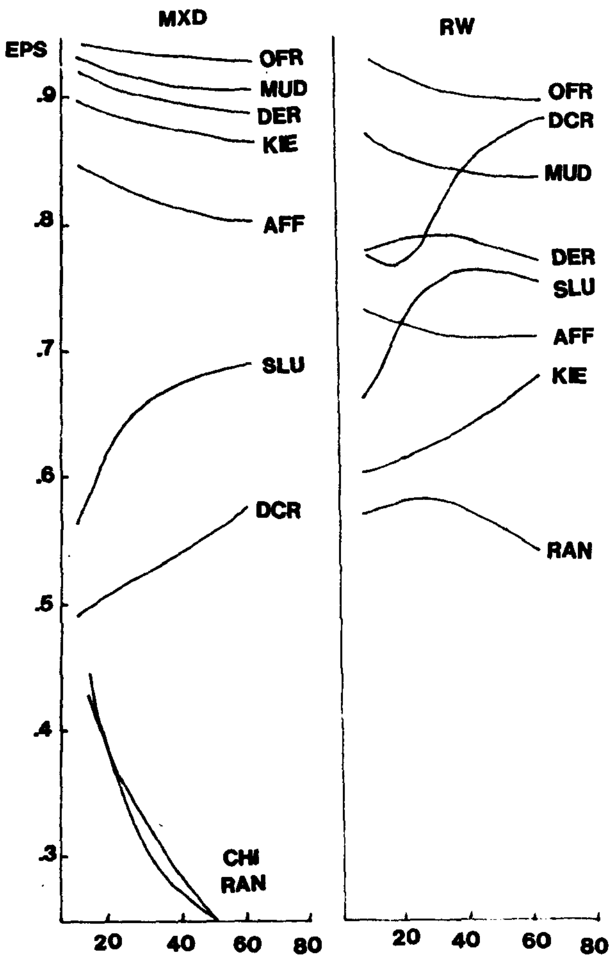
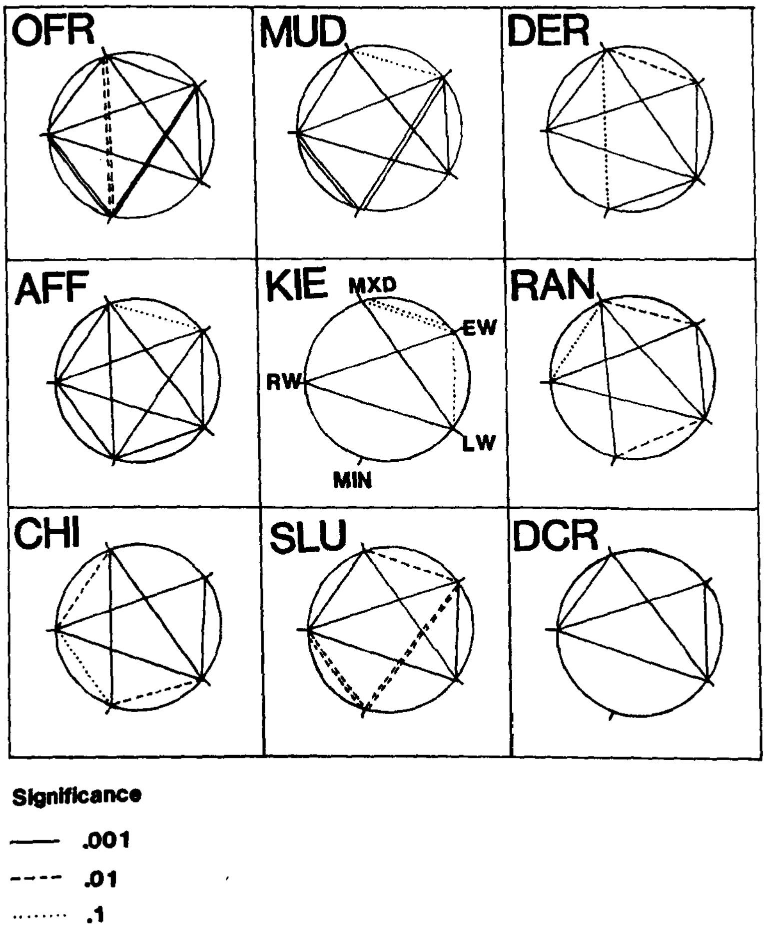

MXD
RW
EPS
.9
.8
.7
.6
.5
.4
.3
OFR
MUD
DER
KIE
AFF
SLU
DCR
CHI
RAN
20
40
60
80
OFR
DCR
MUD
DER
SLU
AFF
KIE
RAN
20
40
60
80

Figure 3.4

Correlation between tree-ring variables.

Single line indicates a positive correlation, a double line a negative correlation.


OFR
MUD
DER
AFF
KIE
MXD
EW
RW
LW
MIN
RAN
CHI
SLU
DCR
Significance
.001
.01
.1

D. SPATIAL PATTERNS OF RELATIONSHIPS BETWEEN CHRONOLOGIES.

a) Spatial relationships in density and ring-width chronologies.

The spatial coherence of the 5 parameters has been examined by considering the correlations between the seven modern sites. The correlation coefficients and their significances are given in table 3.7 and illustrated in figure 3.5. The MXD chronologies show the strongest common signal, a common signal is detected between both low altitude sites (in Northern Ireland and eastern England), and the site in central Sweden at 800m a.s.l. There is a common signal between both Scottish sites and the site at Muddus in northern Sweden some 2300 km apart. All closer sites show significant MXD correlations. LW is the next best parameter with respect to the strength of a spatial signal although its range is less extensive. RW and EW in general show relatively poor intersite crossdating. The Randalstown and Kielder chronologies are more closely related to Glen Affric than to Glen Derry with respect to EW. EW also shows a stronger relationship between the Scottish and the Swedish chronologies than does LW, but the most southerly chronology at Chippenham does not correlate with any of the other sites on EW. This suggests that either there is very little climatic signal in the Chippenham EW chronology or the climate factors affecting EW in eastern England are different from those influencing EW further North.

Schweingruber et al. (1979) make a similar comparison of the ring characteristics of pine, spruce and larch in humid, cool sites in southern England, eastern Scotland, west Scotland, the mediterranean and at subalpine levels in the European Alps. MXD shows strong relationships between sites in similar regions (for example between all British sites and between all central Alpine sites). The British sites also show good agreement with the central alpine sites although not with the Mediterranean sites. MIN shows the next best agreement between the British sites themselves, and weak connections (0.02 significance) between some of the Alpine sites. RW shows a similar pattern to MIN, with some weak connections between the Alps and UK. LW and EW show good agreement between the British sites but practically no connections between these and the Alpine chronologies. A unit of spatial similarity based on MXD is considered to be applicable to pine and spruce on sites in the cool, humid regions of Scotland, England, southern Sweden and the central European Alps.

Subsequent analysis of further data from the European tree-ring network from summer cold-moist sites in subalpine and northern timberlines has shown that material from ecologically similar sites crossdates over large areas (Schweingruber 1985). The sizes of the areas are considerably larger based on MXD than on RW values. Based on calculations of the percentage of agreement between chronologies, on average MXD shows 10% better agreement between sites than RW. Spatial similarity based on the Scottish chronologies extends to the Pyrenees, the eastern Alps, central Sweden and southern Finland.

b) <u>Correlations between 28 European chronologies.</u>

In order to assess the degree of similarity between the British and European chronologies a CORRELATION MATRIX has been constructed using an additional 21 <u>P.sylvestris</u> ring-width chronologies from European sites. Most of the sites are located in Norway, Sweden and Finland. Site 17 is further south in Lithuania, sites C and A are located to the east of the Black Sea, in Turkey and the Ukraine, B is in central Spain. Map 3.2 shows the locations of the sites. The data have been obtained from the IPID project by permission of Dr M. K. Hughes. Below is the full list of chronologies used.

Table 3.8 Chronologies used in PCA.

No:	Site.	Lat.	Long.	Submittor.
1	Jondalen	59 40	09 29 E	Briffa & Jones
2	Muddas 2	66 51	20 22 E	ITRDB Jonsson & Harlan
3	Arjeplog	66 20	18 27 E	ITRDB Jonsson & Harlan
4	Ostersund	62 49	14 48 E	ITRDB Harlan
5	Arosjak	67 52	19 25 E	ITRDB Harlan
6	Pyan-Hakin	62 51	25 29 E	Schweingruber
7	Lofoten	68 29	16 02 E	Schweingruber
8	Laagenus	67 00	27 07 E	Schweingruber
9	Savdazyersk D	62 45	33 00 E	Bitvinskas/LaMarche
10	Murmansk	68 30	32 00 E	Bitvinskas/LaMarche
11	Chipinsk	66 15	36 00 E	Bitvinskas/LaMarche
12	Kandalakshesk	67 15	32 45 E	Bitvinskas/LaMarche
13	Topozersk	65 15	32 30 E	Bitvinskas/LaMarche
14	Kestengsk	65 50	32 15 E	Bitvinskas/LaMarche
15	Kemski	65 00	33 30 E	Bitvinskas/LaMarche
16	Kalevalsk	65 00	31 30 E	Bitvinskas/LaMarche
17	Musteikos	54 10	24 30 E	Bitvinskas/LaMarche
18	O Frostsjoasen	62 19	12 48 E	Briffa et al.
19	Muddus	66 47	20 08 E	Briffa et al.
A	Karinca Duzu	40 50	42 40 E	Kuniholm
B	Navaceradda	40 48	04 02 W	Schweingruber
C	Pkinya A	42 30	41 30 E	Bitvinskas/LaMarche
20	Coulin	57 32	05 21 W	Cartwright/Schweingruber
21	Glen Derry	57 00	03 35 W	Swain
22	Glen Affric	57 15	04 55 W	Swain
23	Kielder	54 55	02 30 W	Briffa/Swain
24	Randalstown	54 46	06 18 W	Swain
25	Chippenham	52 24	00 10 W	Cartwright/Swain

ITRDB = International Tree-Ring Data Bank.

Map 3.2

Location of sites used in PCA.

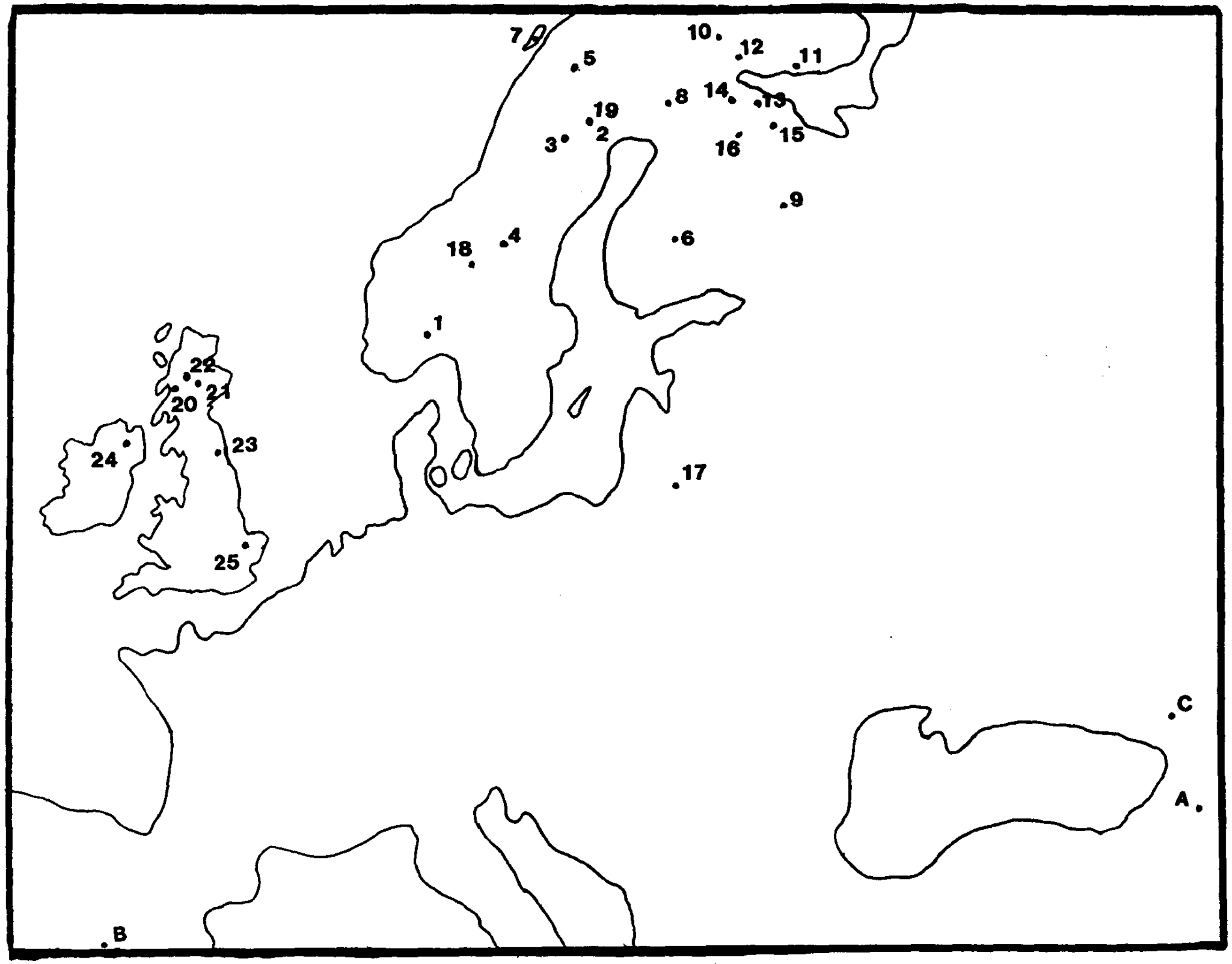
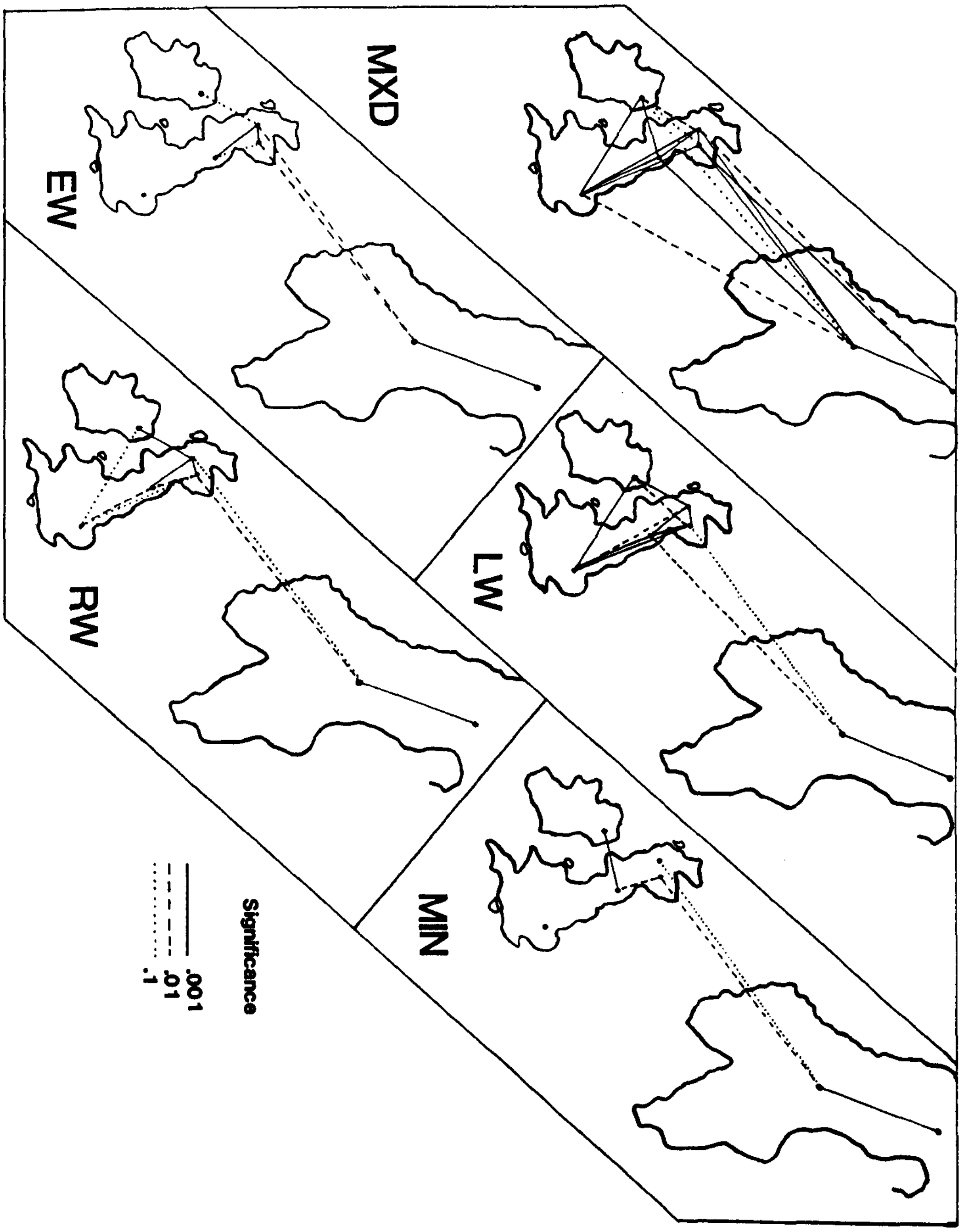

7
10
12
11
5
19
2
8
14
13
3
16
15
9
18
4
6
1
22
21
20
23
24
17
25
C
A
B

Figure 3.5

Correlation between sites using different variables.


MXD
LW
MIN
EW
RW
Significance
.001
.01
.1

A period of 110 years from 1860 to 1969 was used in the calcuations. The results of the correlation analysis are given in table 3.9, significant positive and negative correlations are listed. Most of the the northern Scandinavian sites are highly significantly correlated with each other. Sites 1 in southern Norway, 7 on a coastal island off Norway and site 17 in Lithuania are poorly correlated with the majority of the Finnish and Scandinavian sites. Site 1 also shows inverse correlation with the British sites. It is interesting to note that the maritime site 7 on the northern Norwegian coast only correlates strongly with the Turkish site near the Black sea. Weak links exist between some of the Scandinavian and British sites. There are some moderately significant links between two of the British sites and the Spanish site.

Certain of the negative correlations may be due to changing circulation patterns in the weather (Briffa et al. 1986a). A high pressure zone is often found across Europe in the summer months, the position of this zone may vary in latitude, being located over Scandinavia in some years and further south over the mediterranean in others. Thus opposing weather patterns may operate to cause negative correlations in growth between trees from the two areas even though the trees are responding to climate in the same way. Climatic patterns which favour growth in some areas whilst limiting it in others may also be responsible for negative correlations between maritime and high altitude (or inland) sites.

c) Principal component analysis of European sites.

Further investigation of the spatial characteristics of the interrelationships between tree-ring variables has been possible by conducting principal component analyses (PCA). This allows a more detailed picture of the nature of variation between sites to be constructed, than by using a simple correlation analysis. Statistical details are given in Fritts (1976). As the database of chronologies is increased it has become possible to use PCA to examine spatial tree growth patterns over large areas. This technique has been used in the analysis of climate patterns (Jones et al. 1983, Richman and Lamb 1985, Wigley et al. 1984a) and tree-ring chronologies for Europe (Briffa et al. 1986c), North America and for the whole of the northern hemisphere (IPID, in preparation). There are certain statistical anomalies which have to be considered resulting from the fact that the external factors affecting the spatial patterns of the chronologies may themselves be correlated. If orthogonal PCs are used it may be impossible to interpret them in terms of any real effect. Richman (1986) describes the use of rotated PCs to overcome this problem. The use of rotated PC's can also overcome the difficulties arising when an area is split up and seperate principal component analyses are done on each area. Richman has shown that by using rotated PCs the same pattern is generated using small areas as when the total area is analysed at once, which is not always the case with a conventional PCA. However it is stated that a PCA using unrotated PCs can be used to good effect in many situations (Richman 1986). It is suggested that by mapping the patterns of correlation between the individual sites, the spatial patterns can be verified. In this work such maps have been produced using the data from table 3.9 and they do confirm the groupings indicated in the subsequent PCA. In many cases the spatial patterns associated with the PCs can be explained in terms of known climatic effects which gives weight to the argument that the patterns are real. Principal component analysis has been done using the data for the sites for the 110 year common period, with and without the three southern sites (A, B and C) included. The first four principal components explain 21.6, 9.8, 9.0 and 6.4% of the variance respectively with the southern sites and 24.1, 10.4, 9.9 and 6.6% without these three sites. Thus approximately half the total variance is explained by these first four eigenvectors. Tables 3.10 and 3.11 show the weights on the first three PC's for each of the chronologies for the two analyses. The exclusion of the three southern sites has very little effect on the loading pattern of the first PC but there is considerable difference on the higher order component loadings. Figures 3.6 and 3.7 illustrate the loading patterns on the chronology networks for the first three PC's. The first PC gives strong weightings at all sites especially for the most northerly Scandinavian sites. There is little difference in the first PC when the southern sites are excluded. A strong positive first PC is generally found in the Northern Hemisphere, this has been attributed to a commmon response to climate (notably temperature). The second PCA explains about 10% of the variance. It separates the British and Finnish sites from the central Scandinavian sites. The southern sites, Britain and Finland are weighted positively and Sweden, Lithuania and the Black sea sites are negative. (In fact the actual signs of the values are arbitary). Without the three southern sites, Britain, Finland and Karinca are again separated from central Scandinavia. The third PC gives the British sites a positive weighting, a smaller positive weighting to the Swedish sites and a negative weighting to the Finnish sites in both instances.

The second PC may be reflecting differences between the mediterranean and the northern European sites at the same time as associations between maritime and continental sites. The third PC may also be associated with the differences between maritime and continental sites. A recent european PCA using 75 chronologies, both conifers and hardwoods from sites throughout western Europe shows quite complex patterns of differentiation between the mediterranean, central Alpine and Scandinavian sites (Briffa et al. 1986c).

Both the correlation analysis and the PCA indicate that the British chronologies are generally responding as a coherent unit although the associations between chronologies are not strong. The data reflect patterns which are both common with and in opposition to those from groups of trees in other regions of Europe. Associations extend across the whole of northern Europe.

d) PCA using ring-width and density parameters.

A further study has been carried out on the seven sites for which density measurements are available. Table 3.12 shows the results of the PCA for the first three PCs using MXD, MIN, EW, LW and RW chronologies. MXD shows the greatest weighting on the first PC followed by LW, RW, EW and finally MIN. The weightings on the remaining PCs are similar for all variables. Apart from the calculations based on MIN, the first PC shows a similar pattern at all sites (either all positive or all negative). The strongest weightings are for the Scottish sites which occupy a central position. The second PC separates the two Swedish sites from the remainder and the third PC separates the Irish site (and also the East Anglian site on RW and EW) from the rest.

The percentage variance attributed to the first PC is an indirect measure of the amount of common variance in the chronologies. This allows the variables to be ranked in order of amount of common variance. Using this criterion the MXD chronologies contain the highest proportion of common variance, followed by the LW, RW, and EW chronologies. The pattern of variation in MIN indicates that there is no common pattern between sites.

For identifying regional climatic patterns (and ultimately climatic reconstructions), MXD appears superior to ring-width parameters. Chronologies of LW are likely to be better than those based on EW since they contain a greater proportion of regional information.

Table 3.9
Correlation Matrix for IPID sites and British chronologies 1860-1969
Values for correlation coefficient, r x 100.

Site.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2	.													
3	.	70												
4	18	48	33											
5	.	68	69	42										
6	23	29	26	40	42									
7	-17	.	45	.	33	.								
8	.	46	42	33	41	60	.							
9	.	37	18	.	36	38	.	33						
10	.	48	30	.	43	23	.	53	32					
11	.	.	.	.	.	.	.	18	.	38				
12	.	21	24	.	28	38	.	54	.	64	46			
13	.	25	19	21	28	42	.	46	43	50	32	43		
14	-23	30	32	25	44	41	18	33	43	39	18	38	63	
15	.	20	16	.	22	35	.	32	25	44	30	43	57	25
16	.	.	.	20	23	22	.	.	19	30	17	33	53	34
17	-30	.	19	.	.	.	.	.	16	.	.	.	16	26
18	.	59	43	40	45	.	.	.	.	.	-23	-17	19	26
19	.	67	55	32	59	30	.	38	33	32	.	17	.	21
A	.	35	19	.	.	43	17	.	.	.	.	.	.	.
B	.	.	.	22	.	.	.	.	.	17	.	.	.	19
C	.	.	.	.	.	.	.	.	.	.	.	.	.	-16
20	.	.	.	.	.	.	.	.	-16	.	.	.	.	.
21	21	.	.	.	.	.	.	.	.	.	.	19	.	.
22	.	.	19	17	.	.	.	.	.	20	.	18	19	.
23	.	18	.	.	.	.	.	.	.	26	.	.	21	19
24	24	18	.	.	.	.	.	.	.	.	.	.	.	.
25	.	.	.	.	.	.	.	.	.	19	.	22	.	.

Site.	15	16	17	18	19	A	B	C	20	21	22	23	24
16	42												
17	.	.											
18	.	.	.										
19	16	.	.	40									
A	.	.	.	.	-17								
B	.	.	16	18	.	.							
C	.	.	.	.	.	18	.						
20	.	.	.	.	.	.	.	.					
21	.	19	.	.	.	.	30	.	36				
22	19	.	.	18	.	.	21	.	49	61			
23	.	.	.	.	.	-33	24	.	26	19	34		
24	18	.	.	.	.	.	.	.	.	.	26	.	
25	.	.	.	.	.	.	.	.	.	.	.	16	18

Significance; > 16 = .1 . = non-significant.
> 24 = .01
> 31 = .001

List of sites is given in the text, table 3.8.

Table 3.10

The weights (x1000) on the 3 major principal components of the correlation matrix of the network of 28 European chronologies (listed in table 3.8).

Chron.	PC1(21.6%)	PC2(9.8%)	PC3(9.0%)
1	19	108	207
2	299	-212	193
3	269	-253	161
4	207	- 96	202
5	308	-194	141
6	247	24	- 55
7	77	-257	- 1
8	281	- 3	-109
9	204	-148	-192
10	283	136	-149
11	107	239	-252
12	238	210	-231
13	272	181	-225
14	263	34	-141
15	216	159	-180
16	174	116	-188
17	95	- 19	- 85
18	175	-145	312
19	239	-221	177
20	8	241	325
21	81	319	279
22	124	338	297
23	104	250	177
24	63	110	204
25	55	131	102
A	41	-274	- 74
B	67	168	86
C	4	-111	- 32

Table 3.11

The weights (x1000) on the 3 major principal components of the correlation matrix of the network of 25 northern European chronologies (listed in Table 3.8).

Chron.	PC1(24.1%)	PC2(10.4%)	PC3(9.9%)
1	21	- 13	251
2	301	281	77
3	269	275	55
4	205	182	127
5	308	241	37
6	249	- 38	- 42
7	74	196	- 86
8	283	- 62	- 76
9	206	60	-249
10	284	-182	- 77
11	106	-345	- 99
12	240	-320	- 78
13	274	-245	-138
14	263	- 60	-148
15	217	-242	- 66
16	175	-203	-103
17	93	- 2	-111
18	175	310	169
19	241	296	43
20	1	- 98	429
21	78	-183	410
22	123	-190	437
23	104	-117	240
24	66	- 58	289
25	56	- 78	162

Table 3.12 The weights (x1000) on the 3 major principal components of the correlation matrix of the network of 7 British and Scandinavian chronologies using five parameters of density and ring-width.

MXD	Chron.	PC1(44.8%)	PC2(19.0%)	PC3(14.2%)
	OFR	361	-566	- 28
	MUD	284	-671	-116
	DER	491	158	237
	AFF	480	180	263
	KIE	441	292	104
	RAN	174	150	-866
	CHI	301	252	-315

MIN	Chron.	PC1(22.3%)	PC2(19.1%)	PC3(14.5%)
	OFR	-630	98	313
	MUD	-495	360	203
	DER	-419	- 65	-208
	AFF	127	490	544
	KIE	-350	-455	-495
	RAN	-107	-521	-198
	CHI	175	-369	486

EW	Chron.	PC1(26.9%)	PC2(17.3%)	PC3(16.5%)
	OFR	389	-585	- 7
	MUD	350	-538	- 329
	DER	486	64	389
	AFF	552	315	160
	KIE	238	436	- 67
	RAN	202	221	-629
	CHI	11	158	-560

LW	Chron.	PC1(35.6%)	PC2(20.1%)	PC3(13.2%)
	OFR	-246	-606	- 26
	MUD	-141	-686	-143
	DER	-495	246	145
	AFF	-518	271	- 3
	KIE	-435	- 68	430
	RAN	-279	133	-878
	CHI	-372	- 65	39

RW	Chron.	PC1(30.2%)	PC2(18.3%)	PC3(15.0%)
	OFR	301	-603	258
	MUD	229	-695	- 78
	DER	494	243	333
	AFF	546	263	251
	KIE	404	140	- 84
	RAN	301	71	-549
	CHI	243	- 7	-666

Figure 3.6

Principal component analysis using 28 European sites.
% variance accounted for by each PC is given.

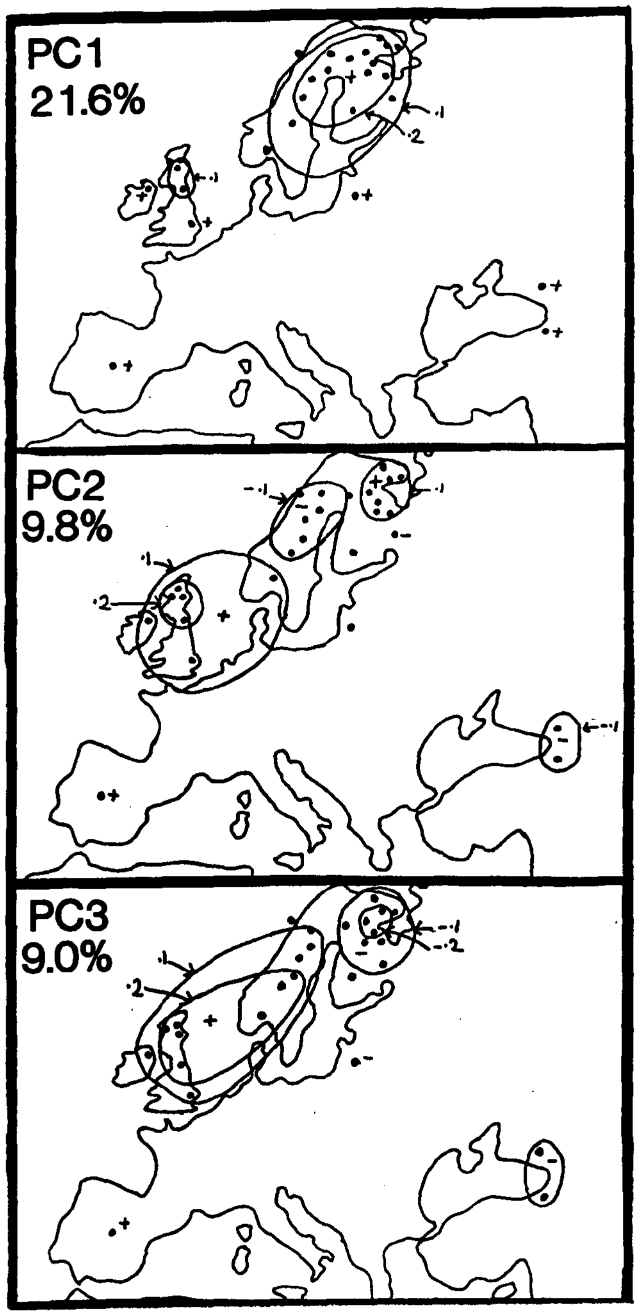
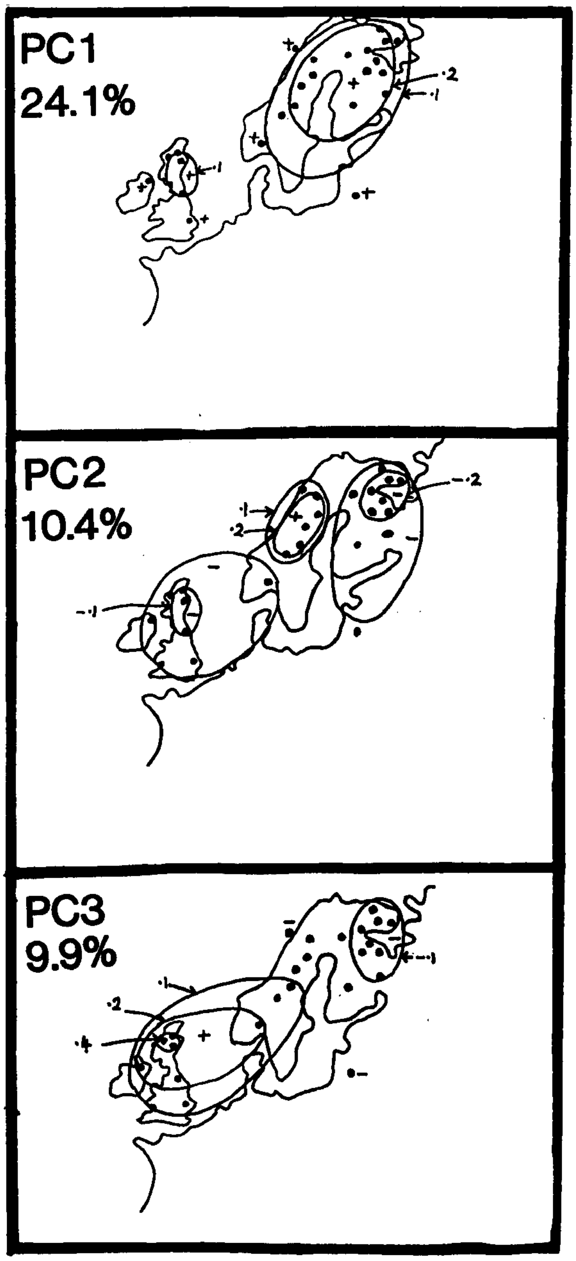

PC1
21.6%
.1
.2
.1
PC2
9.8%
-.1
-.1
.1
.2
-.1
PC3
9.0%
.1
.2
-.1
-.2

Figure 3.7

Principal component analysis using 25 northern European sites, giving % variance accounted for by PC's.


PC1
24.1%
·2
·1
·1
PC2
10.4%
·1
·2
-·2
-·1
PC3
9.9%
·1
·2
·4
·1

E. CONCLUSIONS.

The properties of chronologies from seven modern sites in Britain and Sweden, and two sub-fossil sites in Ireland have been examined. Chronologies have been produced for five tree-ring parameters; maximum density, minimum density, earlywood width, latewood width and ring-width.

Chronology statistics have been obtained using the program FSTAND devised by K. Briffa from the Climate Research Unit, University of East Anglia. Standardisation methods are discussed. In this case a 30-year Gaussian filter has been fitted to the data, indexed series are produced by subtracting the actual values from the curve values for the density parameters, and dividing the actual by the fitted value for the ring-width parameters. Correlations between tree-ring series using MXD indicate highly significant correlations between trees on the high altitude Scottish and Swedish sites and the moderate altitude site at Kielder in northern England. No significant MXD correlations are apparent for the low altitude modern sites although MXD correlates well between trees on the two sub-fossil sites. RW crossdates better than MXD within the sub-fossil and low altitude sites. The properties of the sub-fossil chronologies are different from those from any of the modern sites.

The statistical quality of the mean chronologies is expressed in terms of an Expected Percentage Signal (EPS) value. Briffa (1984) suggests an EPS value of 0.85 as a standard for determining the suitability of a chronology for climate reconstruction. Only the MXD chronologies from the high and moderate elevation sites have EPS values as high as this. A lower figure such as 0.70 is probably more realistic when considering British chronologies. It would still be necessary in some cases to sample a larger number of trees to obtain EPS values of 0.70 for both ring-width and density parameters. EPS statistics indicate that there is a moderate amount of common information in chronologies using all parameters except MIN on most sites. The difference in strength of common signal between high and low altitude sites is more strongly marked in the case of MXD than for RW. The RW chronologies show the greatest common signal between trees from the high altitude sites, but the low altitude sites still have a moderate amount of common signal. MXD however is better than RW at the higher elevations but the MXD signal is very weak between trees from the low level sites.

Correlations between the five variables have been performed for each site. MXD is strongly correlated with LW on all sites but only sometimes correlated with EW. Between sites correlations are strongest and geographically most far reaching with MXD. LW also correlates well between all sites although EW only shows a correlation over short distances between the closer sites.

A principal components analysis using an additional 21 sites mostly from Scandinavia gives all sites a positive weighting on the first PC (explaining approximately 25% of the variance). The British and Finnish sites are separated from those in Sweden on the second PC. The third PC gives the British sites a positive weighting and the Finnish sites negative weightings with Swedish sites having lower positive values. In some years the British chronologies are responding the same way as trees from Finland and differently from the central Scandinavian chronologies, in other years the opposite is true.

The following table ranks the five parameters in terms of their relative values for some of the within and between site statistics.

Table 3.13

	WITHIN SITES					BETWEEN SITES
	msens.	scorr.		EPS(10)		corr. or PC1
		high alt.	low alt.	high alt.	low alt.	
HIGH	MXD	RW	RW	MXD	RW	MXD
.	MIN	EW	EW	LW	LW	LW
.	LW	LW	MXD	RW	EW	RW
.	EW	MXD	LW	EW	MXD	EW
LOW	RW	MIN	MIN	MIN	MIN	MIN

Where msens.= mean sensitivity, scorr.= serial correlation for one year lag, corr.= mean correlation between sites, PC1 is the percentage variance loading on the first principal component.

Regional comparisons suggests that MXD gives the most spatially coherent signal, followed by latewood width, RW, then EW. MIN is the weakest variable. The within site characteristics of the MIN tree-ring series show more variability. EPS(10) at the higher altitude sites reflects the regional pattern, although the low altitude sites give RW as the strongest variable followed by LW, and MXD performs weakly. This suggests that whilst the common signal at the high altitude sites is associated with the regional climatic response, this is not the case at the low altitude sites. Mean sensitivity ranks MXD as the most sensitive variable, and LW better than EW, MIN is also ranked high. This statistic is probable not of great use in comparing these chronologies since it varies little from one variable to another. The lower the serial correlation the more likely the tree-rings will simply reflect the current year's climatic conditions. MXD has a lower serial correlation than RW or EW, but it is higher than for LW on the low altitude sites. The values for MIN are in fact negative for the high altitude sites. Whereas part of the cause for the lower common signal in RW and EW may be due to high autocorrelation from one year to the next, this is not true for MIN where there is low autocorrelation and a minimal common signal.

