Growth rings in secondary xylem. their
formation and interpretation
through geological time.

A thesis submitted for the degree of

Doctor of Philosophy

in the University of London
(Bedford College)

by Geoffrey Tremain Creber

ProQuest Number: 10098481

ProQuest 10098481

ABSTRACT

The secondary wood formed by cambial activity in the growth of trees records with varying degrees of precision the amount of seasonality and other aspects of the climate under which it grew. A survey is presented of the extent to which this climatic 'data-store' can be directly 'read back', based on the extensive literature on the environmental control of wood formation in modern plants. This led to the investigation of growth ring characters in selected fossil and recent wood in the course of which a cyclic phenomenon. apparently under endogenous control. was demonstrated.

The potential of this information to deduce aspects of the palaeoclimate from fossil wood (of age extending back some 370 million years) is then considered. Attention was directed particularly to three intervals of geological time. namely the Upper Devonian. the Permo-Carboniferous and the later Mesozoic in which growth ring characteristics present features of particular interest. A classification of growth ring features is developed and five categories are defined. Some of these data are derived from direct observation of fossil wood material by the author and some from the literature. Growth ring characteristics are plotted on palaeo-reconstruction maps and the climatic significance is considered in relation to other indicators of palaeo-climate.

Consideration is given to the phenomenon of tree growth (and very substantial increments) in high latitudes during two phases of geological time - the Permian and the later Mesozoic. At these times major forest growth evidently extended far beyond the present latitudinal range. Consideration of the radiation energy input at high latitudes. and the effect of a generally more isothermal global climate suggests that these growth ring phenomena can be explained in uniformitarian terms without the need to invoke shift in axial inclination or similar processes as some have advocated.

DEDICATION

To my wife Hilda

THE EARLIEST RECORDED REFERENCE TO GROWTH RINGS IN WOOD

"...... the wood of the silver-fir has many layers. like an onion: there is always another beneath that which is visible and the wood is composed of such layers throughout."

Theophrastus Ca. 300 B.C. "Enquiry into plants" transl. Sir Arthur Hort.

PROBABLY THE EARLIEST RECORDED DETAILED PALAEOCLIMATIC INTERPRETATION OF GROWTH RINGS IN FOSSIL WOOD

"... this specimen (of fossil wood from the Upper Jurassic of East Sutherland) furnishes curious evidence that the often-marked but little understood law. which gives us our better and worse seasons in alternate groupes (sic). various in number and uncertain in their time of recurrence. obtained as early as the age of the Oolite. The rings follow each other in groupes of lesser and larger breadth. One group of four rings measures an inch and a quarter across. while an adjoining group of five rings measures only five-eighth parts; and in a breadth of six inches there occur five of these alternate groupes. For some four or five years together. when this pine was a living tree. the springs were late and cold. and the summers cloudy and chill. as in that group of seasons which intervened between 1835 and 1841: and then for four or five years more springs were early and summers genial. as in the after group of 1842. 1843. and 1844."

Hugh Miller Ca. 1850. Published posthumously in "The cruise of the Bet'sey". 1858.

ACKNOWLEDGEMENTS

PREFACE

In the course of this work, parts of it were published separately and some inevitable overlap occurs between published work, manuscripts in press or prepared for publication and sections of the thesis. Although the thesis may be read as bound, in order to provide a logical reading sequence it is suggested that Appendix III, the four published papers 1972-1977 should be read in chronological order first. Part I then provides introductory material for all of the remainder. Appendix II, a paper in press, has cross-references to Parts II and III which may be read when referred to. Part IV, a manuscript prepared for publication, should be read last. The Fossil Wood Records in Appendix I have been drawn upon when required for Appendix II and Parts III and IV.

TABLE OF CONTENTS

1. Gymnospermous wood from the Kimmeridgian of East
Sutherland and from the Sandringham Sands of Norfolk.
G.T. Creber. 1972. Palaeontology 15. 655-661.

2. Growth rings in fossil woods as evidence of past
climates.
W.G. Chaloner and G.T. Creber. 1973. In 'Implications of
continental drift to the earth sciences' (Eds. D.H. Tarling
and S.K. Runcorn).
pp. 425-437. Academic Press. London.

3. The effects of gravity and the earth's rotation on the
growth of wood. G.T. Creber. 1975. In 'Growth rhythms and
history of the earth's rotation' (Eds. G.D. Rosenberg and
S.K. Runcorn).
pp. 75-87. Wiley, London.

4. Tree rings: A natural data-storage system.
G.T. Creber. 1977. Biological Reviews 52, 349-383.

INTRODUCTION

This work is a study of tree growth from the earliest known trees in the Upper Devonian through to the present day. Without exception, the wood or secondary xylem in these trees develops from a single layer of actively dividing cells, the cambium. The activity of the cambium, particularly in the temperate climatic regions of the work, is subject to periodic bursts of activity and quiescence. Due to the fact that on renewed activity, the cell radial diameters are often larger, boundaries arise between cells of markedly different dimensions. Thus growth rings appear in the wood. (Creber, 1977; fig.1)

PART I

THE ACTIVITY OF THE VASCULAR CAMBIUM

1. <u>Development of the Terminology</u>

The use of the term cambium has a long history; Lorch (1967) traces it back for hundreds of years. He was less concerned however to produce a precise definition but rather to study how, through the ages, it has been regarded as a growth-producing mechanism. Viewed with hindsight he seems rather dogmatic in stating that the cambium is a single <u>layer</u> of actively dividing cells. In doing this he was making an assumption of universal acceptance in a subject that has been at the focus of heated debate for many years. Indeed, at its height, a plant anatomist might have found his scientific rigour judged by his attitude to the exact nature of the cambium. It became almost an act of faith to regard it as a precisely defined layer of cells that was distinct from contiguous layers even though the distinction could not, in the 1930's, be experimentally demonstrated. At the present day, a more pragmatic attitude prevails and authors are concerned to produce a working definition that requires no special pleading.

In 1955, Bannan pointed out that considerable confusion existed in the literature in the use of the word 'cambium'. He cited 8 works in which the narrow definition of the cambium as a single layer of cells was used. Included were: Bailey (1943), Eames & MacDaniels (1947) and Esau (1953). Contrasted with these were 20 who used the concept of a broader cambial zone; they included: Bower (1923), Priestley (1930) and Unger (1847). At the time Bannan was writing, the current debate was whether the term cambium should designate only the uniseriate initiating layer or the broader zone, including the tissue mother cells. Eames & MacDaniels (1947) supported the first of these usages on the grounds that only the cells of the initiating layer were self-perpetuating and, in any case,

cells in the other layers sooner or later maturate into vascular elements. The emhasis was thus placed, not on the function of producing the vascular tissues, but rather on the permanently meristematic nature of the initial cells. However, it was obvious that if capacity for perpetuation were to be made the criterion for delimiting meristems. only very small portions of the regions of growth generally classed as meristems would so qualify.

Use of the word cambium in the broader sense to include the tissue mother cells in addition to the initiating layer has attracted support in the past. Historically the term in the modern sense, has been used to designate the site of generation of secondary xylem and phloem without regard to the constitution of the generating zone. A definition in keeping with this tradition was provided by Esau (1953) who stated that the vascular cambium was the lateral meristem that formed the secondary vascular tissues. What was in doubt was the amount of the cambial zone that was actually meristematic. As will be shown later, mitotic activity during the development of earlywood is actually greater among the xylem mother cells than in the initiating layer. The dividing and redividing xylem mother cells must be rated as meristem cells since they constitute a region of tissue production.

The ontogenetic sequence in the cambial region has features of resemblance with that in the apical meristem of higher plants. In the latter a small number of initials produces central mother cells which in turn give rise to the tissue systems of the stem. The common practice with reference to the stem apex is to consider the apical meristem as including the initials and their immediate derivatives. When used in the same sense, the term cambium. as the designation for the lateral meristem producing wood and bast, should include the tissue mother cells.

Bannan preferred this usage of the term cambium to denote the combined initiating layer and derived tissue

mother cells, or in other words, the zone of periclinal division. Thus he was clearly a 'zone' man and although he states his case in a very persuasive manner there were authoritative plant anatomists at that time, e.g. Bailey, who would have firmly disagreed with him. One wonders, too, how far he was justified in stating so categorically that the use of the word cambium in the broader sense was by custom, as at this date (1955) there was still considerable divergence of opinion.

In fact the concept of the cambium as a single initiating layer has a lengthy history, its first powerful protagonist being Sanio (1873). He demolished Hartig's (1853) theory that it consisted of two layers, one producing secondary xylem and the other secondary phloem. He pointed out that as mitotic cell division results in the formation of an entire protoplasmic membrane and new cell wall around each daughter cell, a very thick tangential wall would arise between the two proposed initials. This effect would be expected to have become very marked in older trees but it had never been observed. A further objection made by Sanio was that the secondary vascular tissues always existed in continuous radial files which showed simultaneous origin and loss. If two initials were involved, one would expect to see the occasional loss of either the phloem or the xylem file separately; again, this only occurs in certain exceptional circumstances and not as frequently as would be the case if Hartig's mechanism operated.

Chronologically, after Bannan's (1955) paper there appeared one by Newman (1956), who studied both apical and lateral meristems in Pinus radiata D.Don. Early in his paper he felt impelled to state his position with regard to cambial definition. He said that a logical case could be made for the existence of one or a very few contiguous initiating cells (apical cells) in the apex and in the same way a case could also be made for one cell (or at most two continuous cells) as an initiating cell (cambium initial) in

each radial row of the cambial zone. However having clearly stated his case in this way, he also felt the need to have a long explanatory note equating his terminology with that of other workers in this field. He said that if the initiating cells in the apex are 'apical cells' then the initial cells in the cambium should be 'cambial cells'. He felt, though, that this apposition of terms would be confusing at that time (1956) for the term cambium had been used frequently in both of two senses - as the ring of initial cells or as the whole growing zone between mature wood and phloem. This confused use even occurs in Sanio's classic paper (1873). More recently, Wight (1933) used the terms 'cambium', 'cambial cells', 'cambial layers' indiscriminately in reference to the zone of dividing or divisible cells between xylem and phloem. The words 'cambium' or 'cambial' in his text could be replaced by 'meristem' or 'meristematic' without significant change of meaning. This author was not concerned with specifying particular initials. Therefore, although Newman used apex and apical cells, to save misunderstanding, he also used 'cambial zone' (= Bannan's 'cambium') and 'cambial initials'.

Newman emerged, therefore, as one supporting the single layer and zone concepts of the cambium, not quite as Bannan did, but by using 'cambial' as an adjective in each case he makes himself much clearer in his terminology than did Bannan. In the wide cambial zone of P.radiata Newman was able to locate the initials most easily in the rays as they were distinguishable from the maturing ray cells by their dense cytoplasm and short radial dimensions. Having located them in the rays he was then able to follow them through the regions between rays, not necessarily in edge-to-edge contact, using characters of partitioning and wall thickness. Whereas Newman worked with transverse sections, Bannan used longitudinal sections and identified the cambial initials as the shortest cells between the xylem and phloem mother cells.

Typical of the history of this disputed terminology is the discussion that followed Wilson's (1964) paper at the 2nd Symposium on 'The Formation of Wood in Forest Trees' (1963, Maria Moors Cabot Foundation for Botanical Research). Among others the discussion involved Bailey, Esau, Barghoorn and Wilson himself. The latter maintained that any cell division in the zone between obviously differentiated secondary phloem and xylem was 'cambial' division but Bailey could not agree. Barghoorn felt, too, that he was only happy with the view that the cambium was a single layer of cells. Esau suggested that the single initial in each file of cells should be called the 'cambial initial' and that the term 'cambial zone' should include that initial together with the dividing xylem and phloem mother cells. Bailey finally agreed at the end of the discussion that the use of the word 'zone' might be acceptable provided that it was clearly defined.

In his paper, Wilson did not feel constrained to define his terminology; as emerged in the discussion he used the word 'cambium' to cover the entire region in which cells could be observed to be undergoing division. The actual object of his study will be deferred to a later section, we are concerned here with the evolution of the terms.

By 1964 therefore, when this Symposium book was published there was a fairly generally accepted view that there were cambial initial cells within a broader meristematic zone. In that year however there appeared a paper by Catesson (1964) which presented a strongly dissenting view. She claimed that the proliferative activity of the vascular cambium in Acer pseudoplatanum L. was not limited to a single initial layer or to a single cell in each file. It appeared to her that there existed a broad zone in which all cells possessed equal properties of multiplication. She did not use Newman's technique in attempting to locate an initial cell but rather depended on observing mitotic frequency to search for the most active

zone. Within this zone she could not find cells with a higher activity than others. Philipson et al. (1971) appear to lend support to her view of the cambium but when analysed fundamentally it is difficult to see how, in practice, in any given radial file of cells in the cambial zone there can be more than one cell producing xylem and phloem initials. Whilst it is true that all cells, especially those of the cambial zone, are totipotent and may produce any type of tissue if provided with a suitable environment (Steward. et al., 1964) there can be only one cell in the file that is actually producing both types of initials. In Fig. 1. 'A' is the single cell which has given rise to 'B' and 'C'. The latter will then differentiate into xylem and phloem cells respectively. If 'C' say, does not mature into a xylem cell but instead remains meristematic and gives rise, as 'A' has done up until this moment, to xylem and phloem initials, then 'A' must relinquish this function and as it is on the xylem side of 'C' it must become a xylem cell. Were this not to be so, a confused jumble of xylem and phloem initials could arise in the radial file. It is of course accepted that there may not exist in the cambial zone a continuous layer, as such, of Type 'A' cells in precise lateral contact with one another. Newman showed quite clearly that such cells were 'out of step' tangentially across the radial files.