The sub-fossil pine chronologies from Northern Ireland resemble the low level sites more than the high altitude sites with respect to their chronology properties. However, there are some major differences in their behaviour. RW crossdating is very strong in the sub-fossil trees. Inspection of the data indicates that there is a complex pattern of periodicity in the RW series. MXD gives a higher Expected Population Signal for the sub-fossil trees than for the low level modern trees. From the results obtained here it seems likely that the growing conditions found at Derrycrow and Sluggan at the time of sub-fossil tree growth were different to those present on the modern tree sites. The peculiarities of the modern sites may partly account for this. Other palaeoclimatic and palynological evidence for this is considered in chapter 5.

Chapter 4.

CLIMATE-GROWTH INVESTIGATIONS USING RESPONSE FUNCTION TECHNIQUES.

A. INTRODUCTION.

The simplest method of determining an association between climate variation and tree growth is to perform a DIRECT CORRELATION analysis between the ring index and the particular climate variable. This approach is described by Pilcher (1976) in an investigation of the effect of monthly precipitation on the growth of Irish oaks. However this method requires the *a priori* selection of climate variables likely to be affecting growth. Generally a large number of climatic factors have an influence, hence MULTIPLE LINEAR REGRESSION must be used. This defines the tree growth index in terms of a set of partial correlation coefficients associated with each individual climatic predictor, scaling each to its relative effect on the mean growth estimate (Fritts et al. 1971, Fritts 1976).

The multiple linear regression equation can be represented as follows;

$$Y_t = b_o + b_1 x_{1t} + b_2 x_{2t} + \ldots . b_n x_{nt} \qquad 4....1$$

Where Y_t is the predicted growth at year t

b (1 to n) are the partial regression coefficients associated with each climatic predictor variable x (1 to n).

Autocorrelation between tree-ring series however limits the number of degrees of freedom so that only a limited number of variables can be entered into the regression (Fritts 1976, Guiot et al. in Hughes et al. 1982).

The individual predictor variables of climate are generally highly correlated which limits the applicability of a normal multiple regression analysis. By use of a STEPWISE MULTIPLE REGRESSION all coefficients are examined seperately; the one that is best correlated is selected and a regression using that variable to estimate growth is performed. The process is repeated selecting the next best correlated predictor. Additional variables are added as long as the residual variance is reduced by a significant amount (defined at a preset level). This method however may result in the rejection of some climatic information.

The effect of intercorrelation between the climate variables is ultimately overcome by transforming them into orthogonal variables called PRINCIPAL COMPONENTS (or eigenvectors). The selected set of predictor eigenvectors which have been used in the correlation are transformed back to a new set of coefficients which correspond to the original correlated variable. This is called the RESPONSE FUNCTION.

The response function technique was developed and described by Fritts et al. (1971). It is reviewed in detail by Fritts (1976), and again by Blasing and Fritts (1976) with examples of its use with North American conifers. The more recent work and controversy is discussed by various authors in 'Climate From Tree Rings' (Hughes et al. 1982) and by Blasing et al. (1984). Response functions have been used to examine the climatic signals in oaks in Britain (Hughes et al. 1978, Milsom 1979, Gray and Pilcher 1983) and the effects of rainfall on the growth of elms (Brett 1978). Similar dendroclimatic studies in Europe including work on *Pinus sylvestris* L. have recently been undertaken by Kienast (1985) and Tessier (1984). A comprehensive response function analysis of *P. sylvestris* in the Scottish Highlands is described by Hughes (1986).

The response function provides a powerful and tested tool in the identification of the climate-growth response although there are certain problems. The attribution of significance to non-significant variables is a major hazard, as indicated by results obtained from simulation analyses described by Cropper (in Hughes et al. 1982). The other problem concerns the treatment of persistence in the tree-ring data. The two main strategies for dealing with this are either forcing non-orthogonal prior growth variables into the equation (Fritts 1976) or 'pre-whitening' the tree-ring data before response function calculation (Guiot et al. 1984).

The aims can be outlined as follows.

1) To investigate the relationship between tree growth and climate for a set of modern British and Scandinavian sites using response function analysis.
2) To identify anomalies in the response function approach which require more detailed examination.
3) To attempt to interpret the climate-growth response on the basis of current knowledge of tree physiology.

B. RESPONSE FUNCTION ANALYSIS.

a) Methods.

The response function employs the procedure of a stepwise multiple regression on the orthogonal principal components (or eigenvectors) of the climate data. The program used here is the original version (A) of the GENSTAT program written by Mr. D. Brett from Royal Holloway college. It is described in Brett (1978), and further discussed by Brett (in Hughes et al. 1982). The method of calculation essentially follows the procedure of Fritts (1976), with one or more vectors for prior growth included in the stepwise regression with the principal components of the climate variables.

The first stage is to derive the principal components or eigenvectors from the set of climate variables. The equation can be written as follows

$$\hat{P}_{1n} = R_{1p} X_{pn} \qquad 4....2$$

Where $\hat{P}$ (1 to n) are the estimated ring indices for n years, and R (1 to p) are the significant partial multiple regression coefficients associated with each of the amplitudes of the selected set of p eigenvector amplitudes. The particular values assigned to the regression coefficients are used in assessing the relative importance of each of the eigenvectors X (1 to n) in determining growth. The derived eigenvectors include the same information as the original climate data (or prior growth) variables, the most important eigenvectors accounting for a large proportion of the variance of the data. The least important eigenvectors express only minor variations in the original data set, so by ordering the vectors from the most to least important, the original climate data is concentrated into a small number of variables.

Conversion of the eigenvectors back to predictors of the original (climate) variables is done by using a transformation of the original equation, thus

$$\hat{P}_{1n} = R_{1p} E_{pm} F_{mn} = T_{1m} F_{mn} \qquad 4....3$$

Where T (1 to m) now represents the response function elements and F (m to n) the normalised climatic data. Since the elements of T are associated with the original climatic variables, each element can be interprted in terms of anomalies in those particular variables. The climate data used in this case is monthly temperature and precipitation for a 12 month period beginning in September of the previous year running through to August of the year of current growth. A twelve month period only is considered, so as to avoid problems associated with multicolinearity in the data, where current year and lag effects may not be seperable (Cropper 1984). Three seperate variables for the previous three years of prior growth are also included to take account of possible effects of lag on the ring index. The rationale behind the choice of climate period is based on the need to consider the effects of climate on five tree-ring parameters (MXD, MIN, EW, LW and RW). It was not possible to use seperate climate periods for each analysis. Current September climate is likely to affect MXD and LW, but not EW, MIN and RW (which will be affected more by the previous September's climate). Simple correlations have been done between monthly temperature (1900-1979) and both LW and MXD at Glen Derry and Glen Affric. (>.21 = .1 significance).

		Previous September	Current September
AFF	LW	-.258	.217
	MXD	-.249	.297
DER	LW	-.322	.084
	MXD	-.327	.321

The results show that previous September temperature is negatively correlated with both variables at the two sites. Current September temperature is positively correlated with MXD at both sites and LW at Glen Affric but not Glen Derry. October temperature shows no significant correlations. The effect of the quasi-biennial oscillation in temperature is clearly found in September temperatures; a correlation of -.15 is found between for the first order autocorrelation in Sep tember temperatures. This may partially account for the negative effect of previous September temperature on growth.

Results of response functions from previous work carried out at Liverpool Polytechnic, including both previous and current September climate as predictors of MXD and RW are reported here. The climate year from the previous September to the current August is therefore chosen to best represent the climate-growth relationships for the remaining parameters.

The next stage involves stepwise multiple regression using the amplitudes of the climatic eigenvectors R (1 to p) to estimate growth. Each step utilises an increasing number of eigenvectors, at each stage. transformation to the response function (equation 4....3) is carried out. The percentage of the tree-ring data variance accounted for by the response function is computed at each stage, the amount of additional variance explained by the inclusion of an additional eigenvector is compared with the residual variance and hence a t-value can be calculated defining the significance of the additional information. A significance level of 0.05 (t = 2.01 for 54 df.) has been used to select the number of eigenvectors to be included in each case.

As more eigenvectors are included the response function becomes better defined. It is necessary to avoid overdefinition by the inclusion of too many eigenvectors. The more steps included the greater the amount of the data variance that is explained. A point is reached where the additional steps are no longer meaningful and the extra eigenvectors will only be contributing noise. The cut-off point here is defined as the position where an eigenvector is not adding a significant amount of extra information. Blasing et al. (1984) tested the significance of response functions by performing simple correlation analyses on the individual climate-growth responses calculated from the response function. It was determined that a larger number of elements could be included than was originally thought especially where the significance levels were low. In the case of the low level sites and the less responsive parameters at least four eigenvectors have been included although the amount of extra variance added by each is not necessarily significant at 5%. Table 4.1 shows the percent variance accounted for by successive eigenvectors of climate and prior growth for the Glen Derry chronologies. Figure 4.1 shows how the response function shape changes as increasing numbers of eigenvectors are included for MXD at Glen Derry.

Table 4.1. Percentage variance accounted for by climate and prior growth eigenvectors at Glen Derry.

Vector no.	MXD %	RW %	EW %	LW %	MIN %
1	21.4	8.0(p)	8.6	14.6	11.6
2	21.1	8.2	6.4	9.5	11.3
3	7.2	6.6	5.8	8.1	4.4
4	7.2	6.2	5.1	7.9	3.9
5	5.5	5.5	4.8	5.5	
6	4.3	5.1	4.0	4.3(p)	
7	2.4(p)			3.0	
8	2.1			2.9	
9	1.4(p)				
TOTAL	71.3	40.6	34.7	55.6	31.4

Where p indicates a prior growth vector.

b) Results.

Response function analysis has been performed on the chronologies from the five sites in U.K. and two from Sweden using five tree-ring parameters in each case. The climate data used are the mean monthly rainfall and temperature data obtained from the nearest weather station to the site, supplying an adequate length of record. British figures are published in Meteorological Office Monthly Weather Reports. The following table lists the sources of climate data.

Table 4.2.

Site.		Station.	Distance. (km)	Lat.	Long.	Alt. (m)
OFR	PPT	Falun	250	60°36'N	15°36'E	200
	TEMP	Grid point 7	300	60 00N	10 00E	
MUD	PPT	Haparanda	190	65 08N	24 12E	10
	TEMP	Grid point 4	200	65 00N	20 00E	
DER	PPT	Braemar	11	57 00N	3 24W	339
	TEMP	Braemar	11			
AFF	PPT	Inverness	45	57 29N	4 13W	4
	TEMP	Achnashellach	36	57 29N	5 16W	67
KIE	PPT	Allenheads	56	55 14N	2 34W	201
	TEMP	Durham	80	54 46N	1 35W	102
Ran	PPT	Belfast	48	54 33N	5 58W	35
	TEMP	NI mean				
CHI	PPT	Cambridge	24	52 12N	0 08W	12
	TEMP	Cambridge	24			

The Northern Ireland regional mean monthly temperature (of 7 meteorological stations) has been used in the Randalstown response function calculation. The monthly temperature means are calculated from the average of the daily means of the maximum and minimum temperature. The Swedish temperature data are from the grid point surface air temperature set for the Northern Hemisphere (Jones et al. 1985, Jones et al. 1986). The Swedish rainfall data are from the Northern Hemisphere climate data bank (Bradley et al. 1985). It has been demonstrated (Hughes et al. 1978) that the distance of the climate station from the site can have a significant effect on the percentage variance accounted for by the response function especially in mountainous regions. A response function from an oak site in North Wales related 45% of the chronology variance to climate using rainfall data from a station 3km away, as opposed to 34% using data from a station 75km away. However it is usually more important to obtain a reasonable length of climate data since there is always the danger of overcalibrating a response function if too short a time period is used. Monthly temperature fluctuations are known to be consistent over wide areas even though the actual mean values may be different, hence choice of meteorological station is likely to have little effect on the response function calculation (Briffa 1984). Precipitation varies more on a local scale so a nearby rainfall record is preferable. Length of record and nearness of station have been balanced to select the best choice of climate station for each site. The distances above are in keeping with those generally accepted for response function analysis (Briffa 1984).

The climate data used are the 12 month period from September of the previous year to August of the current year. Guiot et al. (in Hughes et al. 1982) examine various possibilities of selecting the climate variables to be included in the response function. The use of different numbers of climatic and prior growth predictor variables is considered. A 12 month climate period with seperate vectors for growth persistance is considered to be a valid option in some situations. The choice of climate period to predict growth inevitably depends on the growing conditions and species being considered. The seperation of climate and prior growth in different eigenvectors is preferable both statistically and biologically. Inclusion of seperate monthly climate data from the previous growing season as predictors is unlikely to give valid results for P. sylvestris (hence a 12 month rather than a 14 or 16 month period is used). Physiological studies would indicate that the influence of climate on the following year's growth will begin in September of the previous year when substrate begins to be translocated to the storage organs (Wodzicki 1971). Correlation between the climate variables themselves will tend to invalidate information gained by including monthly climate variables from the previous growing season. The inclusion of prior growth as a predictor will take account of the effect of the previous growing season conditions on the physiological state of the tree. In fact prior growth is likely to be a better estimate of the effect of previous year's climate than the previous growing season climate data itself.

A 12 month period is used, this enables lag effects can be distinguished from response elements. Three years of prior growth are included in the investigation. Since needle retention is upto four years in pines (Bialobok and Zelawski 1967) and the major contribution to photosynthesis is from the current and second-year needles, a three year lag period is chosen as this is likely to be the maximum length of influence on growth directly attributable to climate. The analysis in all cases extends over the 60-year period from 1913 to 1972 (with the 3 years of prior growth 1910-1912 also being included in the calculation). This is the period for which complete climate data are available for all sites.

The results of response function analysis of RW and MXD chronologies from an additional nine locations in Scotland are also included. This work was carried out at Liverpool Polytechnic by D. Cartwright and is reported in Hughes (1986). The sites have been grouped into West coast and East coast sites according to the response function results. Response functions were calculated using temperature and precipitation data for a 16 month period from June of the previous year to September of the current year. The west coast response functions were calculated using temperature data from Achnashellach and precipitation data from Portree, the east coast sites used Braemar climate data. A 60-year period has been used in the analysis from 1911 to 1970. The site details for these nine sites are given below.

Table 4.3

Site.	Code.	Latitude. deg. min. N	Longitude. deg. min. W	Altitude m a.s.l.
East.				
Mar lodge	MAR	57 01	03 34	457
Glen Affric	AFF	57 17	05 00	300
Inverey	INV	57 00	03 35	500
Ballochbuie	BAL	56 57	03 19	381
Dimmie	DIM	56 07	03 20	200
West.				
Loch Maree	LMA	57 31	05 21	100
Coulin	COU	57 32	05 21	250
Plocton	PLO	57 20	05 38	100
Mallaig	MAL	57 00	05 48	50

Table 4.4 summarises the results of all the response function analyses. Results for the seven sites previously described are given for the MXD, MIN, EW, LW and RW. Data for RW and MXD responses are given for the nine additional Scottish sites. The percentage signal due to climate and prior growth is given along with the number of significant eigenvectors included. The results of the east and west Scotland analyses are not directly comparable with the other calculations since a 16 month period rather than a 12 month period has been used. The effects of climate during the previous summer are seperated from the prior growth response when a 16 month climate period is used. MXD gives the best climate response in all cases except at Muddus and Randalstown. A percentage climate signal of 50% or greater is found in the MXD chronologies at most sites above 300m a.s.l. The greatest climate signal is for MXD in the eastern Scottish sites. These sites are located at or near to the altitudinal climatic limit of the species range and thus a high climatic signal might be expected. The east Scotland RW signal is not as strong as the MXD signal and a larger

prior growth element is detected.

The climate response of EW is superior to that of LW at Glen Affric, Randalstown, Muddus and Kielder whereas the converse is true for the sites at Glen Derry, O Frostsjoasen and Chippenham. The correlations between sites (table 3.8) however indicate that LW shows a better regional climate signal than EW. The higher percentage of response function variance in EW attributed to climate may be because a different set of climatic factors may be influencing EW at each site. The best climatic responses in MIN are for Glen Affric, Glen Derry and O Frostsjoasen.

The response function can identify climate growth relationships that may later be used in the calculation of transfer functions that predict climate from tree growth. The temporal stability of the transfer function is tested before it is used for reconstruction. Hughes (1987) verifies the simple relationship between MXD and July-August temperatures for P. sylvestris in Scotland by reconstructing the temperature record for two 80-year periods and verifying this with the actual temperature data. The reconstructions explained 64 and 59 percent of the variance in the actual data. This indicates that temporally stable relationships may be identified in the climate growth response. This would indicate that the response function results are likely to be applicable to the climate-growth relationships in other periods.

The significant response function results for the 12 month period analysis are shown in figure 4.2, the Scottish results are illustrated in figure 4.3.

The MAXIMUM DENSITY RESPONSES show the strongest resemblance between sites. On all sites there is a strong positive response between MXD and July and August temperatures. Spring temperatures (April or May) shows a positive response at most sites. A negative response to late summer and spring rainfall is detected. This may be partly due to the association between low rainfall and high temperatures. There is a negative response to previous Autumn temperature (September) for the Scottish and northern England sites. A positive response on some sites to winter (November and December) temperatures and precipitation is also detected. The results for east and west Scotland in figure 4.3 confirm the findings from the other sites. There is a degree of variability in the responses which serves to indicate that individual site responses must be interpreted with caution. These results also show that some degree of climatic response is found in almost all seasons of the year indicating that for P. sylvestris in Scotland, physiological processes may be going on in the tree throughout the whole year (or that the meteorological data are correlated).

The LATEWOOD RESPONSE like that of MXD is positive to late summer (July and August) temperatures, and inversely related to late summer precipitation. The higher altitude sites also show a negative response of LW to June temperature. A negative RW response to June temperature and an absence of a positive EW response would suggest that high June temperatures were not acting to prolong EW growth at the expense of the LW, but they were affecting LW growth detrimentally. Late winter and early spring temperature (February to April) have a marked positive effect on LW and also on total RW.

The EARLYWOOD RESPONSE is less clear, the climate signal in EW is weaker than for LW at the higher altitude sites. EW responds positively to winter temperatures (December and January) and also to temperatures in the previous Autumn. The eastern Scottish sites show a positive RW response to temperatures from January through to August. A negative response to June temperature has not been detected here. A general negative response to previous summer and autumn temperatures is seen for both west and east Scottish sites. The west coast sites have a high prior growth signal and a low percentage climate signal in the RW chronologies.

The climate signal in the MIN chronologies is also low. MIN does show a generally positive response to previous autumn and winter precipitation. On the higher altitude British sites MIN is negatively affected by winter temperatures (December and January) but a positive temperature response is seen with temperatures in February to April.

Table 4.4. Climatic signals in tree ring chronologies from response functions.

Var.	Site	Prior growth %	Climate signal %	Total %	No. of vectors N	Altitude (m)
MXD	OFR	0.3	49.1	49.4	6	800
	MUD	5.2	14.1	19.3	2	450
	DER	16.0	55.3	71.3	7+2	450
	AFF	0	47.7	47.7	6	300
	* AFF	0.1	57.3	57.4	6	300
	KIE	11.9	47.3	59.2	5+1	200
	RAN	3.1	8.0	11.1	2+1	50
	CHI	2.2	45.2	47.4	3+1	15
	East MAR	13.1	65.3	78.4		460
	Scot AFF	6.7	63.2	69.9		300
	INV	18.3	58.8	77.1		500
	BAL	3.4	68.8	72.2		380
	DIM	14.3	59.8	74.1		200
	West LMA	21.9	42.7	64.6		100
	Scot COU	4.2	49.6	53.8		250
	PLO	0	37.6	37.6		100
	MAL	27.7	62.8	90.5		50
RW	OFR	27.8	32.4	60.2	8+1	
	MUD	11.5	24.6	36.1	3	
	DER	8.0	32.6	40.6	5+1	
	AFF	0	29.7	29.7	4	
	* AFF	3.1	21.9	25.0	4	
	KIE	10.4	26.9	37.3	3+1	
	RAN	26.0	25.4	51.4	2+2	
	CHI	5.2	27.9	33.1	4	
	East MAR	31.8	38.6	70.4		
	Scot AFF	16.6	20.6	37.2		
	INV	18.2	11.6	29.8		
	BAL	33.1	39.7	72.8		
	DIM	48.4	32.3	80.7		
	West LMA	75.9	2.3	78.1		
	Scot COU	57.5	22.2	79.7		
	PLO	31.6	28.3	59.9		
	MAL	57.4	12.3	69.7		
EW	OFR	27.9	21.9	49.8	4+1	
	MUD	4.9	19.9	24.8	3	
	DER	0	34.7	34.7	6	
	AFF	0	32.2	32.2	4	
	KIE	10.3	38.6	48.9	5+2	
	RAN	15.6	39.6	45.2	3+1	
	CHI	-	-	-	ns.	
LW	OFR	4.5	38.5	43.0	5	
	MUD	3.2	15.0	18.2	2+2	
	DER	5.8	49.8	55.6	7+1	
	AFF	3.8	20.6	24.4	3+1	
	KIE	2.8	22.5	25.3	3+1	
	RAN	17.7	14.4	32.1	1+2	
	CHI	4.8	36.5	41.3	4+1	
MIN	OFR	1.1	24.9	26.0	3	
	MUD	-	-	-	ns.	
	DER	0	31.4	31.4	4	
	AFF	0	33.4	33.4	5	
	KIE	0	19.9	19.9	1	
	RAN	0	17.5	17.5	2	
	CHI	-	-	-	ns.	

N = Eigenvectors included in the response function, Climate + prior growth.
* - Recalcuated using Braemar rainfall and temperature data.

Figure 4.1

Stepwise progression in response function analysis.
Glen Derry, MXD, 9 steps.
Significance of predictors and thier lower 95%
confidence limits are shown.

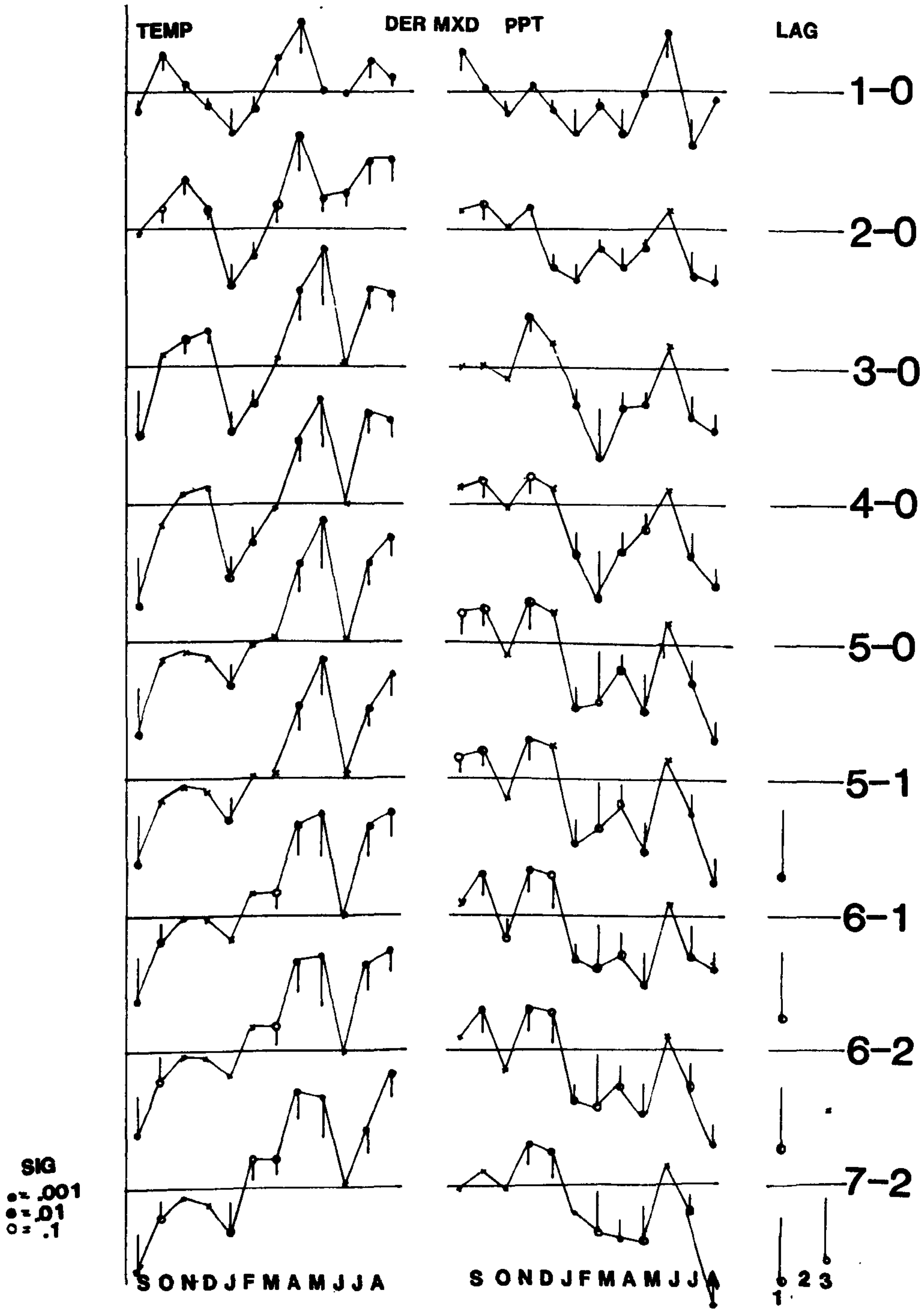

TEMP
DER MXD
PPT
LAG
1–0
2–0
3–0
4–0
5–0
5–1
6–1
6–2
7–2
S O N D J F M A M J J A
S O N D J F M A M J J A
1 2 3
SIG
● = .001
● = .01
○ = .1

Figure 4.2 Significant response function elements for rainfall, temperature and prior growth predictors.

	TEMPERATURE												PRECIPITATION												PG.		
	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	1	2	3
MXD																											
OFR	■						.	.			■	■	■			■	+	●				+		0			
MUD		.		●	●	●		.			■	■	+		o	■					●	o	0	o			
DER	0	.			o	+	●	■	■		■	■				■	+		.	0	o		o	0	o		.
AFF	0				o			●			■	■			■				●		0		0	0			
KIE	0		■		0			■	■	+	●	■	■					.		.	0	■	0	0			0
RAN				●				+		.			●	.			●						.			.	
CHI		.	.	■		0		■	0		■	■	●	■	0	●				0	+	●	0	0		.	
MIN																											
OFR	■			0		.		.			o		■			.		+					.	■			
MUD		●				.			.						●	●	●		+								
DER		●	■	o			●	o		0	.		■	●		■	■				■	0	0	0			
AFF				.	o	■	■			o		0		■	■			●	0			o	o				
KIE				0		■		■		+	.	●	+	■	+			.	+	0	0			.			
RAN					o	.		●		+	●	●		o	.		●							●			
CHI	0		.	.	0	0		■	o	0	0	+	0	+	.	■	●	.		o		●	0	●			
EW																											
OFR			●	■		0		.			●	●	0			.			+	●		0	.		■		
MUD	0	+		●	■	o	+	■			+				+			0		■	+		■	+			
DER				■			0	●			■	0		o							0			0			
AFF	■		o	■		0	+	o	●	●	●	0	0	o	0		●	■	o	o	0	.		o			
KIE			■		■	■			0	0	+	o	0	0	0		o			●	o		0		+		.
RAN	■		0	.	■	■	■	■	0			0	■	■	■	■	0	0	.	.		0	0	■	■		
CHI		.	o		.		.	.	o	.						o				o	.						
LW																											
OFR	■						■	■			■		●				+	■	■				■	o			
MUD	+		o	●	+					0	■	■	o			o	.		■	.		●		0	+		o
DER	0	.		.		0		●		0	+	■		.					o	0		■	o	o			o
AFF	.		.	+			●	●		0	■	■	●	●				●	o			+	.				
KIE		●			●	■	■	■			■	■		o	.	.	.		o				o	0	+		
RAN	■	■	o	.		●	■	+	.	●			■		■	●	.	.		+		.	.	+	■	o	
CHI	.	+	■		.	■	■					●		■	0			0	●		0					o	
RW																											
OFR			●	■	.	.	■				■		0			.		■	■	■							
MUD	0		o	●	■	o		●		0	■	+			+	o		0	.	■		+	0				
DER	o		■		+	●		●		.	■	■	.			■	0				0		o				0
AFF				+	+					.		●	+				+			.			o	o			
KIE	.	■	●		■	■	+	■	0	0			.	0	o			■	0		.	■	o	o	●		
RAN	■	■	0	.	■	■	■	■	0			0	■	■	■	■	0	0	+		■	0	0	●	■	o	
CHI					+			.	o	+			o	●	o				+								

Significance 0 = .001, o = .01, + =+.1, . =-.1
Black squares indicate a positive relationship.
Open squares indicate an inverse relationship.

Figure 4.3
Significant response function elements for rainfall
and temperature functions for Scotland.
(Data from work done by D. Cartwright, reported in Hughes 1986).

```
  TEMPERATURE                     PRECIPITATION                  PG.
  J J A S O N D J F M A M J J A S.J J A S O N D J F M A M J J A S
MXD                              .
M.  O O   O   Ø       Ø     Ø Ø  .          Ø       Ø   O O Ø     1
A.    O       Ø Ø         Ø Ø Ø  .    Ø Ø                         Ø1
I.O   O       Ø             Ø Ø Ø.O       Ø Ø O Ø         O Ø Ø   1-3
B.    O       Ø   Ø   Ø     Ø   Ø.          Ø O       Ø   O Ø Ø   1
D.  Ø         Ø Ø Ø Ø O     Ø   Ø.                      Ø Ø   O       O12
                                 .
L.  O O         O         Ø Ø Ø O.Ø     O O           Ø         O   1
C.  O O                   Ø Ø Ø  .Ø           O       Ø O     Ø
P.              O       Ø Ø Ø Ø  .      O     O       Ø     O Ø
G.    O     Ø O O     Ø O       Ø.Ø Ø O Ø Ø   Ø Ø   O Ø Ø Ø Ø O Ø-3
                                 .
RW                               .
M.  O   O O O         Ø Ø Ø Ø Ø Ø.O   Ø     Ø   O           Ø Ø   12
A.      O         Ø   Ø Ø Ø Ø  .O Ø     Ø     O             Ø     1
I.  O   O O       Ø   Ø Ø Ø Ø  .O Ø Ø   Ø     O             Ø     12
B.  O     O     Ø Ø Ø Ø Ø Ø Ø Ø  .O Ø Ø     Ø   O                   2
D.  O     O O   Ø Ø Ø Ø Ø Ø Ø Ø  .    Ø                     Ø     1
                                 .
L.  O O   O               Ø Ø  .                      Ø             1
C.  O O Ø O Ø   Ø     O     Ø    .      Ø         Ø   O O Ø       O1
P.Ø   O   O                      .O                     O         O1
G.        O                     Ø.                        O       O1
```

Ø = positive element
O = negative element
Significant at 5%.
Significant prior growth (PG) functions shown, (- = negative PG).
M - Mar, A - Glen Affric, I - Inverey, B - Balmoral, D - Dimmie,
L - Loch Maree, C - Coulin, P - Plocton, G - Mallaig.

C. DISCUSSION AND CONCLUSIONS.

a) Interpretation of results.

The results of the response function analysis may be explained in part from our knowledge of tree physiology. Where such explanations are possible, the results of the response function calculations can be considered to represent a real and direct response to climate. The physiological mechanisms summarised in figures 2.2 - 2.5 have been used in the interpretation of the response function results. Table 4.5 summarises the physiological explanations and the evidence for the effects of climate on growth.

The response of trees to climate in the winter indicates that in *Pinus sylvestris*, physiological processes are occuring during the winter months. It is possible that in the relatively mild British winters a certain amount of photosynthesis is taking place on warm winter days. The minimum temperature for photosynthesis to occur has been shown to be about -3°C (Bialobok and Zelawski 1967). The roots may also be active during the winter since soils are rarely frozen. On Swedish sites low temperatures in winter can cause damage to the photosynthetic apparatus in the needles which may not be fully repaired until the following June (Linder and Troeng 1980). The changing response to climate during the winter and the differentiation between high and low altitude sites may be due to the interaction between climate and the physiological changes occurring in the tree.

Warm temperatures in February and March may have a significant effect on the accumulation of reserves in the second-year needles. Warm temperatures in late winter and early spring may mean that there is a good store of carbohydrate reserves in the second-year needles ready for flushing and providing energy for the growth of the new shoot and needles. It has been shown that net assimilation (that is the balance between photosynthesis and respiration) may sometimes be negative at the time of flushing. When a good quantity of stored carbohydrates is available, the length of the new needles and shoot will be greatest. Higher winter temperatures may result in a depletion of carbohydrates as a result of increased respiration. This might occur when photosynthesis is not able to compensate for increased respiration. This could occur when higher than average temperatures occur at night, when warm temperatures are associated with cloudy days and low light levels or when the needles are physiologically unable to photosynthesise efficiently.

High February and March temperatures may induce early flushing. The production of EW coincides with the period of shoot elongation which itself is more or less constant. Early flushing will thus result in an early transition LW production and hence wider LW.

After shoot growth has ceased there may be a lull before active photosynthesis from the new needles commences. High temperatures at this time (June) may be detrimental to growth since they may increase respiration whilst photosynthetic rates cannot be maintained. Since the time of transition from EW to LW may vary from year to year, June may coincide with the period of EW formation, LW formation or the transition period. In Scotland June is generally a dry month and high June temperatures may also be associated with low precipitation and water stress on the tree.

At the time of LW formation, the current year's needles are providing the majority of the photosynthates. If early spring conditions have been favourable, a well developed current year shoot will have formed. The number and length of the current year's needles will thus affect the amount of photosynthesis that can take place whist the LW is being laid down. High rates of assimilation may be associated with wider LW and higher MXD. High temperatures during July and August are generally associated with a lack of cloud cover and greater light intensities. This will also affect the rate of photosynthesis during LW formation. Temperature is known to affect the rate processes in the processes of cell production and development (Ford et al. 1978). High carbohydrate availability may coincide with greater rates of cell production, a wider wall thickening zone, and it will allow the maintenance of a higher rate of cell wall thickening. This would result in a wider latewood and a higher MXD (refer to chapter 2). Low precipitation is associated with high temperatures and a lack of cloud cover and vica versa. July and August precipitation is inversely related to MXD and LW. This implies that the effect of precipitation is a result of the effect on photosynthesis (due to cloud cover) and the rate processes governing cell dimensions (due to temperature). If precipitation was acting through the effect of water stress on the rate of cell expansion, MXD would be inversely related to precipitation but LW would be responding positively to the amount of precipitation. In some years however, when lack of precipitation is causing drought stress to the tree, water stress may result in a reduction in cell diameter (an increase in MXD and a reducion in LW).

The response function results from the work by D. Cartwright indicate that current autumn temperature (September) has a greater influence on

MXD than on RW. September temperatures are likely to have more effect on the wall thickening of the maturing cells than on the number of cells produced. Since wall thickening takes 8-10 weeks, cells produced in July will still be maturing in September.

b) Problems associated with response functions.

Response functions can be used to identify the statistical relationships between climate and growth but it cannot prove that the response is real. The response function elements (in this case the climate factors) need not be directly related to tree growth. Any factors that are correlated with temperature and precipitation may affect the response function relationship. Examples of such factors are, insect attacks associated with particular weather conditions and the effects of water table fluctuations.

It has been demonstrated that the results of single site response functions should be interpreted with care. When response functions are constructed for a number of sites in a geographic region it is possible to use them to identify systematic patterns associated with the climate and growing conditions on particular sites. The differences in climate-growth responses between high and low altitude sites in Britain have been demonstrated as well as differences between west coast and eastern Scottish sites. In a study P. sylvestris and Quercus pubescens for several sites in France, Tessier (1984) was able to identify different populations of each species associated with their patterns of response to monthly precipitation and temperatures. Kienast (1985) also describes a spatial analysis for four regions in Switzerland, Colorado and Cyprus using sites of varying elevation, in dry and moist areas. When response functions are calculated for each site, clear gradations in the response function patterns can be seen as the sites become increasingly dry or higher elevations are reached. Several methods of interpreting response functions are described by Fritts (1976). Cluster analysis has been used for a number of sites in western North America (Fritts 1974).

Interpretation of the significance of single response function elements must be made with care. Blasing et al. (1984) performed simple correlations between the significant growth responses calculated from the response function and the climate variables. They showed that the level of significance of the response function elements has in the past been overestimated. (This is also confirmed by Fritts, personnal communication). The use of summary response functions from several sites will usually eleviate this problem (Gray and Pilcher 1983).

One limitation of response function analysis is that it does not differentiate between the high and low frequency effects of climate on growth. A modification of the response function program can be made to distinguish between high and low frequency variation (Guiot et al. in Hughes et al. 1982, Guiot 1980). The technique involves the use of spectral multivariate analysis. It has proved to be successful in demonstrating the influence of some important parameters not shown by other methods. A sufficient length of data was not available here to perform a spectral analysis.

One problem in interpreting response functions is that monthly weather conditions in any year are often correlated. It is necessary to examine the individual weather patterns for each year to determine if certain hypotheses about the climate growth relationships derived from response functions are sound.

c) Extension of response function study.

While there can be no doubt as to the reliability of the most strongly defined climate growth responses the relationships using parameters other than MXD seem to be less well defined. There may be certain threshold values for the climate variables beyond which there is a growth response. The response function is probably unable to pick up this kind of response if the climatic threshold is reached on only a few occasions during the time period being investigated.

Response functions only indicate the net effect of a climate growth response, the effect of an individual climatic factor may only be apparent in certain years when conditions become limiting. In order to interpret the climatic response in physiological terms it is necessary to examine the effects of climate on growth on a year to year basis. This has been attempted in four regions by Kienast (1985). He considers specific climatic patterns such as cold moist years, warm dry years and cold dry years. The effect on MXD of each type of year is considered on all sites from each region, ranging from the low to high elevation sites and the dry to moist sites. Distinctive spatial dendroecological diagrams can be drawn for each year showing a different pattern according to the type of year. Thus a cold moist year shows increased MXD on the low altitude dry sites and a lower than average MXD on the high altitide sites. The opposite pattern is exhibited in a warm dry year.

In chapter 6 the annual variation in ring density across the whole ring is examined for trees from Glen Affric and Glen Derry. Monthly weather and density are examined on a year to year basis. The results are used to test the hypotheses about the climate-growth relationships derived from the response functions.

Table 4.5 Physiological mechanisms explaining the response function results.

\+ indicates a positive response. A response may be via:
a) an increase in col. 1 causing an increase in col. 3.
b) a decrese in col. 1 causing a decrease in col. 3.
c) both may operate.

\- indicates a negative response. A response may be via:
a) a decrease in col. 1 causes an increase in col. 3.
b) an increase in col. 1 causes a decrease in col. 3.
c) both may operate.

Numbers in brackets refer to the number of significant responses from the total of 7 sites.

CLIMATE	RESPONSE	MECHANISM	EFFECT
EARLYWOOD WIDTH			
Prior autumn, winter temps.	Nov(2) Dec(4) Jan(4)	Photosynthesis affects substrate availability in spring.	+
Spring temperature.	Apr(4) May(1)	Rates of cell production and enlargement in spring.	+
Early spring precipitation.	Apr(5)	Rate of cell expansion in spring.	+
Late spring precipitation.	May(3) Jun(3)	Date of transition to LW production.	-
LATEWOOD WIDTH			
Late winter temperature.	Feb(4) Mar(5)	Dates of commencement of EW and LW production.	+
Spring temperature.	Apr(5)	Area of current year foliage, thus summer photosynthesis.	+
Early summer precipitation.	Jun(3)	Rate of cell expansion, soil moisture availabilty.	+
Summer temperature.	Jul(5) Aug(5)	Rates of cell production and expansion. Cell prod. via growth regulators and substrate.	+
Summer precipitation.	Jul(4) Aug(4)	Cloud cover and temp. affect photosyn. and cell production.	-
MINIMUM DENSITY			
Prior autumn temperature.	Sep(2) Oct(1) Nov(1)	Storage reserves available in spring.	+
Winter temperature.	Feb(3) Mar(2)	Storage reserves available in spring. Photosynthetic capacity of old needles.	+
Spring temperature.	Apr(3)	Rates of cell production and respiration.	+
Spring ppt.	Apr(2)	Rate of cell expansion.	-
MAXIMUM DENSITY			
Winter temperature.	Dec(3) Feb(3) Mar(2)	Efficiency of old needles and storage reserves > spring growth and current year needles.	+
Spring temperature.	Apr(7) May(2)	Current needle area.	+
Spring precipitation.	Apr(3) May(3)	Cloud cover and temp. affects spring photosynthesis > summer substrate avail. & soil moisture.	-
Summer temperature.	Jul(6) Aug(6)	Rates of cell prod., expansion and thickening. Photosynthesis> substrate avail.>wall thickening.	+
Summer precipitation.	Jun(2) Jul(5) Aug(6)	Cloud cover and temps. Opposite effect to temperature.	-

Chapter 5. INVESTIGATION OF SUB-FOSSIL PINE.

A. INTRODUCTION.

Studies of the vegetation changes since the last ice age have been possible by investigating the plant material forming layers in peat accumulations. Pollen analysis of peat and other sedimentary formations such as lake deposits has also yielded valuable information on vegetation history (Godwin 1956). Tree stumps are often found in distinct strata in the peat layers indicating that at one time conditions were suitable for tree growth on the peat. The cold temperatures and anaerobic conditions in the peat inhibit decay of the stumps and have allowed the stumps to be preserved where peat growth has been rapid. This preserved timber is termed sub-fossil wood, since it will remain in the peat almost indefinately without decaying if left undisturbed. Generally sub-fossil wood in Europe is of relatively recent origin, upto 10,000 years old. Radiocarbon dating on stumps of Agathis Australis preserved in peat in New Zealand indicate that sub-fossil wood here is 40,000 years old (Ogden 1982, in Hughes et al. 1982). The true petrified forests from the Carboniferous era however, are millions of years old. In Britain sub-fossil timber of several species has been found including oak, scots pine, birch and willow (Pilcher 1973, O'Sullivan 1977).

The occurrence of sub-fossil pine at high altitudes in the Cairngorm mountains of Scotland is described by Pears (1968 and 1970) in a study of post-glacial tree-lines. Radiocarbon dating of stumps was carried out in conjunction with pollen analysis to place the pine layer a the stratigraphic sequence (Birks 1975). The sub-fossil trees from blanket peats on the island of Lewis have been studied by Wilkins (1984). Radiocarbon dates of pine stumps on Lewis were found to range from 4870 yr. B.P. (before present) to 3910 yr.B.P. The occurrence of sub-fossil remains from the south Pennine uplands in England is described by Tallis and Switsur (1983). In none of these studies was any year by year tree-ring measurement undertaken. The descriptions indicate that the material collected was not sufficiently well preserved for tree-ring sequences to be distinguished.

Dendrochronological studies on sub-fossil pines have been carried out in Ireland (McNally and Doyle 1984, Pilcher 1971), south west Scotland (Ward et al. 1987) and the Netherlands (Munaut 1966a, b), in all cases indicating the potential for further study in this field. An extremely well related set of ring-width chronologies has been produced by Munaut from a group of recently exposed pine stumps preserved under silt at

Terneuzen on the coast of the Netherlands. The stumps were all well preserved, tree-growth had ceased when the area was flooded by the sea in 300 B.C. The trees were crossdated simply by matching the graphs of ring-width. The tree-ring series were sufficiently similar to permit reliable crossdating by this method. A mean chronology 230 years in length, containing 52 contemporanous trees was constructed. All trees were 100-200 years old and it appeared thar only one generation of trees grew here.

McNally and Doyle (1984) used dendrochronological methods to produce three site master chronologies up to 500 years in length from pine stumps in the Irish Midlands. Nearly 50 pieces of timber were crossdated, with radiocarbon dating placing the chronologies from 4000 to 3500 years B.P.

A large number of sub-fossil pine and oak timbers exposed by peat cutting and road building in Northern Ireland have been collected by Dr. J. R. Pilcher and colleagues from Queen's University, Belfast (Pilcher 1973). Oak material has been crossdated successfully over wide areas. It has been used in conjunction with bog oaks from Germany and northern England to produce an 7272-year chronology from 5210 yr. B.C. to the present (Pilcher et al. 1984). Radiocarbon dating on the pine material indicates that the trees were growing intermittently at different sites between 4000 and 9000 yr. B.P. The positioning of the pine stumps in the stratigraphic sequences produced from pollen diagrams is described by Pilcher (1973). Many of the stumps are extremely well preserved and ring-width measurements on many hundreds of samples has allowed crossdating of some specimens and the production of several short chronologies, upto about 300 years in length. It was decided to use some of the best samples from the sites in Northern Ireland for the initial study of sub-fossil pine.

After the last glaciation P. sylvestris began to colonise much of Britain. Initially the reinvasion was slow. The origin of the Caledonian pine may have been from invasion from the continent as the ice receded, there is also evidence that recolonisation occurred from refugia in the outer Hebrides and the west coast of Ireland where isolated areas of scots pine had survived the ice age (Moore 1987, Kinloch et al. 1986). The greatest extent of pine growth in Britain was in a short period during the Boreal era, 4000-7000 yr. B.P. This is an important time in our recent climatic history, coinciding with a relatively warm dry period (the so called altithermal) when peat bogs dried out sufficiently to allow substantial tree growth.

Dendroclimatological studies on sub-fossil trees may yield valuable information on temperatures during this period. Maximum density in pines is known to yield more information about temperatures than ring-width at high altitude trees (Hughes et al. 1984, Hughes 1986). Temperatures during the altithermal might be similar to those expected in the near future due to the effect of increased carbon dioxide insulation of the upper atmosphere (Kellogg 1987).

The main aims of this part of the work are as follows;

1) To determine whether it is possible to carry out density measurement on sub-fossil pine.
2) Attempt to increase the length and number of trees included in the Irish sub-fossil pine chronology using crossdating based on maximum density.
3) Locate a high altitude site in Scotland for the production of a high altitude sub-fossil pine chronology.
4) Consider how the ring-width and density properties of sub-fossil pine chronologies compare with those of modern trees.
5) Attempt to relate properties of chronologies from trees on sub-fossil sites with those of modern trees growing under similar conditions with a known response to climate.

B. COLLECTION AND CROSSDATING.

a) IRISH MATERIAL.

i) Methods and Results.

Sub-fossil pine from Ireland was obtained from four peat sites at Sluggan, Derrycrow, Sharvogues and Fallahogy. Peat cutting had exposed the material which occurred in distinct strata at levels between 0.5 and 2.0m below the surface of the peat. Usually all that is preserved is the base of the stump and some of the larger roots. Sample collection by researchers from Belfast involves cutting a transverse disc from the stump with a chainsaw, as high up the stem as possible to reduce the effects of the influence of the roots but avoiding any rot. Many of the samples still included bark on the outside, which had improved the state of preservation. Much of the material was very resinous which had again helped to preserve it. The stumps could be upto a meter in diameter. Ring counts indicated that many of the trees were 200 years old or more. On some specimens rings were upto 6mm wide, but on most there were periods of very poor growth and sections with barely discernable rings, sometimes only one cell wide or absent along part or all of the ring.

The procedure for ring-width measurement and crossdating is described in chapter 3. Ring-width measurements had been made in Belfast on a large number of trees from these four Irish sites, numbering about 150 trees in all. Three radii per tree had been measured and mean-tree ring-width series had been produced where crossdating between radii made this possible. Crossdating between trees had been attempted visually, by matching the graphical plots and statistically, using the crossdating programme CROS. Crossmatching between trees was poor or non-existent in most cases, although some significant 't' values were found. A number of tentatively crossdated series from each site had been found. It was hoped that by measuring density on these samples it might be possible to confirm the ring-width dating and improve crossdating to produce robust mean density chronologies.

A set of 15 trees from Derrycrow, 12 trees from upper and lower levels at Sluggan, four from Fallahogy and two from Sharvogues were selected for ring-width and density measurement in Liverpool. Two distinct layers of pine stumps were found at Sluggan, at different levels in the peat. Remeasurement of ring-width on the Derrycrow trees yielded a master site chronology 211 years in length, based on the ring-width series of seven trees. Four of these seven sections are from fallen trunks rather than stumps. The remaining eight trees did not crossdate and could well not be contemporaneous. Figure 5.1 shows the positions of overlap of the seven trees constituting the ring-width master. These crossdating results were the same as the tentative crossdating that had previously been done at Belfast. A radiocarbon date on a piece from the 10th to 20th year of the chronology gives a date of 4635 +/- 55 years B.P. (Smith et al. 1973). Similarly for the site at Sluggan, six trees from the lower layer of stumps have been crossdated, and are shown in figure 5.1. A mean ring-width chronology 235 years long has been produced. The radiocarbon date on a piece from the early part of the chronology from Sluggan lower was 7095 +/- 115 years B.P. The remaining trees could not be significantly crossdated on ring-width.

ii) Discussion.

The situation on raised bogs in the Irish Midlands, described by McNally and Doyle (1984) shows a high proportion of material crossdating over a relatively short period. It is suggested that the occurrence of pines on the bog coincided with a raising of the bog surface above the water table, when the peat dried out sufficiently to allow the trees to grow. As it dried the trees would respond increasingly to the prevailing climatic conditions and less to the changes in water levels within the bog. This might suggest that part of a chronology at any site may include a regional climatic signal and thus be potentially crossdateable with other sites. Bog oaks are known to crossdate well between sites, suggesting that oaks probably grew in drier areas than the pines. Crossdating between sites may depend on the regionality of the changes in bog hydrology. The site at Glashabaun, (McNally and Doyle 1984) contained pines for a period of 500 years, hence regeneration was occurring. Radiocarbon dates indicate that these trees grew between 4000 and 3500 yrs. B.P. which is later than the trees from the Northern Irish sites. The site at Terneusen on the Belgian coast (Munaut 1967) only supported one generation of trees. Wilkins (1984) considered that a catastrophic change in climate resulted in the demise of the pines and a sudden increase in the rate of peat growth on the island of Lewis. A possible explanation for the decline of pines on a peat bog site is an increase in the height of the bog water table. Flooding causes a lack of aeration to the roots. The roots die back because they cannot respire, at the same time acid conditions in the soil result in the transformation of nitrogen into toxic componds, resulting in further root dieback. This would also reduce seed germination and survival as well as affecting the growth of the mature trees (Kozlowski 1985). The occurrence of three layers of pines in Sluggan bog suggests that intermittent drying of the bog surface had occurred. This interpretation is supported by the presence of layers of moss peat which occur under these conditions (Pilcher personnal communication). There is no additional information on the vegetation associations in the pine layers in the Northern Irish peat. It is still also not certain how widespread these changes in bog hydrology were. McNally and Doyle (1984) suggest that these phases of drying accompanied by tree growth occurred at different times in different areas.

The prevalence of sections of trunks rather than stumps in the crossdatable trees may be because sections from low in the tree bole are more strongly affected by local water table fluctations and growing conditions around the individual tree which may mask even a common site signal.

The evidence would suggest that there may only have been a short period (perhaps only one generation) of pine growth on the Derrycrow site and at each level on the Sluggan site. The bogs may never have dried out sufficiently during this time for the trees to be influenced by yearly weather conditions. The primary influence on growth was bog hydrology. The lack of crossdating may be primarily because the sections are mostly taken from stumps. The growth of annual rings in this part of the tree is strongly influenced by root growth and the effects of prevailing climate conditions are minimal.

b) SCOTTISH MATERIAL.

i) Methods and Results.

In Scotland preserved pine stumps occur over a wide area and sub-fossil remains can be found almost everywhere that peat is present, except in the far North which was probably beyond the range of the pines in the Boreal era. Pine stumps can be found on sites upto 790m a.s.l in the Cairngorms (Pears 1968, 1970). Peat growth was generally much slower in Scotland than in Northern Ireland, especially at higher altitudes and hence the sub-fossil stumps have not been as well preserved, since decay began before the stumps were fully buried in the peat (Birks 1975). Pine stumps are rarely more than a meter below the peat surface and in many places they have been exposed where the peat is eroded. Further North where growth of deep peat was more extensive, P. sylvestris was at the northern limit of its range. No pine remains have been found on the east coast north of the Dornoch Firth. The most northerly site investigated was at the Aultnamain Hotel on the Struie (GR. NH 665 813), where the stumps rarely exceeded 10cm in diameter and were not more than 100 years old (although under 1.5m of peat). Map 5.1 shows the locations of the Scottish sites.

A fairly extensive exploration was carried out to locate possible sites in the Cairngorm mountains and along the Pass of Drummochter, 30-40 km south of Inverness. Areas where peat had recently been removed by construction work, forestry operations and natural erosion were explored. An accessible site of well preserved stumps could not be found. Although sub-fossil pine was seen in most areas, it rarely constituted more than parts of the upper root crown.

A large scale excavation of sub-fossil material, exposed by forestry operations, from further south on a moderate altitude site in Tayside had been carried out by Dr. R. Ward from City of London Polytechnic (Ward et al. 1987). Samples were obtained from this collection, consisting of 52 trees from two sites, Corrie Sheilich (GR. NN 350 465) and Clashgour (GR. NN 256 425) 305m and 195m a.s.l. respectively (Map 5.1). These pieces were well preserved but small, 10-30cm in diameter. Many of them showed great variability in ring-width between radii, with frequent discontinuous rings. Much of the wood was from just above the root crown, which may have accounted for this.

The Scottish material from Clashgour and Corrie Sheilich differed from the Irish pine. The material was often smaller in diameter, less resinous and contained fewer rings. The trees were on average 100 years old compared with specimens frequently over 200 years old on the Irish sites. The major work on the material from Rannoch has been carried out by Dr.R.Ward at the City of London Polytechnic. Several hundred samples have been obtained from the two sites but only a small number of trees have been tentatively crossdated. Remeasurement of ring-widths on 27 trees from Clashgour and 24 from Corrie Sheilich was carried out by myself in Liverpool. Three radii were measured on each section. There was limited statistical evidence of crossdating between trees for five ring-width series from Clashgour and four series from Corrie sheilich. By performing x-ray densitometry on these nine trees it was hoped that it could be determined if crossdating using MXD would improve and confirm the crossdating between trees. It was found that the wood was not sufficiently well preserved for the x-ray densitometry procedure to be carried through. Thin sections could not be cut from most of the discs because there was too much fracturing at the ring boundaries. Density was successfully measured on two radii from three of the trees. It has been possible to compare the crossdating between radii for ring-width and MXD. In all cases the MXD series does not crossdate as well as ring-width between radii. One might infer from this that MXD would less effective than ring-width measurement for crossdating between individual trees. This is similar to the situation with the Irish sub-fossil pines.

ii) Discussion.

There are several factors that could account for the lack of crossdating. First there is the problem with missing rings; when comparing the ring-width measurements between radii periods of very narrow and absent rings were often encountered over part of a series. If rings are not absent on all radii it is possible to locate the positions of absent rings, where rings are missing on all radii, it is not possible to identify them. The marked asymmetry of radial growth is partly because the discs were taken close to the root buttress area. The samples are small, in some cases with less than 100 rings preserved. Material from the base of a tree is likely to be more strongly affected by the growth of the roots (and hence local water regimes) than the portion nearer the tree crown (which is the major interceptor of a climate signal). The ring patterns suggest there were periods of good growth followed by long periods where the rings were very narrow and growth was more or less non-existent. This type of ring pattern is likely to be due to the effects of local hydrological factors, suppression by shading or tree tilt rather than the effects of changes in climate.

Differences of over 1000 years in the radiocarbon dating between stumps only 10m apart on Scottish sites has been found. This has been attributed to a low intensity of sampling (Birks 1975). This would suggest that several generations of trees may have been growing on the Scottish sites. A low stand density and very slow growth (with periods of missing rings in the lower tree bole) may attribute to the lack of crossdating. Several generations of trees may have grown at the Tayside sites, reducing the chances of finding contemporaneous trees. No radiocarbon dating has been done on the Tayside trees. Pollen anaylsis carried out at the City of London Polytechnic indicates that pine forest was present at Clashgour as early as 6500 yr. B.P. There was continuous pine growth on this site for a period of 2000-3000 years after this (Ward et al. 1987).

There was a decline in the pine forests and widespread blanket bog formation about 4000 B.P. over much of Scotland (O'Sullivan 1977). It was probably not accompanied by as rapid an increase in the rate of peat growth as in Ireland since conditions were cooler, hence substantial decay of the stumps occurred before they were buried in the peat. It is considered that in the north west of Scotland this occurred before the impact of man. In the eastern Highlands it appears that it was largely human activity which led to the destruction of the forests (O'Sullivan 1977).

Map 5.1

Sub-fossil pine in Scotland.
Striped area indicates the suggested maximum extent of pine dominated forest in the Scottish Highlands (from McVean and Ratcliffe 1962). Black area are remnants of native pinewoods. Glen Derry (DER), Glen Affric (AFF) and Coulin (COU) have been studied.

X - Areas explored for suitable sub-fossil pines.

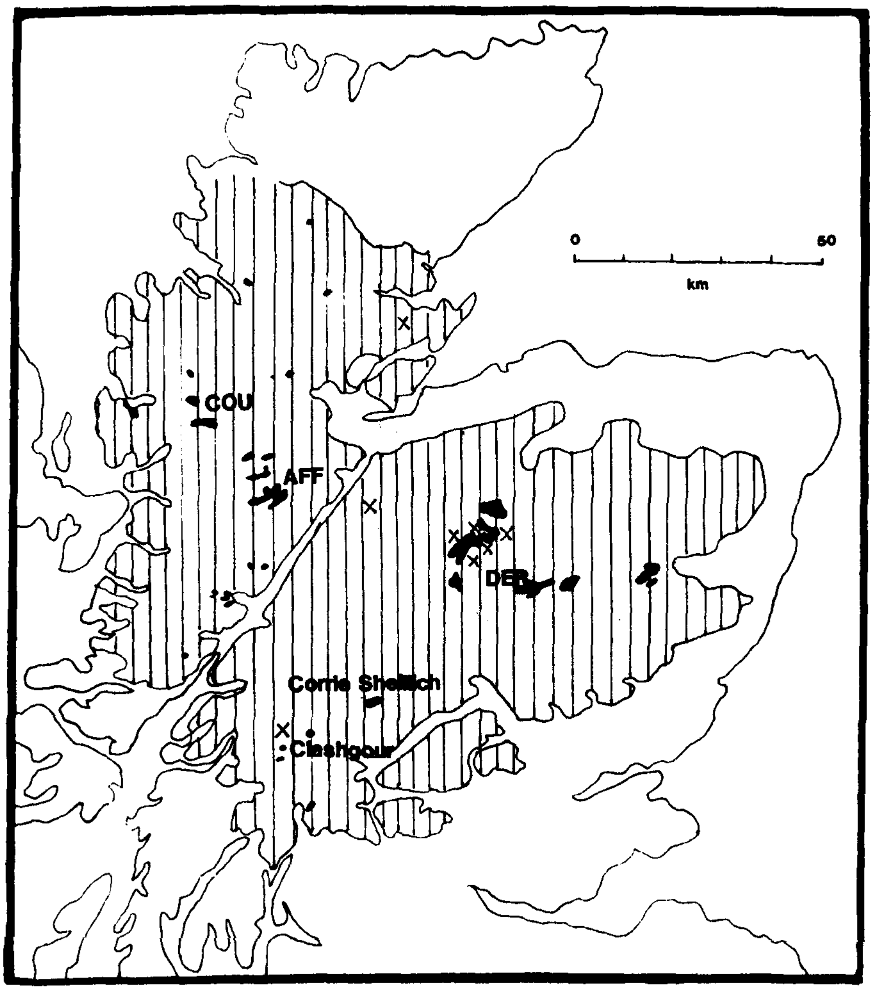
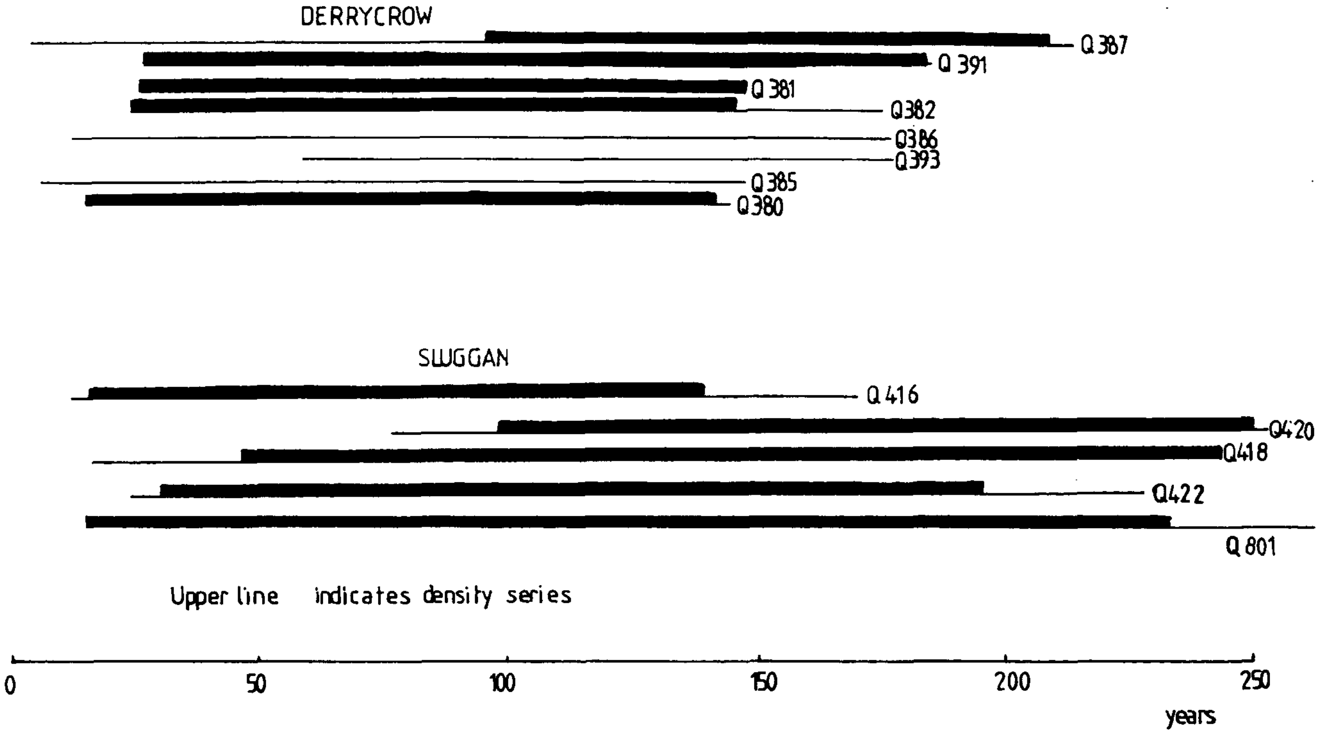

0
50
km
COU
AFF
DEB
Corrie Sheilich
Clashgour

Figure 5.1

Positions of overlap of sub-fossil trees.
Sluggan and Derrycrow, Northern Ireland.

Positions of overlap of subfossil trees



Upper line indicates density series

C. COMPARISON OF PROPERTIES OF SUB-FOSSIL AND RECENT SCOTS PINE.

a) Densitometry.

Details of the method of density measurement and recording are given in chapter 6, section B. It was demonstrated that densitometry could be successfully performed on some sub-fossil timbers but that it did not give improved crossdating.

X-ray density was measured on a total of 33 trees from four Irish sub-fossil sites and successfully on three trees from Tayside in Scotland. All trees had previously been measured for ring-width and some had been tentatively crossdated. One radius per tree was x-rayed for the Irish material (two for the Scottish). There was inevitable loss of some portions of the sample during the resin extraction and cutting processes. The correlation coefficients obtained for crossdating between trees using ring-width measurements from the densitometry scan were slightly lower than those obtained by crossdating the original ring-width series. The lengths of the series obtained by densitometry were shorter due to loss of material during resin extraction and cutting. Only one radius per tree was used which had a small effect in reducing the correlation coefficient.

Density measurement on sub-fossil material poses several problems. Sub-fossil sections have a tendency to fracture at the ring boundaries when cut, thus the lengths of the pieces for densitometry are reduced. Not all the material is well preserved especially near the outside of the section. Preservation is often adequate for the ring boundaries to be distinguished even though much of the cell structure is no longer present. Extraction of resin is also difficult. Often the better preserved pieces are very resinous. If the extraction process is carried on for too long it will denature the cell walls as the cellulose breaks down. Resin is more opaque than wood tissue to x-rays and its presence would lead to meaningless density readings. Periods of several decades when the rings are very narrow are frequent in sub-fossil trees. These periods may crossdate on ring-width, but the density values are not accurate using the present system of measurement since the rings themselves are only a few cells wide. Use of a logarithmic calibration wedge in the densitometer which enhances small density values so that small rings can be measured has been tried successfully on modern pine material and it is found to help in overcoming this problem. This facility was not available when the sub-fossil pine was being measured.

b) Comparison with modern sites.

There are no living trees growing on any of the sites in Northern Ireland where sub-fossil pines are found. In fact there are no native pinewoods remaining in Ireland. The nearest area to the sub-fossil sites where trees of a reasonable age are growing on peat, is a location near Randalstown. It is a small area of scots pine woodland remaining by the edge of a new road. Only about 20 trees are growing here, they are all suffering from the effects of disturbance due to wind blow, competition and soil disturbance.

Four other modern British chronologies have been produced from trees growing on peaty soils (refer to Chapter 3). Chippenham Fen is on fenland in the east of England, these trees might be expected to show similarities to trees growing on raised bogs in Northern Ireland since tree growth here may be affected by fluctuations in the water table. Both are low altitude sites.

The Scottish sites on peaty podsols are altitudinal tree-lines. Sub-fossil pine remains are found at these sites although the tree-line was at a higher altitude during the Boreal era. Temperate is the primary factor limiting the tree-line in these area. It might be expected that the properties of sub-fossil pines would be similar to these trees if temperature was the primary factor affecting the growth of the sub-fossil trees.

The ring-width and density series for Sluggan and Derrycrow were standardised and chronology statistics obtained using the FSTAND program described in chapter 3. The properties of the sub-fossil series using the five parameters MXD, MIN, EW, LW and RW are compared with those of the modern tree ring series. Table 3.4 summarises the correlation statistics between the individual trees from FSTAND. The chronology statistics are given in tables 3.6 and 3.7, showing the correlation between variables.

Table 3.4 gives the mean correlation coefficient between trees (r) and the Expected Percentage Signal (EPS) for the five parameters. Both mean r and EPS are greater for the RW series than the MXD series on the sub-fossil sites. This is only true of the modern trees at the two low level sites, Chippenham and Randalstown. However whereas Chippenham and Randalstown give mean r's of .291 and .216, Sluggan and Derrycrow give values of .395 and .470 for RW crossdating. EW also crossdates substantially better than LW at Derrycrow, which is similar to the two Swedish sites. The sub-fossil trees crossdate better than Chippenham and Randalstown using MXD, but not as well as any of the higher altitude sites. With respect to crossdating between trees using the five ring-width and density parameters, the sub-fossil trees behave differently from trees on any of the other sites.

Table 3.5 gives the mean sensitivities and serial correlations for the five tree-ring parameters. Mean sensitivity for the sub-fossil trees is generally lower for all parameters than for the modern sites. This suggests that there is less short term variation in the sub-fossil chronologies. The serial correlation is much higher than on any of the modern sites. Growth is strongly related to that of the previous years. Visual comparisons of the ring-width plots indicates that the long term trends are synchronous between trees. This suggests that growth was being affected by water table fluctuations which impose long term fluctuations on growth.

Figure 3.3 gives EPS for different filter lengths. Whereas EPS decreases with filter length on the modern sites, there is an increase in EPS for the sub-fossil series. Both MXD and RW behave similarly suggesting that the same periodic fluctuations are affecting these two parameters. EPS generally increases with increasing filter length suggesting that there may be long-term periodic fluctuations in growth. These sites may in fact be constantly changing throughout the time period of the chronology. Conditions for growth were becoming less and less favourable as time went on, until eventually the trees stopped growing altogether and peat accumulation again took over. The rings are extremely narrow towards the outside of many of the trees indicating very slow growth.

Table 3.6 shows the correlations between the density and ring-width variables. There is a high correlation between MXD and RW on the sub-fossil sites. This suggests that maximum latewood density and ring-width are governed by similar factors. At the higher altitude modern sites (Muddus, Glen Derry and Glen Affric), RW and MXD are also highly correlated. Response functions indicate that this is due to the effect of temperature on both these variables. Temperature is not neccessarily the factor influencing sub-fossil pine growth.

On these raised bogs of the Irish sub-fossil sites the primary influence on growth is probably the water supply. If the water table rises too high the roots may become waterlogged and some of the roots may be killed, as is the case with living Pinus contorta on waterlogged sites in Scotland (Miller 1984). Tree growth is retarded not only during the wet period but also for a period following this when roots are recovering. If the water table in the peat drops, the peat dries out, aeration of the roots is increased resulting in improved tree growth. Eventually if the peat dries further, growth will be affected by current climate conditions. It is likely that such relatively dry conditions were never attained at the two Northern Irish sub-fossil sites. The sites at Chippenham and Randalstown are relatively dry peat sites. The trees at Chippenham may have been affected by water table fluctuations as a result of the opening and closing of the lock gates. There are unfortunately no data available on these changes.

D. CONCLUSIONS.

Sub-fossil pine is abundant throughout much of Britain where there are deposits of peat. In Scotland and Ireland it dates largely from about 8000-4000 years B.P. The material is well preserved where peat growth has been rapid, as in many parts of Ireland. Evidence suggests that in Ireland trees grew on many sites for only a few hundred years when the peat dried out sufficiently. Thus trees from a site are likely to be contemporaneous. The well preserved specimens where rings are not too narrow are suitable for densitometry. Such material has been found in lowland peat bogs in Northern Ireland.

In Scotland peat growth was too slow at higher altitudes to preserve much other than the roots and basal part of the stump. Several generations of sparsely distributed trees may have grown on many sites, hence a lack of crossdating between trees on a site may be because they were not growing contemporaneously even if the timbers are found in close proximity. No Scottish sub-fossil trees suitable for densitometry have so far been located. Ward et al. (1987) suggest that the most promising sites for finding crossdatable pine in Scotland would be in isolated locations where trees grew for only a short period. Physical and chemical analysis of the sub-fossil wood and comparison with modern analogues may also yield valuable information on the conditions prevailing during the Boreal era.

The problems of crossdating sub-fossil pine have been discussed. Many of the problems are due to the fact that the material is from the root buttress area. Sections of fallen logs are found to crossdate better than stumps.

The statistical properties of sub-fossil pine indicate that the trees from Sluggan and Derrycrow in Northern Ireland are quite different from any growing on the modern sites that have been investigated. The sub-fossil chronologies are largely constructed from root buttress material whereas the modern trees are produced from cores at breast height. This may account for some of the variation in statistical properties. The sub-fossil chronologies show long term continuous trends in growth as well as some shorter period growth fluctuations. All variables are highly autocorrelated from one year to the next. RW gives better crossdating than MXD although they are strongly positively correlated. Local site conditions such as water table fluctuations are likely to have been the main factors influencing tree growth.

Deductions about past climate from sub-fossil pine are thus at present limited to inferences associated with our knowledge of the growing conditions necessary for P. sylvestris to survive and the nature of the material. Further attempts to relate the growth of scots pine to that of oak may be profitable. Crossdating between modern oak and pine is occasionally possible (Pilcher, personal communication). It may be possible to crossdate the floating P. sylvestris chronologies with the oak chronologies now that the oak chronology has been extended back before 7000 yr. B.P. (Pilcher, personnal communication). The dendroclimatic information obtainable from both oak and pine chronologies considered together may be of additional value.

Chapter 6. EXAMINATION OF DENSITY VARIATION.

A. INTRODUCTION.

The strong link between maximum density (MXD) and July/August temperatures in Pinus sylvestris L. forests in Scotland and Scandinavia has been used very successfully to produce reconstructions of past temperatures from spatial patterns of tree-ring width and maximum density (Hughes et al. 1984, Hughes (1987), Briffa et al. 1987). The physiological causes of this response are not fully understood. Response function analysis suggests that the climate-growth relationships are moderately complex (Chapter 4, Hughes et al. 1982). The results in chapter 4 also demonstrate that the climate-growth response varies between sites.

The procedure of density measurement and recording using x-ray densitometry is described first. It is shown to be feasible in terms of data storage capacity to record the whole density curve for moderately narrow rings (1.2mm) from high altitude Scottish Pinus sylvestris. Systematic densitometric measurements in the past have generally been confined to recording only the maximum and minimum densities, earlywood width and latewood width for each ring. Several studies have been made using other density parameters. Huber (1976) uses not only maximum and minimum density but also mean density and percentages of the ring above three fixed density levels in a dendroclimatological comparison of P. sylvestris sites in eastern France. Indices such as the number of 'significance years' (in which a given percentage of the trees all exhibit an increase or decrease in density in the same direction) are used to compare the density parameters. MXD still proved to be the most useful parameter for crossdating between sites.

Kienast (1985) examines the characteristics of the density variation across the ring for several conifer species including P. sylvestris. Scots pine tends to show an abrupt change in density between earlywood and latewood. The density of the latewood is uniformly high in pines and the peak in density can be at any point in the latewood, not necessarily at the end of the ring as in many conifer species.

The microanatomy of cell structure is considered. The variations in cell wall thickness and lumen size across the annual ring are described. The calculated percentage wall area is compared with the x-ray density and a linear relationship between the two is found.

Using trees from high altitude sites in Scotland, systematic measurement of cells of P.sylvestris has been undertaken. The technique was developed in Germany by Diaz-Vaz et al. (1975). It has been used in a subsequent study of P. sylvestris growing at low altitude near Hartheim by Merkel (1984). A set of 10 trees were chosen from this site. Measurements of lumen diameter and wall thickness were taken progressively along ten files of cells within each ring for a period of seven years from 1973 to 1979. Density was calculated from these measurements using a formula which assumed the cells to be rectangles in discrete cell files. The calculated density was strongly correlated with density measured by x-ray densitometry. It was possible to determine how wall thickness, lumen diameter and density were changing across the rings. The density, wall thickness and lumen diameter curves for each year were plotted against the mean curves for each of these parameters. The annual deviations from the mean density pattern were significantly different. These differences could be attributed almost entirely to changes in cell wall thickness, with lumen diameter having a small effect. Deviations in cell size were found to be related to the amount of precipitation in the growing season for these trees and not to temperature or the amount of solar radiation. It was concluded that the water regime caused changes in density by its effect on cell diameter.

The trees from Scotland growing near the altitudinal limit of P. sylvestris are known to be influenced primarily by growing season temperatures rather than the amount of precipitation. Ring-width and hence the number of cells per ring is about a third that of the German trees (rings on average are 1.2mm compared with 3.5mm in the German trees). The initial microanatomical investigation showed that it was possible to construct 'Merkel type' wall thickness, lumen diameter and density profiles for the Scottish trees.

Image Analysis equipment has been used to enable a large number of sections to be scanned and to enable properties of the cell shapes to be measured and recorded. The potential and limitations of the image analysis technique are described. It was not feasible to obtain sufficient replication and a long enough run of years for the systematic patterns of wall thickness and lumen size measurements to be analysed quantitatively. However this work has enabled the relationship between cell dimensions and density to be explored for a limited number of rings.

The systematic variation in density across the annual ring has been studied using x-ray density measurements. In order to standardise the 'density profiles' for each year, cubic splines have been fitted to the data. Density profiles for an 80-year period from Glen Affric have been constructed. The statistical and graphical properties of the density profiles are described. The density profiles are considered in relation to the findings using response functions (chapter 4) and current physiological knowledge (chapter 2).

The aims of this part of the work are as follows.

1) To investigate the relationship between density and cell dimensions along the ring.
2) To study the density pattern along the ring in order;
   a) to examine the relationship between maximum density and the density pattern of the rest of the ring.
   b) to identify density patterns associated with a response to climate.
3) Relate the findings to the response function results.
4) Attempt to explain the climate-density response in a physiological context.

B. DENSITOMETRY MEASUREMENT AND RECORDING.

An account of x-ray densitometry, equipment testing and density verification, using the apparatus at Liverpool is given in Milsom (1979), although this work predates the installation of an Apple computer. The procedure of density determination is outlined here under the following headings: extraction and sample preparation, cutting, x-raying, densitometry and data handling.

a) Extraction and sample preparation.

Before x-raying, any resin and impurities in the wood must be extracted. Increment cores are small enough to be cleaned without cutting. Where sections are being used, radial pieces must be cut from the section. This is done using a small electric bandsaw. These pieces should not exceed 1cm x 1cm in cross section and they are cut radially, as near perpendicular to the grain as possible. Specimens are labelled with indian ink, the samples are boiled in water for three to six hours (depending on their size) to soften them, help remove trapped air and remove any water soluble extractives. The wood is then refluxed using a Soxhlet apparatus in 95% ethanol for about 48 hours.

Samples are mounted on wooden blocks using a strong balsa cement prior to cutting. The cores or sections are mounted with the grain angle horizontal. It is then usually neccessary to sand down the surface of mounted sections to obtain a level surface above the mounting block. A special jig has been made for cutting sections or cores (plate 6.1). A small twin blade circular saw mounted on a Bridgeport milling machine is used for cutting. It incorporates two hollow ground, metal slitting blades, 40mm in diameter with 200 teeth, set at 1.0, 1.2 or 1.6mm apart according to the material. The block is held firmly in the jig and the revolving saw moves along the sample at a rate of 10mm/s. The angle of the block can be changed relative to the direction of movement of the saw blades. It is important to ensure that the wood is cut at right angles to the fibre direction. The revolving saw blades are passed along the sample two or three times, cutting deeper at each stage. Great care is needed to prevent the blades sticking and breaking the wood. If the blades become too hot or if a small piece of wood becomes caught between them, the distance between the blades will increase, and the thickness of the section will not remain constant. This is one of the major problems associated with this method of cutting.