Catesson's work was criticised by Mahmood (1968) on the grounds that a study of the mitotic frequency at a given moment does not provide a reconstruction of past events in the cambial zone. He felt that if she had studied the cellular relationships resulting from a sequence of divisions (as Newman did) she might have identified a single initial cell in each radial file. Mahmood. working in Newman's laboratory, produced photographic evidence from Transmission Electron Microscopy for the wall characters of
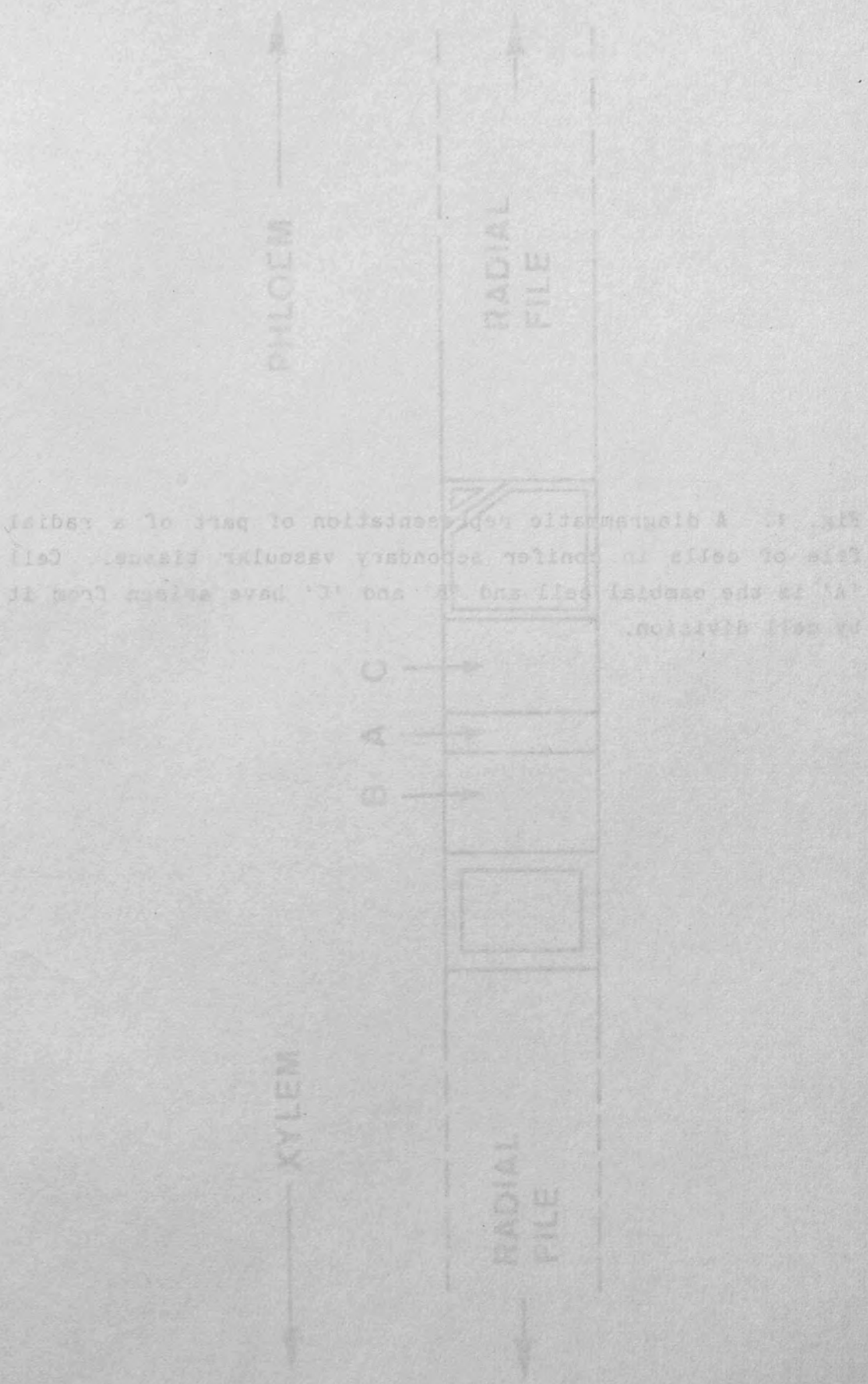
Fig. 1. A diagrammatic representation of part of a radial file of cells in conifer secondary vascular tissue. Cell 'A' is the cambial cell and 'B' and 'C' have arisen from it by cell division.

Fig. 1. A diagrammatic representation of part of a radial file of cells in conifer secondary vascular tissue. Cell 'A' is the cambial cell and 'B' and 'C' have arisen from it by cell division.
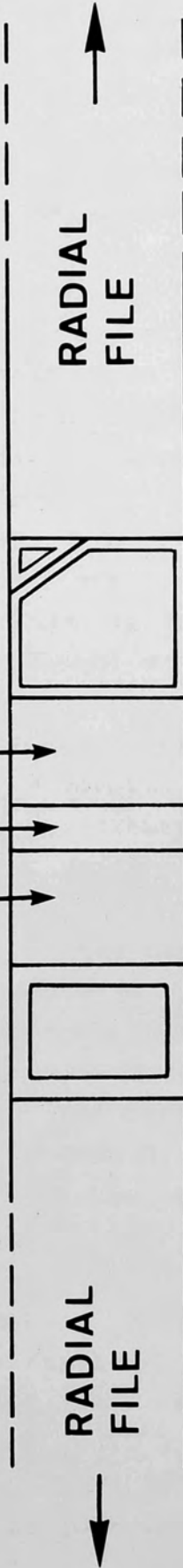
the daughter cells resulting from xylem mother cell division. He thus confirmed Newman's hypothesis based on Light Microscopy. He was able to show convincingly (Fig.2) that subsequent division of xylem mother cells in the cambial zone of Pinus patula resulted in the appearance of multiple walls around the daughter cells.

Murmanis (1970) working on cambial material from P. strobus was able to show that this multiplicity of tangential walls also occurs in this species. She cites Mahmood and fully supports his conclusions. Philipson et al. (1971) in reviewing the foregoing literature present what is now the present day view of the vascular cambium. They felt it was clear that in conifers the cell pattern in the xylem and phloem is determined by a single cambial initial in each radial file; anticlinal divisions being of the oblique type. It may well be significant, however, that the evidence for a single, permanent initial is derived from conifers, while the chief recent dissenter from this view, ie. Catesson (1964) worked on a dicotyledon. Cambial behaviour is complex and fairly uniform throughout the conifers. In dicotyledons, on the other hand, it varies from a condition similar to that in the conifers to a much simpler one with anitclinal divisions of the radial longitudinal type not involving the loss of fusiform initials. Fusiform initials are converted to ray initials by simple transverse segmentation. The small amount of data available for the distribution of anticlinal divisions in dicotyledons shows that they may be either virtually restricted to a single layer (Cumbie, 1967) or distributed over several layers (Catesson, 1964; Cumbie, 1963). The width of the initiating layer may prove to be similarly variable; certainly existing evidence is insufficient to indicate that a single initiating layer is invariable or even general in dicotyledons.

It seems likely, therefore, that the terms 'cambial initial' and 'cambial zone' will be generally acceptable and

Fig. 2.   Diagrams illustrating the formation of parental primary walls as a result of the divisions of the cambial cell and its daughter cells.

A.   The division of the cambial cell giving rise to the xylem initial.

B.   A theoretical construction of successive divisions of the xylem initial showing the origin of parental primary walls surrounding each cell. $\underline{d}$. daughter cells of xylem mother cell; $\underline{i}$. xylem initial; $\underline{m}$. xylem mother cell; $\underline{t}_1$. $\underline{t}_2$. Sanio's 'groups of four' formed from two daughter cells (re-drawn after Mahmood, 1968).

A

c   i

B

i   m   d   d t_1 t_1 t_1 t_1 t_2 t_2 t_2

will not require prior definition. It is significant that Torrey et al. (1971) use them in their general survey of cytodifferentiation in xylem; at no stage in their paper do they place the terms in quotation marks nor are there any formal definitions. Similarly Wodzicki & Peda (1963) define the term cambial zone but Wodzicki (1971) uses it without first giving a definition. Wilson, Wodzicki & Zahner (1966) proposed the following terminology:

1. The cambial zone. composed of the initial cell and mother cells capable of further division;

2. A zone of radially enlarging derivatives no longer dividing;

3. A zone of maturing derivatives where secondary wall thickening occurs;

4. The mature derivatives. In his book, Roberts (1976) adopts this terminology in its entirety and it would appear that we now have a terminology that has wide acceptance.

2. Cellular variation

It has been noted previously (Creber, 1975) that the decline of tracheid diameter from earlywood to latewood across growth rings is not regular but has a cyclic factor impressed upon it. Unfortunately, early attempts to study the cyclic effect made use of a moving average technique which tended to exaggerate it by what is known to statisticians as the Slutzky effect.

A different approach was therefore adopted in order to process the data without introducing spurious effects. A bivariate regression program (Nie etal. 1975) was used to fit a straight line to the data. In the program, values of the dependent variable are predicted from a linear function of the form

$$Y^1 = A + BX$$

where Y^1 is the estimated value of the dependent variable Y. B is a constant by which all values of the independent variable X are multiplied, and A is a constant which is added to each case. The independent variable X is the cell number in the ring, starting with the first earlywood cell. The difference between the actual and the estimated value of Y for each case is called the residual, ie. the error in prediction, and may be represented by the expression

$$Residuals = Y - Y^1$$

The regression technique involves the selection of A and B such that the sum of the squared residuals is smaller than any possible alternative, ie. it is a 'least squares' solution. This may be expressed as

$$(Y - Y^1)^2 = SS_{res} = minimum$$

The total sum of squares in Y (which is the total variability of the dependent variable Y) can be partitioned into components that are (1) explained or accounted for by the regression line, denoted by SS_{reg} and (2) unexplained (the sum of the squared residuals). SS_{res} which may be expressed as

$$SS_{res} = (Y - Y^1)^2$$

This partition may be written as

$$SS_y = SS_{reg} - SS_{res}$$

A measure of prediction accuracy and strength of linear association is the ratio of explained variation in the

dependent variable Y to the total variation in Y.

$$\text{Thus } r^2_{xy} = \frac{SS_{reg}}{SS_y} = \frac{SS_y - SS_{res}}{SS_y}$$

This ratio, r^2, is also called the coefficient of determination. In the table, r^2 is given for groups of contiguous files of cells from some extant woods and one fossil specimen, <u>Metacedroxylon scoticum</u>. It is evident that in some cases eg. the fossil wood, that much of the variation (up to 89.9%) is explained by the regression line. Whereas in the case of the <u>Cupressus</u> specimens the unexplained variation may be as high as 84.6% (100 - 15.4%).

The use of this program however was not limited to obtaining a measure of r^2 for the data. a further object was to pass the residuals into a Maximum Entropy Spectral Analysis program which was designed to search for periodicities. It was thought better to use the residuals for this purpose rather than the raw cell data since it is now shown that, at least for the fossil wood and the specimen of <u>P. strobus</u>, a high proportion of the significance of the cell data can be due to a straight line decline in cell size. The periodicities are also given in the Table 1; one of the sequences of residuals (that for <u>M. scoticum</u>, file 1.) is plotted in the graph.

In an attempt to simulate data for the radial diameters, Mahmood's (1968) paper was used. Here, as already mentioned, he was able to show that the file of immature cells left behind by the cambium is not totally homogeneous but consists of cells surrounded by differing numbers of wall layers. Assuming that possibly, those cells with a larger number of layers might not attain to such a size as those not quite so constrained. a sequence of cell radial diameters has been estimated. The sequence was then converted to the residuals of a straight line regression

Table 1. Periodicities in the files of cells.

NAME	FILE	CELLS	r²	%	PERIODICITIES				
					4-7	7-10	10-13	13-25	Above 25
Metacedroxylon scoticum	1	70	0.739	73.9%	5.98	8.5	12.4	-	41.6
	2	70	0.846	84.6%	5.5	-	10.3	22.2	-
	3	70	0.899	89.9%	5.96	-	-	20.8	-
Cupressus Ring 1	1	91	0.273	27.3%	6.0	8.2	12.1	20.6	55.5
	2	91	0.32	32.0%	6.0/6.9	-	10.5	15.7	39.9
	3	91	0.154	15.4%	4.5/6.9	-	11.0	19.0	41.6
	4	91	0.383	38.3%	4.6/5.5	9.1	-	-	40.7
Cupressus Ring 2	1	66	0.562	56.2%	6.3	8.3	-	13.1	34.4
	2	66	0.485	48.5%	-	7.6	-	21.5	-
	3	66	0.277	27.7%	4.7/6.6	-	11.2	23.5	-
	4	66	0.269	26.9%	-	7.1	-	15.9	30.2
P. strobus Ring 2	1	51	0.755	75.5%	4.7	9.76	-	-	37.0
	2	51	0.757	75.7%	-	8.4	-	18.9	-
	3	51	0.837	83.7%	-	7.3	-	18.8	-
Theoretical cell data	1	112	-	-	5.98	8.95	-	17.8	-

which in turn were passed through the MESA program. The periodicities thus found appear in the Table as Theoretical Cell Data. It is seen that they could well be a set of actual cell data. Whilst it is accepted that this is no proof of the causal mechanism, it is also true that the hypothesis is not immediately ruled out by the results of the analysis.

A possible interpretation of the variability of the radial diameters of tracheids across the growth rings of gymnospermous wood was published by Ford et al (1978). They describe work done on a dominant tree in a Forestry Commission Sitka spruce plantation in Dumfrieshire. Samples of bark/sec. phloem/cambium/immature sec. xylem/ part of the previous year's sec. xylem were taken from an internode at 12h intervals for 15 days (27th June - 11th July). This frequent sampling interval had not been used by any previous workers and it represented an attempt to seek changes in xylem production and maturation that might be due to short-term changes in the weather. Their resulting data was in the form of measurements of tracheid tangential and radial diameters together with wall thicknesses.

Their main methods of analysis were correlation and autocorrelation. They found a widespread significant positive correlation of radial tracheid diameter and wall thickness. Along three files of cells they found positive values of autocorrelation which they interpreted as an indication that consecutive cells along the radial files had similar diameters (as I have also found). They did not use their results to explore the groups of cells involved but from one of their graphs it could be seen the autocorrelation falls to zero at about the 5th-6th cell distance along the files. It is rather disturbing that they apparently used raw cell data in their autocorrelation calculations.

They also present results of simple correlations between contiguous files of cells. To do this, they took

the measurements (radial diameters) of cells that had most (or all) of their radial walls in contact with one another across the boundary of two contiguous files. This was done in preference to correlating the entire lists of cell data from two complete files; they accepted that there was a loss of cell data in using this method. It was argued, however, that there was a greater significance in the remaining data since, they said, the pairs of cells so selected were those that had expanded together radially at the same time when a certain environmental factor was acting on the tree. Whereas, the argument goes, if one takes cell No. 5, say, in each file, these may well not be in contact with one another in the two files and were therefore not expanding at the same time. The results of their correlations produced significant positive coefficients between files which they said indicated a simultaneous causal mechanism affecting all of the files together. An alternative explanation might well be that this particular region of the growth ring had a similar capacity for expansion in all of the files of cells due to their simultaneous ability to expand. Ford (pers. comm.) was critical of my original procedure (1975) of superimposing the graphs of moving averages of cell diameters to show apparently out-of-phase situations along the files. Instead, he said that we should use his technique of correlating only those cells which shared a substantial common boundary in parallel contiguous files. When this was done some very conflicting results were obtained which are given in the Table 2.

Table 2.   Correlations between files of cells.

NAME AND
FILE NUMBERS   r

Metacedroxylon   Residuals $^1/_2$ − 0.067
scoticum   Files $^1/_2$ + 0.705
                      Residuals $^2/_3$ + 0.202
                      Files $^2/_3$ + 0.870

P. strobus   Files $^1/_2$ + 0.776
                      Files $^2/_3$ + 0.901

Cupressus   Files $^1/_2$ + 0.388
Ring 1   Files $^2/_3$ + 0.487
                      Files $^3/_4$ + 0.393

Cupressus   Files $^1/_2$ + 0.542
Ring 2   Files $^2/_3$ + 0.381
                      Files $^3/_4$ + 0.528

Files $^1/_2$ indicates File 1 correlated with File 2

It is seen that for some pairs of files the
coefficient may be very high (eg. Pinus strobus Files 2/3.
+0.901) but others it may be as low as +0.381. It looks as
if more woods should be examined to broaden the database.
For Metacedroxylon scoticum some further data were available
in the form of the residuals from the regression program.
Correlation of these produced quite different results from
those obtained from the raw data; in the case of Files 1 & 2
in Metacedroxylon scoticum a negative figure results instead
of a quite strongly positive one (+0.705). Again, it looks
as if more work would be desirable.

3. Nuclear variation

Another possible source of cell size variation is polyploidy. Early workers (eg. Schacht (1856) and Russow (1882)) thought that the cells of the cambial zone were multinucleate but Strasburger (1893) doubted the accuracy of their work. In a very detailed study Bailey (1920) was able to show conclusively that these cells were uninucleate. Earlier reports to the contrary had been the result, apparently, of observations of two or more transparent cambial cells super-imposed one upon the other; the impression had been given of a bi- or tri-nucleate cell.

The nuclei in gymnosperm cambial zone cells tend to be very large; according to Strasburger (1893) they may attain a length of 9,000μm with a volume of $10 \times 10^6 \mu m^3$. Strasburger's measurements led him to believe that there was a close correlation between cell size and nuclear size, a conclusion strongly supported by Gerassimow (1902). After the publication of the latter paper there was a considerable controversy among zoologists and botanists as to whether the so-called nucleo-cytoplasmic relation was a constant and self-regulating ratio. In the cambial zone of Pinus strobus, Bailey (1920) was able to show, however, by a series of detailed measurements that in fusiform initials the nucleo-cytoplasmic ratio was not constant.

Boveri (1902, 1905) found that the size of the nuclei in echinoderm larvae was dependent upon the number of chromosomes which enter into the nuclei. Some years later it was shown by Gates (1909) that in Oenothera gigas De Vries, a tetraploid of O. lamarckiana, the cells were much larger than those of the diploid from which it originated. Winkler (1916), in a general survey of cell sizes and chromosome numbers in higher plants concluded that there was a close correlation between cell size and chromosomal mass. He found, too, that many differentiated plant cells were polyploid. However, again, Bailey (1920) checked the

cambial zone of P. strobus and found that all of the cells that he observed, regardless of size were uniformly diploid (2n = 24).

Erdmann (1908) found that in sea urchin cells the chromosomal mass was the size-determining factor rather than the chromosome number. Other workers on animal cells supported this view but Bailey (1920) found that ray initials with a volume range of 3 to 10 x $10^3 \mu m^3$ had chromosomal masses indistinguishable from adjoining fusiform initials with a volume range of 1 to 5 x $10^6 \mu m^3$.

Although Bailey's work on P. strobus would seem to settle the matter of nucleo-plasmic volume in the conifer cambial zone there is a considerable body of literature that supports the view that polyploidy is widespread in differentiating primary xylem. For example in Zea mais root metaxylem cells the DNA content of the muclei was found to fall into a frequency distribution having peaks at the 4-, 8-, 16- and 32- ploid equivalent. The DNA content had a high positive correlation with nuclear volume in the overall growth of the metaxylem cells (List. 1963). List also studied widely diverse genera such as Acorus and Peltandra (Araceae) and Marsilea and Dennstaedtia (Filicales) and found similar correlations of cell volumes and polyploidy in differentiating xylem. List's work is typical of much other work in this field and the widespread occurrence of polyploidy in differentiating cells (not only xylem) led Evans and Van't Hof (1975) to investigate whether or not it was an essential feature of plant cell differentiation. They found that in Pisum sativum polyploidy was present in roots, sepals, pods, pistils and stamens but not in petals or leaves. In Triticum aestivum some leaf cells exhibited polyploidy but the root cells did not. No polyploid cells could be found in any of the tissues of Helianthus annuus. They therefore came to the conclusion that polyploidy was not essential to cell differentiation in spite of its widespread occurrence.

It still remains a possibility therefore that the variation in cell radial diameter observed along files of cells in gymnosperm secondary xylem might be due to different levels of polyploidy in the initials during differentiation. However the apparently cyclic variation exhibited is not very likely to be due nuclear variation as the latter seems to occur in rather a random fashion. At the moment the matter remains unresolved because the techniques for the investigation of polyploidy in primary tissues are not usable in tissue such as secondary xylem.

LITERATURE CITED

Bailey, I.W. 1920. The cambium and its derivative tissues;
III. A reconnaissance of cytological phenomena in the
cambium. Amer. J. Bot. 7, 417-34.

Bailey, I.W. 1943. Some misleading terminologies in the
literature of "plant tissue culture". Science, 98, 539.

Bannan, M.W. 1955. The vascular cambium and radial growth in
Thuja occidentalis L.
Canadian Journal of Botany, 33, 113-38.

Boveri, T. 1902. Ueber mahrpolige Mitosen als Mittel zur
Analyse des Zellkerns. Verh. Physik.
-Med. Ges. Würzburg, 35, 597-8.

Boveri, T. 1905. Zellen-Studien.5. Ueger die Abhängigkeit
der Kerngrösse und Zellenzahl der Seeigel-Larven von der
Chromosomenzahl der Ausgangzellen. Jena.

Bower, F.O. 1923. Botany of the Living Plant. 2nd ed.
Macmillan, London.

Catesson, A.M. 1964. Origine, fonctionnement et variations
cytologiques saisonnières du cambium de l'Acer
pseudoplatanus L. (Acéracées).
Ann. Sci. nat. (Bot.) 12e ser. 5, 229-498.

Creber, G.T. 1975. The effects of gravity and the earth's
rotation on the growth of wood in 'Growth rhythms and
history of the earth's rotation', eds. G.D. Rosenberg
and S.K. Runcorn, pp.75-87, Wiley, London.

Cumbie, B.G. 1963. The vascular cambium and xylem
development in Hibiscus lasiocarpus. Amer. J. Bot. 50,
944-51.

Cumbie, B.G. 1967. Development and changes in the vascular
cambium of Leitneria floridana. Amer. J. Bot. 54,
162-75.

Eames, A.J. & MacDaniels, L.H. 1947. An introduction to
plant anatomy. 2nd ed. McGraw-Hill, New York.

Erdmann, R. 1908. Experimentelle Untersuchung der
    Massenverhältnisse von Plasma, Kern und Chromosomen in
    dem sich entwickelnden Seeigelei. Arch. Zellforsch. 2,
    76-136.

Esau, K. 1953. Plant anatomy. Wiley, New York.

Evans, L.S. and Van't Hof, J. 1975. Is polyploidy necessary
    for tissue differentiation in higher plants?
    Amer. J. Bot. 62, 1060-1064.

Ford, E.D., Robards, A.W. and Piney, M.D. 1978. Influence of
    environmental factors on cell production and
    differentiation in the early wood of Picea sitchensis.
    Ann.Nbot. 42, 683-692.

Gates, R.R. 1909. The stature and chromosomes of Oenothera
    gigas De Vries. Arch. Zellforsch. 3, 525-52.

Gerassimow, J.J. 1902. Die Abhangigkeit der Grosse der Zelle
    von der Menge ihrer Kernmasse.
    Zeitschr. Allgem. Physiol., 1, 220-58.

Hartig, T. 1853. Ueber die Entwicklung des jahrringes der
    Holzpflanzen. Bot. Zeit., 11, 533-66, 569-79.

List, A. 1963. Some observations on DNA content and cell
    nuclear volume growth in the developing xylem cells of
    higher plants. Amer. J. Bot. 50, 320-329.

Lorch, J. 1967. The elusive cambium. Archives
    internationales des sciences 80, 253-83.

Mahmood, A. 1968. Cell grouping and primary wall generations
    in the cambial zone, xylem and phloem in Pinus.
    Australian J. Bot. 16, 177-96.

Murmanis, L. 1970. Locating the initial in the vascular
    cambium of Pinus strobus L. by electron microscopy.
    Wood Science and Technology, 4, 1-14.

Newman, I.V. 1956. Pattern in meristems of vascular plants.
    1. Cell partition in living apices and in the cambial
    zone in relation to the concepts of initial cells and
    apical cells. Phytomorphology, 6, 1-19.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K.and
    Bent, D.H. Statistical package for the social sciences
    (SPSS). 2nd ed. McGraw Hill, New York.

Philipson, W.R., Ward, J.M. & Butterfield, B.G. 1971. The
    vascular cambium. Chapman & Hall. London.
Priestley, J.H. 1930. Studies in the physiology of cambial
    activity III. The seasonal activity of the cambium.
    New Phytol. 29. 316-54.
Roberts, L.W. 1976. Cytodifferentiation in plants.
    Cambs. Univ. Press. London, New York.
Russow, E. 1882. Über den Bau und die Entwicklung der
    Siebröhren und Entwicklung der secondären Rinde der
    Dicotylen und Gymnosperm. Sitzungsber.
    Naturf. Gessell. (Dorpat), 6, 257-327.
Sanio, K. 1873. Anatomie der gemeinen Kiefer (Pinus
    silvestris L.). Jahrb. wiss. Botan. 9, 50-126.
Schacht, H. 1856. Lehrbuch der Anatomie und Physiologie der
    Gewächse. Müller, Berlin.
Steward, F.C., Mapes, M.O., Kent, A.E. and Holsten, R.D.
    1964. Growth and development of cultured plant cells.
    Science 143, 20-27.
Strasburger, E. 1893. Histologische Beiträge V. Ueber die
    Wirkungssphäre der Kern und die Zellgrosse. Fischer,
    Jena.
Torrey, J.G., Fosket, D.E. & Hepler. P.K. 1971. Xylem
    Formation: A paradigm of cytodifferentiation in higher
    plants.
    American Scientist 59, 338-52.
Unger, D.F. 1847. Botanisches Beobachtungen III. Die
    Intercellular-substanz und ihr Verhältnis zur
    Zellmembran bei Pflanzen. Botan. Ztg. 5, 289-300.
Wight, W. 1933. Radial growth of the xylem and the starch
    reserves of Pinus sylvestris: a preliminary survey.
    New Phytol. 32, 77-96.
Wilson, B.F. 1964. A model for cell production by the
    cambium of conifers. in 'The formation of wood in forest
    trees', ed. M.H. Zimmermann, pp. 19-36, Academic Press,
    New York.