After cutting, the samples are prised out from the blocks using a knife, labelled and layed out in trays. The thickness of the samples is measured using a screw guage micrometer, three measurements are taken along the length of the sample. If the variation in width is greater than +/- 10%, due to problems mentioned above, samples must be broken so that variation on any individual piece is not more than +/- 5%.

b) X-ray densitometry.

The moisture content of the wood must first be standardised. As long as the moisture content does not rise above 12% there is no significant effect on x-ray density (Parker and Kennedy 1973). The process of extraction in alcohol dehydrates the wood to about 10% moisture content, absorption of moisture from the air during the subsequent cutting may raise the level to 12%, but it is unlikely to rise higher than this in a centrally heated winter atmosphere. For at least 12 hours prior to x-raying the samples are kept in desiccator trays. These consist of covered perspex trays approximately 40cm x 25cm by 3cm deep containing a vial of a concentrated solution of calcium chloride. This solution is hygroscopic and has the effect of maintaining the wood moisture content around 10% prior to radiography.

The x-ray method used employs a moving carriage and a short x-ray beam. The focal point of the x-ray beam is 94mm from the sample. The beam is passed through an 8.4mm collimator slit 29mm above the film, which reduces parallax in the beam to an effective source-film distance of 27m. The x-ray tube contains a beryllium window to filter out unwanted short wavelength x-rays. The nature of the x-rays can be changed by altering the voltage and the tube current. For the 1.2mm to 1.6mm thick scots pine samples, a current of 7mA and a voltage of 10kV gave the best levels of exposure and maximum subject contrast.

The samples were laid out in trays with a base of thin clingfilm polythene (which does not impair the passage of x-rays) along with a stepped glacetal calibration wedge. This material is composed of the elements carbon, hydrogen, and oxygen in the same proportions as occur in wood and is more robust than a wooden wedge. The tray is laid on the unexposed x-ray film (in darkness) on the top of the carriage. The whole carriage assembly is located in a lead lined drawer, which must be closed before x-raying can proceed. The layout of the x-ray unit is shown in figure 6.1. The carriage is moved by means of a horizontal screw driven by a synchronous electric motor. This ensures smooth movement and a constant speed. Once the drawer is closed the x-rays are turned on and the carriage is passed under the x-ray source at a speed of 2.75 mm/s.

The film used is Kodak type M, double emulsion, fine-grained x-ray film. The film is developed immediately after exposure using the recommended Kodak developers and developing procedure.

c) Densitometry.

Density measurements are made directly from the x-ray negative, using a Joyce Loebl microdensitometer 3.C.S.. A source beam of light is split so that half passes through the x-ray negative and half through a standard optical wedge of known opacity. The negative is tracked beneath the light beam and a servo-motor system matches the nominal x-ray density to density in the wedge. This is connected via a chain drive to a potentiometer; the electrical signal from this is sent to an Apple computer where it is converted to a number between 0 and 255 by a single channel analog to digital interface.

The portion of the negative viewed at any one time is governed by the size of the slit that the light passes through. The usual effective slit size is 20µ wide and 850µ high. This gives a small enough area to detect minor changes in density and yet is large enough to include a sufficient number of cells to give a true density estimate. The optical stage is moved by a stepper-motor driven lead screw under software control from the Apple computer, capable of moving in 2.5µm increments. Useing the standard density programme the stepper motor moves in 10µ steps in the latewood and 30µ steps in the earlywood. The earlywood-latewood boundary is defined in terms of a constant density value which is input at the start of the density measuring programme. A value of .6 g/cc is used in most cases since this cuts the steepest part of the density curve, and is consistent with the boundary defined by anatomical methods (see later in this chapter).

d) Data recording.

The digital signal from 0 to 255 is converted to an absolute density value by the computer by reference to a calibration equation. Before a scan is made the radiographic image of the stepped glacetal calibration wedge is scanned. The glacetal wedge consists of seven steps ranging in thickness from 0.2mm to 1.4mm of known constant density. This calibration procedure allows the differences in the exposure between the x-ray negative to be compensated for.

The relationship between radiographic optical density and wood physical density follows an approximation to the reciprocal squares relationship when soft x-rays are used (Milsom 1979).

Thus

$$(\quad y=1/x^2 \quad) \qquad 6....1$$

Where y is the radiographic optical density and x is the density of the wood.

On scanning the x-ray negative half the split beam passes through the negative and half through a compensation wedge in the back of the densitometer. The compensation wedge changes in opacity non-linearly so that it gives a straight line relationship between wood density and radiographic density. An absolute calibration between x-ray density and wood density in P.sylvestris has been performed relating x-ray density to actual wood density measured on small wood blocks (Milsom 1979). The imporatance of this type of calibration are outlined by Fletcher and Hughes (1970). The stepped glacetal wedge is scanned and knowing the thickness of the wood sample, the coefficients of the straight line regression relating the digital output to radiographic density are determined. Different compensation wedges are needed for different species since the relationship between radiographic density and actual wood density varies. The resolution of the measurements is determined by the properties of the light passing through the slit. The geometric resolution of this apparatus is +/- .0025mm (Milsom 1979).

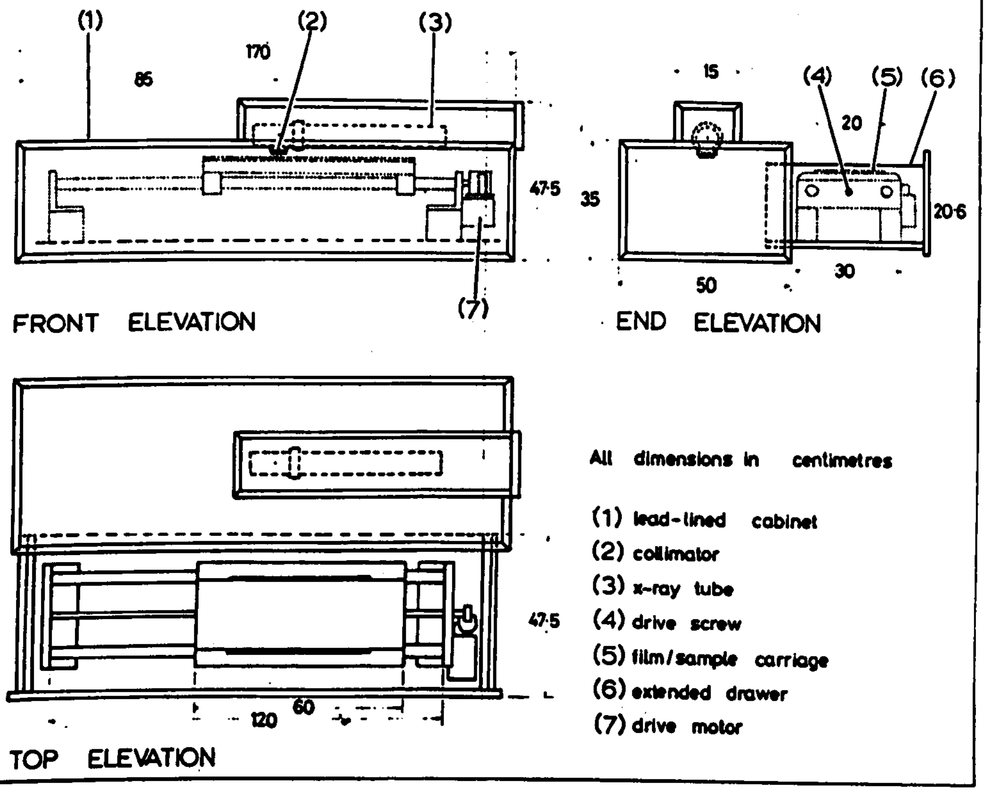
Several programs have been used which record different parameters from the densitometer scan (the methods are illustrated in figure 6.2). It is possible to record every density value measured, at 30µm and 10µm steps (in earlywood and latewood respectively) for the whole length of the scan (program COUNT3.1). This records the density profile of each ring. This generates a lot of data and it is not possible for more than a few rings to be measured because of the limitations of the computer memory (the maximum length of sample that can be scanned at 30µm steps is 3.6mm). The use of 30µm steps in the latewood as well as in the earlywood is usual on this type of scan (COUNT3.3). A comparison of data from scans using 10µm and 30µm steps in the latewood showed no significant loss of densitometric detail using 30µm steps except when measuring extremely narrow rings.

In general four values only are recorded for each ring, these are maximum density, minimum density, width of earlywood and width of latewood. This program (COUNT) uses 10µm steps in the latewood and 30µm steps in the earlywood. Programs are available for editing, printing and crossdating these data.

Figure 6.1

Layout of x-ray unit.

X-RAY UNIT. cabinet and carriage assembly



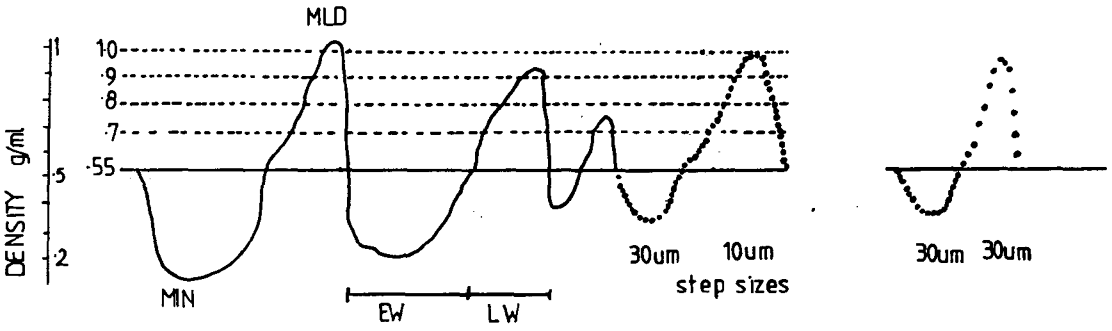
All dimensions in centimetres

(1) lead-lined cabinet
(2) collimator
(3) x-ray tube
(4) drive screw
(5) film/sample carriage
(6) extended drawer
(7) drive motor

Figure 6.2

Density trace as seen on the video monitor whilst scanning an x-ray negative. The EW-LW boundary is set at .55 g/ml.

Densitometry recording

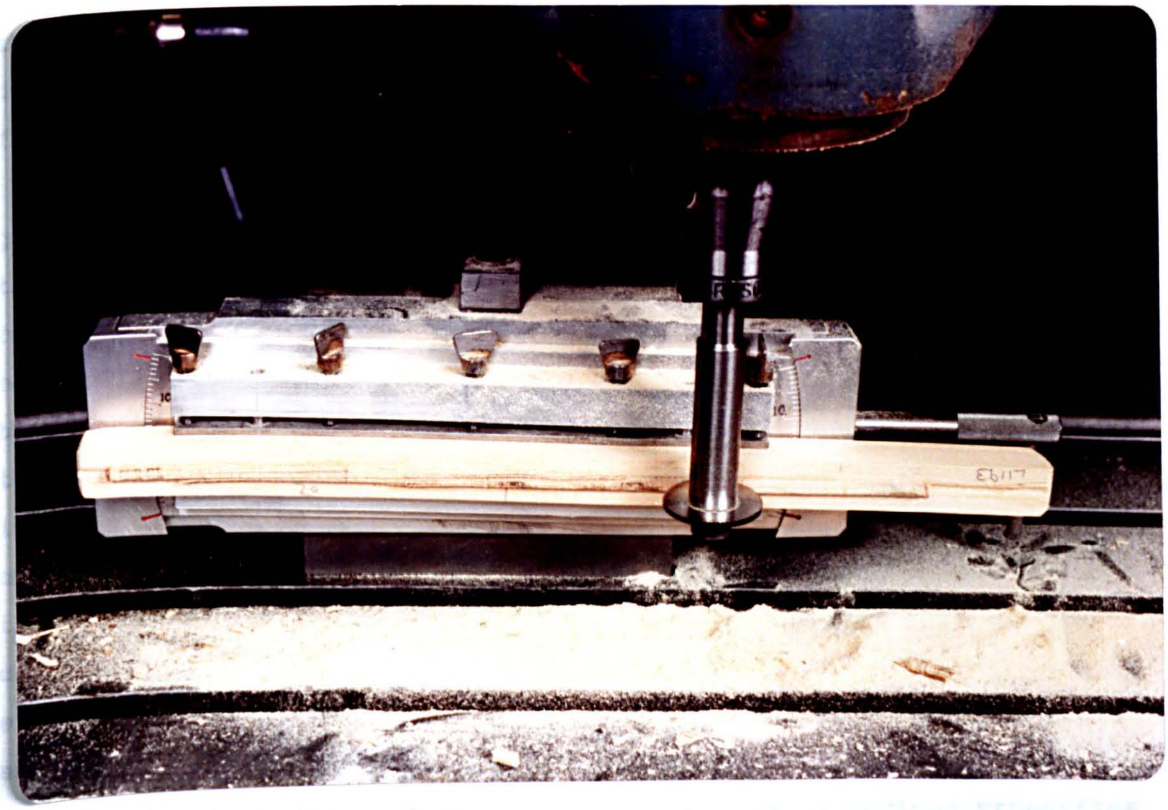


OPTIONS.

1. Record all points
2. Record maximum density, minimum density, earlywood width and latewood width.

Plate 6.1

Cutting jig with twin-blade saw.


10
10
RISC
2.6
Eb117

C. WOOD MICROANATOMY IN RELATION TO DENSITY.

a) Introduction.

The aim of this study is to investigate the changes in wall thickness and lumen diameter across the width of the growth ring in order to explain the changes in density. Physiological research suggests that wall thickness and lumen diameter are controlled by independent internal mechanisms and could therefore vary independently. Changes in the external environment are known to affect wall thickness and lumen diameter in different ways, hence there are two different sets of factors controlling density (section 2).

The first part is concerned with measurements made using an eyepiece graticule on a simple light microscope. The relationships between wall thickness, cell lumen diameter and density are investigated. The relationships between two anatomical definitions of the earlywood-latewood boundary and the densitometrically determined boundary are considered. The second part describes work carried out at the Laboratory of Tree-Ring Research at the University of Arizona using image analysis equipment. The aim here was to examine the possibility of using quantitative microanatomical analysis on tree-rings to study the variation in cell dimensions over an extended time period. Using a computer-based image analysis and data storage system it is possible to examine a sufficient number of rings for the ring structure to be analysed for a period of several decades. It would then be possible to investigate the effects of environmental factors on various properties of the ring structure.

Vaganov (1986) describes the production and use of 'tracheidograms' (plots of cell wall thickness and cell diameters across rings) for P.sylvestris in U.S.S.R.. An automated measurement system is used to measure cell sizes across the rings. The effects of seasonal temperature and precipitation on ring structure are examined and interpreted in terms of durations and rates of wall thickening and cell expansion. The technique is still being perfected, but it illustrates the use of an automated sytem of measurement of cell dimensions. The importance of recording cell dimensions (as opposed to density alone) as indicators of a climate-growth response is emphasisd.

b) Cell structure and density.

Previous work has shown that the variation in lumen diameters and wall thickness across rings of pines can be determined by measuring cell dimensions in the radial direction along successive files of cells (Diaz-Vaz et al. 1975, Merkel 1984). Since the cells of pines are aligned in distinct radial files, it is possible to pick out continuous lines of cells along the length of a ring (plate 6.2). Diaz-Vaz et al. use a specially constructed optical linear micrometer for measuring wall thickness and lumen diameters from thin sections. Measurement of ten radial files is found to be sufficient to give a statistically sound mean measure of how the two parameters behave along the ring. Relative area of cell wall can be calculated using a formula which assumes that the cells are rectangles and tangential cell wall thickness is constant, for the latewood cells in any one year.

The work in Germany (Merkel 1984) used P.sylvestris trees growing at low altitudes with relatively wide rings, primarily influenced by the amount of precipitation. It was necessary to determine whether this method could be applied to scots pines growing at high altitudes in Scotland. It was necessary first to determine how density was related to cell dimensions in both narrow and wide rings.

Thin sections of wood were cut 30µm thick on a freezing sledge microtome, stained with Phloroglucinol (a temporary red stain for lignin prepared with 5g of stain in 100cc 70% ethanol) and permanently mounted in DPX resin. The measurements were made from slides using an optical microscope at 400x magnification. A simple eyepiece graticule was used for measuring cell dimensions. This method had obvious limitations and was very time consuming, although repeatable results were produced on good sections.

Two rings were measured, the first was 1.9mm wide containing 61 cells, year 1900 from the Glen Derry site. The second ring was year 1951 from the same tree, in this case .6mm wide and containing 20 cells.

The means for the cell wall thicknesses and the lumen diameters were calculated from measurements from ten files of cells. Cell dimensions were calculated in terms of the percentage of the distance along the cell, beginning at the start of the earlywood. Figures 6.3, 6.4 and 6.5 show the actual measurements for cell wall thickness, and the mean values for cell wall thickness and lumen diameters with 95% confidence intervals. Wall thickness is more or less constant in the earlywood, it increases to a peak towards the end of the latewood, then decreases at the very end of the ring. Lumen diameter fluctuates little in the EW and decreases gradually towards the end of the ring. Using the formula described by Diaz-Vaz et al. 1975, the relative area of cell wall was calculated at successive points along the ring.

Thus the relative wall area is given by;

$$WA = T(L+D)-L(T-D) / T(L+D) \qquad 6....2$$

Where T=Tangential width of cells, (constant), L=Lumen diameter, D=cell wall thickness (of double wall).

The calculated values of relative wall area were compared to density determined by x-ray densitometry. The work in Germany involving 7 trees for a period of 7 years (1974-1980) has shown that x-ray density is linearly related to relative wall area (Merkel 1984). With *P. sylvestris* Merkel obtained a correlation coefficient of 0.9846. Diaz-Vaz et al. (1975) obtained correlation coefficients between relative wall area and x-ray density of 0.9725 for *Pseudotsuga menziesii* and 0.9578 for *Pinus contorta*. Figure 6.6 shows relationship between density and relative wall area for the two rings of *P.sylvestris* from Glen Derry. The correlation coefficients for the relationship between density and relative area of cell wall, as well as the coefficients for the straight line relationships between the two were highly significant ($p < .001$) for both rings. The slopes of the two straight lines are significantly different ($p < .1$).

Figure 6.6 shows the two straight line relationships. The equations of these are;

Ring 1. $G = .9526p + .1123$ $r = .9014$ 6....3

Ring 2. $G = .8838p + .2115$ $r = .9769$ 6....4

Where G = density and p = percentage wall.

These results suggests that the scottish material does not behave differently from the german material. The results of previous work are confirmed; x-ray density is found to be linearly related to relative area of cell wall in both wide and narrow rings although the actual density of the cell wall material may vary from ring to ring. Cell wall material is more dense in the narrower ring. Current research on deciduous species of trees suggests that there is not always a straight line relationship between density and proportion of wall area within a ring and that the actual density of the cell wall material may vary (Telewski, personal communication).

c) Earlywood-latewood boundary.

The microscopic measurement of wall thickness and lumen diameter have been used to investigate the positions of the earlywood-latewood boundary as defined by Mork, and Creber and Challoner (1984), (see chapter 2). Mork's definition locates the boundary between earlywood and latewood at the position at which the radial diameter of the tracheids is less than twice the value of the wall thickness between cells. By Creber and Challoners' definition the boundary is located at the point of maximum rate of change of cell diameter (decrease) across the ring. These positions have been compared with the position of the boundary defined by specific density values from the x-ray density curve, using figure 6.6. A density value of 0.59g/ml is equivalent to the earlywood/latewood boundary defined by Creber and Challoner (1984) and 0.62g/ml for Mork's definition. Thus a density level of 0.6g/ml to define the earlywood/latewood boundary is consistent with anatomical definitions.

d) Image analysis.

Image Analysis was carried out using a computer based system already in operation at the Tree-Ring Laboratory at the University of Arizona. The reliability of this method and the feasibility of image analysis to measure and record the microanatomical features on a large number of rings were tested.

i) Sectioning and preparation of slides.

A detailed account of the techniques used in botanical sectioning is given by Berlyn and Miksche (1976). The method employs a technique where the wood is embedded in paraffin wax before sectioning on a sledge microtome. This was followed by staining and then mounting of the sections in a permanent medium.

The wood samples were already cut to approximately 1.2mm thick transverse sections with a twin blade saw. The width is 5mm (as determined by the core size), the pieces were cut to a length of approximately 3cm to fit on the microtome blocks. The first stage involved boiling the wood samples in dilute potassium hydroxide (.001M) for three hours to soften the cell walls and help to remove any trapped air bubbles. (Removal of resin and water soluble extractives had been carried out prior to x-ray analysis.) The wood was then taken through a sequence of increasing concentrations of ethanol to dehydrate it. The samples were subjected to a vacuum during the first few stages to increase the penetration of the alcohol and remove any air bubbles in the wood. The ethanol was then replaced in stages by xylene and finally by heated paraffin wax at 57°C. The following table outlines the process.

Section dehydration and wax embedding.

1. Boil in dilute KOH	3hrs.
2. 30% Ethanol	3hrs.
3. 50% Ethanol	3hrs.
4. 70% Ethanol	3hrs.
5. 95% Ethanol	3hrs.
6. 95% Ethanol	3hrs.
7. 100% Ethanol	3hrs.
8. 100% Ethanol	3hrs.
9. Xylene	3-5hrs.
10. Xylene	2hrs.
11. 50:50 wax/Xylene, 57°C	8-10hrs.
12. wax 57°C	3-5hrs.
13. wax 57°C	3-5hrs.

The wax impregnated pieces of wood were then taken out of the oven, laid flat in small aluminium trays and covered with more warm wax. When the wax had solidified the moulds could be removed from the trays, cut to size and mounted on blocks of wood ready for sectioning.

A sledge microtome was used for cutting the sections (plate 6.3). It was necessary to moisten the surface of the wax block to prevent shattering of the section and better results were obtained when the block was cooled with a lump of ice. The cut sections were transferred to a water bath at 40°C for a few minutes to soften the wax and allow the section to flatten out before being lifted onto slides coated in gelatine. The waxed sections could then be left to dry out on a hot plate at 35°C for several hours. Sections as thin as 10µm were obtained on the better pieces, however in general they could not be cut thinner than 20µm without shattering the cell walls.

The sections were then dewaxed and stained. The warm slides were transferred to Coplin jars where they went through the following sequence of washes.

Dewaxing and staining schedule.

1. Xylene	15mins.
2. 100% Ethanol	15mins.
3. 50% Ethanol	10mins.
4. Stain-Acradine Orange in aqueous Phosphate buffer.	15mins.
5. Rinse in distilled water.	
6. 50% Ethanol	5mins.
7. 100% Ethanol	10mins.
8. Xylene	10mins.

The water soluble Acradine-Orange stain was chosen because of its property of fluorescing under ultra-violet light. Use of this stain meant employing rather an extended staining schedule but it produced much better results for image analysis than a conventional stain such as saphranin. The sections were then mounted on slides in a permanent resinous mounting medium and left to harden on a hot plate (35°C).

Problems in the preparation of sections.

The production of good sections was time consuming and on many samples a good section was not obtained. Problems arose at all stages of the procedure despite experimentation using different methods. Good sections were obtained from a limited number of samples.

If the wood had not been adequately softened, it was too brittle to be sectioned. The process of dehydration of the wood in xylene often resulted in the cell walls becoming brittle and the inner part of the wall breaking away from the outer cell wall. If cells were not adequately dehydrated, the wax could not be impregnated and the samples fragmented on sectioning. The earlywood suffered from most distortion due to the dehydration process because the cell walls were thinner.

The material was in the form of 1.2mm thick sections from 5mm cores, thus the pieces were sufficiently small for good wax impregnation to be obtained. The number of attempts at cutting a good section however was limited since the wood tended to come away from the wax when it became less than .5mm thick. This also meant that a section at right angles to the ring boundaries had to be obtained on the first few sectioning trials.

Sections sometimes could not be removed cleanly from the microtome blade without breaking or curling. If too thin, sections broke up in the water bath. A major problem was making the sections adhere to the slides during the dewaxing and staining schedules. If too much gelatine was used this took up the stain and could be seen on the final slide, if too little gelatine was used, the section would fall from the slide in the coplin jars. The dewaxing procedure again caused breakage of the cell walls, but it is essential to remove all the wax. The thicker the section the less likely fracturing of the cell walls would occur but the longer the dewaxing period, and the greater the risk of the section slipping from the slide.

ii) Image Analysis Procedure.

The Image Analysis system is located in the Laboratory of Tree-Ring Research at the University of Arizona. It uses the DARWIN system (Digital Analysis of Resolvable Whole-pictures by Image Numeration). A full description of this method is given by Televski et al. (1983). The layout of the equipment used is shown in plate 6.4.

The slide is placed on the microscope stage and is illuminated from above by ultra-violet light. The fluorescing specimen can be viewed through the microscope objective or else the image can be transferred by means of the video camera and digitizer to the television screen.

The u.v. light source to the microscope only provides a single intensity of illumination. The intensity of the image on the screen can be controlled by the external camera control box.

The digitizer converts the analog video signal from the camera to a digital signal. This is a value on a "grey scale" from 0=black to 255=white for a matrix of 512 x 480 points on the screen. The image analysis program can select any part of the total area on the television monitor for scanning. On scanning the grey scale values for the points within that area are returned to the computer via the interface card. Analysis of this image then takes place according to the program that has been loaded.

The program used in this study is Topographer III. Once the coordinates of the area to be scanned have been set, upper and lower grey level limits are chosen to distinguish the object from the background. Scanning is performed from top to bottom and left to right within the image area, the grey level values for each point are compared with the upper and lower grey levels and adjacent pixels are determined to be either object or background. The seperate objects are constructed and can be individually identified.

The program can draw the objects on the microcomputer monitor and a print-out of this can be requested. The total area occupied by the objects can be calculated, as well as the area of individual objects and their coordinates. An editing facility for deleting, joining and separating objects is also available. By means of a set of paddle controls the objects seen on the television monitor can be located for editing.

Problems associated with the image analysis proceedure.

There were several problems associated with image analysis. The main drawback is that the choice of the grey levels to seperate object from background is subjective. This affects the size of the objects and to a greater extent, the thickness of the cell walls. On very thin sections cut exactly at right angles to the grain, changes in the grey level boundaries would have little effect, but most of the sections used here were thick enough for differences to be apparent.

The process is time consuming because only a small area can be scanned at a time and it may take several scans before the grey level boundaries are considered to be correct. Adjustment of the light levels and image intensity also requires a certain amount of skill. The intensity of the u.v. light source cannot be altered and if the section is illuminated for too long it will burn. Thus a limited number of scans can be performed on each section (usually not more than three). The size of the area that can be scanned is also limited because of distortion at the edges of the screen.

iii) Results of image analysis.

Firstly it was necessary to test the validity of the image analysis results and determine whether percentage object area in an individual scan is correlated with x-ray density.

After experimenting with different sizes of image area, a convenient size of 40 x 185 units on the screen was chosen for analysing latewood. (The longest side being tangential, that is along the line of the ring boundaries.) This converts to 57 x 264µm, which is about twice as wide and a quarter as long as the normal slit size on the densitometer. It is about 3-4 cells wide by 7 high in the latewood.

The latewood of each ring was scanned, starting with a block at the end of the ring and proceding with adjacent blocks backwards to the earlywood. The latewood only was measured because initial trials with scans along the whole ring indicated that cell dimensions were more or less constant in the earlywood. It was also more difficult to obtain good sections of the earlywood since the thinner cell walls tended to break up during sample preparation.

The scanning was repeated on a different set of cells three times for each ring. Problems in the sectioning and the image analysis when the quality of sections was not adequate meant that the number of rings scanned was limited. Image scans of 40 x 185 units for the latewood have successfully been obtained for the following trees and years.

Glen Derry.

N57	1924-1940
N60	1929-1940
S51	1930-1932, 1938-1940

Glen Affric.

N38	1930-1939
S45	1930-1935

For each scan the percentage object area was determined, the objects in this case are the cell lumens. A hard copy print-out of the image itself was also obtained. Appendix II shows the pictorial images for the trees, S57 and N60 (reduced in size four times from the original plot size).

The x-ray density had been measured on all the above rings. It was possible to correlate density with the percentage wall area (100 minus percentage object area). The density had been measured with the densitometer using a slit size of 30x1000 µm and a step size of 30µm, so for each area scanned the percentage wall area (a mean of the three values at each position in the ring) was associated with approximately two values of density measured using the densitometer.

Of the five trees which were scanned across the latewood, all gave straight line relationships between x-ray density and percentage wall area. Mean correlation coefficient between the two straight lines of .98 was obtained. Figure 6.7 shows the regression for trees N38 and N60. These two lines were sufficiently alike to be pooled.
The equations of the lines are as follows;

Tree N38	$G=.9809p+.0915$	
Tree N60	$G=.9299p+.0524$	
Pooled equation.	$G=.9537p+.0841$	6....5

Where G = density, p = proportion wall area.

The possibiltiy of obtaining measurements of wall thickness and lumen diameters from the image analysis pictures was then investigated. From the image pictures (Appendix II) it was possible to count the number of vertical and horizontal cell walls in the image area since the cells are generally arranged in a regular pattern with the cell walls aligned horizontally and vertically. Assuming the cells to be rectangles with walls of equal thickness, it was possible to calculate indices for mean wall thickness and mean lumen area for each image using the formula in equation 6...2. The calculated values of wall thickness and lumen area (along with the values for percentage wall area) for N60 are plotted in figure 6.8. This diagram indicates that there is an increase followed by a decline in cell wall thickness across the LW. At the same time there is a gradual decrease in lumen area towards the end of the ring. Both wall thickness and lumen size are controlling percentage wall area in the LW. The greatest percentage wall area occurs at the end of the latewood in the narrow rings but before the end in wider rings. It usually occurs shortly after the peak in wall thickness.

This study indicates the potential for this kind of approach to anatomical study. It could be used in determining the relative effects of lumen diameter and wall thickness in controlling density on different sites and in different years. Unfortunately there is inadequate replication here to allow any such comparisons to be made.

e) Conclusions.

There are many problems associated with the sectioning methods in the production of slides for image analysis. Pinus sylvestris from high altitudes is very difficult to section to the standard required for image analysis. The preparation of slides is time consuming. The standard of quality of slides necessary for image analysis is very high and this means that only the very best material can be used. It is difficult therefore to produce sections of long continuous periods.

Woody material is inherently difficult to section (Berlyn and Miksche 1976). An image analysis technique being developed at the Commonwealth Forestry Institute at Oxford uses reflected light from the wood surface to produce the images (Hughes J.F. personal communication). This requires a sophisticated method of wood surfacing but it avoids problems associate with sectioning.

The image analysis procedure itself has limitations. Despite the fact that data manipulation and storage is carried out in a sophisticated program, setting up and adjusting of the image is time consuming and is done manually and is subjective. Image scans are not exactly repeatable. The size of the image that can be scanned at any one time is small and at each new scan the system must be recalibrated. The degree of subjectivity in the image adjustment allows only a qualitative approach to the study of anatomical features of cells.

The percentage object area calculated from the image analysis scans correlates significantly with x-ray density. There is a straight line relationship between density and percentage wall area for individual rings from one tree. This suggests that the absolute density of the cell walls is not changing throughout a growing season and that the changes in density across a growth ring are due entirely to changes in the cell wall thickness and lumen size. Other workers suggest that in some species, density of the cell walls themselves may change along the rings (Televski, personal communication). This is currently being investigated on birch trees using the image analysis system in Tucson.

Image analysis ia an effective technique for obtaining quantitative information on tree-rings. The potential of image analysis lies in the fact that detailed examination of the annual variation in cell size parameters can be made and the results stored easily on computer disc. It can give information on the cell sizes which could be used to provide valuable information about the relationship between wall thickness, lumen diameter and percentage wall area. Given adequate replication it would be possible to examine the effects of climate on cell anatomy through the course of the growing season.

Figure 6.3

Measurements of cell wall thickness for 10 files of cells plotted against the percentage of the distance along the ring.

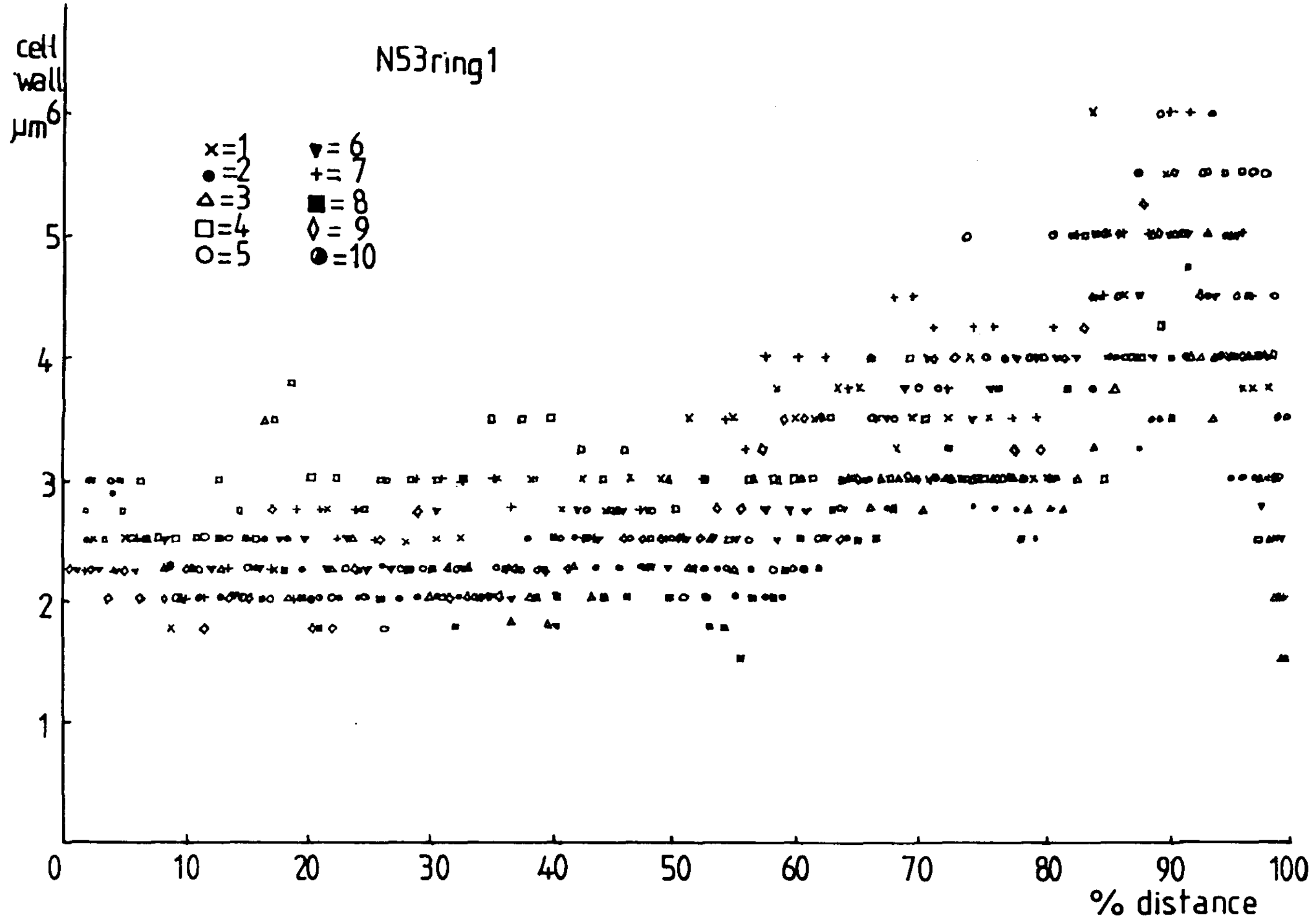
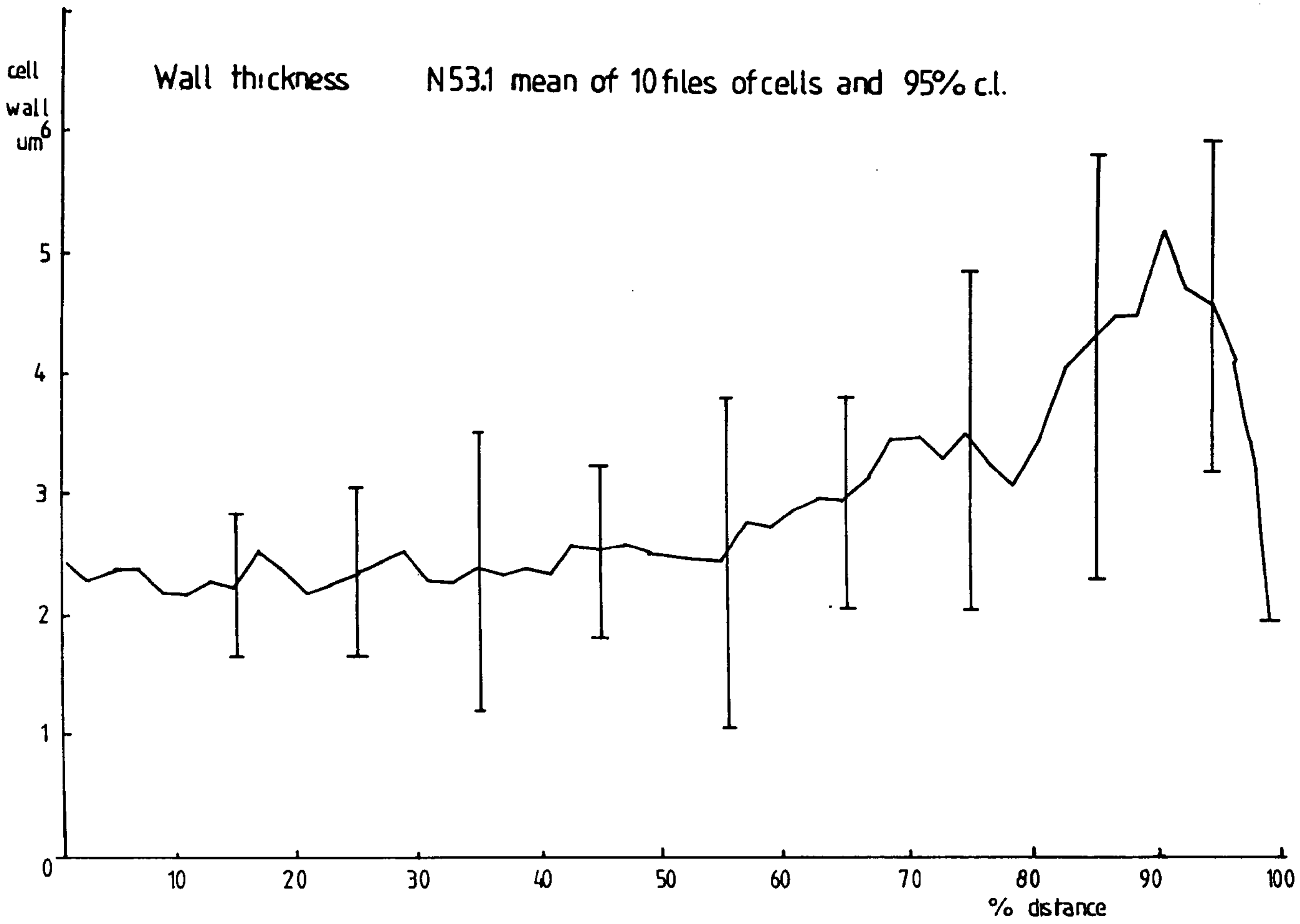
N53ring1
cell wall µm
x=1
●=2
△=3
□=4
○=5
▼=6
+=7
■=8
◊=9
●=10
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
90
100
% distance

Figure 6.4

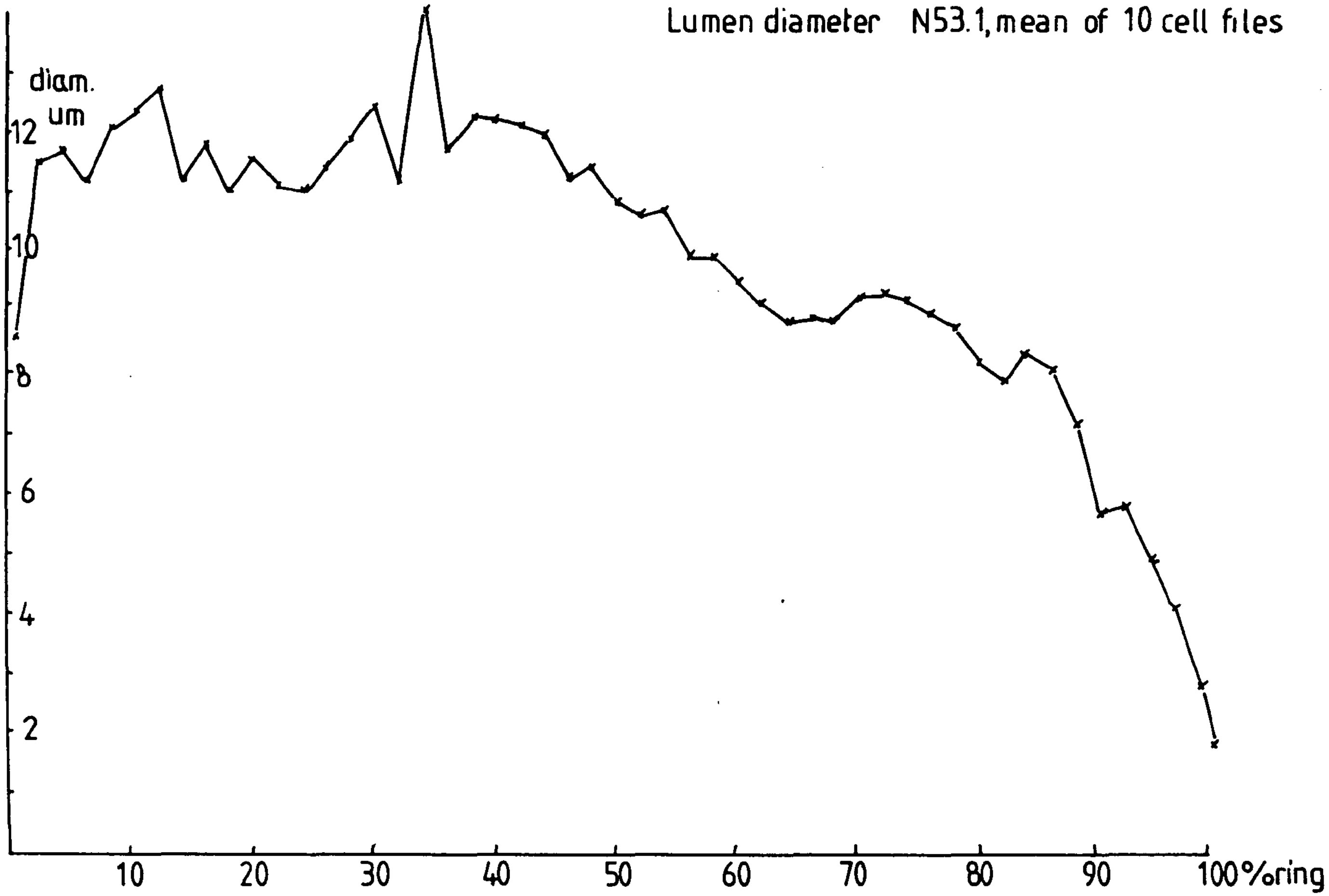
Variation in wall thickness across an annual ring. Calculated from the mean of measurements of 10 files of cells.