Wilson, B.F., Wodzicki, T.J. & Zahner, R. 1966.
    Differentiation of cambial derivatives: Proposed
    terminology.
    Forest Science 12, 438-40.
Winkler, H. 1916. Über die experimentelle Erzeugung von
    Pflanzen mit abweichenden Chromosomenzahlen.
    Zeitschr. Bot., 8, 815-70.
Wodzicki, T.J. 1971. Mechanisms of xylem differentiation in
    Pinus sylvestris L. J. Exp. Bot. 22, 670-87.
Wodzicki, T.J. & Peda, T. 1963. Investigation on the annual
    ring of wood formation in European Silver Fir
    (Abies pectinata D.C.). Acta Soc. Bot. Pol. 32, 609-18.

PART II

CHANGES IN THE EARTH'S OBLIQUITY

(a) Change due to the interaction of the earth and the
     moon.

     The interaction of the earth and the moon is well
established since it is susceptible to rigorous mathematical
treatment and, in recent years has been checked
experimentally. The subject is very much a live one in
astronomical research at the present time because (i) it is
providing a means of detecting a possible change in G and
(ii) it is one of the constraints on theories of the origin
of the moon.
     As long ago as 1695. Edmund Halley reported that the
motion of the moon seemed to be changing with time.
However, the first person to put the whole subject on a firm
mathematical basis was G.H. Darwin (2nd son of C.R.). In
two papers (1879,1880, republished 1908, 1962). rightly
described by one worker in this field (Macdonald, 1964) as
monumental, Darwin laid the foundations for all later work
on this subject. Even now, 100 years later. virtually every
author cites these papers (e.g. Hughes. 1981; Stephenson,
1981; Ringwood, 1979; Singer 1977).
     The slowing down of the rotation of the earth is due to
the friction of the tides that are raised in the oceans by
the sun and the moon. Because the earth's rotation is
decreased, conservation of angular momentum demands that the
moon moves to a larger orbit about the earth. This movement
causes a change in the earth's obliquity because (O'Keefe.
1980, pers. comm.):

     1. The earth's total angular momentum can be resolved
         into two components, one perpendicular to the
         ecliptic, the other in the ecliptic plane.
     2. The recession of the moon leads to an increase of
         its angular momentum compensating for an equivalent
         loss by the earth.

3. Because the moon's orbit lies nearly in the plane of the ecliptic the moon takes only that component perpendicular to the ecliptic.

4. Hence the ratio of the two components of the earth's rotational angular momentum vector is changing; this ratio is the tangent of the obliquity which therefore changes in the direction of increasing obliquity.

Nobody disputes this process of obliquity change but the difficulty is that the astronomers and planetary physicists cannot yet put a hard and fast time scale on the changes in the rate of recession of the moon. Whilst they can say, thanks to the lunar laser ranging experiment, that at the moment the moon is receding at about 4cm/yr, they also point out that this rate of recession extrapolated back through geological time brings the moon catastrophically close to the earth less than 1.5×10^9 y BP. This is because it is a non-linear process, the rate being inversely proportional to the 6th power of the earth-moon distance.

Such a close approach of the moon to the earth, as Piper (1978) explains, would be a devastating event in earth history (Lamar et al., 1970; Tarling, 1975) initiating widespread partial or complete melting of crust and mantle. The event itself is known as the 'Gersterkorn event'. The absence of such an event after 3.0×10^9 y BP is taken as evidence that the moon was already a satellite at this time. At one time it was hoped that the widespread low-grade Archaean greenstone terrains could be taken as an indication of a global thermal event. However further study showed that they were formed at various times between 3.5 and 2.2×10^9 y BP. Additional evidence of the age of the earth-moon system comes from the 3.8×10^9 y BP Isua supracrustal sequence of West Greenland. Atmospheric oxygen was necessary for the production of ferric oxide in that formation; the blue-green algae that presumably produced the

oxygen could not have survived the thermal event of a close lunar approach. Consequently the view now is that the earth-moon association may well date back almost to the formation of the earth itself, i.e. ca. 4.6×10^9 y BP.

A more or less simultaneous origin of the earth and moon (Ringwood, 1979; Smith, 1982) is becoming more plausible since actual moon rock has been available for study. Thus one must contemplate a long period of association in the earth-moon system and also a long time-scale of gradual change in the obliquity. Having followed the arguments of the various authors on the subject it is necessary to summarise the present position and try to decide what reasonable figures we can put upon the obliquity at the points that concern us in the geological time-scale. Fortunately two of the principal workers in this field, MacDonald (1964) and Goldreich (1966), give some indication of what may have taken place. Their results are in close agreement and are as follows:

OBLIQUITY ($^{\circ}$)	GEOLOGICAL AGE 10^9 y BP
22	0.5
21.5	1.0
21	1.5
20	2.0
19	2.5
17	3.0
14	3.5

With the overwhelming evidence that a 'Gersternkorn event' has not taken place during the last 4×10^9 y it is necessary to examine whether or not the present value of tidal friction and its consequent recession of the moon is perhaps at a rather high value. There has been a long-standing controversy in the study of tidal friction as to whether deep oceans or shallow seas are of greater

importance.

The pioneer work on this aspect of tidal friction was carried out by Taylor (1919) who calculated the frictional losses from tidal currents in the Irish Sea. Jeffreys (1920) then extended the work to the rest of the world. Thus the shallow seas school of thought got off to a good start and held sway for some 40 years. In 1960, however, Munk and MacDonald pointed out that in Taylor's and Jeffreys' calculations some of the terms had been set too high and they maintained that tidal dissipation in shallow seas had been exaggerated. A telling point of criticism concerned the Bering Sea; with an area of 1×10^6 km^2 and with much of it less than 60m deep it is a very important shallow sea. However, if one used Jeffreys' figures, the amount of tidal dissipation apparently there would amount to about $^1/_3$rd of the world total. Since this patently could not be so, the shallow seas faded in importance and Munk & MacDonald also pointed out that dissipation along open coastlines had been neglected by Jeffreys. The latter in 1968 admitted this and it is noticeable that in the 1976 edition of his textbook (The Earth) he includes a new paragraph on this topic.

Whilst this controversy continued, a 10 year survey with more instrumentation than ever previously used was being carried out around the Northeast Atlantic by Cartwright et al. who published their results in 1980. They conclusively show that Taylor and Jeffreys, whilst somewhat astray in their original calculations, were basically correct in that shallow seas and coastlines are the more important causes of tidal dissipation with the oceans being correspondingly minor.

At the present time the shallow seas / deep oceans controversy has somewhat receded into the background and its place has been taken at the forefront of research by the work of Brosche and Sündermann in Germany. With the availability of palaeomaps (Smith et al., 1981) now it is

possible also to work on the ocean areas delimited by the position of the continents through geological time. Brosche and Sündermann (1978) carried out numerical modelling of palaeotidal effects using the ocean distribution for (a) the Upper and (b) the Lower Permian. For (a) their model produced a figure for tidal friction of about $\frac{2}{3}$ of the present day figure whilst for (b) it was only $\frac{1}{3}$. At first it appeared strange that tidal friction should differ so much in two oceanic distributions that were essentially very similar. Somewhat prophetically as it turned out, Stephenson (1981) thought that it indicated that even moderate changes in the shape of oceans and adjacent seas might substantially affect tidal action. This statement was soon demonstrated to be true by Brosche (1981) who showed that different values of tidal friction arise in models in which the widening of the Atlantic Ocean is simulated in steps of a few degrees of longitude at a time as it took place in continental drift. Brosche conluded that for realistic calculations of the history of the earth-moon system many closely spaced models would be required; the present day value for tidal friction may not be a representative average for even the last 10×10^6 y. Krohn and Sündermann (1982) have also shown that in other geological periods including the Upper Cretaceous the calculated value for tidal friction was at a reduced figure.

It would appear therefore that evidence is accumulating to the effect that obliquity change due to the interaction of the earth-moon system is likely to have been very slow. It is interesting in this connection to note that Darwin was of the opinion that such change during the last 500×10^6 y was probably no more than one degree. It has to be borne in mind, too, that this low figure would be largely masked by the Milankovitch wobble.

(b) <u>Change due to the rotation of the plane of the ecliptic</u>
    <u>about the sun.</u>

Williams (1972,1973,1975) put forward a theory of obliquity change that was due to the rotation of the plane of the ecliptic about the sun with a period of 2.5×10^9 y. He claimed that this rotation had its origin in the plume of gases drawn out of the sun and which eventually coalesced to form the planets. (This, incidentally is not the only model for the formation of the planets (Ringwood, 1979; Smith, 1982)). In spite of the rotation of the plane of the ecliptic Williams claimed that the planets would behave as gyroscopes and maintain their axial orientations relative to space and thus undergo a cyclic change of obliquity with respect to the plane of the ecliptic.

One of the major criticisms that can be levelled at Williams' theory is that he does not in any way explore all of the consequences of the obliquity changes that ensue from it. He uses the changes principally to explain the occurrences of ice ages but he does not, for example, examine the effects that the changes would have on the ocean tides. Furthermore, he proposes that during the Cretaceous the earth's axis was virtually vertical (i.e. zero obliquity) but in fact the present study shows that in the high latitudes during that geological period there were strongly marked growth rings in the wood of the trees growing at that time. This seems quite incompatible with what would be a seasonless situation all over the world.

LITERATURE CITED

Brosche, P.(1981). Oceanic tides and the rotation of the
    earth. European Regional Meeting in Astronomy.
    Dubrovnik.

Brosche, P. & Sündermann, J.(1978). Numerical computation
    of tidal friction for present and ancient oceans. In
    Tidal friction and the earth's rotation (eds. P. Brosche
    & J. Sündermann), pp.125-43. Springer-Verlag. Berlin &
    New York.

Cartwright, D.E., Edden, A.C., Spencer, R. & Vassie,
    J.M.(1980). The tides of the northeast Atlantic Ocean.
    Phil. Trans. Roy. Soc. A 298, 87-139.

Darwin, G.H.(1879). On the precession of a viscous spheroid
    and on the remote history of the earth.
    Phil. Trans. Roy. Soc. A 70, 447-530.

Darwin, G.H.(1880). On the secular change in the elements
    of the orbit of a satellite revolving about a tidally
    distorted planet. Phil. Trans. Roy. Soc. 171, 713-891.

Goldreich, P.(1966). History of the lunar orbit.
    Rev. of Geophysics. 4, 411- 39.

Hughes, D.W.(1981). Why is the moon slowing down?
    Nature, London 290,190.

Jeffreys, H.(1920, 1976). The earth. Cambs. Univ. Press.
    Cambs. & London. 1st, 6th edn.

Krohn, J. & Sündermann, J.(1982). Paleotides before the
    Permian. In Tidal Friction and the Earth's Rotation II
    (eds. P. Brosche and J. Sündermann). pp.190-209.
    Springer-Verlag. Berlin.

Lamar, D.L., McGann-Lamar, J.V. & Merifield, P.M.(1970).
    Age and origin of the earth-moon system. In
    Palaeogeophysics (ed. S.K. Runcorn). pp.41-52.
    Academic Press. New York & London.

MacDonald, G.J.F.(1964). Tidal friction.
    Rev. of Geophysics 2, 467-541.

Miller, G.R.(1966). The flux of tidal energy out of deep
    oceans. J. Geophys. Res. 71, 2485-89.

Munk, W.H. & MacDonald, G.J.F.(1960). The rotation of the
    earth. Cambs. Univ. Press., Cambs. & London.

O'Keefe, J.A.(1980). Pers. comm. NASA: Goddard Space Flight
    Centre, Greenbelt, Maryland 20771, U.S.A.

Piper, J.D.A.(1978). Geological and geophysical evidence
    relating to continental growth and dynamics in the
    hydrosphere in Precambrian times: a review and analysis.
    In Tidal friction and the earth's rotation (eds. P.
    Brosche & J. Sündermann), pp.197-239. Springer-Verlag,
    Berlin & New York.

Ringwood, A.E.(1979). Origin of the earth and moon.
    Springer-Verlag, Berlin & New York.

Singer, S.F.(1977). The early history of the earth-moon
    system. Earth-Science Reviews 13, 171-89.

Smith, A.G., Hurley, A.M. & Briden, J.C.(1981). Phanerozoic
    palaeocontinental world maps. Cambs. Univ. Press.
    Cambs. & London.

Smith, J.V.(1982). Heterogeneous growth of meteorites and
    planets, especially the earth and moon.
    J. Geol. 90, 1-125.

Stephenson, F.R.(1981). Tidal recession of the moon from
    ancient and modern data.
    J. Brit. Astron. Assoc. 91, 136-47.

Tarling, D.H.(1975). Geological processes and the earth's
    rotation in the past. In Growth rhythms and the history
    of the earth's rotation (eds. G.D. Rosenberg & S.K.
    Runcorn), pp.397-412. Wiley, London & New York.

Taylor, G.I.(1919). Tidal friction in the Irish Sea.
    Phil. Trans. Roy. Soc. A 220, 1-93.