Wall thickness N53.1 mean of 10 files of cells and 95% c.l.

Figure 6.5

Variation in lumen diameter across an annual ring. Calculated from the mean of measurements of 10 files of cells.



Lumen diameter N53.1, mean of 10 cell files

Figure 6.6

Relationship between x-ray density and wall area.

Wall area percent is calculated from measurements of wall thickness and lumen diameter. Seperate straight line relatioships apply to each ring.

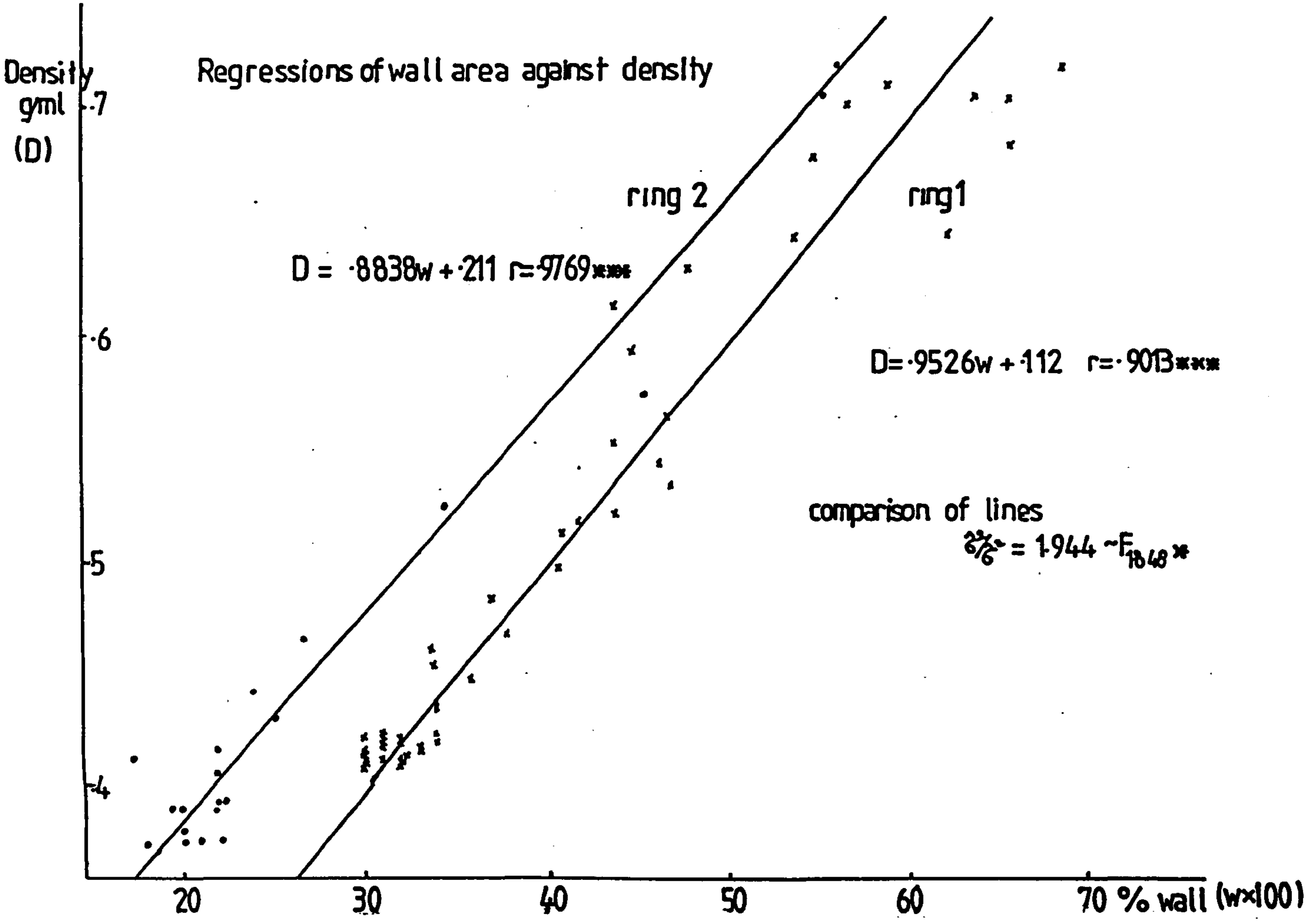

Regressions of wall area against density
Density
gml
(D)
·7
·6
·5
·4
20
30
40
50
60
70 % wall (w×100)
ring 2
D = ·8838w + ·211 r=·9769***
ring1
D=·9526w + ·112 r=·9013***
comparison of lines
δ^2/δ^2 = 1·944 ~F_{1848}*

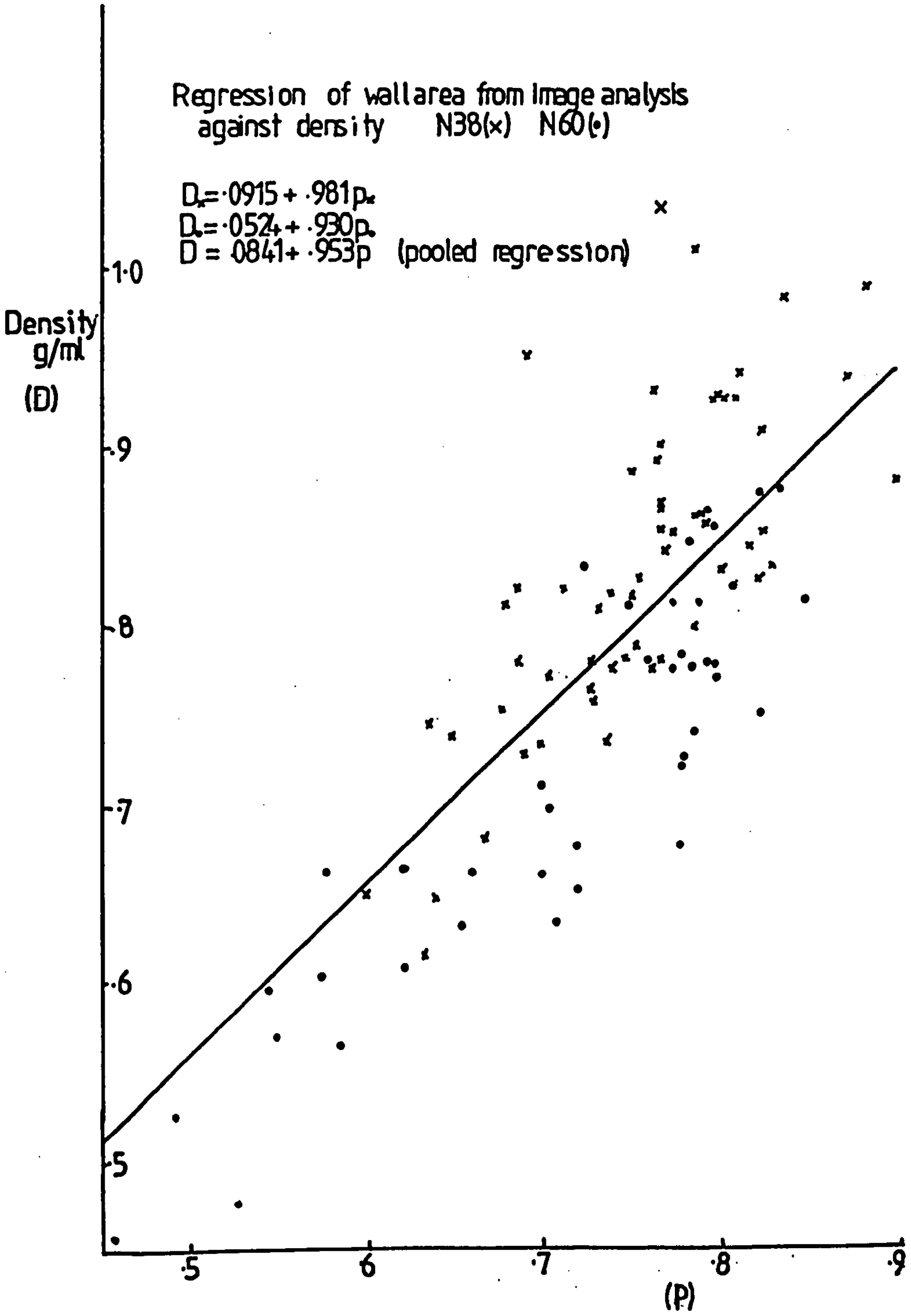
Figure 6.7

Relationship between x-ray density and wall area.

Wall area is calculated from the percentage object area derived from image analysis.

p is the proportion of cell wall in the image.

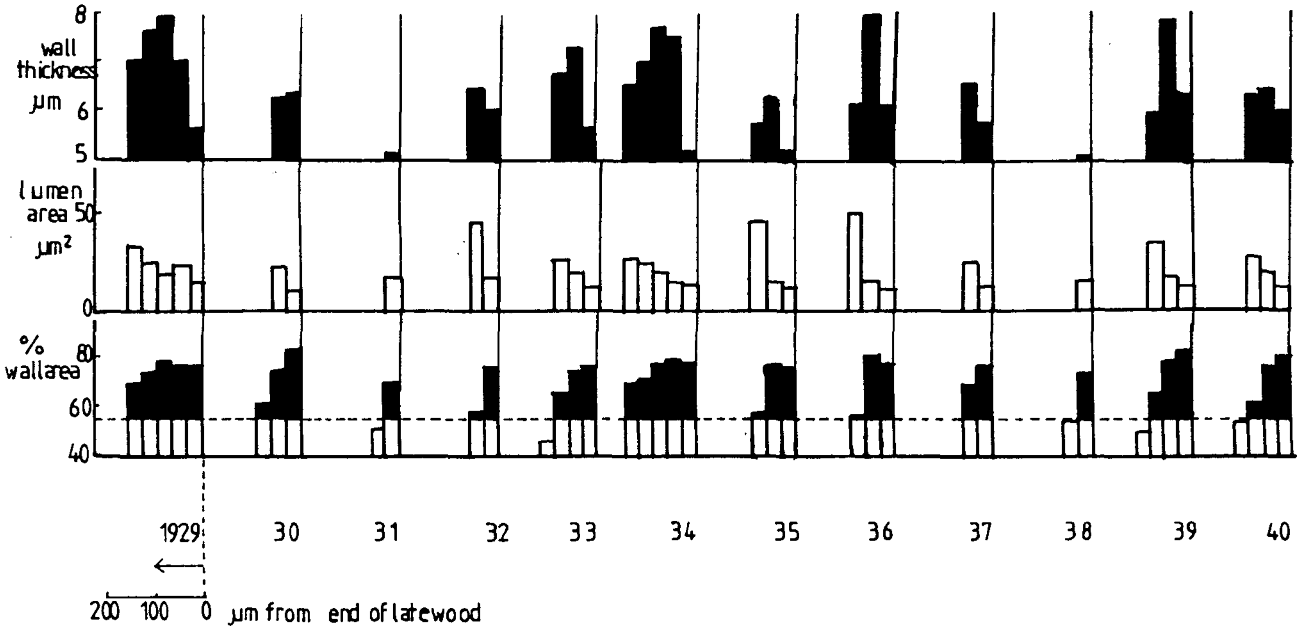
One straight line relationship applies to both rings.



Regression of wallarea from image analysis against density N38(×) N60(•)
$D_{\times} = \cdot 0915 + \cdot 981 p_{\times}$
$D_{\bullet} = \cdot 0524 + \cdot 930 p_{\bullet}$
$D = \cdot 0841 + \cdot 953 p$ (pooled regression)
Density g/ml
(D)
1·0
·9
·8
·7
·6
·5
·5
·6
·7
·8
·9
(P)

Figure 6.8

Image analysis results.



wall thickness µm
8
6
5
lumen area µm²
50
0
% wallarea
80
60
40
1929
30
31
32
33
34
35
36
37
38
39
40
200
100
0
µm from end of latewood

Plate 6.2

Radial section of scots pine wood.

Thin wall earlywood cells are seen on the left, thicker walled latewood on the right. The section is stained with phloroglucinol is fluorescing under illumination with u.v. light.

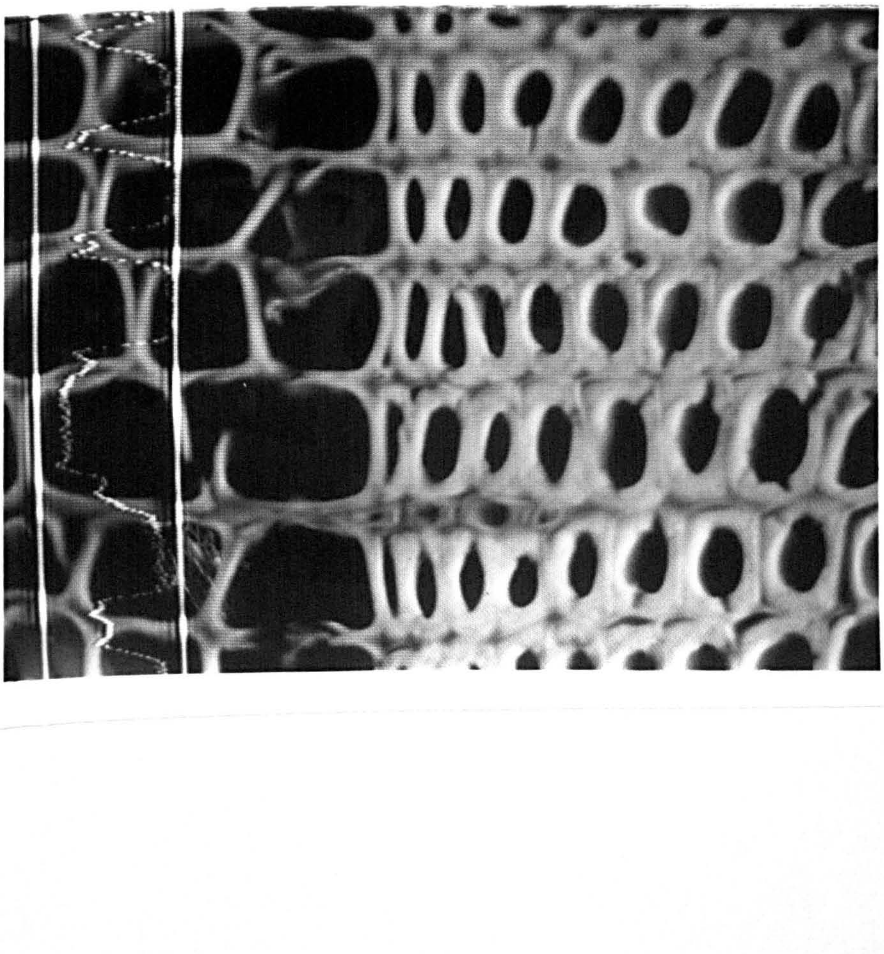


Plate 6.3

Sledge microtome used for cutting thin sections for image analysis.

In this study the mounted sections were only 30mm in length.

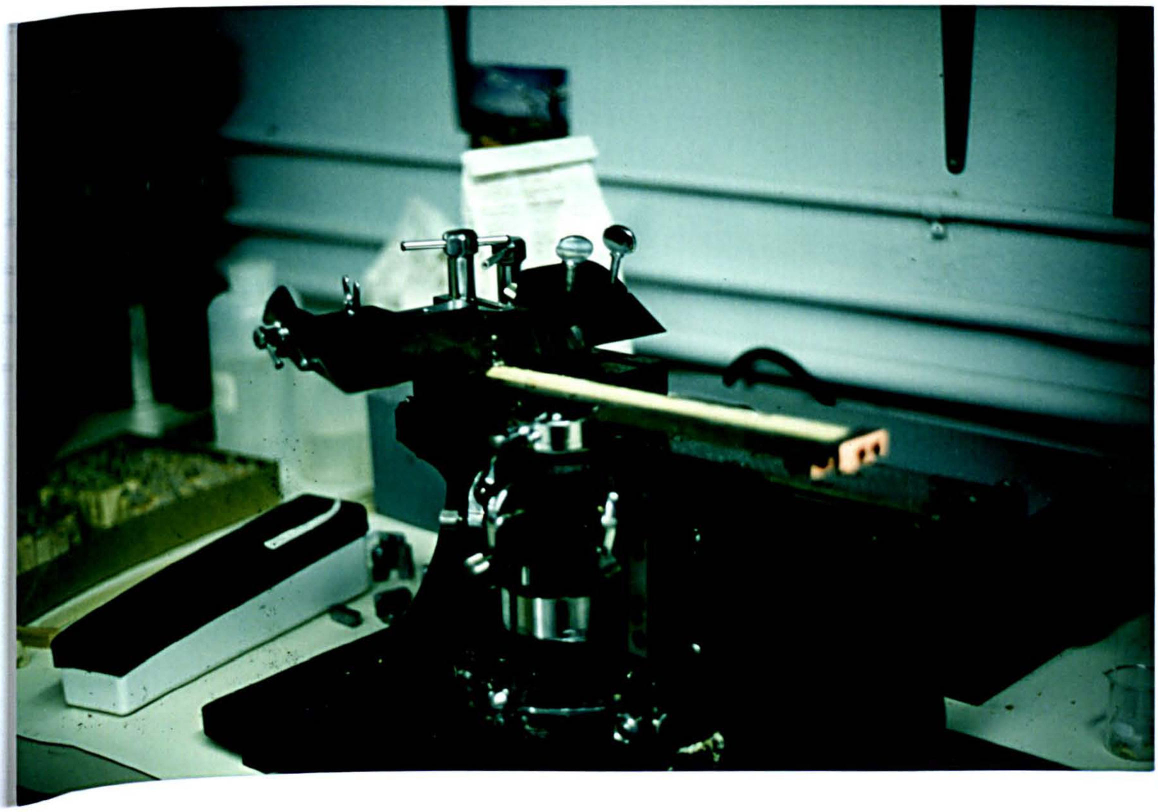


Plate 6.4

DARWIN Image Analysis system.

A = Control box.

B = Video camera.

C = Microscope.

D = Digitizer.

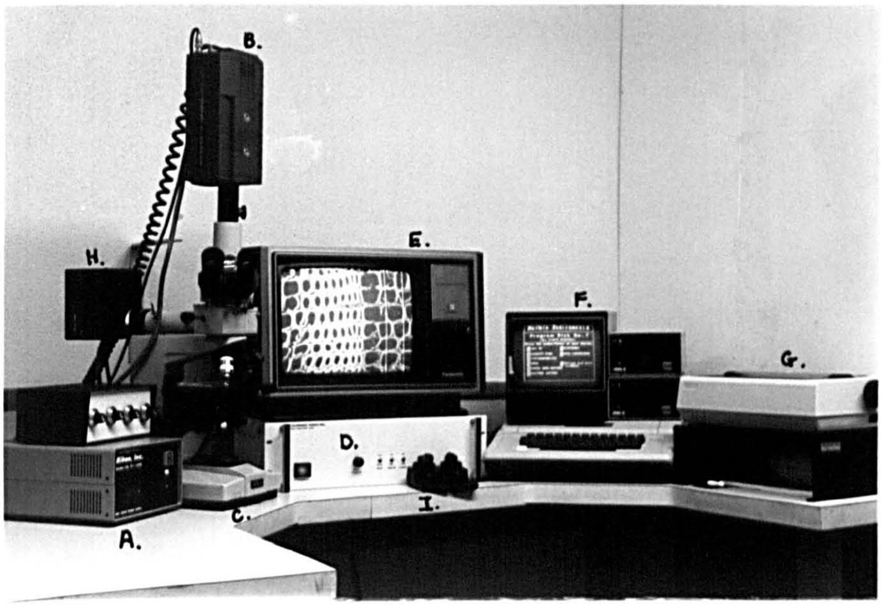
E = Video monitor.

F = Apple IIe computer.

G = Printer.

H = u.v. light source.

I = Paddle controls.


B.
E.
H.
F.
G.
D.
I.
C.
A.

D. ANALYSIS OF THE DENSITY PROFILE.

a) Introduction.

The density profile for a single year records the variation in density across the ring from the beginning of the earlywood to the end of the latewood. Density profiles may be constructed by recording the density at equal intervals across the ring, using the method of x-ray densitometry.

The density profiles of individual trees from certain sites are found to exhibit similar patterns, characteristic for each year. Merkel (1984) found a strong association between the shapes of the density profiles and the amount of precipitation for Pinus sylvestris from low altitudes in Germany. Merkel (1984) described profiles of density, lumen diameters and cell wall thickness for a period of seven years. This study attempts to examine the effects of environmental factors on density for a longer time period.

Density profiles for 80 years from 1900 to 1979 have been constructed from x-ray density curves of a sample of trees from two Scottish sites. Cubic spines have been fitted to the density profiles to assist in the comparison of density profiles. The deviations in the density profiles of individual years from the mean density profile for that tree have been investigated. The potential of a mathematically defined density profile as a tool in dendroclimatology is investigated.

The main aims are;

a) Investigate relationship between MXD and density of the rest of the ring.

b) Examine similarities and differences in density profiles between trees.

c) Examine relationship between climate and density.

d) Attempt to relate findings to physiological evidence.

b) Methods.

i) Density measurement.

The analysis is conducted for a period of 80 years from 1900 to 1979. The density data are produced from a densitometer scan of x-ray negatives with a step size of 30µm for both the earlywood and latewood, using program COUNT3.3 (see section 6B for a full description of densitometry). Trees from two sites in Scotland, at Glen Affric and Glen Derry are considered. Computer plots of the x-ray density data were produced for all trees so that rings could be identified and examined individually. Figure 6.9 shows examples of x-ray density plots for the trees used, for the periods 1900-1910 and 1911-1920.

Inspection of the x-ray density plots indicates that many of rings were not sufficiently well defined for density profiles to be constructed. This is a result of a poor quality x-ray negative or factors associated with the growth rings themselves. The selection of appropriate periods for density profile construction is based on several criteria deduced from inspection of the x-ray density plot. These are:

1. Definition of the rings.
2. Width of rings.
3. A period of at least 20 consecutive years.
4. Mean ring density fairly constant.

The x-ray negative must not be blurred, as the ring boundaries must be clearly defined. Rings of width greater than 3.0mm and less than .6mm were not used. In many trees there are alternating periods of wide and narrow rings and sections of compression wood. There should be a reasonably even density pattern for a period of at least 20 years.

The density values have been recorded at equal (30µm) intervals along the ring. Since there is considerable variation in the width of the rings, the number of values recorded per ring varies. The number of density values recorded for each ring ranges from 20 in the narrow rings to over 100 points for the widest rings. In order to compare density profiles and construct mean density curves, a standard number of points from each ring. This is achieved by fitting a cubic spline function to the original density profile and obtaining density values at 1% intervals along this curve. Each density profile is then described by 101 density values. The advantage of using a cubic spline rather than a polynomial curve is that it is constrained to pass through all the points. Since changes in density across a ring may be somewhat abrupt and these fluctuations may be important in climate-growth interpretation, it is necessary to fit a curve which follows the density profile as closely as possible. Figure 6.10 shows a fitted cubic spline along with the original data values for a single ring.

ii) Spline fitting.

Fitting of cubic splines was carried out on each ring seperately using a modification of a BASIC programme (Heilborn 1981). All computing was carried out using the Apple IIe micro-computer. The densitometry programme stores upto 1000 density values as they are measured, they are not distinguished as seperate rings. The spline fitting programme (SPLINE) first asks for the number of the first density value and then for a value for the earlywood-latewood boundary. The data are read from the file starting at the given value proceeding until the boundary from LW back to EW is crossed. The sequence number of this point is then recorded so that the start position for reading the next ring is known. SPLINE fits a cubic spline curve to each ring in turn, stores 101 points for each ring then proceeds to the next ring. The programme will continue to a specified end point or until the 1000th data point is reached.

The first stage of cubic spline fitting is to fit a parabola to each set of three adjacent points in turn. It is then possible to calculate the slope of the parabola at the position of the central point. Thus the slopes $D(j)$ at each of j points are computed as functions of the x and y coordinates of the density values. Thus;

$$D(j) = F(x(j-1), x(j), x(j+1), y(j-1), y(j), y(j+1)) \qquad 6....6$$

Seperate cubic polynomial curves are then fitted between each point to give the closest fit to the points and the intersecting slopes. A set of j polynomials are obtained, of the form

$$z = y(j) + f(j)w + g(j)w^2 + h(j)w^3 \qquad 6....7$$

Where $f(j)$, $g(j)$ and $h(j)$ are the cubic spline coefficients and w is a function of the increment along each spline. Thus the value of y at any point can be calculated by reference to the appropriate polynomial equation. 101 points at equal intervals were taken from each curve and stored on disc.

iii) Calculation of means.

A total of 12 trees from Glen Affric have been examined, five of which include data from two cores. Computer plots of the splines were made. These were inspected against the densitometer plots for incorrect reading of the ring or anomalous rings. The density plots indicate that density of the rings varies considerably between trees and according to the age of the tree when the ring was formed. For each tree, periods of even growth 20 to 35 years long, have been selected from the density chronologies. Mean density profiles for these periods have been calculated. It was possible to calculate the mean of any number of density profiles by calculating the mean value at each point using a BASIC programme MEANSPLINE. There is considerable variation in the mean profiles from tree to tree.

The density profiles have been plotted along with the means for each year and each tree, Apppendix III. The deviations from the profiles illustrate where density has been higher (black) or lower (striped) than normal. The numbers on theleft indicate the number of density values used to construct the spline, this is directly related to the width of the ring. In some years deviations in the profiles for the individual trees all show a similar pattern, in other years the pattern is less well defined. Since the samples were only taken from the dominant trees in the stand similar density curves might be expected. Had trees from other parts of the canopy been used, it may have been necessary to compare density profiles from each canopy class seperately, since the dates of onset and termination of growth are known to vary according to the position of the tree in the canopy.

The total area above or below the mean curve for each year (and tree) can be computed. This is the deviation (DEV). An analysis of variance to examine the effects of years and on the DEV. It has been carried out for 8 trees for 21 years, 1900-1920. Deviations (DEVS) have been computed as the differences between the individual profiles and the overall mean profile for the 21 years and 8 trees. The results are shown in the table below.

Source	df	SS	MS	VR	
Trees	7	2.912	.416	2.869	**
Years	20	4.680	.234	1.614	*
Resid.	140	20.30	.145		
Total	167	27.89			

The tree effect on DEV highly significant (p =.01), years are also significant (p =.1).

The significant tree effect would indicate that the profiles for individual years must be compared with the mean tree profile (rather than an overall mean profile) in order for the year effect to be distinguished. A further analysis of variance has been carried to investigate the effect of trees within years. In this case DEVS are computed as differences between the profile for each year and the 21-year mean profile (1900-1920) for that tree. The results are shown below.

Source	df	SS	MS	VR	
Between trees within years	140	10.41	.0744	.44	ns
Residual	27	4.778	.1769		
Total	167	15.19			

These results show that there is no significant effect of trees within years, this indicates that if the tree effect is removed a common pattern in DEVS is found.

Figure 6.9

X-ray density plots. Glen Affric trees. 1900-1910.

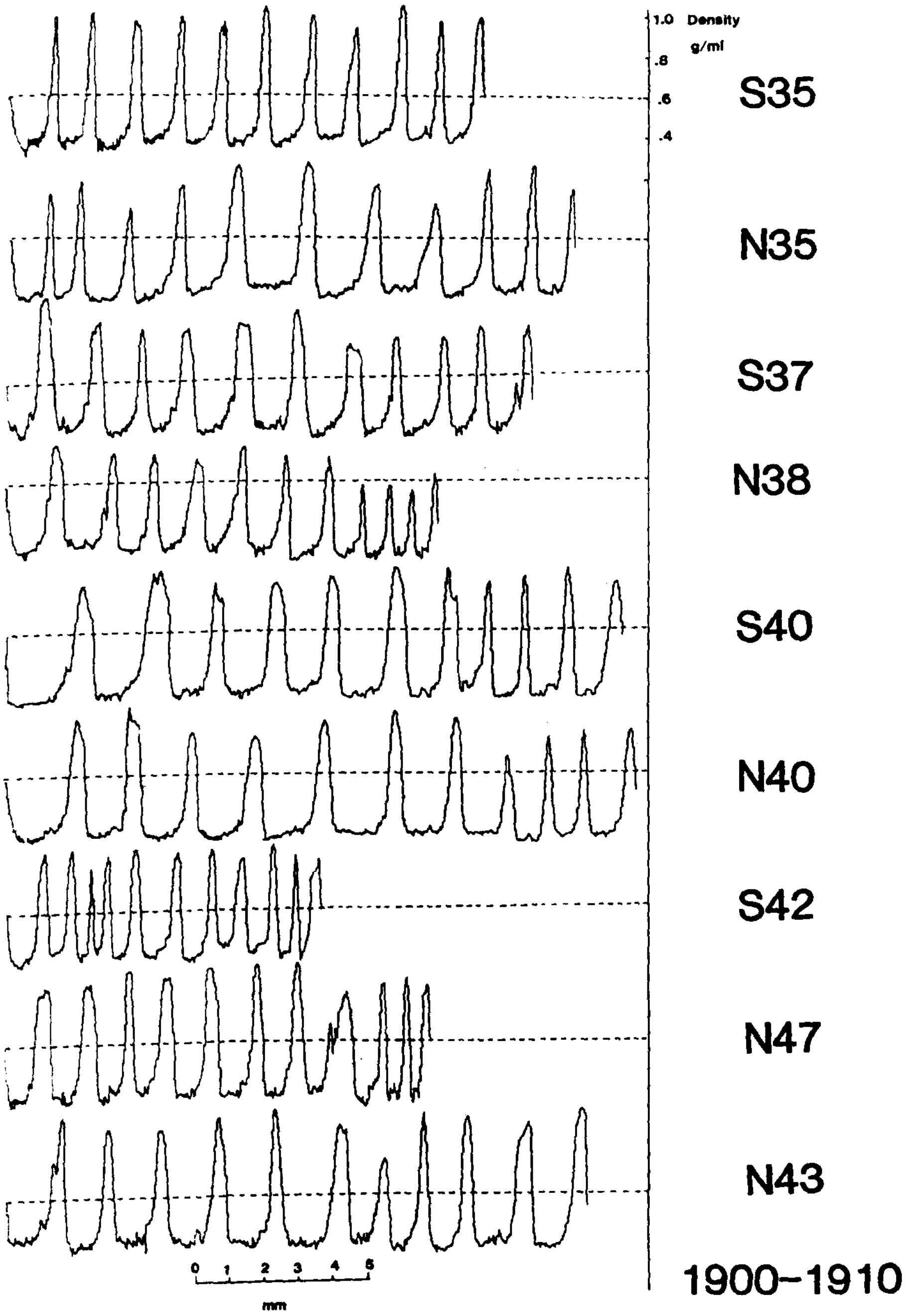
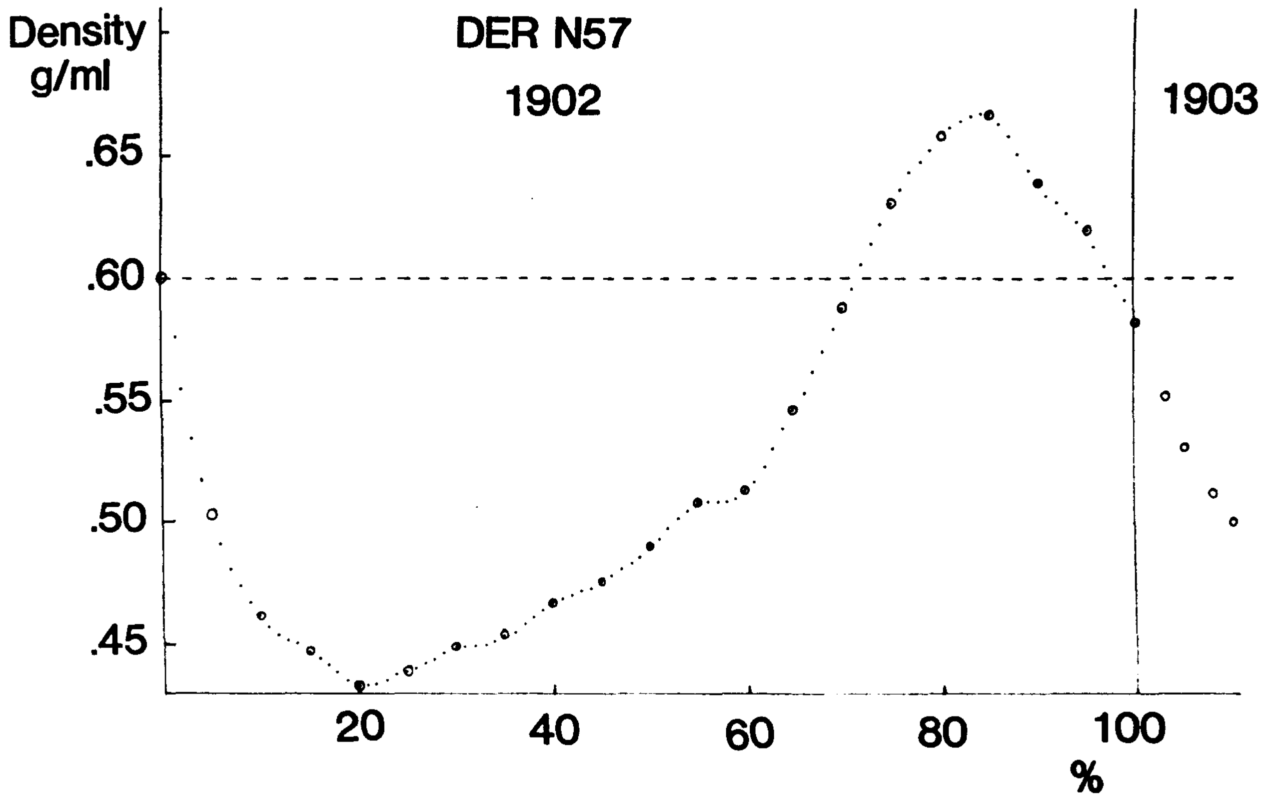

1.0 Density
g/ml
.8
.6
.4
S35
N35
S37
N38
S40
N40
S42
N47
N43
1900-1910
0 1 2 3 4 5
mm

Figure 6.10

Method of fitting the cubic spline.

o = Original data value.