Williams, G.E.(1972). Geological evidence relating to the
    origin and secular rotation of the solar system.
    Mod. Geol. 3, 165-81.

Williams, G.E.(1973). Geotectonic cycles, lunar evolution,
    and the dynamics of the earth-moon system.
    Mod. Geol. 4, 159-183.
Williams, G.E.(1975). Late Precambrian glacial climate and
    the earth's obliquity. Geol. Mag. 112, 441-465.

PART III

THE ESTIMATION OF TRUNK WOOD PRODUCTION BY TREES

(a) Annual wood production

The wood in the trunk of a tree may be regarded as a
cone with a vertical height considerably larger than its
basal radius.   In circumstances where the tree produces one
increment of wood per year. the volume of wood produced is
the difference between the volume of the trunk wood cone at
the beginning of the year and that at the end.

The formula for the volume of a cone is:

$$\frac{\Pi r^2 h}{3} \quad \dots\dots\dots\dots\dots \quad (1)$$

where r is the radius of the cone base and h is the cone
height.   Thus the volume of trunk wood produced in a year
will be:

$$\frac{(\Pi (r+x)^2 h)}{3} - \frac{(\Pi r^2 h)}{3} \quad \dots\dots\dots \quad (2)$$

where x is the ring width for the year.

The mass of wood formed can be found by multiplying the
volume obtained from formula 2 by the gravimetric density;
for conifer wood this can be taken as $0.4g\ cm^{-3}$.   Such
calculations enable the annual wood production of a tree to
be estimated.

If the number of trees per unit area of forest is
known. an estimate may be made of its annual trunk wood
productivity.   The accuracy of such a calculation may be
high if the forest is an even-aged stand.   As an example of
the order of magnitude of conifer wood growth that may take
place, that given by Moore (1976) may be cited.   He reported
the annual wood increment of a Sitka spruce plantation in
Northern Ireland as $1000g\ m^{-2}$.   This is a very high figure
and would place the trees in Forestry Commission yield
class 24.   Yield class 12, for instance, would only produce
$400g\ m^{-2}$ (Hamilton and Christie. 1971).

(b)   Percentage efficiency

Having calculated the mass of wood being produced annually per unit area of forest it is possible to calculate the efficiency of the wood production process in utilising solar energy.   To do this. there is a need to know the solar input to the forest canopy.   There are various sources of information that may be used to obtain the necessary data; for instance solar radiation maps of the world are published (Löf, Duffie and Smith. 1966; Hall. 1978) in which it is evident that the British Isles receives between 3153MJ m^{-2} and 4730 MJ m^{-2} annually.   Alternatively an author may cite a figure for temperate latitudes e.g. Grace (1983) gives 3200 MJ m^{-2} as a typical figure for the annual solar input at ground level.   Some authors give a very local figure for the actual area of forest studied e.g. Ovington (1961) gives 3212MJ m^{-2} as the solar input to the forest at Thetford that he was currently studying.

Using the figure of 400g m^{-2} as the wood production by Yield class 12 Sitka spruce it is possible to calculate the energy contained in the wood by multiplying the mass by the calorific value of the wood (21 x 10^3J gm^{-1}).   If the solar input to the forest was 3500MJ m^{-2} yr^{-1} then the percentage efficiency of conversion would be:

$$\frac{400 \times 21 \times 10^3 \text{ J}}{3500 \times 10^6 \text{ J}} \times \frac{100}{1} \% \qquad \ldots\ldots\ldots \quad (3)$$

In this case the efficiency is 0.24%

This figure is of course only for the trunk wood production process in the tree; for total dry matter production the overall percentage is about 1-2% (Ovington. 1961; Grace. 1983).   A range of examples is given in Table 1.   Of the solar energy actually incorporated as dry matter production it is estimated that about 40% goes into the trunk wood (Kozlowski. 1962).   That is to say about 0.4% of

TABLE 1

Percentage efficiencies of various tree species in utilising light energy.

Authors	Forest type or Tree species	Dry matter production	% Efficiency
Ovington (1961)	Pinus sylvestris	19.9×10^6 g ha^{-1} yr^{-1}	1.0%
Blackman & Black (1959)	Fagus sylvatica L.	23.5×10^6 g ha^{-1} yr^{-1}	1.5%
Helms (1970)	Pinus ponderosa	198×10^3 g ha^{-1} day^{-1}	1.5%
Miller (1955)	Pinus contorta Dougl.	15×10^6 g ha^{-1} yr^{-1}	1.0%
Hall (1978)	Evergreen forest	22×10^6 g ha^{-1} yr^{-1}	0.8%
Hall (1978)	Deciduous forest	15×10^6 g ha^{-1} yr^{-1}	0.6%

the total solar input. The result of 0.24% in calculation 3 is seen to be of the right order of magnitude for a rather low yielding forest plantation.

(c) Interception of solar energy

In order to intercept the necessary solar energy a tree must have a crown of a suitable shape. In high latitudes with low angles of sunlight, Jahnke and Lawrence (1965) have shown that a very effective crown shape is a cone with a height/basal radius ratio of at least 8. The formula for the area of light interception of a cone illuminated by sunlight at a given angle above the horizon is:

$$A = (T + \Pi r^2 - S) \sin \theta \qquad (4)$$

T is the area of the shadow cast by the cone and is found by the following formulae:

$$T = a_1 b \qquad (5)$$
$$a_1 = b \tan \phi \qquad (6)$$
$$b = r \sin \phi \qquad (7)$$

S in formula 4 is found from:

$$S = \frac{\Pi r^2 \phi}{180} - \frac{r^2 \sin 2\phi}{2} \qquad (8)$$

ϕ in formulae 6, 7 and 8 is found from:

$$\phi = \text{arc cos} \left(\frac{r}{h} \tan \theta \right) \qquad (9)$$

In the above formulae, h is the height of the cone, r is the basal radius of the cone and θ is the angle of the sun above the horizon.

The areas of solar energy interception for three conical crowns are given in Table 2. Since the main interest in the present work is solar energy in high latitudes, only low angles of sunlight have been considered. At a latitude of 70^0N. the sun's angle above the horizon ranges from 1^0 to 40^0 each day between May 21st and July 21st; in the southern hemisphere the dates are November 21st to January 21st. In both hemispheres the sun is above the horizon for 24 hours each day between these dates (List, 1971).

At these low angles of sunlight the area of interception of a cone is very close to its area of vertical section. This, in a right cone, takes the form of an isosceles triangle whose base is the diameter of the cone. Its area is found by multiplying half the length of the base, i.e. the radius of the cone base by the length of the perpendicular line from the mid-point of the base to the vertex of the cone, i.e. the cone height. Hence, for the first cone in Table 2 the vertical section area will be 10 x 1, that is $10m^2$. The calculated interception areas for this cone for sunlight angles of 1^0, 5^0, 19^0, 35^0 and 40^0 are $9.9m^2$, $9.8m^2$, $9.7m^2$, $9.0m^2$ and $8.6m^2$ respectively. Thus even at a solar altitude of 40^0 the area of interception calculated by formulae 4 to 9 is still 86% of the vertical section area. Since the latter is so much simpler to calculate, it is possible to use it for most purposes in high latitude studies.

Whereas the area of interception of a conical crown is informative when dealing with direct sunlight, the total external area of the conical crown must be known if its capacity to receive diffuse light needs to be calculated. The external surface of a cone, excluding the circular base, is found from the formula:

$$\Pi r S \quad \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots \quad (10)$$

TABLE 2   ILLUMINATED AREAS (m²) OF CONICAL TREE CROWNS INTERCEPTING SUNLIGHT

| CONE DIMENSIONS | | | LATITUDE 70°N   May 21st to July 21st | | | | | | | |
| | | | LATITUDE 70°S   November 21st to January 21st | | | | | | | |
h	r		MIDN'T	3 AM	6 AM	9 AM	12 NOON	3 PM	6 PM	9 PM
		θ	1°	5°	19°	35°	40°	35°	19°	5°
10m	1m	A	9.9	9.8	9.7	9.0	8.6	9.0	9.7	9.8
		%I	99	98	97	90	86	90	97	98
14m	1.25m	A	17.4	17.35	17.32	15.7	15.05	15.7	17.32	17.35
		%I	99	98	97	90	86	90	97	98
18m	1.75m	A	31.2	31.0	30.5	28.4	27.1	28.4	30.5	31.0
		%I	99	98	97	90	86	90	97	98

h and r are the cone height and basal radius respectively; θ is the angular altitude of the sun above the horizon; A is the calculated area (m²) of the illuminated part of the conical crown; %I is the interception area expressed as a percentage of the vertical section area of the cone (i.e. the median bisection plane).

where r is the radius of the cone base and S is the slant height of the cone which is the length of its sloping side.

(d) Calculations based on published data for two fossil
     forests

(i) Jefferson's Forest. Alexander Island. Antarctica (Jefferson. 1982)

In one continuous exposure there were 31 gymnosperm tree stumps in an area of $550m^2$; a density of 1 tree per $17m^2$.

Conical crowns ((c) above) of height 17m and basal radius 1.6m could have been borne by these trees without the lower branches being in contact. Such a crown has a vertical section area of 17 x 1.6 = $27.2m^2$. With the approximation described in (c) above this may taken as $25m^2$ to allow for the sun rising to $40°$ at noon at latitude $70°S$. the palaeolatitude at which Jefferson's Forest is thought to have been located in the Lower Cretaceous.

A typical tree in the forest had a trunk diameter of 37cm and height of 20m. Ring width was 0.25 cm and hence the volume of wood grown in a year would have been, using formula 2:

$$\frac{3.14 \times 18.75^2 \times 2000}{3} - \frac{3.14 \times 18.5^2 \times 2000}{3} \quad cm^3$$

$$= 19494.17 \ cm^3$$

When multiplied by the density of wood, this is 7797.6g of wood. The energy content of this mass of wood is 7797.6 x 21.000J = 163.75MJ.

From solar energy measurements taken at Halley Bay $(75°S)$ (Farman and Hamilton. 1978) and Southice (a base on the 1955-58 Trans-Polar Expedition at $81.9°S$. (La Grange,

1963) the first was shown to receive 3452MJ m^{-2} yr^{-1} whilst the second received 3664MJ m^{-2} yr^{-1}. Taking the lower of these two figures it is seen that the tree with its 25m^2 interception area could have a solar input of 86.300MJ. Therefore the 163.75MJ in the annual production of wood only represents:

$$\frac{163.75}{86,300} \times \frac{100}{1} = 0.19\% \text{ efficiency}$$

Thus the annual wood production only represents 0.19% of the total light input as against the more usual 0.4% mentioned in (b) above. It would appear therefore that the light input at this high latitude is adequate for the wood production indicated by the fossil tree stumps and their ring widths. Also. a rate of annual production of wood of 7797.6g per 17m^2 is only 458.6g m^{-2} which. if compared with the examples cited in (a) above. is seen to be a relatively low rate of production and would allow for some shading of the trees by their neighbours. Although in this connection it has to be pointed out that at this high latitude the sun travels through 360° in 24 hours and thus the light would be more evenly distributed among them. In any event the trees are widely spread out at 1 per 17m^2.

The total crown surface area of such trees, using formula 10 would be:

$$3.14 \times 1.6 \times 17.075 = 85.78m^2$$

Such a total crown area would provide a substantial surface for the interception of diffuse light.

(ii) The Purbeck Fossil Forest (Francis. 1983)

In this forest a typical tree had a basal trunk diameter of 1m. a height of 20m and a mean annual ring width of 1.13mm. Using these data in formula 2 it is possible to

estimate the annual wood production of one tree as:

$$\frac{3.14 \times 50.113^2 \times 2000}{3} - \frac{3.14 \times 50^2 \times 2000}{3}$$

$$= 23681.4 \text{ cm}^3$$

When multiplied by the density of wood. this is 9472.56g of wood. The energy content of this mass of wood is 9472.56 x 21000J = 198.92MJ.

If this quantity of energy is taken as being 0.4% of the total light energy incident upon the tree as indicated in (b) above it is possible to estimate the minumum area of crown required by the tree to intercept the necessary light energy.

At the palaeolatitude at which this forest grew (36°N) the present day solar input is about 6300MJ m^{-2} yr^{-1}. Taking the 198.92MJ in the wood as representing 0.4% of the total incident light energy then the tree would require to intercept 49730.9MJ during the year. At an input rate of 6300MJ m^{-2} yr^{-1} a foliage surface area of 7.9m^2 would suffice. This rather sparse foliage is well illustrated in the author's reconstruction of a typical Purbeck tree (Francis. 1983. p.289).

The conventional method of expressing forest productivity is in terms of mass of dry matter per unit area of forest as in (a) above. However in the case of a fossil forest there is always the problem of determining whether or not all of the stumps represent trees which were living contemporaneously. This problem did not arise in the case of Jefferson's Alexander Island Forest because the reason for estimating the productivity was to show that the light input would be adequate to support it and therefore a 'worst case' was chosen in which all of the stumps were assumed to have been living contemporaneously. If it were argued that some of the stumps were dead when fossilised then the

adequacy of light supply would become much easier to demonstrate.