The EW - LW boundary is shown at a density of .60 g/ml.


Density
g/ml
DER N57
1902
1903
.65
.60
.55
.50
.45
20
40
60
80
100
%

E. PROPERTIES OF THE DENSITY PROFILE.

a) Similarities between density profiles.

Certain years show a greater degree of similarity between profiles than others, as indicated for Glen Affric in appendix III. 1920 for example has rings with both high and low DEVS. Other years such as 1926, 1916, 1933, 1938, 1945 and 1951 clearly show a common response between trees. MEAN PROFILES (calculated as the mean of the individual trees for each year) are only meaningful in the years when all profiles are of similar shape. MEAN PROFILES have been calculated for each year in order to examine the statistical relationships between DEVS for each year and the data relating to climate and other tree-ring characteristics.

In order to examine the similarity of the density profiles in a spatial context, profiles from a second site at Glen Derry have been constructed. This site is approximately 60 km from Glen Affric at a higher elevation (450m compared to 300m a.s.l.). In general the trees have narrower rings but they respond more closely to climate. The average ring-width at Glen Affric is 1.25mm compared to 1.05mm for Glen Derry. The strength of the a common signal between trees is indicated by Expected Percentage Signal (EPS) values (table 3.4). Using MXD at Glen Derry, EPS10 (for 10 trees) is .888 compared to .849 for Glen Affric, thus the signal is stronger at Glen Derry. For RW, ESP10 is .585 for Glen Derry and .751 for Glen Affric. Response function statistics using monthly precipitation and temperature data indicate that the climate signal is greater at Glen Derry. The following are statistics for the percentage of the growth response in three parameters that can be explained by principal components of climate (see table 4.4).

	Glen Derry.	Glen Affric.
MXD	55%	57%
RW	33%	30%
LW	50%	21%

The narrower rings for the Glen Derry trees makes them less suitable for density profile construction, on average 25 rather that 42 points are available for spline fitting. Mean profiles have been made for Glen Derry in the same manner as for Glen Affric. Three trees have been used. Since so few trees have been available for use at Glen Derry, the Glen Derry profiles serve only as a comparison with Glen Affric.

Appendix III shows the density profiles from Glen Derry. The smoother outlines and more obvious DEVS of these profiles is a result of the narrowness of the rings. Deviations in density are more closely related to MXD in the Glen Derry trees than in the Glen Affric trees. The Glen Derry profiles show similar patterns of deviation to Glen Affric. In the years when all Glen Affric profiles behave in the same way, the Glen Derry profiles also exhibit that pattern. This suggests that a regional climate signal is responsible for these density deviations.

Table 6.1.

Correlation between indexed MXD, spline MXD, spline deviation and summer temperature.

	GLEN AFFRIC.				GLEN DERRY.		
	MXD Index	MXD Spline	DEV	J/A (Ach)	MXD Index	MXD Spline	DEV
MXD S	.846						
DEV	.558	.621					
J/A(Ach)	.527	.443	.388				
MXD I	.792	.809	.732	.491			
MXD S	.508	.436	.564	.335	.568		
DEV	.261	.227	.571	.201	.427	.713	
J/A(Bra)	.694	.611	.514	.737	.640	.406	.285

Significance >.21 = .1, >.32 = .01, >.44 = .001.
Period of 80 years 1900-1979, (79 d.f.).

At both sites the indexed MXD correlates better with climate than with spline MXD, probably because more trees were used to produce the indexed chronology, also the indexing process filters out some of the noise in the data. A correlation of .846 between the two MXD series for Glen Affric suggests that MXD is reasonably well constructed from the splines. Visual inspection of the plots of MXD (index) and MXD (splines) shows up no anomalies. MXD for Glen Derry is less well constructed since fewer trees are used. DEV correlates less well with the July and August temperature mean than MXD. DEV correlates better between the two sites than MXD (from the splines), giving a correlation coefficient of .571 for DEV compared with .436 for MXD. The statistics confirm the visual impression that DEV is more strongly correlated with MXD at Glen Derry than at Glen Affric with a value of .713 at Glen Derry and .621 at Glen Affric.

It is notable that DEV and MXD at Glen Affric correlate better with the July-August temperature at Braemar (60 km away) than the data from the station at Achnashellach (25 km away), suggesting that the trees at Glen Affric are responding closely to widespread temperature effects associated with altitude. The climate data from Braemar may be reflecting this widespread temperature effect more than the Achnashellach station which is at a lower altitude and a more maritime location closer to thewest coast.

b) Relationship between density profiles and climate deviations.

To facilitate visual comparison between the density profiles and temperature data, the monthly temperature data are represented as deviations from the average for the period 1900-1979. Appendix III shows the annual temperature deviations alongside the density profiles. March and April temperatures are represented as broken lines, May to August temperatures as solid lines, other months are shown as dots. Rainfall data is much more variable and this kind of representation is not very useful. The amount of rainfall is known to have less effect on the rings than temperature. Only the periods of unusually high and low precipitation are considered here.

First it was necessary to test whether decadal trends in the temperature data are represented in the density profiles. The DECADAL MEAN density profiles are calculated as the mean of all profiles for all trees in each ten year period. Figure 6.11 shows the decadal mean density profiles plotted against the OVERALL MEAN density profile (all years and all trees). The deviations in the decadal means in climate data from the 1900-1979 mean are also represented. Visual inspection indicates that decadal deviations in density profiles are related to decadal deviations in climate data. The following table gives the correlation coefficients between the profile DEVS and decadal temperature deviations* for Braemar. * from the monthly mean.

Table 6.2

J	F	M	A	M	J	J	A	S	O	N	D
-26	-07	44	38	52	-23	16	58	41	56	-33	18
				*			*		*		

Values are for r x 100, * indicates significance at 10%. 8 Decades 1900-1909 to 1970-1979 are used, (7 d.f.).

With only 7 degrees of freedom the significances are low. It appears that decadal variation in spring temperatures (March to May) are positively correlated with decadal DEVS. Late summer and autumn temperatures show positive correlations also. September to October temperatures are likely to be affecting the ring of the following year as is August temperature to a certain extent. There is no distinction between current year effect and prior growth effect here.

A comparison between monthly climate deviations for each year and three parameters taken from the splines has been carried out. Maximum density has been calculated from the splines as well as ring-width (which is obtained from the number of points used to calculate the original spline curves). The results are shown below, the correlation coefficients x 1000 are shown.

Table 6.3.

	preS	preO	M	A	M	J	J	A	S
RW	-035	-004	201	056	-066	006	009	-112	-029
MXD	-166	-054	-015	306	176	126	484	343	240
DEV	-201	-189	272	421	111	-015	301	147	228
RWxDEV	-080	-044	084	154	-035	006	159	-072	-082

AUT - RW = 246, MXD = -046, DEV = -015, RWxDEV = 223

Temperatures are Braemar means, tree-ring data is for Glen Affric, AUT= First order autocorrelation in the parameter. Significance 210 = 10%, 353 = 5%, 412 = 1%. A period of 80 years 1900-1979 is used, (79 d.f.).

It is clear that DEV is responding to spring temperatures to a greater extent than MXD or RW. The affect of March temperature on DEV is apparent. May and June temperatures have little influence on density whereas July and August temperatures affect MXD more than DEV. Current September temperature correlates positively with DEV and MXD but not RW. Previous September temperature is negatively correlated with MXD and DEV (although not significantly). A negative autocorrelation in September temperature (r = -.155) may partly account for this. RWxDEV is not a valid indicator of climate influence on the ring although it might be assumed to represent the amount of wall material laid down better than DEV alone. Physiological interpretation of these findings and further discussion is considered later in this chapter.

c) Comparing yearly density profiles.

Examination of the density profiles and deviations in temperature data (appendix III) can aid in the interpretation of the results from the response function analysis. Effects of temperature in three periods are considered:

i) late winter and early spring (February and March)

ii) spring (April and May)

iii) late summer (July and August)

The response functions and physiological mechanisms responsible for the climate-growth response have been discussed (Chapter 4, part C). In order to examine the effects of each period on the ring, the 80 years (1900-1979) have been partitioned into 27 blocks according to whether the temperatures have been high, moderate or low in each of the three periods. The classification is based on the temperature deviations illustrated in appendix III, the years are partitioned into quartiles, the highest and lowest 20 values are used in the classification.

Table 6.4 gives the results and describes the type of density profile formed. Figure 6.12 illustrates diagramatically the typical forms of density profiles associated with different weather patterns in the growing season. Physiological explainations are considered.

High late summer temperatures are consistently associated with high

MXD. A season with low temperatures from February to May and high July and August temperatures does not occur in this period so the effect of such a year cannot be evaluated. A moderately high MXD can also be associated with high April and May temperatures even when summer temperatures are not above average.

Higher than average February and March temperatures are associated with wide latewood and a more gradual transition from earlywood to latewood. The response functions indicate that EW is inversely related to February temperature at Glen Affric (and in Sweden) and inversely to March temperature at Glen Derry. LW is responding positively to February temperature at Glen Derry and March and April temperatures at Glen Affric. This effect is clearly seen in the density profiles from 1933, 1938, 1945, 1961 and 1944. The converse (low February and March temperatures associated with narrow latewood) only applies where low temperatures are maintained in the later part of the spring, as in 1951, 1916 and 1941. It is difficult to classify the effects of temperature in the early part of the growing season since monthly temperature data are crude indicators of the start of the growing season.

The image analysis data from 1933 would suggest that the gradual increase in density from EW to LW is associated with a gradual reduction in lumen area at the same time as a gradual increase in wall thickness. Physiological evidence (chapter 2) would suggest that these high early spring temperatures were affecting the date of spring initiation of growth. Warm March temperatures may lead to early flushing. Earlywood cells will be formed initially until the new needles are mature and begin to transport carbohydrates. Since the period of time necessary for the new needles to begin translocating carbohydrates (which triggers the thicker walled latewood cells to form) is generally constant, latewood cells will begin to be formed earlier in the season. Temperatures are still quite low so the amount of photosynthate available for wall thickening is limited. The rates of cell enlargement and wall thickening may remain quite slow until higher temperatures are reached later in the season hence a gradual transition to LW is seen.

Long growing seasons with high September temperatures, where growth may have continued into the autumn months are noticed where latewood density is high and a sharp drop in density at the end of the ring as in 1921, 1936, 1949, 1953 and 1959. High September temperatures allow the latewood cells to continue wall thickening well into the autumn, hence latewood density is high. The rate of cell production in the autumn is however slow. The sharp drop in density is a result of a small lumen size and very thin walls of the last few cells produced. Growth may have ceased before the final cells are fully enlarged.

Certain features can also be interpreted as the effects of rainfall although patterns here are hard to identify and are not always consistent. Low rainfall would be expected to result in a smaller lumen size and hence higher density. This may be the case in 1913 where there is a low July rainfall yet moderate growing season temperatures. However since low rainfall is generally associated with higher than average temperatures, it is difficult to separate the two effects.

Figure 6.11

Deviations of density profiles and monthly temperature data from the decadal means. of monthly temperatures.

Temperature data is from Braemar.

Density profiles are means for all trees from Glen Affric, numbers of left indicate relative amount of deviation (arbitary units).

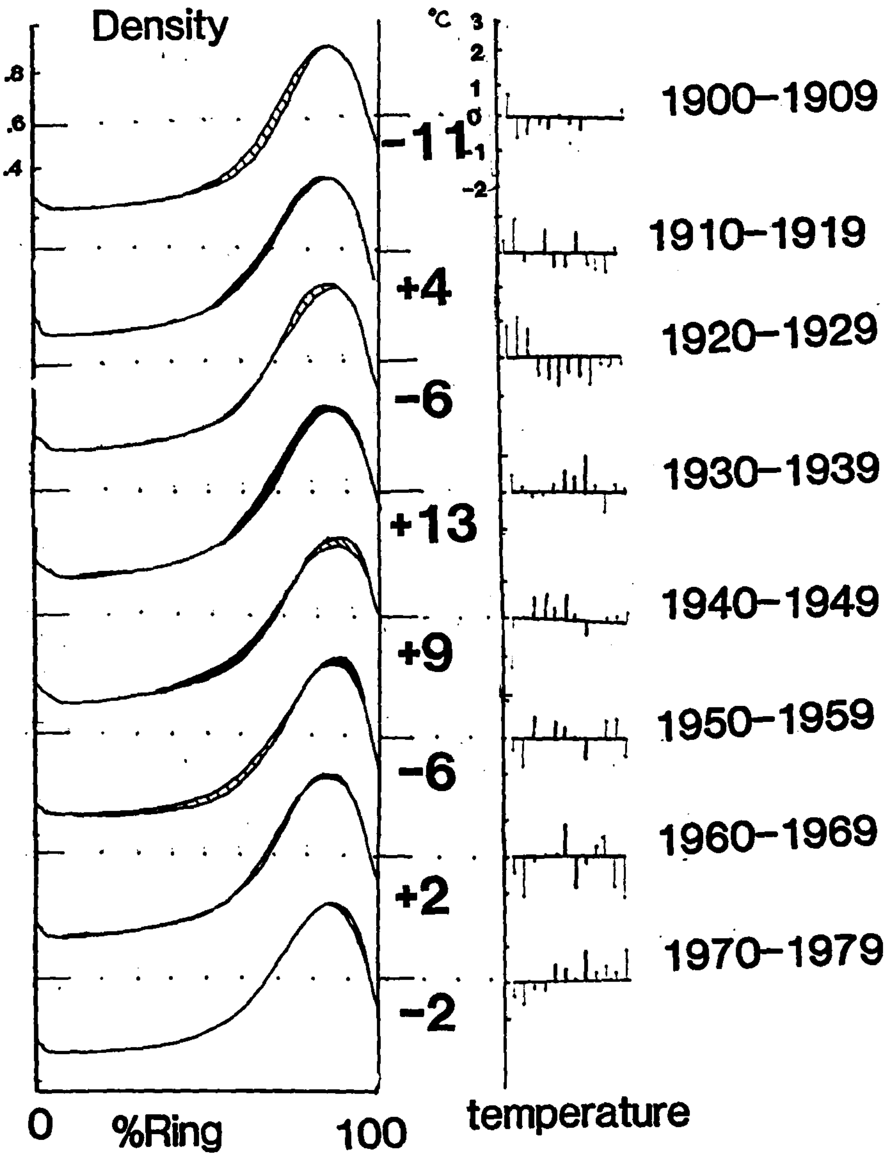

Density
.8
.6
.4
°C
3
2
1
0
-1
-2
-11
+4
-6
+13
+9
-6
+2
-2
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
0
%Ring
100
temperature

Figure 6.12 Effects of climate on the density profile.

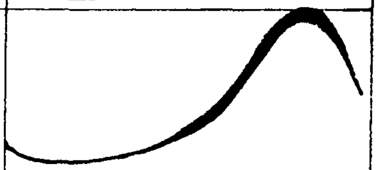
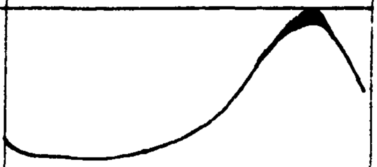
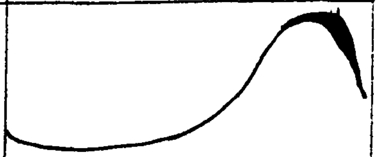
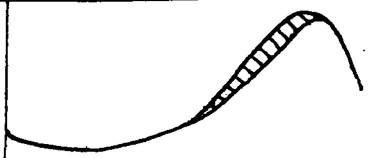
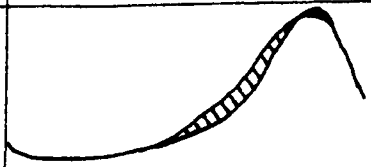
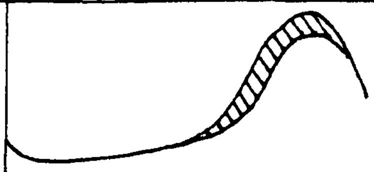
CLIMATE	MECHANISM	RING
High temps. in all seasons	Early LW production, good current shoot growth, high summer photosynthesis. Inc. rate of wall thickening.	
High temps. late winter to end of spring.	Early initiation of EW, early transition to LW production, large cells in early part of LW.	
High spring & summer temps.	Well developed current year shoot. High photosynthesis in summer. Higher rate of cell development and thickening.	
High summer temps.	Inc. photosynthesis in summer. Inc. rates of wall thickening and cell prod.	
High autumn temps.	Wall thickening in LW prolonged.	
Low spring temps.	Late EW production, late transition to LW.	
Low spring, high summer temps.	Late transition to LW. High photosynthesis in summer.	
Low late winter to end of spring temps. Low spring summer temps.	Late EW initiation, late LW initiation. Reduced growth of current shoot, reduced spring and summer photosynthesis. Reduced current shoot development. Reduced photosynthesis and wall thickening in summer.	

Table 6.4 Classification of temperature variation and effects on the density profiles.

1.2.3	RING TYPE	YEAR
H.H.H	Wide LW, high MXD	45, 33, 11, 59*
H.H..	Wide LW, mod. high MXD	38, 18
H...H	Wide LW, high MXD	44, 26
H....	No common type	71,67,53,48,46,29,21,10
H...L	Variable, narrow LW	61, 20*, 12
H.L.H	High MXD, narrow LW	35, 34
H.L..	Low MXD, narrow LW	50, 32, 27, 23
H.L.L	Low MXD, narrow LW	24, 22, 07*, 03
..H..	Moderately high MXD	64, 60, 57, 40, 49
..H.L	Average ring	52
....H	High MXD	25, 76*, 75, 73
.....	High MXD in 1913	54, 39, 13*
....L	No common type	65, 36, 28
..L..	Narrow LW	78, 77, 15
..L.L	Narrow LW, low MXD	72, 66, 62, 02
L.H.H	High MXD	55*, 01
L.H..	Low MIN, narrow LW, mod high MXD.	52, 37, 08, 09
L.H.L	High MXD, low MIN, wide LW	47
L...H	Average ring	69
L....	No common type	63,58,31,30,19,04*,00
L...L	Low MXD, wide LW 1917	42, 19, 17
L.L..	Narrow LW, low MXD	51, 41*, 16

1 = Late winter, early spring temperatures (February, March).
2 = Spring temperatures (April, May).
3 = Late summer temperatures (July, August, September).
* - indicates the possible effect of low precipitation in the summer months.
L - Lower, . - moderate, H - higher than average temperatures.

F. DISCUSSION AND CONCLUSIONS.

The preceding section has indicated that density profiles constructed from x-ray densitometry scans can provide a useful tool for interpreting the climate-growth effects in high altitude *P. sylvestris*. It provides a method of evaluating the climate-growth relationships derived from response functions. A more detailed picture of the climate-growth response can be developed with year by year anomalies identified. This may be important if climate reconstruction is to be attempted. The differentiation between effects which exhibit a more or less linear relationship with density and those which only take effect in certain years (or in one direction) is made possible using density profiles. The study of density profiles from a network of sites may be useful in distinguishing between local and regional climatic effects. This would also allow for the effects of weather patterns on different parts of the ring to be studied since the growing season is likely to be slightly different at different sites.

The density profile patterns allow a greater degree of physiological interpretation of the response functions. By relating the climate data directly to the density profile the effects of changing conditions during the growing season can often be seen. The degree of deviation from the average density profile (DEV) gives more information about the climate in the early and late parts of the season than maximum density (table 6.3). It would be possible to determine separate components of early season and late season density DEVS. The DEV could be a useful parameter in reconstruction of climate during the early and late parts of the growing season.

More adequate data on the relationship between climate and wall thickness, lumen diameter and density are still essential. Preliminary image analysis work has shown that useful information about the above relationship can be obtained from image analysis data. The production of good sections and the image analysis procedure are both time consuming which limits the numbers of trees and years that can be examined.

One of the limitations of the study of ongoing seasonal trends is in the climate data. Monthly indices from distant weather stations are rather crude estimators of changing weather conditions. A measure of daily (or weekly) temperature or solar radiation is required. This has been used in a short term study (for a period of 15 days) of the effect of temperature on cell structure (Ford et al. 1978, see section 2). Other growth models based on cumulative indices have been used in connection with the effect of rainfall on drought sensitive trees. Zahner uses such an index to predict the growth of Loblolly pine (Zahner, to be published). Density profiles may also prove useful in the identification of climate growth responses which might be useful in growth modelling (Fritts personal communication, Ford to be published). The advantage of the density profile approach is that it allows a reasonably large number of accurate, easily replicated plots of rings to be produced relatively quickly. A possible application of density profile studies may be in relating the growth of one tree species to another. If features of P. sylvestris density profiles could be identified that related to the growth of oak it may be possible to use this information to provide a method of identifying 'signature years' that would crossdate between the two species. Oak ring-width is known to respond to temperature in April and May (Milson 1979). So far crossdating between oak and pine has been unsuccessful (Pilcher personal communication). This would then be useful in the study of sub-fossil pine, and it may provide a method of dating and hence building up a long pine chronology.

Chapter 7. CONCLUSIONS.

Several of the topics examined in this work are currently being investigated by other researchers. Further work is still needed on some of the fundamental principles relating to dendroclimatology, especially aspects concerning the physiological mechanisms behind the climate-growth response. Sub-fossil pine in Scotland is currently being studied at the City of London Polytechnic (Lowe personal communication). A great deal of untapped information is also still available from the sub-fossil pine in Northern Ireland. This study has shown that densitometry can sucessfully be performed on the Irish sub-fossil trees. It has not yet been possible to date any of the Northern Irish chonologies. Current work being undertaken to investigate the direct effects of climate on cell dimensions is reported (and in most cases it still being carried out) for example in U.S.A. (Televski personal communication, Ford to be published), Germany (Diaz-Vaz et al. 1975, Merkel 1984), U.S.S.R. (Vaganov 1987) and in Britain (Denne and Dodd 1980).

Density analysis of sub-fossil pine using x-ray densitometry is possible on well preserved specimens. Such material has been found in Ireland but so far there has been no success with material from Scotland. The statistical properties of the ring-width and density chronologies from the Irish subfossil trees have been compared with those of modern tree chronologies from several sites in Britain and Sweden. The sub-fossil chronologies behave differently from the modern chronologies. Maximum density is found to be inferior to ring-width for crossdating between sub-fossil trees, although a reasonably strong common signal (between trees from a site) is still present in the MXD chronologies. The problem of comparing sub-fossil and modern trees is compounded by the fact that many of the sub-fossil tree-ring series are taken from just above the root stump, thus the rings are strongly influenced by root growth rather than the crown. Thus more information is needed on the relationship between growth at the root buttress and tree-ring growth at breast height. It is also desirable to locate specimens of sub-fossil material where the whole stem has been preserved.

Further investigation of sub-fossil pine in Scotland (involving dendroclimatological work) is being undertaken at present by Dr. J. Lowe and colleagues from the City of London Polytechnic. The work involves a comprehensive study of the peat stratigraphy, pollen analysis and dendrochronological study of the sub-fossil pine from several sites in the Rannoch moor region. Radiocarbon dates of the key horizons in the peat are currently being obtained. The way forward in investigating the climate conditions since the last glaciation and especially during the 'altithermal' would seem to be an approach based on a more comprehensive study of the peat bog horizons. Dendrochronological work is of special importance since it can allow dating to an exact year. This may only be achieved if a set of good specimens can be found. They must have been growing contemporaneously, be well preserved, at least 100 years old, with reasonably wide rings and preferably be trunks. If it is possible to find an 'enclave' of sub-fossil pine where the trees grew densely for a relatively short period, a short chronology could perhaps be constucted. The use of densitometric analysis on such specimens may be of great value. Rannoch moor is at a higher altitude than the Northern Irish sites (200-350m a.s.l. as opposed to 50m in Ireland) which might be expected to give improved crossdating using MXD. Densitometry is likely to increase the chances of crossdating with a chronology from another site, or possibly with an oak chronolgy. The growth characteristics of the sub-fossil trees may also yield information about the climatic and ecological conditions at the time.

Response functions have been calculated on modern trees from 7 sites in Britain and Sweden. Further investigation of density at two of these sites (in Scotland) has been possible by fitting cubic splines to the density curves and examining the pattern of deviation of yearly density curves from mean density curves. The work on modern trees using response functions and cubic spline functions has indicated the importance not only of July and August temperatures but also of early an late season temperatures in determining maximum density. This is similar to the situation with Picea rubens in Eastern North America (Conkey 1986) where spring temperatures (April and May) are found to correlate better with MXD than summer temperatures. Her conclusions relating to the biological basis for the climate-density response are similar to those deduced by the author in relation to Pinus sylvestris at high altitudes in Scotland.

The physiological evidence has been examined as it relates to the effects of climate on maximum and minimum densities, earlywood width and latewood width. Figures 2.2 - 2.5 summarise the relationships that are known to apply to P. sylvestris. These diagrams have been used in the interpretation of the response functions and density profiles. The importance of early season temperatures in influencing the growth and development of the current year needles which affects density in the latewood is noted. The mechanism by which summer temperature affects cell dimensions through rates and durations of cell production, expansion and wall thickening has been explored. The influence of growing season length on the ring is also seen. The density profile analysis has proved a useful technique in examining the year to year climate-growth response. The value for the deviation from the mean density curve (DEV) may be a useful parameter for reconstructing of climate in the early part of the growing season.

The effects of water stress on cell diameter in the growing season ultimately affecting MXD is stressed by Conkey (1986) and has also been noted by other workers (Little and Wareing 1981, Jacoby and Ulan 1981, Zahner 1978). The importance of water stress at high altitudes in Scotland where the climate is oceanic has not been adequately assessed. The interaction of low precipitation and high temperatures (hence a greater amount of solar radiation) is apparent. The additional effect on density of water stress in low rainfall years, causing a reduction in cell diameter has not been determined. Evidence from the density profiles would suggest that low rainfall does result in increased density in addition to the effect due to increased solar radiation.

Preliminary work using image analysis techniques has shown the potential for gaining information about the climate-growth response from detailed analysis of wall thicknesses and lumen diameters across the rings. The method use here is dependent on the production of very good quality sections. The way forward in image analysis would seem to be with the use of a surface image analysis technique. This avoids the problems involved in obtaining good sections and distortion of the cells in sectioning. Image analysis is likely to be very useful in determining the impact of water stress on cell dimensions (and hence its contribution to density).

The use of monthly means of temperature and precipitation data is not necessarily the most appropriate method for investigating the climate-growth response. Other workers have demonstrated that a stronger climate-growth signal can been obtained using degree days rather than monthly temperature means (Jacoby and Cook 1981, Jacoby et al. 1985, Zahner personal communication). The use of a cumulative index of temperature or solar radiation such as this is likely to be a good indicator of the growth response in P. sylvestris in Britain. Such an index would be especially useful for examining the climate-density response using density profiles.

REFERENCES.

Baillie M.G.L. and Pilcher J.R. (1973). A simple crossdating programme for tree ring research. Tree Ring Bull. 33: 7-14.

Barnett J.R. (1981). Xylem cell development. Castle House Pubs.

Becker B. and Giertz-Siebenlist V. (1970). Eine uber 1100 jahrige mitteleuropaische Tannenschronologue. Flora 159: 310-346.

Bennet K.D. (1984). The post-glacial history of <u>Pinus sylvestris</u> in the British Isles. Quat. Sci. Rev. 3: 133-155

Berger A. (1980). Climatic variation and variability: facts and theories. D. Reidel Pubs. London.

Berlyn G.P. and Miksche J.P. (1976). Botanical microtechnique and cytochemistry. Iowa State Univ. press, Ames Iowa.

Bialobok S. and Zelawski W. (Eds) (1967). Outline of Physiology of Scots Pine. Translated from Polish. U.S. Dept. Agric. Washington 1976.

Birks H.H. (1975). Studies in the vegetational history of Scotland. IV. Pine stumps in Scottish blanket peats. Phil. Trans. R. Soc. Bot. 270: 182-226.

Blasing T.J., Duvick D.N. and Cook E.R. (1983). Filtering the effects of competition from ring width series. Tree-ring Bull. 43: 19-30.

Blasing T.J. and Fritts H.C. (1976). Reconstruction of past climatic anomalies in the North Pacific and Western North America from tree-ring data. Quat. Res. 6: 563-579.

Blasing T.J., Solomon A.M. and Duvick D.N. (1984). Response functions revisited. Tree-ring Bull. 44: 1-16.

Boyer W.D. (1970). Shoot growth patterns of young loblolly pines. For. Sci. 16: 472-482.

Bradley R.S., Kelly P.M., Jones P.D., Diaz H.F. and Goodess C. (1985). A climatic data bank for the Northern hemishphere land areas, 1851-1980. DoE Tech. Rep. No. TR017. US Department of energy Carbondioxide Research Division. Washington D. C. 335pp.

Braeker O.U. (1981). Der alterstrend bei jahrringdichten und jahrringbreiten von nadelholzen und sein ausgleich. (Age trends in growth ring width and density in conifers and their elimination). Mitteilungen der forstlichen bundesversuch Sonstalt wein. 142: 75-102.

Brett D.W. (1978). Elm tree rings as a rainfall record. Weather 33(3): 79-94.

Briffa K.R. (1984). Tree-climate relationships and dendroclimatological reconstructions in the British Isles. Thesis for Doctor of Philosophy. Climatic Research Unit, Univ. of East Anglia.

Briffa K.R., Jones P.D., Wigley T.M.L., Pilcher J.R. and Baillie M.G.L. (1986a). Climate reconstruction from tree rings. Part 2. Spatial reconstruction of summer mean sea-level pressure patterns over Great Britain. J. Climat. 6: 1-15.

Briffa K.R., Wigley T.M.L. and Jones P.D. (1986b). Towards an objective approach to standardisation. Paper presented at task force meeting "Methodologies of Dendrochronology; East/West approaches", Krakov Poland. June 1986. To be published as an I. I. A. S. A. report.

Briffa K.R., Wigley T.M.L., Jones P.D., Pilcher J.R. and Hughes M.K. (1986c). The reconstruction of past circulation patterns over Europe using tree-ring data. Commission of the European Communities. Contract No. C. L. 111. UK(H).

Briffa K.R., Jones P.D., Pilcher J.R. and Hughes M.K. (1987). Reconstructing summer temperatures in Northern Fennoscandinavia back to 1700 A. D. using tree-ring data from Scots pine. J. of Palaeoclimatology (in press).

Bunce R.G.H. and Jeffers J.N.R. (1977). Native Pinewoods of Scotland. I.T.E. Camb.

Campbell J.B. and Drew L.G. (1973). Manual for using basic chronology programs. Laboratory of Tree-Ring Research, University of Arizona.

Chandler T.J. and Gregory S. (1976). The climate of the British Isles. Longman, London.

Conkey L.E. (1979). Response of tree-ring density to climate in Maine U.S.A. Tree-ring Bull. 39: 29-38.

Conkey L.E. (1986). Red spruce tree-ring widths and densities in Eastern North America as indicators of past climate. Quat. Res. 26: 232-243.

Cook E.R. (1986). A ring-width analysis of four tree species growing in southeastern New York State. M.S. Thesis, University of Arizona.

Cook E.R. and Peters K. (1981). The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-ring Bull. 41: 45-53.

Creber G.T. and Challoner W.G. (1984). Influence of environmental factors on the wood structure of living and fossil trees. Bot. Rev. 50(4): 357-448.

Cremer K.W., Borough C.J., McKinnell F.H. and Carter P.R. (1982). Effects of stocking and thinning on wind damage in plantations. N.Z. J. For. Sci. 12: 244-68.

Critchfield W.B. and Little E.L. (1966). Geographic distribution of the pines of the world. U.S. Dept. of Agric. Misc. Pub. 991.

Cropper J.P. (1984). Multicollinearity within selected western North American temperature and precipitation data sets. Tree-ring Bull. 44: 29-38.

Denne M.P. (1971). Temperature and tracheid development in *Pinus sylvestris* seedlings. J. Exp. Bot. 22: 362-370.

Denne M.P. (1974). Effects of light intensity on tracheid dimensions in *Picea sitchensis*. Ann. Bot. 38: 33-45.

Denne M.P. (1976). Effects of environmental change on wood production and wood structure in Picea sitchensis seedlings. Ann. Bot. 40: 1017-1028.

Denne M.P. (1979). Wood structure and production within the trunk and branches of Picea sitchensis in relation to canopy formation. Can. J. For. Res. 9: 406-427.

Denne M.P. and Dodd R. S. (1981). The environmental control of xylem differentiation. In Barnett J.R. (Ed.) 'Xylem cell development'. Castle House Pubs. pp236-255.

Denne M.P. and Smith C.J. (1971). Day length effects on growth, tracheid development and photosynthesis in seedlings of Picea sitchensis and Pinus sylvestris. J. Exp. Bot. 22: 347-361.

Diaz-Vaz J.E., Echols R. and Knigge W. (1975). Vergleichende Undersuchung der Schwankungen von Tracheidendimension und rontgenoptisch ermittelter Rohdichte innerhalb des Jahrings. Forstw. Cbl. 94: 161-175.

Doley D. and Leyton L. (1968). Effects of growth regulating substances and water potential on the development of secondary xylem in Fraxinus. New Phytol. 67: 579-594.

Douglass A.E. (1936). Climatic cycles and tree growth. Vol III. Carnegie Institute of Washington Publications: 289.

Duff G.H. and Nolan N.J. (1953). Growth and morphogenesis in the canadian forest species. Can. J. Bot. 31: 471-513.

Echstein D. (1972). Tree-ring research in Europe. Tree-ring Bull. 32: 1-18.

Fayle D.C.F., MacIver D. and Bentley C.V. (1983). Computer-graphing of annual ring-widths during measurement. For. Chron. 59(6): 291-293.

Ferrand J.C. (1981). Reflexions sur l'heterogeneite du bois. Wood Microdensity Bull. 1(2): 4-16.

Fletcher J.M. and Hughes J.F. (1970). Use of x-rays for density determinations and dendrochronology. Univ. of B.C. Faculty of Forestry. Bull. 7.

Ford E.D., Deans J.D. and Milne R. (1987). Shoot extension in Picea sitchensis. I The pattern of seasonal variation within a forest canopy. II. Analysis of weather influences on daily growth rate. (to be published).

Ford E.D., Robards A.W. and Piney M.D. (1978). Growth of a sitka spruce plantation: Cell production and the differentiation of xylem in the earlywood. Ann. Bot. 42: 683-692.

Fraser A.I. and Gardiner J. .H. (1967). Rooting and stability in Sitka Spruce. Forestry Commission Bull. 40. HMSO, Lond.

Fritts H.C. (1974). Relationship of ring widths in arid site conifers to variations in monthly temperature and precipitation. Ecol. Monog. 44(4): 411-440.

Fritts H.C. (1976). Tree rings and climate. Acad. Press. Lond.

Fritts H.C., Blasing T.J., Hayden B.P. and Kutzbach J.E. (1971). Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in palaeoclimate. J. App. Meteor. 10: 845-864.

Fritts H.C., Mosimann J.E. and Botherff C.P. (1969). A computer program for standardising tree-ring series. Tree-ring Bull. 29: 15-20.

Fritts H.C., Smith D.G., Cardis J.W. and Budelsky C.A. (1965). Tree ring characteristics along a vegetation gradient in Northern Arizona. Ecol. 46: 393-340.

Godwin H. (1956). The history of the British flora. Camb.

Gordon J.C. and Larson P.R. (1968). Seasonal course of photosynthesis, respiration and distribution of 14C in young Pinus resinosa trees as related to wood formation. Plant Physiol. 43: 1617-1624.

Gray B.M. and Pilcher J.R. (1983). Testing the significance of summary response functions. Tree-ring Bull. 43: 31-38.

Graybill D.A. (1987). A network of high elevation conifers in the western United States for detection of tree-growth response to increasing atmospheric carbon dioxide. Proc. Int. Symposium on Ecological aspects of Tree-Ring Analysis. New York.

Guiot J. (1980). Response functions after extracting principal components and persistence in dendroclimatology. Instiut d'Astronomie et de Geophysique; Universie Catholique de Louvain-La-Neuve, Contribution No. 22.

Guiot J. (1987). Arma techniques for modelling tree-ring response to climate and for reconstructing variations of palaeoclimates. Internal report- to be published.

Hari P. and Siren G. (1972). Influence of some ecological factors and the seasonal stage of development upon the annual ring width and radial growth index. Inst. For. Skogfor. 40.

Heilborn J. (1981). Science and Engineering programs Apple II Edition. Osborne/McGraw-Hill, Calif.

Hodges J.D. and Scott D.R.M. (1968). Photosynthesis in seedlings of 6 conifer species under natural environmental conditions. Ecol. 49: 973-980.

Hoeg O.A. (1956). Growth ring research in Norway. Tree-ring Bull. 21: 2-15.

Huber B. (1941). Aufbau einer mitteleuropaischen Jahrring-Chronologie. Mitteilung Akad. Dtsch. Forstw. 1: 110-125.

Huber F. (1976). Problemes d'interdatation chez le pin sylvestre et influence du climat sur la structure de ses accroissements annuels. Ann. Sci. For. 33: 61-86.

Hughes M.K. (1987). Dendroclimatology of Pinus sylvestris L. in the

Scottish Highlands. In R.G. Ward (Ed). Applications of tree-ring studies. British Archaeological reports. Oxford (in press).

Hughes M.K. (1986). Requirements for spatial and temporal coverage. Paper presented at task force meeting "Methodologies of Dendrochronology; East/West approaches", Krakov Poland. June 1986. To be published as an I. I. A. S. A. report.

Hughes M.K. and Davies A.C. (1987). Dendroclimatology in Kashmir using tree ring widths and densities in subalpine conifers. In 'Methods in Dendrochronology East-West Approaches'. (Ed) L. Kairiukesis IIASA/Polish Academy of Science.

Hughes M.K., Gray B., Pilcher J., Baillie M.G.L. and Leggett P. (1978). Climatic signals in British Isles tree-ring chronologies. Nature 272: 605-606.

Hughes M.K., Kelly P.M., Pilcher J.R. and LaMarche V.C. (1982). Climate from tree rings. C.U.P.

Hughes M.K., Schweingruber F.H., Cartwright D. and Kelly P.M. (1984). July-August temperature at Edinburgh reconstructed from tree-ring density and width measurements. Nature Lond. 308: 341-344.

Huntingdon E. (1914). The climatic factor in the development of peoples. Ronald press NY.

IPID (1987). Northern Hemisphere temperature estimation using blue group Northern Hemisphere 79-chronology set: High latitude and high altitude sites.

Jacoby G.C. (1980). X-ray densitometry in tree-ring studies. In Proc. of Dendrology of the eastern deciduous forest biome. Virginia Polytechnic Institute, Blacksburg Virginia.

Jacoby G.C. and Cook E.R. (1981). Past temperature variations inferred from a 400-year tree-ring chronolgy from Yukon Territory, Canada. Arctic and Alpine Res. 13 (4): 409-418.

Jacoby G.C., Cook E.R. and Ulan L.D. (1985). Reconstructed summer degree days in Central Alaska and Northwestern Canada since 1524. Quat. Res. 23: 18-26.

Jones P.D., Raper S.C.B., Santer B.D., Cherry B.S.G.. Goodess S.C., Bradley R.S., Diaz H.F., Kelly P.M. and Wigley T.M.L. (1985). A grid point surface temperature data set for the Northern Hemisphere 1851-1984. DoE Technical report, TR022, US Dept. of Energy Carbon dioxide Research Division. Washington DC. 251pp.

Jones P.D., Wigley T.M.L. and Briffa K.R. (1983). Reconstructing surface pressure patterns using principal components regression on temperature and precipitation data. Proc. International meeting on Statistical Climatology. Instituto Nacional de Meteorologie e Geofisica. Lisbon. 4.2.1.-4.2.8.

Kellogg W. (1987). Awareness of mankind as a factor in climatic change. Proc. Int. Symp. Ecol. aspects of Tree-ring analysis. N.Y.

Kienast F. (1985). Dendrookologische Untersuchungen an Hohenprofilen aus Verschiedenen Klimabereichen. Dissertation for PhD. University of Zurich.

Kinlock B.B., Westfall R.D. and Forrest G.I. (1986). New Phytologist 104: 703-729.

Kozlowski T.T. (1962). Tree growth. Ronald Press. NY.

Kozlowski T.T. (1985). Soil aeration, flooding and tree growth. J. Arbor. 11(3): 85-96.

Kramer P.J. (1964). The role of water in wood formation. In Zimmerman M.H. (Ed.) 'The formation of wood in forest trees'. Acad. Press.

Kremers R.E. (1964). Cambial chemistry. Tappi 47: 292-296.

LaMarche V.C. (1974). Frequency-dependent relationships between tree-ring series along an ecological gradient and some dendroclimatic implications. Tree-ring Bull. 34: 1-20.

LaMarche V.C., Graybill D.A., Fritts H.C. and Rose M.R. (1984).

Increasing atmospheric carbon dioxide: Tree ring evidence for growth enhancement in natural vegetation. Sci. 225: 1019-1021.

Larson P.R. (1962). Auxin gradients and the regulation of cambial activity. In Kozlowski T.T. (Ed.) 'Tree growth'. Ronald Press. NY.

Larson P.R. (1964). Environmental effects on wood formation. In Zimmerman M.H. (Ed.)'The formation of wood in forest trees'. Acad. Press.

Larson P.R. (1969). Wood formation and the concept of wood quality. Yale Univ. sch. of for. Bull. 74.

Lavender D.P. (1980). Effects of the environment upon the shoot growth of woody plants. In Little C.H.A. (Ed.) 'Control of shoot growth in trees'. IUFRO. pp 76-106.

LeBlanc D.C., Raynal D.J., White E.H. and Ketchledge E.H. (1987). Characterization of historical growth patterns in declining red spruce trees. Proc. International symposium on Ecological aspects of Tree-Ring analysis. N.Y.

Lenz O., Schar E. and Schweingruber F. H. (1976). Methodische probleme bei der radiographische-densitometrischen Bestimmung der Dichte und der Jahrringbreiten von Holz. Holzforschung 30: 114-123.

Linder S. and Troeng E. (1980). Photosynthesis and transpiration of 20-year-old scots pine. In Persson T. (Ed). Ecol. Bull. (Stockholm) 32.

Linder S. and Lohammar T. (1981). Amount and quality of information on CO_2 -exchange required for estimating annual carbon balance of coniferous trees. In "Understanding and predicting tree growth", S. Linder (Ed.) Stud. For. suecica 160. pp 73-87.

Lingg W. (1986). Dendrookologische Studien on Nadelbaumen im alpinem Trockental Wallis (Schweiz). Berichte Report 287. Swiss Fed. Inst. For. Res. CH 8903 Birmensdorf.

Little C.H.A. (1975). Inhibition of cambial activity in Abies balsamea by internal water stress: Role of abscisic acid. Can. J. Bot. 53:

3041-3050.

Little C.H.A. and Wareing P.F. (1981). Control of cambial activity and dormancy in Picea sitchensis by indol-3-ylacetic and abscisic acids. Can. J. Bot. 59: 1480-1493.

Lowe J.J. and Walker M.J.C. (1984). Reconstructing Quarternary Environments. Longman N.Y.

McNally A. and Doyle G.J. (1984). A study of subfossil pine layers in a raised bog complex in the Irish Midlands. I. Palaeowoodland extent and dynamics. II. Seral relationships and floristics. Proc. R. Irish Acad. Sect. B. 84B(6,7): 57-81.

McVean D.N. and Ratcliffe D.A. (1962). Plant communities of the Scottish Highlands. H.M.S.O. (Nature Conservancy Monog. no. 1)

Meko D.M. (1981). Applications of Box-Jenkins methods of time series analysis to the reconstruction of drought from tree-rings. PhD thesis, University of Arizona.

Merkel H. (1984). Uber den witterungseinflub auf die jahrringstruktur der Gemeinen kiefer (Pinus sylvestris L.). Ein beitrag zur dendroklimatologie der nadelholzer. Dissertation University of Frieburg.

Mikola P. (1956). Tree-ring research in Finland. Tree-ring Bull. 21: 16-20.

Mikola P. (1962). Temperature and tree growth near the Northern timber line. In Kozlowski T.T. (Ed.) 'Tree growth'. Ronald Press.

Milsom S.J. (1979). Within- and Between-tree variation in certain properties of annual rings of sessile oak, Quercus petraea (Mattuschka) liebl. as a source of dendrochronological information. Phd. thesis. Dept. of Biol. Liverpool Polytechnic.

Miller H.G. (1984). Water in Forests. Scottish Forestry. 18(1): 165-181.

Milsom S.J. and Hughes M.K. (1978). X-ray densitometry as a dendrochronological technique. In 'Dendrochronology in Europe'. Ed. J. Fletcher. B. A. R. Int. series 51: 317-324.

Mitchell J.M., Pzerdzeevskii B., Flohn H., Hofmeyr W.L., Lamb H.H., Rao K.N. and Wallen C.C. (1966). Climatic change. World Met. Organisational Tech. Note 79. World Met. Org. Geneva.

Moore P.D. (1987). Tree boundaries on the move. Nature 326: 545.

Munaut A.V. (1966a). Recherches dendrochronologiques sur Pinus sylvestris. I. Etude de 45 pins sylvestris recents originaires de Belgique. Agric. (Belg.) 14(2): 193-232.

Munaut A.V. (1966b). Recherches dendrochronologiques sur Pinus sylvestris. II. Premiere application des methodes dendrochronologiques a l'etude de pins sylvestris sub-fossiles. (Terneusen, Pays-Bas). Agric. (Belg.). 14(3): 361-389.

Munaut A.V. (1967). Etudepaleo-ecologique d'un gisement tourbeux situe a Terneusen (Pays-Bas). Berchtenvande Rijksdienst voor het Oudheidkundig Bodemonderzaek. Jan. 1967: 1-27.

Munaut A.V., Berger A.L., Guiot J. and Mathieu L. (1978). Dendroclimatological studies on cedars in Morocco. In Evolution des Atmoshpheres Planetaires et Climatologique de la Terre. CNES Nice.

Munro M.A.R. (1984). An improved algorithm for crossdating tree-ring series. Tree-ring Bull. 44: 17-27.

Necasany V., Jurasek L., Sopko R. and Bobak M. (1965). Formation of lignified cell wall within twenty-four hours. Nature 206: 4784.

Neuwirth G. (1959). Der CO2-Stoffwechsel Einiger Koniferen wahrend des Knospenaustriebes. Biol. Zbl. 78: 559-584.

Nix L.E. and Wodzicki T.J. (1974). The radial distribution and metabolism of IAA 14-C in Pinus echinata stems in relation to wood formation. Can. J. Bot. 52(6): 1349-1355.

Oskretkov M.I. (1959). Ob intyensivnosti fotosinteza konoii sosny. Problemy fotosinteza. A. N. USSR. 642-645.

O'Sullivan P.E. (1977). Vegetation history and the native pinewoods. In Bunce R.G.H. and Jeffers J.N.R. (Eds.) 'Native pinewoods of Scotland'. ITE. Camb.

Parker M.L. (1971). Dendrochronological techniques used by the Geological survey of Canada. In paper 71-25, 1-30. Geol. Survey of Canada, Edmonton, Canada.

Parker M.L. (1976). Improving tree-ring dating in Northern Canada by X-ray densitometry. Syesis 9: 163-172.

Parker M.L. and Henoch W.E.S. (1971). The use of engelmann spruce latewood density for dendrochronological purposes. Can. J. For. Res. 1: 90-98.

Parker M.L. and Kennedy R.W. (1973). The status of radiation densitometry for measurement of wood specific gravity. IUFRO Conf., Pretoria.

Pears N.V. (1968). Post-glacial tree-lines of the Cairngorm mountains, Scotland. Trans. Bot. Soc. (Edin). 40: 361-394.

Pears N.V. (1970). Post-glacial tree-lines of the Cairngorm mountains, Scotland. Some modifications based on radiocarbon dating. Trans. Bot. Soc. (Edin). 40: 536-544.

Persson T. (1980). Structure and Function of Northern Coniferous Forests.- An Ecosystem Study. Ecol. Bull. (Stockholm) 32.

Philipson W.R., Ward J.M. and Butterfield B.G. (1971). The Vascular Cambium. Chapman and Hall, Lond.

Pilcher J.R. (1973). Tree-ring research in Ireland. Tree-ring Bull. 33: 1-5.

Pilcher J.R. (1976). A statistical oak chronology from the north of Ireland. Tree-ring Bull. 36: 21-27.

Pilcher J.R., Baillie M.G.L., Schmidt B. and Becker B. (1984). A 7272-year tree ring chronology for western Europe. Nature 312: 150-152.

Pilcher J.R. and Gray B. (1982). The relationship between oak tree growth and climate in Britain. J. of Ecol. 70: 297-304.

Polge H. (1965). Study of wood density variations by densitometric analysis of x-ray negatives. Proc. IUFRO 41: 1-30.

Polge H. (1970). The use of the x-ray densitometric methods in dendrochronology. Tree-ring Bull. 30: 1-10.

Richardson S.D. (1964). The external environment and tracheid size in conifers. In Zimmerman M.H. (Ed.).'The formation of wood in forest trees'. Acad. Press.

Richardson S.D. (1966). Studies on the physiology of xylem development. III. Effect of temperature, defoliation and stem girdling on tracheid size in conifer seedlings. J. Inst. Wood Sci. 12: 3-12.

Richman M.B. (1986). Rotation of principal components. J. of Clim. 6: 293-335.

Richman M.B. and Lamb P.J. (1985). Climatic pattern analysis of 3- and 7-day summer rainfall in the central United States: some methodological considerations and a regionalisation. J. of Clim. and App. Meteor. 24: 1325.

Schweingruber F.H. (1980). Dichteschwankungen in Jahrringen von Nadelholzern in Beziehung zu Klimatisch Okologischen Faktoren, oder das Problem der Falsechen Jahrringe. Berichte Report 213. Swiss Fed. Inst. For. Res. CH 8903 Birmensdorf.

Schweingruber F.H. (1983). Der Jahrring: Standort, Methodik, Zeit und Klima in der Dendrochronologie. Paul Haupt Berne, Stuttgart.

Schweingruber F.H. (1985) Dendroecological zones in the coniferous forests of Europe. Dendrochronologia 3: 67-75.

Schweingruber F.H. (1986) Site selection and sampling strategy. Paper presented at task force meeting "Methodologies of Dendrochronology; East/West approaches", Krakov Poland. June 1986. To be published as an I. I. A. S. A. report.

Schweingruber F.H., Braker O.U. and Schar E. (1979). Dendroclimatic studies on conifers from central Europe and Great Britain. Boreas. 8: 427-452.

Schweingruber F.H., Fritts H.C., Braeker O.U., Drew L.G. and Schar E. (1978). The x-ray technique as applied to dendroclimatology. Tree-ring Bull. 38: 61-91.

Serre F. (1977). A factor analysis of correspondence applied to ring widths. Tree-ring Bull. 37: 21-32.

Serre F. (1978). The dendroclimatological value of the European larch (Larix Decidua Mill.) in the French Maritime Alps. Tree-ring Bull. 38: 25-34.

Siren G. (1961). Skogsgranstallen som indikator for Klimatfluktuationerina i norra Fennosckandien under historisk tid. Comm. Inst. For. Fenn. 54: 66pp.

Skene D.S. (1969). The period of time taken by cambial derivatives to grow and differentiate into tracheids in Pinus radiata. Ann. Bot. 33: 253-262.

Skene D.S. (1972). Kinetics of tracheid development in Tsuga canadensis. Ann. Bot. 36: 176-187.

Smith A.G., Pearson G.W. and Pilcher J.R. (1973). Belfast radiocarbon dates V. Radiocarbon 15(1): 212-228.

Smith C.J. (1974). Light intensity and substrate availability in relation to tracheid development in Picea sitchensis. Ann. Bot. 38. 347-358.

Smith C.J. (1976). Adaptions to environmental change in Picea sitchensis seedlings- changes in photosynthesis, growth and substrate availability. Ann. Bot. 40: 1003-1015.

Steiner K.C. (1979). Patterns of variation in bud burst timing amongst several pinus species. Sil. Gen. 28(5-6): 185-194.

Steven H.M. and Carlisle A. (1959). The native pinewoods of Scotland. Oliver and Boyde, Lond.

Tallis J.H. and Switzur V.R. (1983). Forests and moorland in the south Pennine uplands in the mid-Flandrian period. I. Macrofossil evidence of the former forest cover. J. of Ecol. 71: 585-600.

Telewski F.W., Wakefield A.H. and Jaffe M.J. (1983). Computer-assisted image analysis of tissues of ethrel-treated Pinus taeda seedlings. Plant Physiol. 72: 177-181.

Tessier L. (1984). Dendroclimatologie et ecologie de Pinus silvestris L. et Quercus pubescens Willd. dans le sud-est de la France. Thesis Univ. of Aix-Marseille for PhD.

Tomaszewski (1967). The Biogenesis of Wood. In Bialobok and Zelawski (1967). 'Outline of physiology of Scots pine'. pp. 97-118.

Tranquillini W. (1979). Physiological Ecology of the Alpine Timberline. Springer-Verlag, NY.

Vaartaga O. (1959). Evidence of photoperiodic ecotypes in trees. Ecol. Monogr. 29: 91-111.

Vaganov E.A. (1986). Histometric analysis of trees rings in ecological and dendroclimatological researches. Paper presented at task force meeting "Methodologies of Dendrochronology; East/West approaches", Krakov Poland. June 1986. To be published as an I. I. A. S. A. report.

Ward R.G.W., Haggart B.A. and Bridge M.C. (1987). Dendrochronological studies of bog pine from the Rannoch moor area, western Scotland. In R. Ward (Ed.) 'Applications of tree-ring studies'. BAR International Series 333.

Weiser and Becker (1975). In Hughes et al. (1982). Climate from tree-rings. CUP.

White E.J. (1974). Multivariate analysis of tree height increment on meteorological variables near the altitudinal tree limit in Northern England. Int. J. Biometeor. 18(3): 199-210.

Whitmore F.W. and Zahner R. (1967). Evidence for a direct effect of water stress on tracheid cell wall metabolism in pine. For. Sci. 13: 397-400.

Wigley T.M.L., Briffa K.R. and Jones P.D. (1984). On the average value of correlated time series, with applications to dendroclimatology and hydrometeorology. J. Clim. App. Meteor. 23: 201-213.

Wilkins D.A. (1984). The flandrian woods of Lewis (Scotland). J. of Ecol. 72: 251-258.

Wodzicki T.J. (1961). Investigations on the kind of Larix polonica Rac. wood formed under various photoperiodic conditions. Acta Soc. Bot. Pol. 30(2): 293-306.

Wodzicki T.J. (1964). Photoperiodic control of natural growth substances and wood formation in larch (Larix decidua D.C.). J. Exp. Bot. 15: 584-599.

Wodzicki T.J. (1971). Mechanisms of xylem differentiation in Pinus sylvestris L. J. Exp. Bot. 22(72): 670-687.

Wodzicki T.J. (1978). Seasonal variation of auxin in stem cambial region of Pinus sylvestris L. Acta Soc. Bot. Pol. 47(3): 225-231.

Wodzicki T.J., Wodzicki A.B. and Zajaczkowski S. (1979). Hormonal modulation of the oscillatory system involved in polar transport of auxin. Physiol. Plant. 46: 97-100.

Worral J.D. (1980). The impact of environment on cambial growth. In Little C. H. A. (Ed.) 'Control of shoot growth in trees'. IUFRO.

Wright J.W. and Baldwin H.I. (1957). The 1938 international union of scotch pine provenance test in New Hampshire. Silv. Gen. 6: 2-14.

Zahner R. (1978). Water deficits and growth of trees. In T.T. Kozlowski (Ed.) 'Water deficits and Plant Growth II.' pp.191-254. Academic Press, New York.

Zajaczkowski S. (1973). Auxin stimulation of cambial activity in Pinus sylvestris. I. The differential cambial response. Physiol. Plant. 29: 281-287.

Zajaczkowski S. and Wodzicki T.J. (1978). Auxin and plant morphogenesis- a model of regulation. Acta Soc. Bot. Pol. 47: 233-243.

Zelawski W. (1967). Gas exchange and water balance in needles. In Bialobok S. and Zelawski W. (Eds). Polish Academy of Sciences.

Zelawski W. and Niwinski Z. (1966). Variability of some needle characteristics in scots pine (Pinus sylvestris L.) ecotypes, grown in natural conditions. Ecol. Pol., Ser. A. 14: 301-308.

Appendix 1. Site descriptions.

CHIPPENHAM FEN.

Lat. 52°24'N, Long. 0°10'W.

Map ref. TL 648 697

Location - East Anglia, 5 miles north of Newmarket in the Cambridgeshire fens. The site is at an elevation of 15m, scots pines are growing on an area of flat peat soil. 10 trees were sampled, 2 cores taken from each tree, collected by D. Cartwright July 1978.

DERRYCROW.

Lat. 45°31'N, Long. 06°29'W.

Map ref. H 987 641

Elevation 18m a.s.l.

The site is in Armagh, Northern Ireland on the Southern side of Lough Neagh 10.2 km north of Portadown. It is a peat bog site and no trees are growing there at present. Extraction of a large number of subfossil stumps was carried out by J.Pilcher et al. from Queens University, Belfast in the early 1970's. A radiocarbon date gives the pine layer as 4639 +/- 60 yrs. BP.

GLEN AFFRIC.

Lat. 57°15N, Long. 04°55'W

GR NH 145 225

Altitude 180-450m.

The area of native scots pine forest that was sampled extends from Badger falls to half way along Loch Affric on the North side. It is partly on shallow slopes (10 degrees) in the lower section and partly on steeper SE slopes of 30 degrees. The soil is sands and gravels in the lower part with some peat between the knolls giving way to shallow well drained peat on the higher slopes.

Sampling was carried out in May 1984 by C. Swain. 14 trees were cored, with 2 cores per tree. Previous sampling had also been carried out by D. Cartwright in July 1977.

GLEN DERRY

Lat. 57°00N, Long. 03°35W.

GR NO 035 932

Alititude 390-555m

The site is partly on the west facing slope (30 degrees) in the upper region of Glen Derry, 1km above Derry Lodge. The north east facing slopes (45 degrees) of Glen Luibeg 1km West of Derry Lodge form the remainder of the site. The trees are growing on peaty soils, the native pines are growing in an open stand with very few young trees.

Sample collection was carried out by C. Swain May 1984. 13 trees were cored, 2 cores/tree. Previous sampling in the same area had been carried out by D. Cartwright in October 1979. The area was further down the Glen and called Mar in this case. An area at the foot of the Glen at Inverey (2.5 km south of the Glen Derry site) had also been sampled in July 1977.

KIELDER CASTLE.

Lat. 54°55N, Long. 02°30W.

GR NY 632 935

Elevation 200m a.s.l.

The area is at Ravenshill wood Northumberland, sampling was done by K. Briffa in 1981. 19 trees were cored, one core from each tree was available for use in Liverpool.

MUDDUS.

Lat. 66°47N, Long. 20°08E.

Elevation 450m a.s.l. The site is in Northern Sweden. Tree ring data for this site is available in the European data bank.

O FROSTSJOASEN.

Lat. 62°19N, 12°48E.

Elevation 800m a.s.l. The site is in central Sweden. Data for this site has been obtained from K. Briffa from Climate Research Unit at University of East Anglia.

RANDALSTOWN.

Lat. 54° 46N, Long. 06°18W.

GR JO 099 025

Elevation 50m.

Antrim, Northern Ireland. The area is on flat peat by the Ballylugan road 2.4km north east of Randalstown. This is a small area of pine trees remaining by the roadside after construction of a new bypass. Sampling was carried out by C. Swain November 1983. 15 trees were cored, two cores were taken from each tree.

SLUGGAN.

Lat. 54°46N, Long. 06°18W.

GR J 009 921

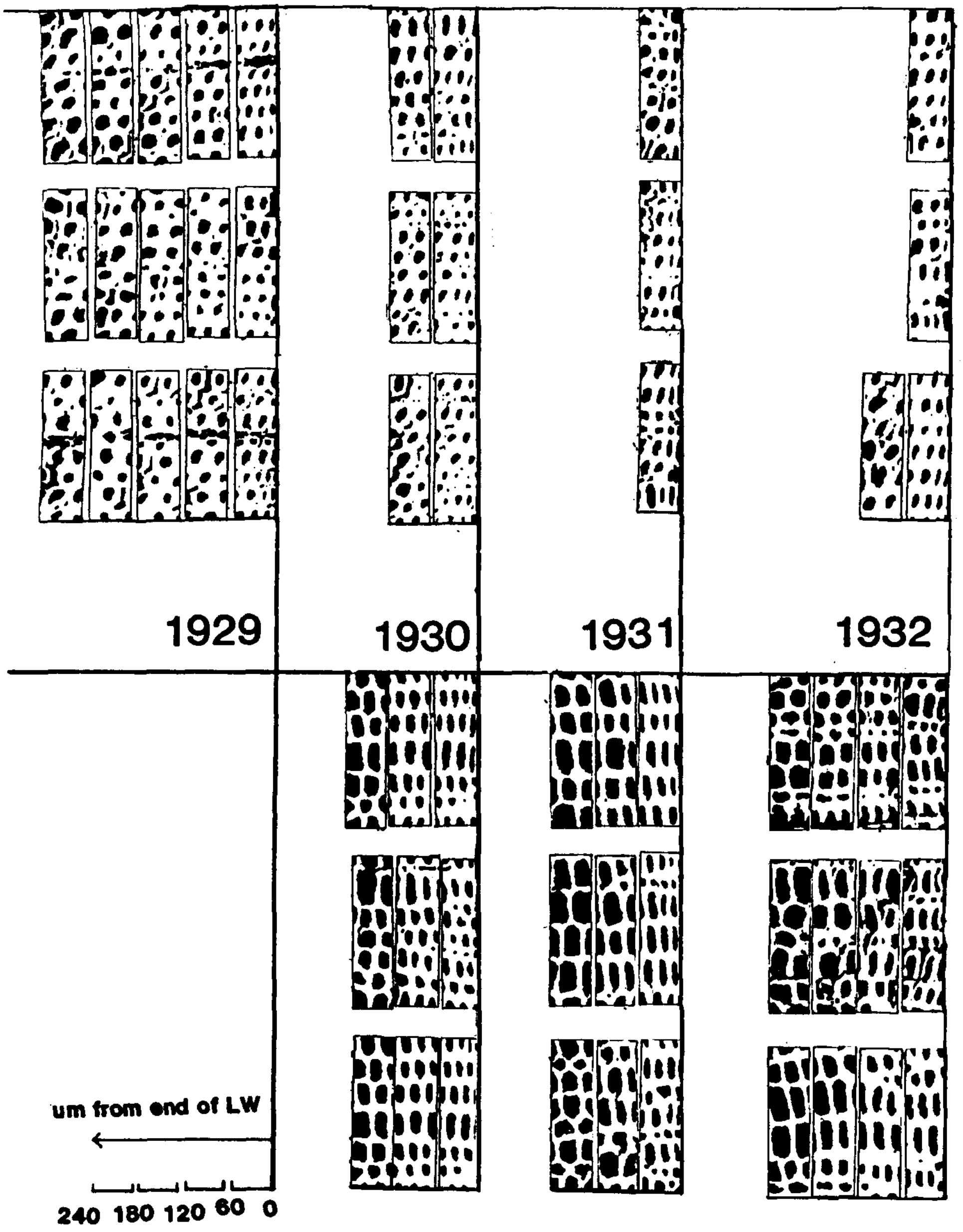
Elevation 50m a.s.l.

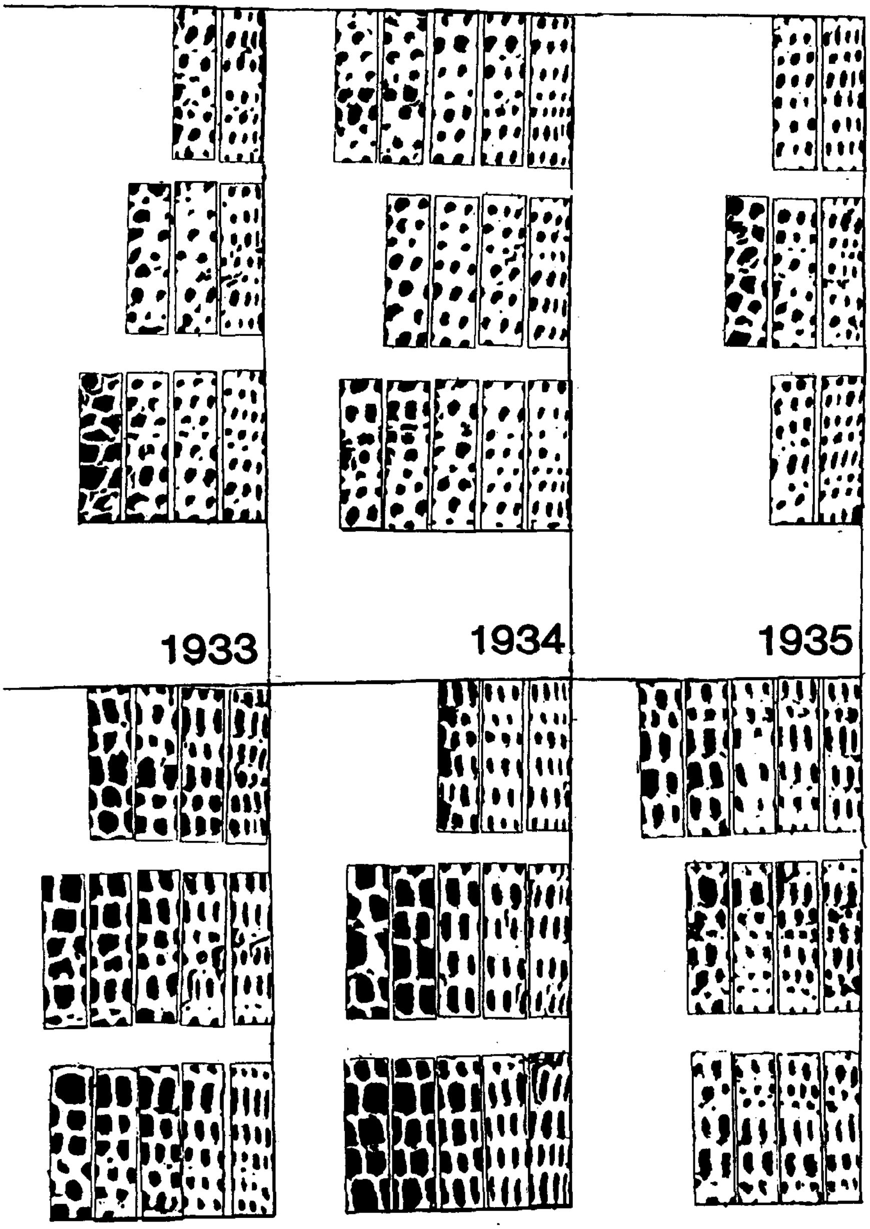
The site is in co. Antrim, Northern Ireland, on the north east side of Lough Neagh, 2.4 km north east of Randalstown. No trees are growing on the site at present. It is an area of raised peat bog with three layers of subfossil pine stumps. The peat is cut yearly, exposing the stumps.

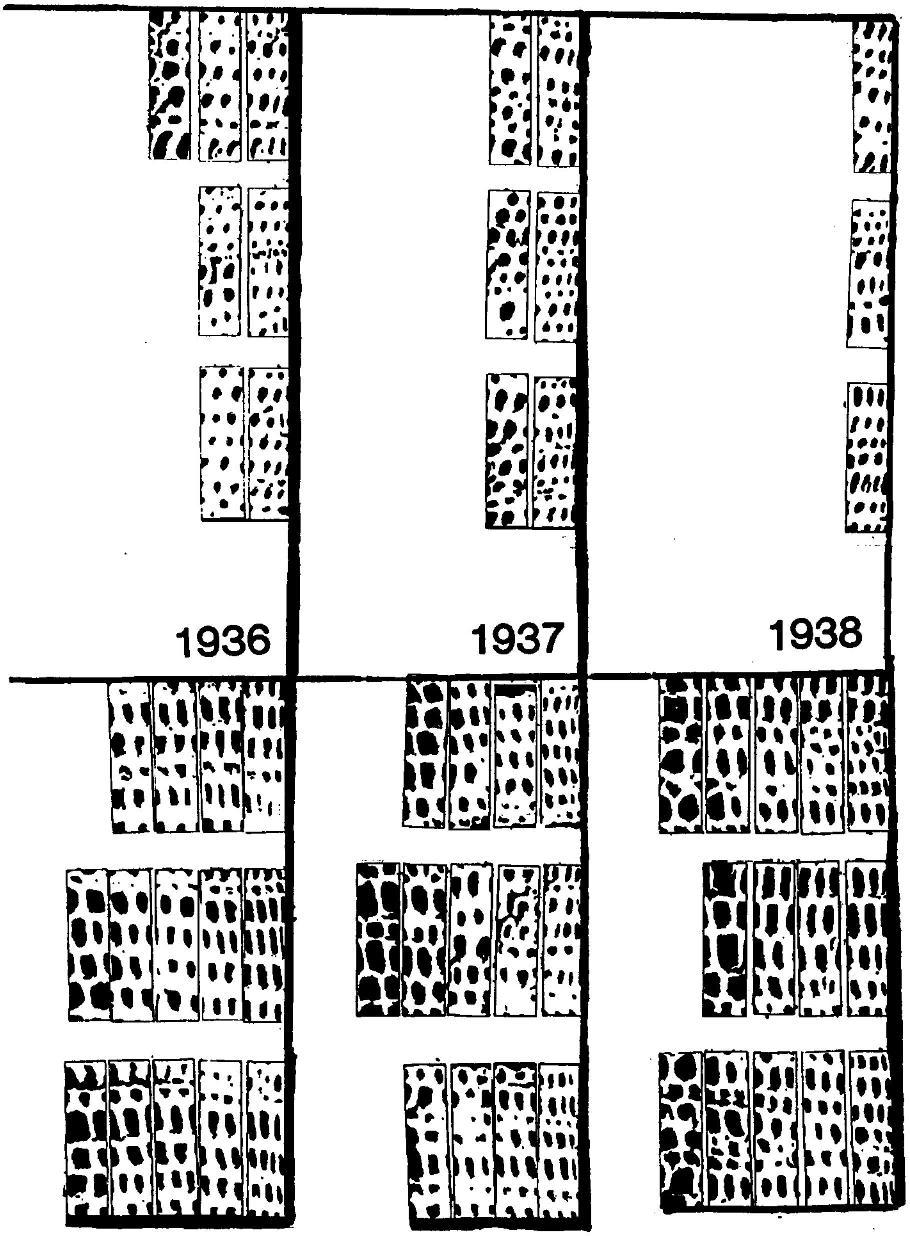
A large number of stumps have been excavated by J.Pilcher. Radiocarbon dates on the Upper, Middle and Lower layers of stumps are 6615 +/- 95, 7005 +/- 65 and 7095 +/- 115 years BP respectively.

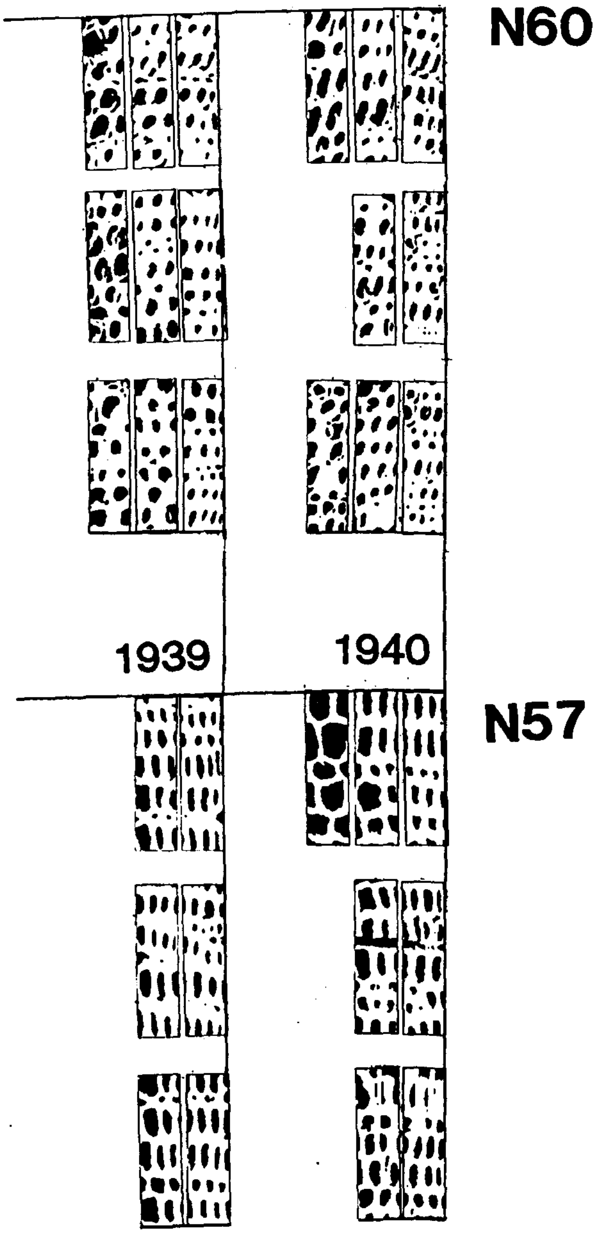
Appendix II.

IMAGE ANALYSIS PICTURES.


1929
1930
1931
1932
um from end of LW
240 180 120 60 0


1933
1934
1935

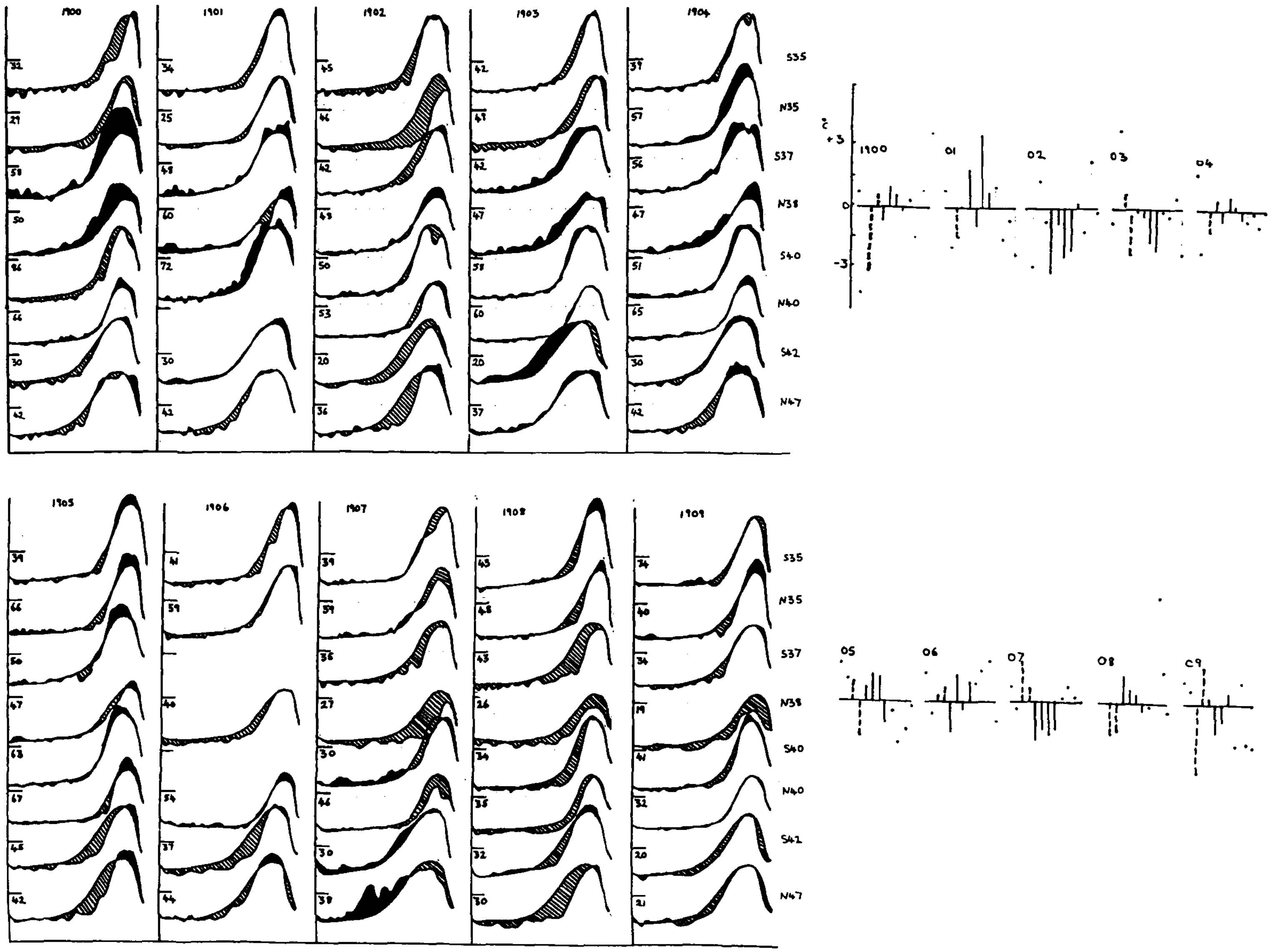

1936
1937
1938


N60
1939
1940
N57

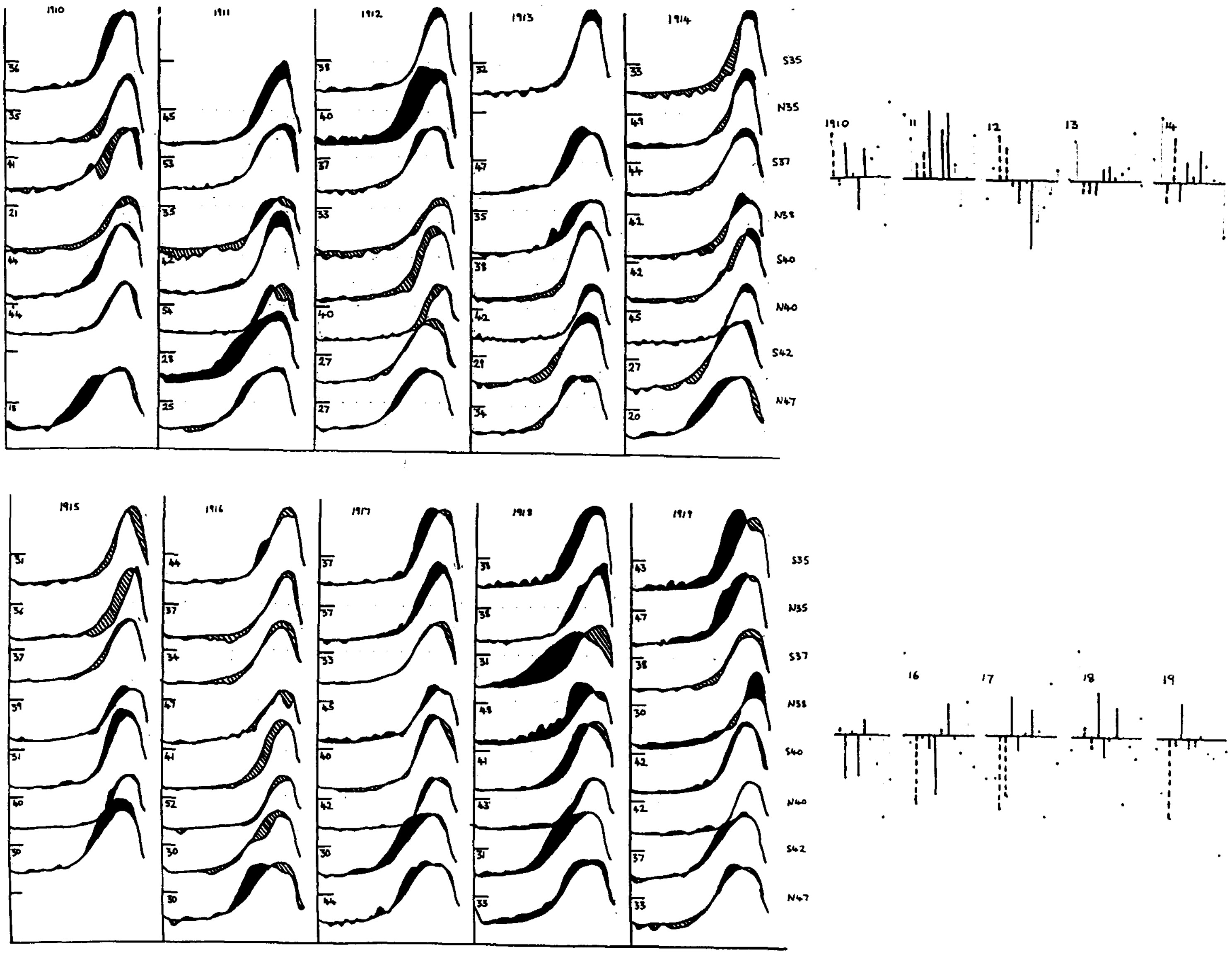
Appendix III.