In studying wood productivity in the Purbeck Forest, therefore, a range of tree densities is taken so as to produce an equivalent range of wood productivities. At one site the stump density was one per $17m^2$ whilst in another it was considered to be half of this figure at one per $34m^2$. The range of wood production is therefore from $557.2g$ m^{-2} to $278.6g$ m^{-2}. In comparison with the figures for wood production in (a) above this forest had low rates which are in keeping with the semi-arid climate in which it was thought to have grown. The geological evidence for the climate consists of evaporite deposits and hypersaline lagoonal sediments, with blackened pebbles, adjacent to the forest site (Francis, 1983).

Another way of tackling the problem of estimating wood production where the tree density is not known for certain is to express the productivity of wood in terms of the trunk surface area (in effect the area of the vascular cambium). Using formula 10, the trunk surface area of a typical Purbeck tree would be:

$$3.14 \times 50 \times 2062 \ cm^2$$
$$= 323734.0 \ cm^2$$

The ratio of the volume of annual wood production to trunk surface area will then be:

$$\frac{23681.4}{323734.0} = 0.073$$

For comparison with this tree 2 examples are chosen, one is a Sitka Spruce taken from the Forestry Commission Forest Management Tables (Hamilton and Christie, 1971). The data cited are for a typical tree in the highest yielding class No. 24. Such a tree, 80 years old, would be 40.3m

high and 56.3cm in basal radius. Its trunk surface area from formula 10 would be:

$$3.14 \times 28.15 \times 4030 \ cm^2$$
$$= 35215.73 \ cm^2$$

Since its volume of annual wood production was 49740.93 cm^3 the ratio of this to the trunk surface would be:

$$\frac{49740.93}{356215.73} \quad = 0.14$$

The second example is a larch (<u>Larix</u> <u>decidua</u>) 8m high with a basal radius of 50cm. This was an extremely low yielding tree growing at an altitude of 2150m in the Alpes Maritimes (Serre, 1978). Its trunk surface area was:

$$3.14 \times 50 \times 802 \ cm^2$$
$$= 125914.0 \ cm^2$$

Its volume of annual wood production was 1870.03 cm^3 and therefore the ratio to trunk surface was:

$$\frac{1870.03}{125914.0} \quad = 0.014$$

Thus the ratios are as follows:

Purbeck tree	0.073
Sitka Spruce	0.14
Larch	0.014

The Purbeck tree therefore had a productivity only half that of the Sitka Spruce but about five times that of the larch. The Sitka Spruce as a tree in yield class 24 would be regarded as having a productivity only achievable under

the best possible conditions in the British Isles. On the other hand the larch was growing at a high altitude under very limiting conditions for tree growth. The productivities of these three trees have to be considered against their ecological backgrounds and the Purbeck Tree is seen to have a productivity that is compatible with its site conditions as determined by the geological evidence.

LITERATURE CITED

Blackman. G.E. and Black. J.N. 1959. Physiological and ecological studies in the analysis of plant environment. XII The role of the light factor in limiting growth. Ann. Bot. (London) 23. 137-145.

Farman. J.C. and Hamilton. R.A. 1978. Measurements of radiation at the Argentine Islands and Halley Bay. 1963-72. British Antarct. Surv. Scient. Rept.. No.99.

Francis. J.E. 1983. The dominant conifer of the Jurassic Purbeck Formation, England. Palaeontology 26. 277-294.

Grace, J. 1983. Plant-atmosphere relationships. Chapman and Hall, London and New York.

Hall, D.O. 1978. Solar energy through biology: could it be a practical energy source? pp.9-38 in H. Clijsters, M. Van Poncke and R. Marcelle (eds). Biological solar energy conversion. Limburgs Universitair Centrum. Netherlands.

Hamilton, G.J. and Christie, J.M. 1971. Forest management tables (metric). Forestry Commission, Her Majesty's Stationery Office.

Helms, J.A. 1970. Summer net photosynthesis of ponderosa pine in its natural environment. Photosynthetica 4. 243-253.

Jahnke. L.S. and Lawrence. D.B. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology 46, 319-326.

Jefferson, T.H. 1982. Fossil forests from the Lower Cretaceous of Alexander Island, Antarctica. Palaeontology 25, 681-708.

Kozlowski, T.T. 1962. Photosynthesis, climate and tree growth. pp.149-164 in T.T. Kozlowski (ed.) Tree growth. Ronald Press, New York.

La Grange, J.J. 1963. Trans-Antarctic Expedition 1955-58
    Scientific Report No. 13. Meteorology 1. Shackleton,
    Southice and the journey across Antarctica.
    Trans-Antarctic Expedition Committee.

List, R.J. 1971. Smithsonian meteorological tables. 6th
    edn. Smithsonian Institution Press, Washington.

Löf, G.O.G., Duffie, J.A. and Smith, C.O. 1966. World
    distribution of solar radiation. Solar Energy 10.
    27-37.

Miller, D.H. 1955. Snow cover and climate in the Sierra
    Nevada, California. Univ. Calif. Publs. Geogr. 11.
    1-218.

Moore, D.G. 1976. The oceanic forest. Irish Forestry 33.
    10-15.

Ovington, J.D. 1961. Some aspects of energy flow in
    plantations of Pinus sylvestris L. Ann. Bot. (London)
    25, 12-20.

Serre, F. 1978. The dendroclimatological value of the
    European larch (Larix decidua Mill.) in the French
    maritime alps. Tree-Ring Bulletin 38. 25-34.

PART IV

A MANUSCRIPT PREPARED FOR SUBMISSION TO 'BOTANICAL REVIEW'

'ENVIRONMENTAL CONTROL OF WOOD GROWTH IN LIVING AND FOSSIL
TREES'

CONTENTS

ENVIRONMENTAL CONTROL OF WOOD GROWTH IN LIVING AND FOSSIL
TREES

1. INTRODUCTION

The laying down of secondary xylem in the trunk wood
and major branches of trees produces a unique 'data store'
of the environment under which the growth occurred (Creber.
1977). At its simplest. this 'data store' includes such
evident information as the seasonal growth rings. indicating
the age of the trunk or limb. Investigation of the factors
controlling wood growth can elucidate quite precise data on
the climate of growth of individual years.

Fossil wood, showing detailed cellular structure. much
as in a modern specimen, occurs in considerable quantity
throughout the geological past back to the Devonian period
(some 370 million years BP). Theoretically such fossil wood
has the potential of revealing a great deal of information
concerning past environments of growth. This may include
such diverse aspects of the environment as temperature and
rainfall, altitude and latitude, and hence physical
parameters such as continent positions and the inclination
of the earth's axis of rotation.

This review attempts to bring together the range and
mechanism of action of those factors which control secondary
wood formation. I have selected from the substantial
literature on this subject (partly from the field of
forestry. partly from plant physiology) work which offers a
basis for 'reading back' the enviromnental 'signal' from
the secondary wood of trees. I then go on to review briefly
some of the more striking results coming from the
application of this approach to fossil woods on a global
scale.

2. THE GROWTH PROCESS

(a) Cambial activity

The wood is formed by the active periclinal division of a cylindrical layer of cells, the vascular cambium. The latter gives rise centripetally to xylem mother cells which may themselves undergo further divisions. There has been much debate as to whether there is a single layer of cambial initial cells; an alternative view is that the entire mitotic zone should be termed the cambium (Priestley, 1930). Newman (1956), however, was able to demonstrate clearly that single initial cells exist and now more recent workers (Wilson et al., 1966) use the terms 'cambial initial' and 'cambial zone'. The former is used for the single initiating layer and the latter for the entire mitotic zone including the cambial initials. The production and later expansion of the xylem cells forces the cambial initial cells outwards and some divide anticlinally to compensate for the increasing circumference of the cylinder. As they move outwards the initials leave behind them trails of cells which differentiate into xylem elements (Fig. 1). They expand radially, they elongate, their walls are thickened and lignified and as their protoplasts die mature xylem elements are formed. In general this is the situation in conifers whose wood consists almost exclusively of tracheids with occasionally some little-differentiated parenchyma cells vertically orientated; much more parenchyma is to be found in the horizontally running rays. In dicotyledons there is not such a series of sharply defined phases in the development of their wood since a relatively few cells. the vessel initials, expand so much more than. say. the fibre initials and thus a heterogeneous pattern arises. This is particularly true of ring-porous species such as oak and ash.

Although for convenience the phases of wood development as shown in Fig. 1 are divided off from one another by convention (Ford et al. 1978: Skene. 1969. 1972: Wodzicki.

Fig. 1. A diagrammatic representation of two files of cells from the secondary wood of a conifer during the formation of earlywood (A), and latewood (B). _a_. cambial zone; _b_. radial expansion zone; _c_. wall thickening zone; _d_. mature tracheids; _e_. latewood of previous year's increment. (Re-drawn after Wodzicki, 1971).

A

a   b   c   d   e

B

a b c   d

1971) the process is of course a continuous one. However, these phases are of some importance since there is evidence that the characteristics of the wood are influenced by the length of time that the cells spend in each phase. as will be seen later. Also, many other influences may leave their marks during these development phases (Denne & Dodd, 1981).

(b) Ring formation

The total number of cells formed during one growing season and the extent to which they expand will determine the width of that season's growth of wood. The latter is known as a growth ring (tree ring) and its boundaries are formed by the juxtaposition of the small thick-walled cells. termed latewood, which are formed at the end of the growing season and the larger thin-walled ones formed at beginning of the next. These rings are seen especially in trees growing in temperate latitudes where cambial activity ceases during the winter and hence results a correspondence between the rings and calendar years. This is the basis of dendrochronology. In the tropics, species vary as to their patterns of wood growth (Coster. 1927-8; Tomlinson & Craighead, 1972); in a mixed forest some species may produce rings whilst others do not. Those that do produce rings may do so strictly annually e.g. Taxodium in Florida, or irregularly according to the vagaries of rainfall as in the case of Diospyros, a mangrove in N. Queensland (Duke et al., 1981).

Therefore with a knowledge of wood growth, it is possible to examine the cross-section of a trunk, branch or root and deduce the influences that were at work as the wood was forming. However, before proceeding further, one must consider the possibility that within the same tree the wood formed simultaneously in its different parts may have different features. One of the most prominent characters which may vary in this way is the ratio of earlywood to latewood within each ring.

(c.) <u>Earlywood and latewood</u>

Those wood elements that form early in the growing season have greater radial diameters, and thus larger lumina, than those formed later (Fig. 1). The earlywood is lighter in weight than the latewood and the relative proportions of each collectively influence the density of the wood. In forestry and wood technology this is of considerable importance commercially since the uses of timber must be suited to its properties (Elliott, 1970).

It might be thought that the ratio of earlywood to latewood was directly reflecting the changing environmental conditions at successive stages through the growing season. While to some extent this is true, there is considerable difficulty both in defining consistently the boundary between early and late wood and in interpreting the significance of these two phases of the wood's growth.

In order to assess the amounts of earlywood and latewood in a given ring it is necessary to make a decision as to where one ends and the other begins. In some ways the situation at the present day is no better than when Mork devised his definition (1928). He defined a latewood cell as one in which the lumen radial diameter was equal to, or less than twice the thickness of the combined cell walls separating that lumen from the one in the adjoining cell (Fig. 2a). The tendency has been for each worker to adopt a definition that gives satisfactory results with his own particular material. Klem et al. (1945) were responsible for a variant on Mork's definition and in this version the boundary was fixed where the tangential diameter of the cells was equal to or greater than the radial one. Dinwoodie (1963) used this definition in his study of the variation in fibre length in members of the species <u>Picea sitchensis</u> (Bong.) Carr. Knigge and Koltzenburg (1964) produced a further version which was based upon the dimensions of three successive cells in a radial file. They regarded a latewood cell as one whose lumen had a radial

Earlywood — — — — — Latewood

Earlywood — — — — — Latewood

Fig. ... A diagrammatic representation of three methods for locating the earlywood-latewood boundary in conifer wood, as ... from cell measurements as explained in the text.

(a) The X-ray density method. A profile plate as ... ... minimum, to ob, maximum (Re-drawn after Nicholls and Brazier, 19xx)

(b) The ... X-ray density method. The earlywood-latewood boundary is arbitrarily drawn determined at 0.5 g cm⁻³, ... the density range from earlywood to latewood (Re-drawn after Cown and Parker, 1979).

Fig. 2. A diagrammatic representation of three methods of positioning the earlywood-latewood boundary in conifer wood.
(a) The Mork method, based on cell measurements as explained in the text.
(b) The X-ray density method. $\underline{w}$, profile width at mid-density position; $\underline{x}$, X-ray density range from AB, minimum, to CD, maximum. (Re-drawn after Nicholls and Brown, 1971).
(c) The basic wood density method; the earlywood-latewood distinction is arbitrarily determined at 0.5 g mc^{-3}. $\underline{g}$, the density range from earlywood to latewood; $\underline{r}$, ring width. (Re-drawn after Cown and Parker, 1979).
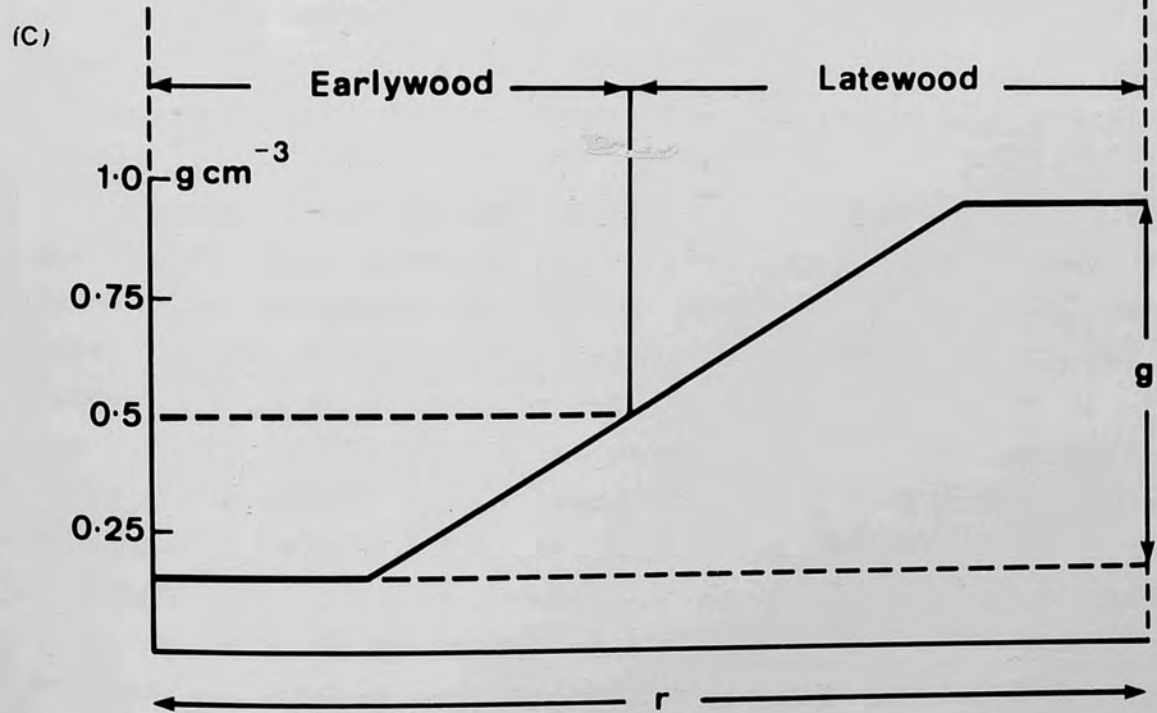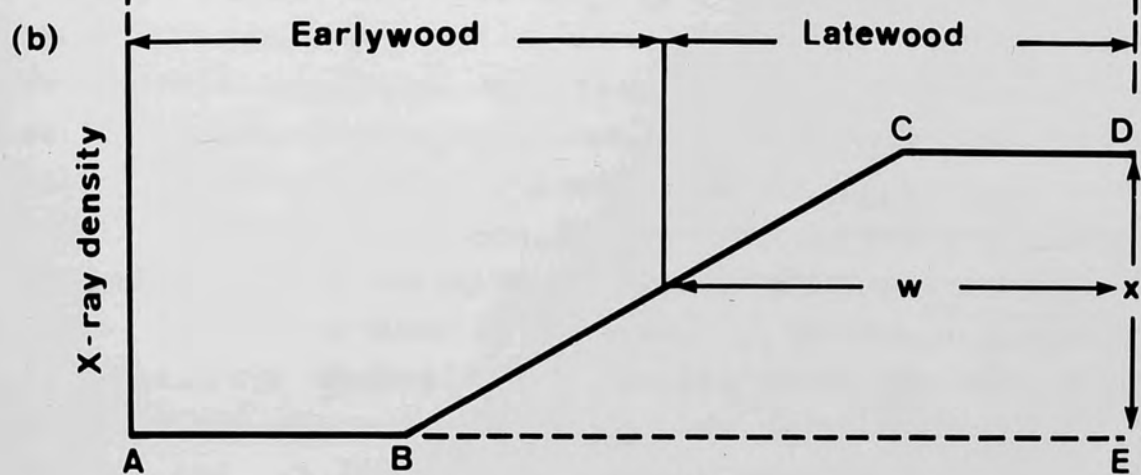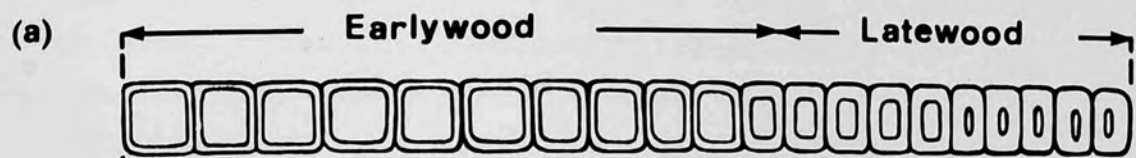
diameter which was equal to or less than half the distance between the nearer margins of the lumina of the cells on each side. Thus the combined thicknesses of the tangential walls on both sides of the cell were involved in this definition.

Yet another definition was produced by Smith (1955) in which the latewood cells were stated as having lumina narrower in the radial direction than the thickness of the walls between successive lumina. Fry and Chalk (1957) found this definition useful in their work on Pinus patula Schl. and Cham., grown in Kenya, because their trees had produced earlywood with unusually thick walls; as thick apparently as those of European latewood. Smith's definition satisfactorily separated the early- from the late-formed part of the ring in P. patula (at least when grown in Kenya), but, as Fry and Chalk point out, it would deny the existence of latewood in many European conifers. Similarly, Green and Worrall's (1963) definition works well with thin timber sections studied by optical densitometry (Creber, 1977, p.363).

Whitmore and Zahner (1966) used both Mork's original definition and also a variation, in their study of developing secondary xylem in young Pinus resinosa Ait. trees. Because they were examining wood before it was fully mature they were faced with the problem of cells which did not yet fit Mork's definition but would do so by the end of the growing season. They therefore instituted a category of 'flattened latewood cells' for those cells which would eventually become Mork latewood. For the purposes of their work, which will be described in detail in a later section, the use of the two definitions simultaneously enabled them to fix two transition dates for latewood, one for the Mork cells and one for the flattened cells.

(d) X-ray densitometry

Polge (1966) pointed out the disadvantages of all of
the earlywood/latewood definitions based on wall/lumen
dimensions; for example, one file of cells may have a
different boundary position from a neighbouring file and
also one may find apparently latewood cells intercalated
between earlywood cells. He was one of the pioneers of the
X-ray technique in which pencil - like sticks of wood,
square in cross-section of side 5mm x 5mm, are shaped from
cores drilled radially out of tree trunks. When prepared
they are laid on X-ray film and irradiated to produce an
X-ray negative. In this way the different densities of
earlywood and latewood become translated into shades of grey
on the negative. This is then run on an optical
densitometer and the varying intensities of light passed by
the negative are then recorded. If the machine is first
standardised by using a piece of translucent synthetic
material with approximately the same density of carbon,
hydrogen and oxygen atoms as in wood, the output of
readings may be obtained directly in terms of grams per
cubic centimetre. Using this technique on Douglas-fir wood,
Polge chose 0.55g cm^{-3} as the boundary density separating
early and latewood. Mean density was calculated from the
mean densities of all of the rings scanned. He showed that
with his technique he could: 1. recognise that a given
specimen of wood came from the central part of a trunk, and
2. deduce the provenance of wood from two separate growth
sites in France by their contrasting densitometric patterns.

The X-ray technique has a number of valuable features.
For example it permits the use of cores from living trees.
Also it has a smoothing effect on insignificant
irregularities in the wood because a 5mm depth of wood is
scanned in one passage of the X-ray beam.

In a later study Nicholls and Brown (1971) arrived at
their estimate for the boundary by a calculation involving
both the maximum and minimum densities. The latter were

read off from the X-ray densitometer profile (Fig. 2b).
Whereas in the past average density has either required a
tedious integration or the positioning of a horizontal line
to divide the space beneath the density curve into two equal
areas. Nicholls and Brown were able to obtain a measure of
the average by using w and r.

The area under the curve ABCDE with respect to the base
line AB is BCDE which also

$$= \ ^1/_2(CD + BE) \quad (\text{max.} - \text{min.})$$

but since $^1/_2(CD + BE) = w$. it follows that the height of
the mean ordinate with respect to the base line

$$= \frac{w(\text{max.} - \text{min.})}{r}$$

In terms of density,

$$\text{average density} = \frac{w(\text{max. density} - \text{min. density})}{r}$$
$$+ \text{min. density}$$

It was then found possible to use the expression $\underline{w}$ as
$$r$$
an earlywood/latewood ratio since it is independent of the
position of the profile with respect to the density scale.

Although this is an elegant technique. it has its
disadvantages. McKinnell and Shepherd (1971) found that the
relationship of wood density with lumen diameter and wall
thickness was not the same between trees of the same
species. This variation in cell dimensions in each of the
two zones calls in question the validity of using the
concept of average density. In a recent study on
Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) Cown and
Parker (1979) combined the X-ray technique with measurements

of the absolute density of the wood: unlike Nicholls and Brown who sought to uncouple the profile from the density scale. They adopted the $0.5g \, cm^{-3}$ density level as their criterion for the earlywood/latewood boundary (Fig. 2c) and it seems to have served them well in their work. It enabled them to show variations in the earlywood-latewood ratio that were allegedly due to the different growing conditions on 5 separate sites in the Pacific Northwest of the U.S.A.

In the section on environmental influences (Section 3c) a new technique is described for the determination of the earlywood-latewood boundary and is used in conjunction with a classification of growth ring types.

(e) The effects of age and position within the tree

Because the principal interest in the present work is the environmental effect on wood growth. attention has to be paid to the possibility that non-environmental factors may influence the relative proportions of earlywood and latewood. Creber (1977. Table 1) lists some of them. One in particular that is widely recognised is due to the age of the tree. As with most aspects of the subject there are many examples which are in conflict (Elliott. 1970); however. there is much evidence that there is a tendency for trees to produce increased amounts of latewood in the outer rings of the trunk. That this is not merely due to the. usually. smaller width of these rings can be shown by choosing rings for comparison that are of equal width.

A further positional effect is that of distance from the crown. As Larson (1969) points out. a young tree is essentially all crown and the current-year shoot at the apex. forming a sizeable proportion of the total tree. dominates wood production. As the young tree grows. lateral branches play a larger role in regulating wood growth. Thus the first rings of young trees contain a high proportion of earlywood due to the close proximity of the foliar organs

producing plant growth regulators. In the current-year internode (used in the forester's sense. as the portion of stem between branch-whorls in conifers) the tracheids produced near to the influence of the leaves are almost exclusively of the earlywood type with some of a smaller diameter being produced at the base of the internode just prior to dormancy. Downwards from this point the percentage of latewood will gradually increase in the rings as the distance from the foliar organs increases. Earlywood tracheids will nevertheless predominate because the branches of young trees are short and vigorous. Larson (1969) introduced the term 'transition latewood' in order to describe the cells typically formed in rings nearer the crown of the tree (Fig. 3). They have walls almost as thick as those of the final cells in the rings but their lumina are larger.

Latewood is initiated at or near the trunk base in trees of all ages and its differentiation progresses upwards as the season advances. The width of the latewood zone therefore tapers upwards. reaching a point of extinction near the apex. This pattern of latewood development is a function of age and distance from the active crown. The abrupt onset of latewood formation in the lower trunk produces a sharp transition from the larger to the smaller cells; higher up nearer the crown the transition becomes less distinct with a zone of Larson's transition latewood in between. Each branch is in effect similar to the upper part of the main axis and thus its wood will have a smaller amount of latewood in the rings than wood from the lower trunk. Thus the effects of age and position are interrelated. the later formed rings in a tree have a different position with reference to the crown.