DENSITY PROFILES AND TEMPERATURE DATA.

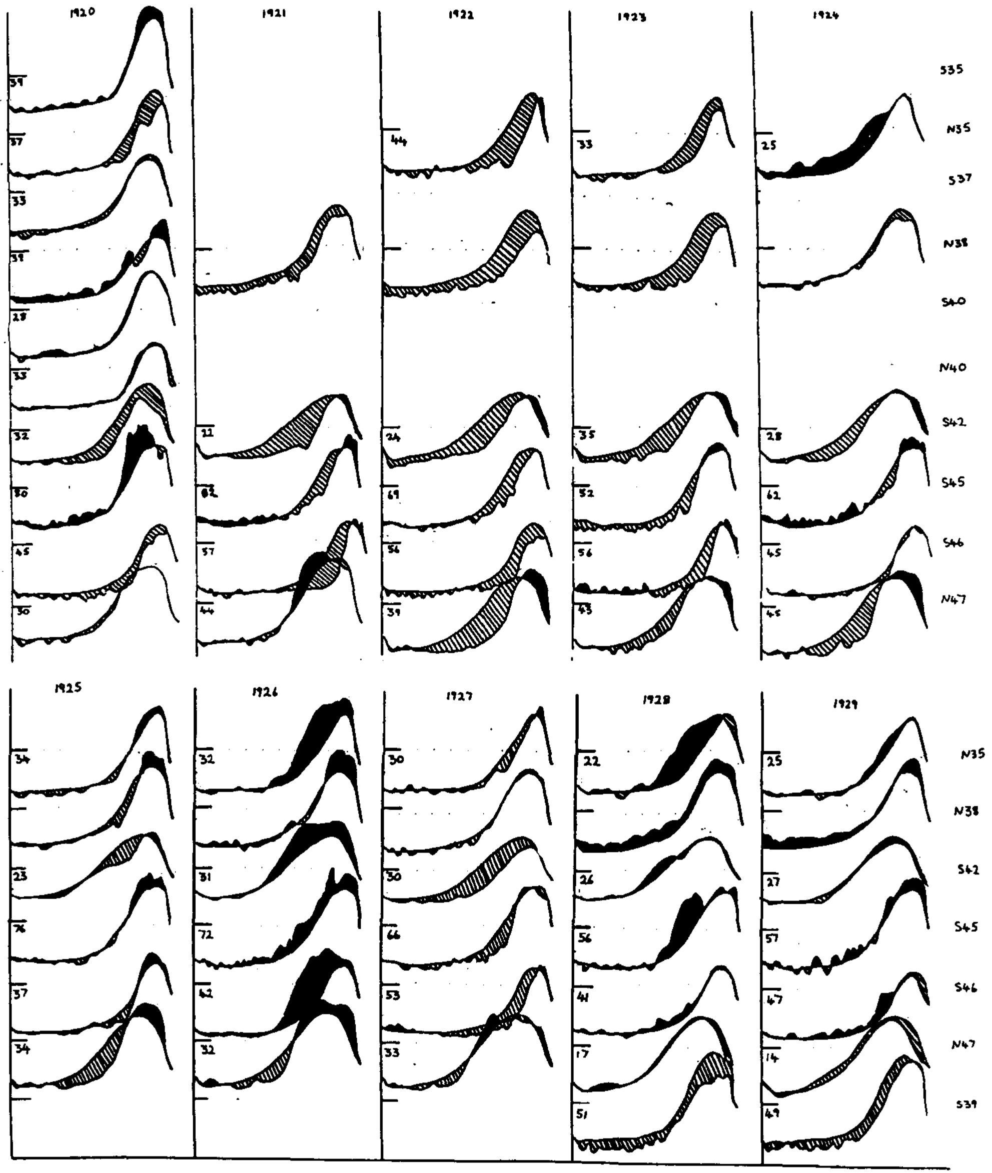
AFF = Glen Affric, DER = Glen Derry.

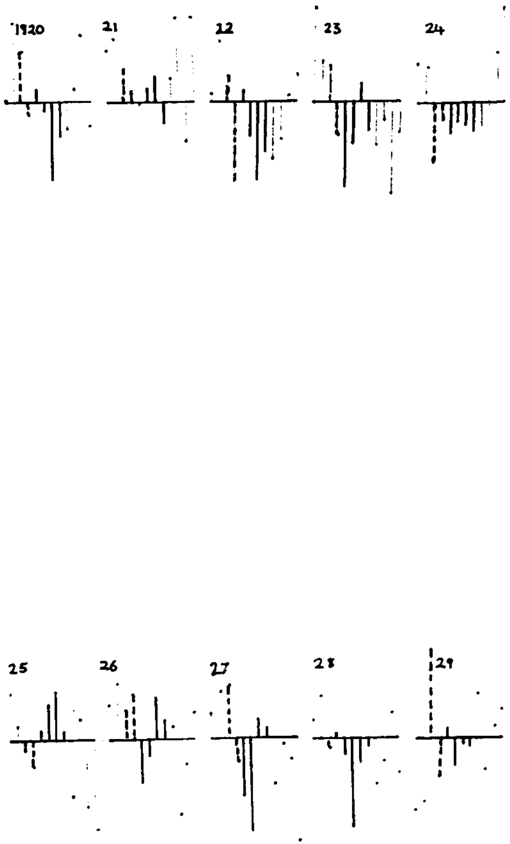

1900
1901
1902
1903
1904
S35
N35
S37
N38
S40
N40
S42
N47
1905
1906
1907
1908
1909
°C
+3
0
-3
1900
01
02
03
04
05
06
07
08
09

AFF


1910
1911
1912
1913
1914
36
35
41
21
44
44
18
45
53
35
42
54
28
25
38
40
37
33
40
27
27
32
47
35
38
42
29
34
33
49
44
42
42
45
27
20
S35
N35
S37
N38
S40
N40
S42
N47
1915
1916
1917
1918
1919
31
36
37
39
31
40
30
44
37
34
47
41
52
30
30
37
37
33
43
40
42
30
44
38
38
31
48
41
43
31
33
43
47
38
30
42
42
37
33
S35
N35
S37
N38
S40
N40
S42
N47
1910
11
12
13
14
16
17
18
19

AFF


1920
1921
1922
1923
1924
59
37
33
39
28
33
32
80
45
30
21
62
57
44
44
24
69
56
39
33
35
52
56
43
25
28
62
45
45
S35
N35
S37
N38
S40
N40
S42
S45
S46
N47
1925
1926
1927
1928
1929
34
23
76
37
34
32
31
72
62
32
30
30
66
53
33
22
26
56
41
17
51
25
27
57
47
14
49
N35
N38
S42
S45
S46
N47
S39


1920
21
22
23
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26
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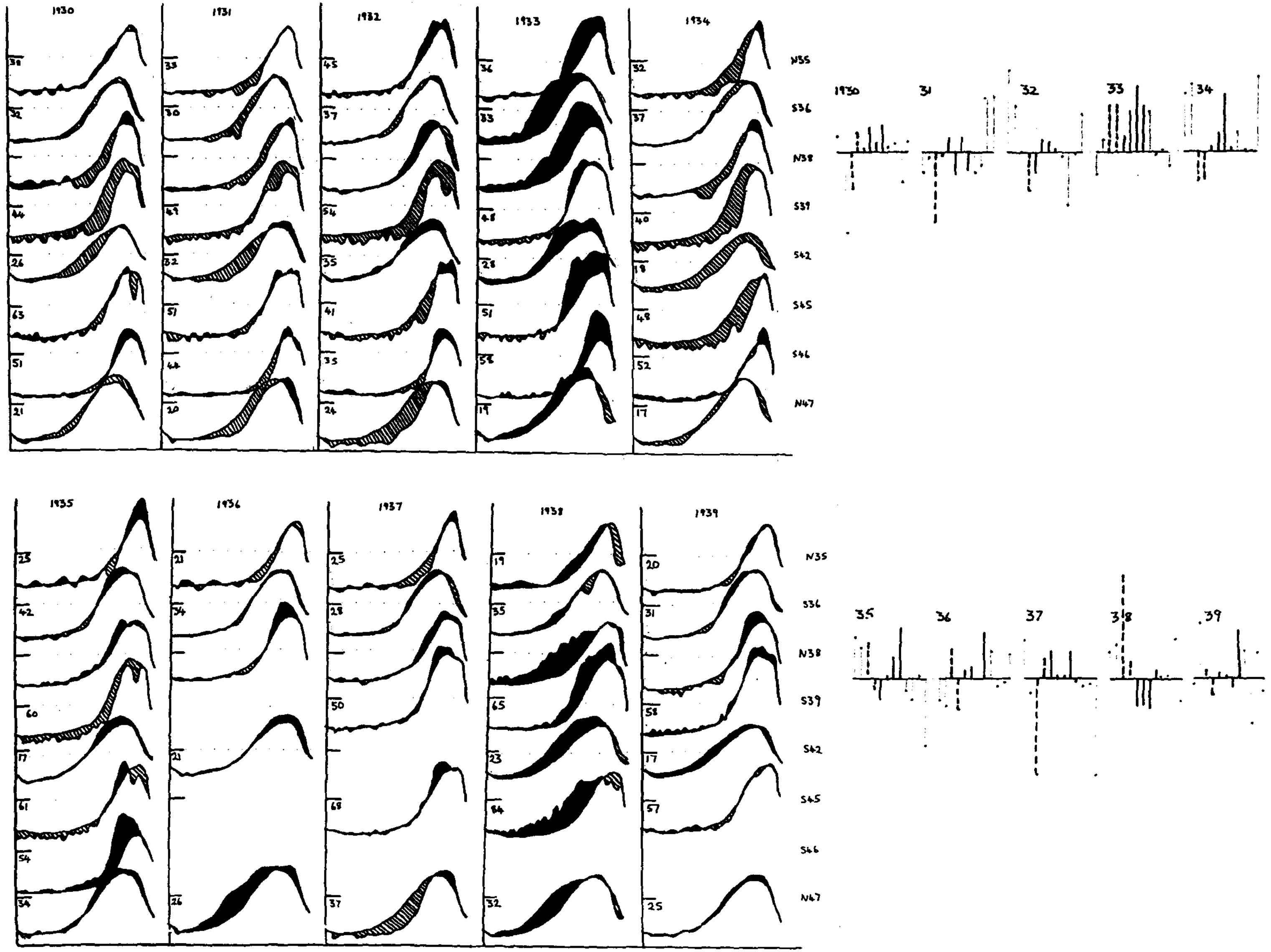
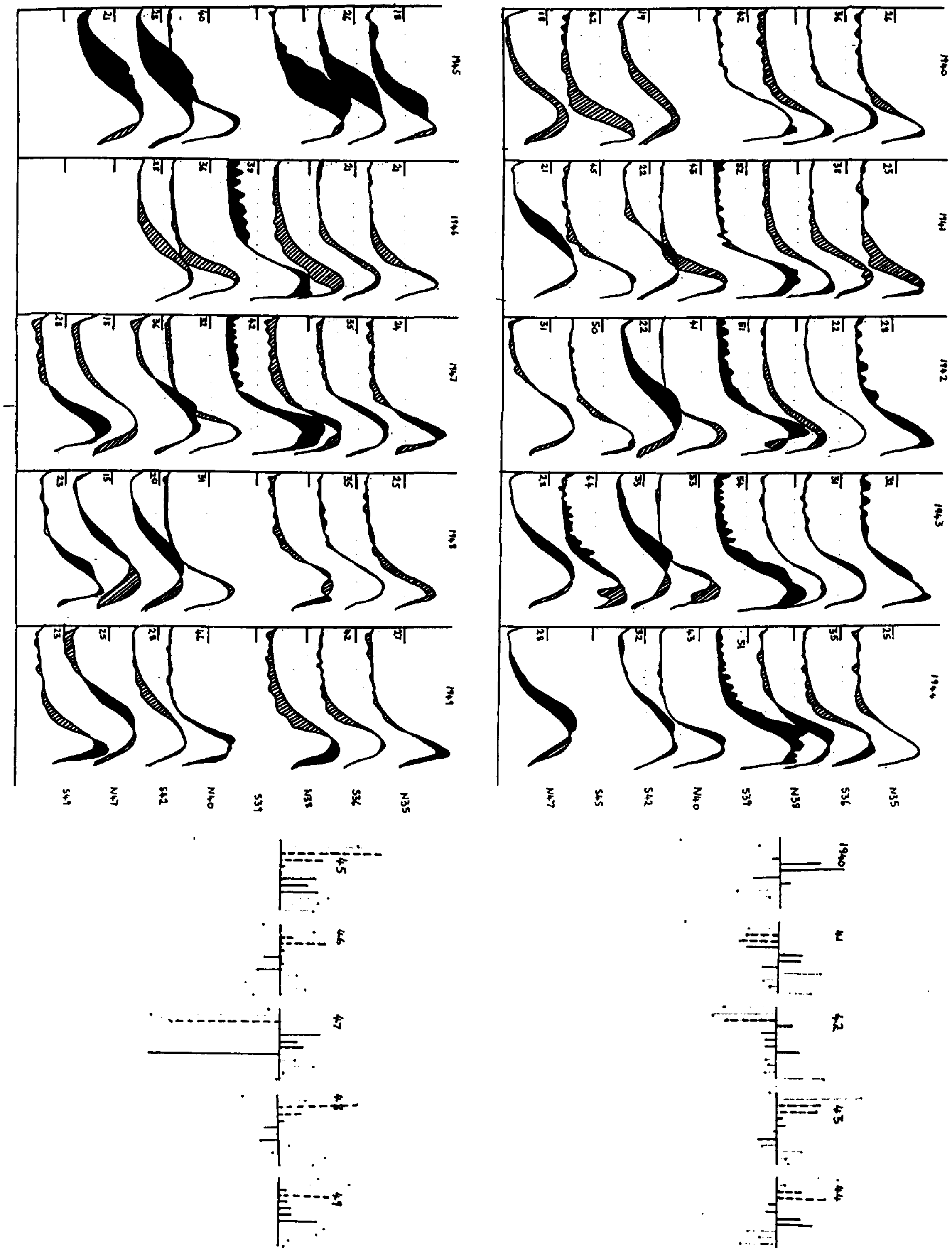
28
29

AFF


1930
1931
1932
1933
1934
1935
1936
1937
1938
1939
N35
S36
N38
S39
S42
S45
S46
N47
1930
31
32
33
34
35
36
37
38
39

AFF


1940
1941
1942
1943
1944
1945
1946
1947
1948
1949
N35
S36
N38
S39
N40
S42
S45
N47
S37
S41
41
42
43
44
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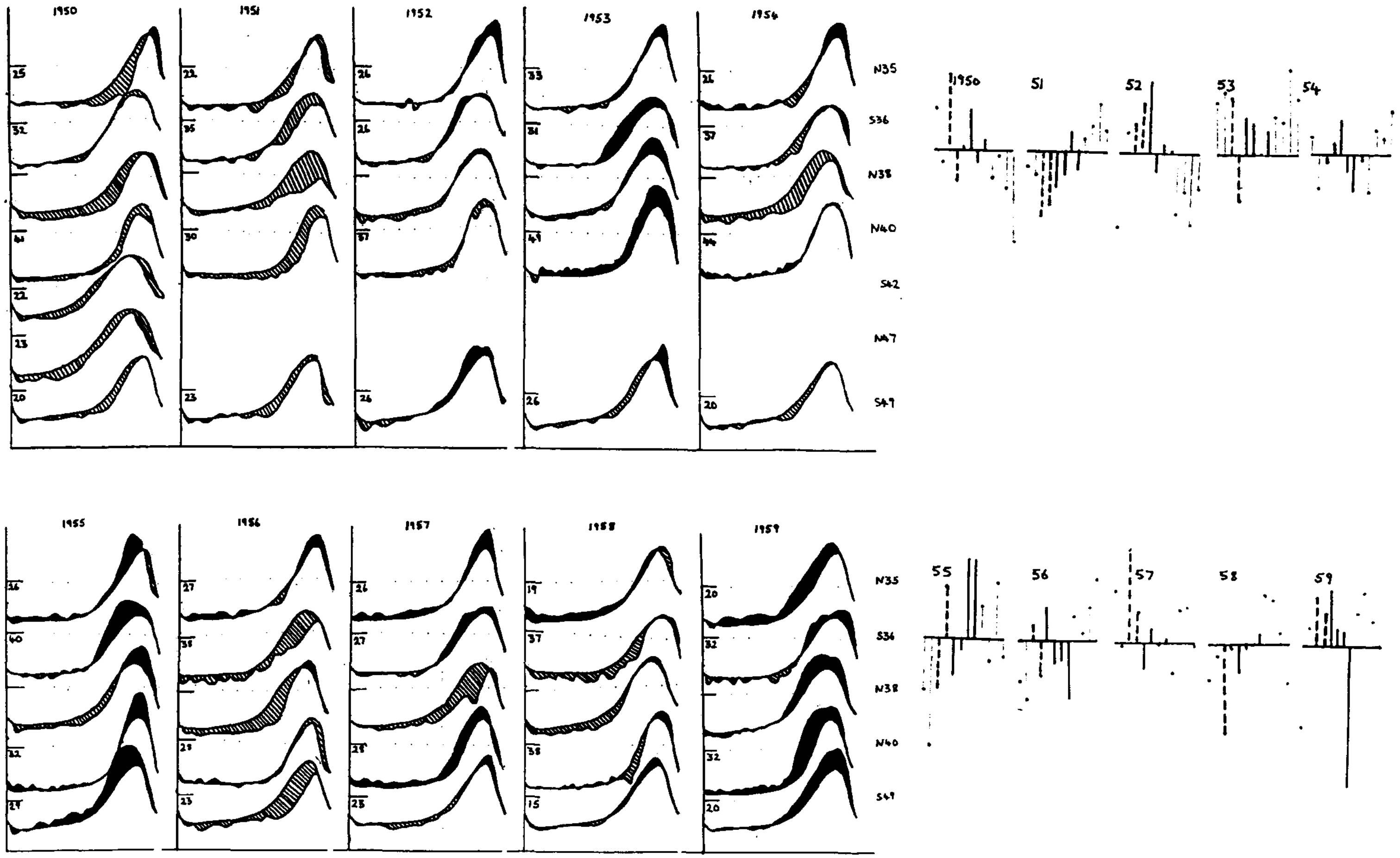
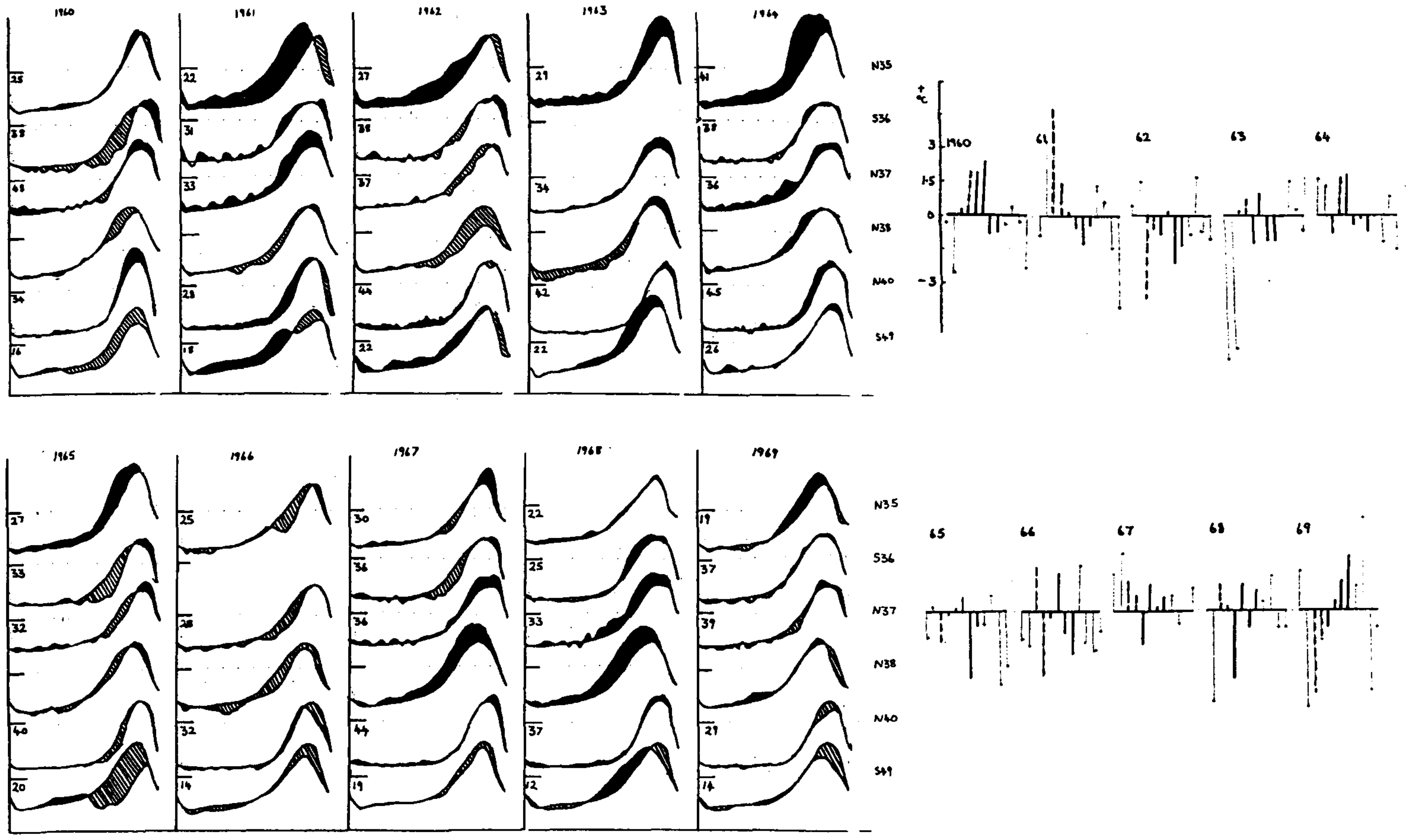
46
47
48
49

AFF

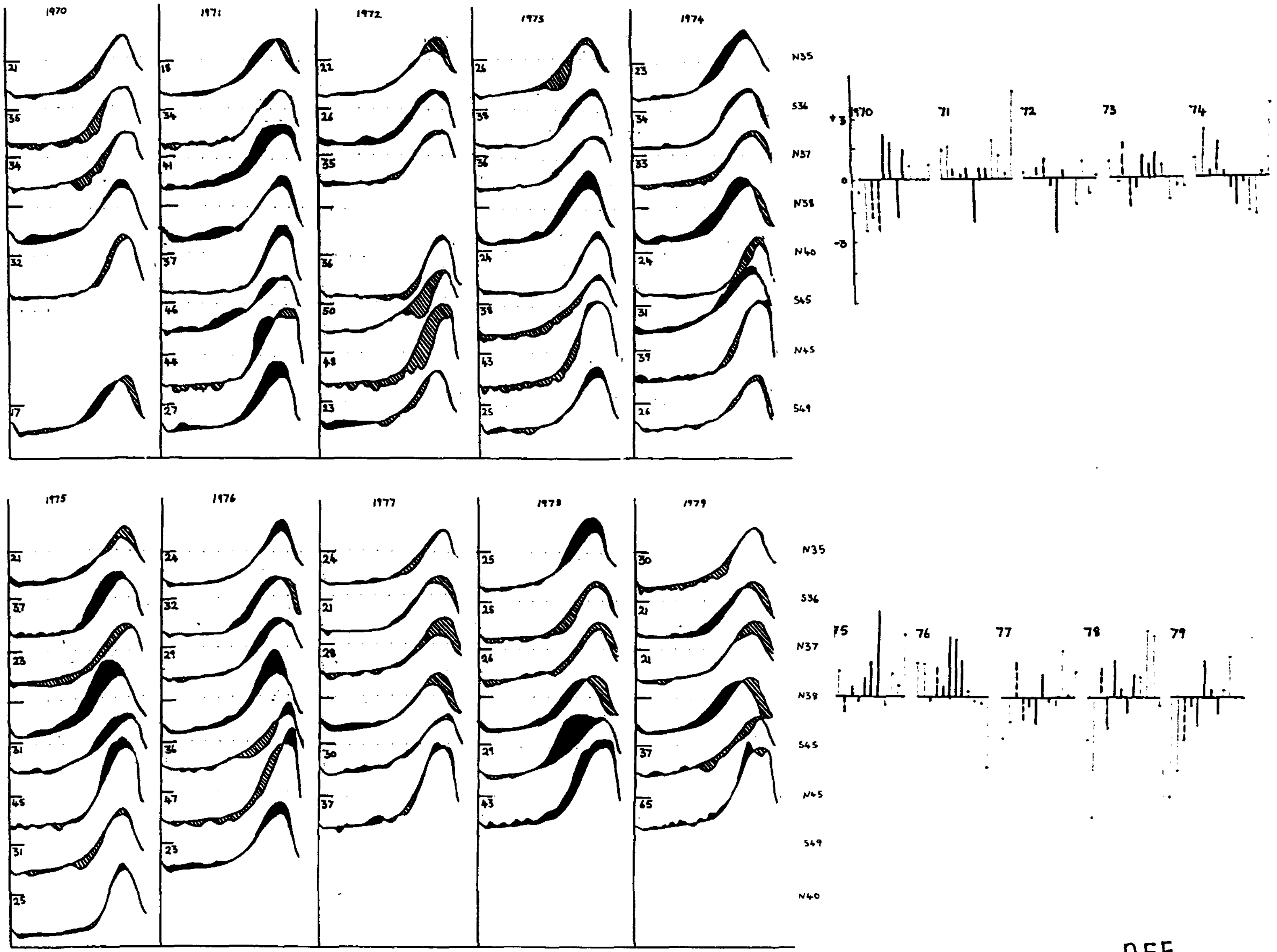

1950
1951
1952
1953
1954
N35
S36
N38
N40
S42
N47
S49
1950
51
52
53
54
1955
1956
1957
1958
1959
N35
S36
N38
N40
S49
55
56
57
58
59

XV

AFF


1960
1961
1962
1963
1964
1965
1966
1967
1968
1969
N35
S36
N37
N38
N40
S49
°C
+
3
1·5
0
-3
1960
61
62
63
64
65
66
67
68
69

AFF


1970
1971
1972
1973
1974
21
36
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32
17
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50
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23
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33
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31
39
26
N35
S36
N37
N38
N40
S45
N45
S49
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1970
71
72
73
74
1975
1976
1977
1978
1979
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36
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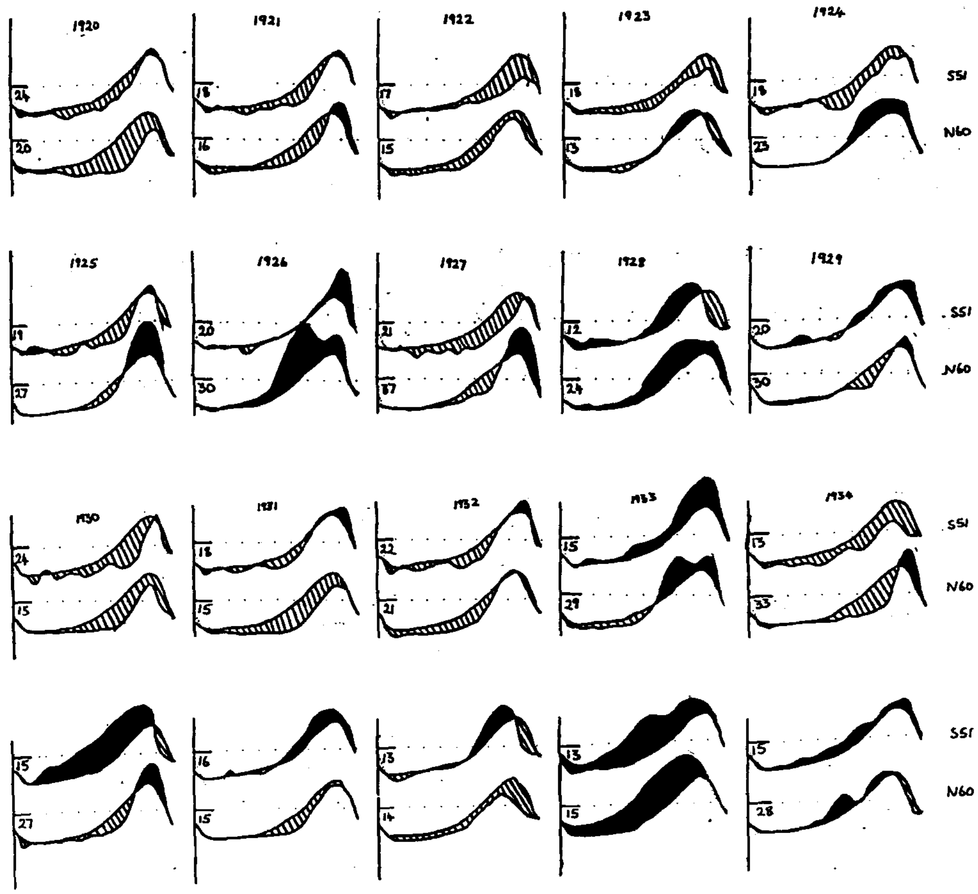
37
25
25
26
29
43
30
21
21
37
65
N35
S36
N37
N38
S45
N45
S49
N40
75
76
77
78
79

AFF


1920
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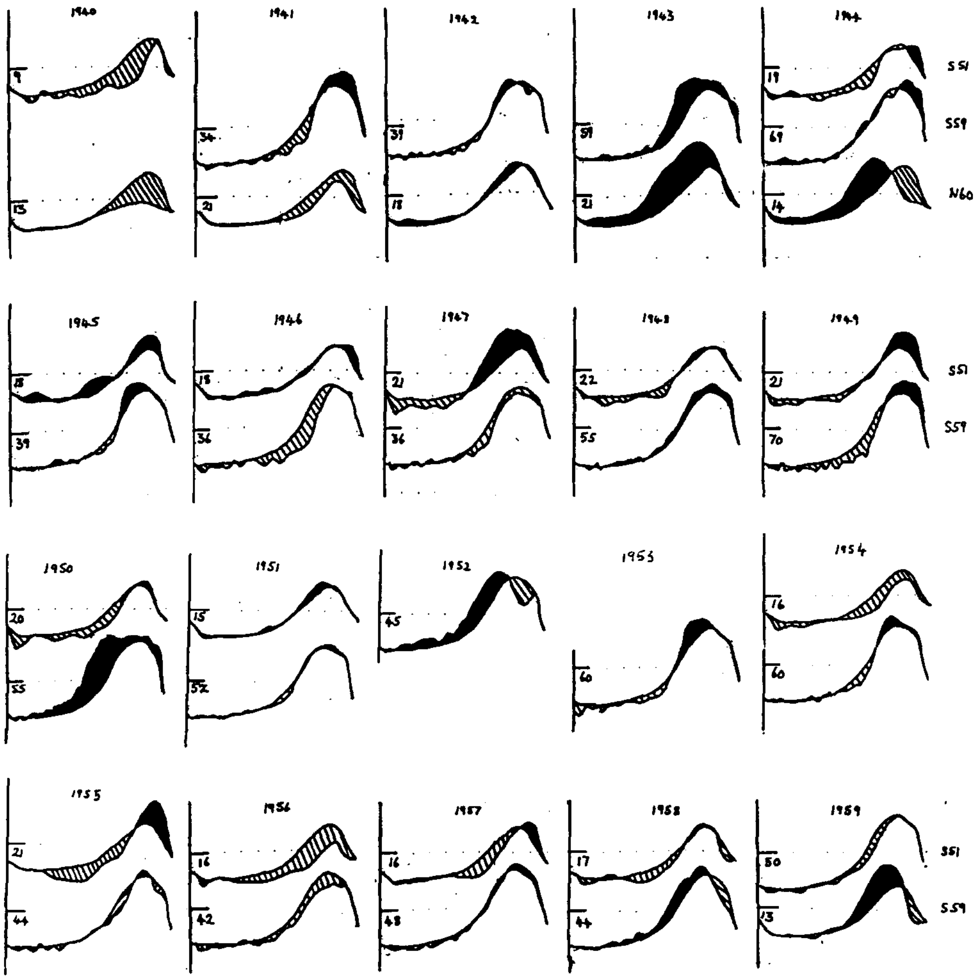
1930
1931
1932
1933
1934
SSI
N60

DER


1940
9
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1941
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1942
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18
1943
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1944
19
69
14
S51
S59
N60
1945
18
39
1946
15
36
1947
21
36
1948
22
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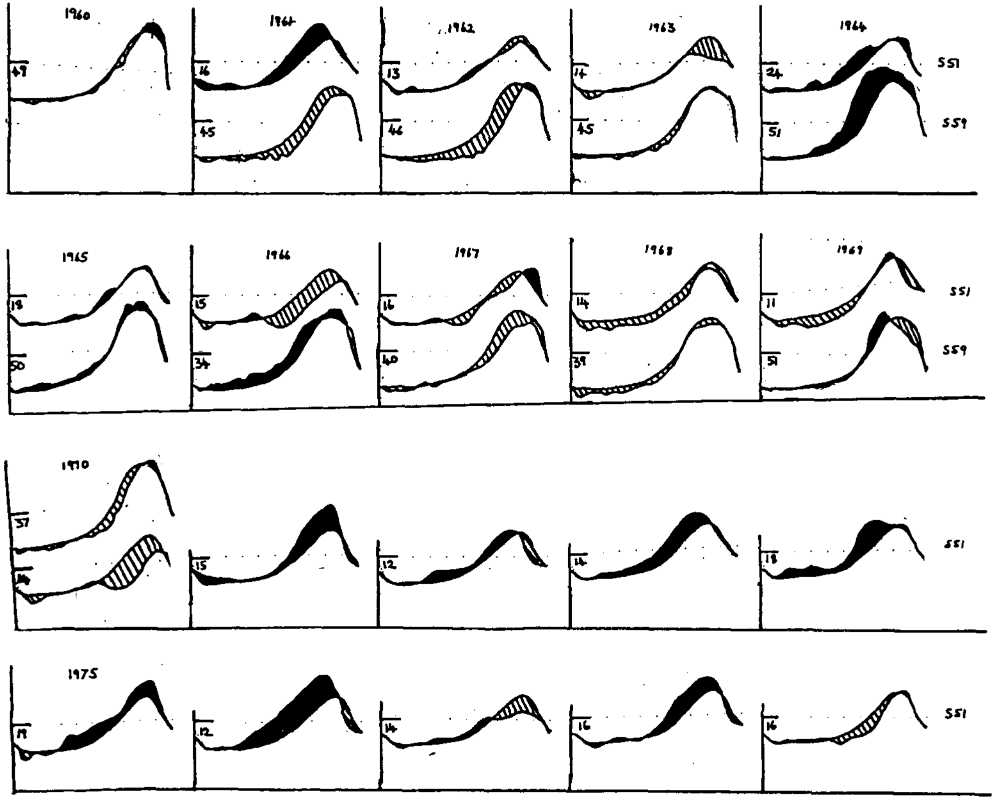
1949
21
70
S51
S59
1950
20
55
1951
15
52
1952
45
1953
60
1954
16
60
1955
21
44
1956
16
42
1957
16
48
1958
17
44
1959
50
13
S51
S59

DER


1960
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1964
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1968
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1969
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1970
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14
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1975
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551

XX

DER