Because root wood is of no commercial importance it has not received the enormous attention that has been devoted to trunk wood by the timber industry. From the few studies that have made it is clear that there is much variation in
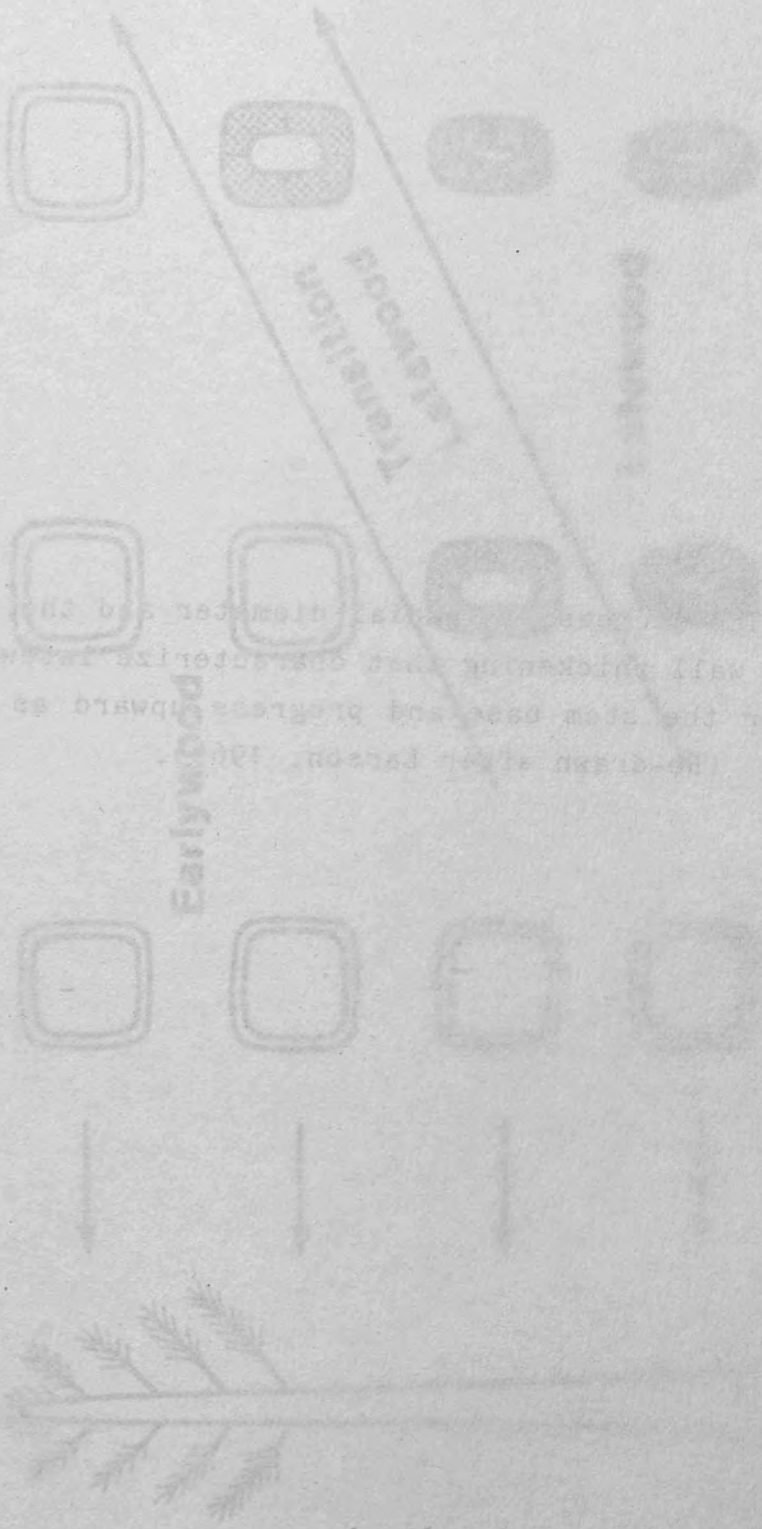
Fig. 3.   The decrease in radial diameter and the increase in secondary wall thickening that characterize latewood usually begin near the stem base and progress upward as the season advances.   (Re-drawn after Larson, 1969).
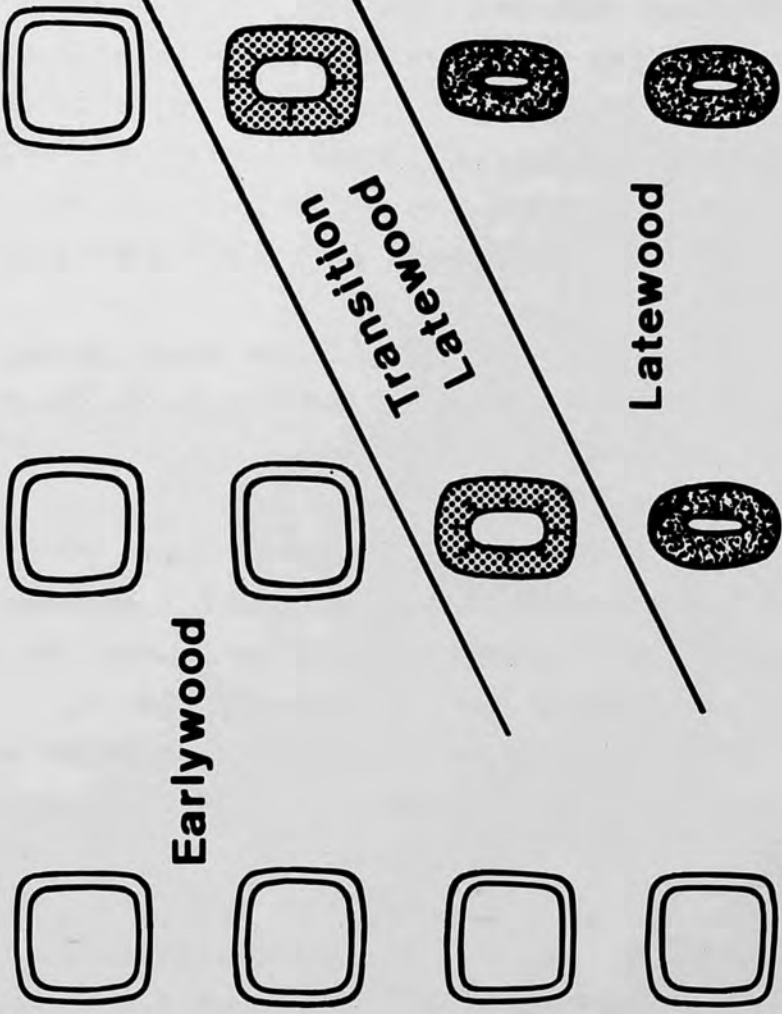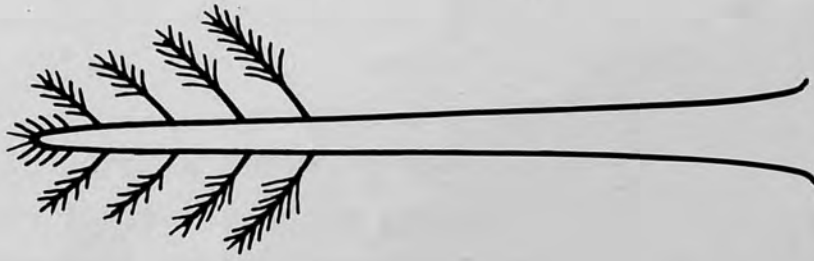
structure depending, it appears, on the depth of the roots in the soil (Bannan, 1962). Such wood has a superficial resemblance to the wood of branches and the inner trunk in that the growth rings terminate abruptly with only a very few latewood tracheids. In this connection Beck's (1953) work on the Devonian fossil genus Callixylon is of interest here in that he was able to designate a new species. Callixylon petryi Beck, based on root material. (See Section 2(f)).

At this point reference is made to Bailey and Faull (1934) who studied specimens of the wood of Sequoia sempervirens (D. Don) Endl. collected by Douglass. Entire cross-sections were secured from different heights in the same tree and from trees growing in different parts of the range of the species. Other specimens from roots, branches and stems were collected by Bailey himself. On studying all of the material it was found that the growth rings varied considerably in width, in the ratio of latewood to earlywood and in the abruptness of the transitions between thin-walled and thick-walled tracheids. In young trees growing under favourable conditions the growth rings may be very wide. During subsequent development, the rings tend to become steadily narrower, and may actually occasionally consist of the theoretical minimum of two tracheids, one earlywood and one latewood. Many specimens had relatively narrow rings throughout their cross-sections or alternating zones of narrow and wide rings since old suppressed trees will form wide rings when released from the competition of dominating neighbours. This effect is also illustrated by Larson (1969) in the context of forestry where the removal of competing neighbours is effected by thinning the stand.

Bailey and Faull found the growth rings of branches and roots to be narrower than those of trunks of comparable age. In narrow rings from the peripheral parts of old stems. branches and roots, the earlywood/latewood ratio was low and the transition between the two was very abrupt; whereas in

wide rings the ratio tends to be higher and the transition may be either gradual, or abrupt. In the inner rings of stems and branches the earlywood/latewood ratio tends to be higher in the wider rings, and the transition between the two to be so gradual that there is no obvious boundary. The latter feature is very much in agreement with Larson's (1969) findings.

Thus the effects of the other factors which influence wood growth must be seen against a background of internal variation within the tree itself.

(f)   Interpretation

Fossil wood frequently occurs in isolated fragments and it is useful therefore to have certain identification features that enable the assignment of a specimen to a certain part of a tree. In the first instance the radius of curvature of the rings is a useful feature. Much curved rings are likely to be those nearest the centre of a trunk, branch or root. If the absolute centre is present, a root may be easily distinguished from trunk or branch by the presence of centripetal metaxylem whereas in the latter organs a pith will be observed. Also, in a root reaction wood is not present (see p.156) and the rings are virtually always very deficient in latewood. A wood specimen with distinctly curved rings and reaction wood is therefore very likely to be a branch; without reaction wood a portion of the leading shoot is indicated, especially if the rings are wide and exhibit Larson's 'transition latewood'. A specimen several centimetres wide in which the ring boundaries appear to be straight, or almost so, is most likely to be a portion of the trunk; very narrow rings with a high proportion of latwood would help to settle the matter.

3. ENVIRONMENTAL INFLUENCES

In the present work it is highly desirable to be able to interpret environmental influences from the proportion of the latewood in the growth rings of fossil wood. There is a considerable literature on this subject (Creber, 1977) and from it can be extracted certain correlations between the environments of trees and the characteristics of their growth rings.

(a) Growing season

A longer than average growing season appears to be one of the factors that causes the development of additional latewood. Two examples are cited which illustrate this effect. The first is a study of the growth of Fraxinus excelsior L. and Pseudotsuga menziesii growing in plantations near Oxford (Chalk, 1930). It was found that increased latewood percentage in the rings was positively correlated with longer growing seasons. In the second case, a similar effect seems to have operated in a study involving the planting in Norway of specimens of Picea abies L. Karst of German provenance (Klem. 1957). These continued to grow much longer into the late summer and autumn than the Norwegian Picea abies and produced correspondingly more latewood. Further information on this topic is given in Section 4(c).

(b) Water supply

However, trees will not continue growing late in the season if the water supply is not adequate. Koehler (1938) showed that artificial irrigation of Pinus palustris Mill. could increase the amount of latewood by 50%. Similarly. Voegeli and Reinhart (1956) found that drought years had the greatest effect on the amount of latewood formed. Orman (1958) was able to establish in a study of Douglas-firs growing in New Zealand, that very little latewood developed

if the annual rainfall was less than 762mm. Furthermore it may not be only the total amount of rainfall that is important but the time at which it falls may have considerable influence as well. Larson (1957) was able to illustrate this very point by studying the growth of Pinus elliottii Engelm. var. elliottii growing in Florida. It proved to be the June and July rainfall that had the highest positive correlation with percentage of latewood. It was also the rainfall of those two months that Fritts (1962) found was most important for latewood development in Quercus alba L. in Illinois.

Not only the percentage of latewood, but also the nature of the earlywood-latewood boundary seems to be at least partly controlled by the water supply. Harris (1955) showed that an abrupt change from earlywood to latewood in Pinus sylvestris L. (a Type 'A' ring, see below). could be caused by a water shortage at that time. A further study that reinforces Harris' findings is that of Kraus and Spurr (1961) who showed very close agreement between the dates of the onset of soil-water shortage and the timing of the earlywood-latewood transition in Pinus resinosa growing in Southern Michigan. Further discussion of the earlywood-latewood boundary is to be found in the section on Water Supply (Section 8).

(c) Classification scheme

In order to make the interpretation of growth rings as systematic as possible. a classification scheme has been devised, to categorise different earlywood-latewood relationships (Fig.4). The earlywood-latewood boundaries have been established by a new technique in which a cumulative algebraic sum is made of the deviations from the mean of the radial cell diameters. The tendency of the latewood to have smaller radial diameters causes the cumulative sum graphs to turn downwards towards zero. The points at which these turns are made are used in each case

to determine the earlywood-latewood boundaries.

Type 'A' rings are those in which there are sharp transitions at the earlywood-latewood boundaries (Fig. 4A). This type of ring occurs when a water shortage sets in abruptly in the growing season. These rings are usually without much latewood as a good water supply is necessary for its formation. In Type 'B' rings (Fig. 4B) the transition to latewood is much more gradual and a wide band of latewood would indicate a long growing season with an adequate water supply. Type 'C' rings (Fig. 4C) are less commonly encountered; they indicate growth in an environment with only a very gradual change during the growing season. Types 'D' and 'E' are essentially somewhat similar (Fig. 4D and E); both indicate growing seasons that are relatively uniform but each has a terminal event representing a cessation or retardation of cambial activity. In 'D' the ring boundary is somewhat more marked whilst in 'E' it is so faint that it almost escapes notice.

Type 'O' growth (Fig. 4O) results from a situation where all the necessities for growth are constantly present. With the knowledge of the possibilities for genetic variation (Section 9) that exist in trees, it is realised that certain of them may not always exhibit growth ring features as precisely as in Fig. 4. It is all the more valuable therefore when an assemblage of fossil wood material is obtainable from a single site. Furthermore, there are certain genera in the Araucariaceae and the Podocarpaceae such as Araucaria and Phyllocladus whose wood under a variety of circumstances tends to have rings of Types 'D' and 'E'. Since the earlywood-latewood ratio is a characteristic of the tree not significantly affected by environmental factors the wood of these genera can really only be used in studies involving analyses of ring widths. Also, as these trees are not widely grown on a plantation basis there is not the vast amount of data available from experiments that is the case for genera such as Pinus. Picea

and _Abies_, for example. The significance of wood of the type exhibited by _Araucaria_ is discussed again in Section 11.

Fig. 4. Six graphs of selected types of growth rings in fossil woods which show how (a) the cell radial diameter changes across the width of each growth (cf. Fig.1.) and (b) the cumulative sum of the deviations from the mean cell radial diameter falls to zero in the latewood phase of each ring. See text for the analysis of the ring types. The data were obtained from the following fossil woods: A, Appendix I No.9; B, No,94; C, No.12; D, No.10; E, No.55; O, Callixylon trifilievi Zalessky.
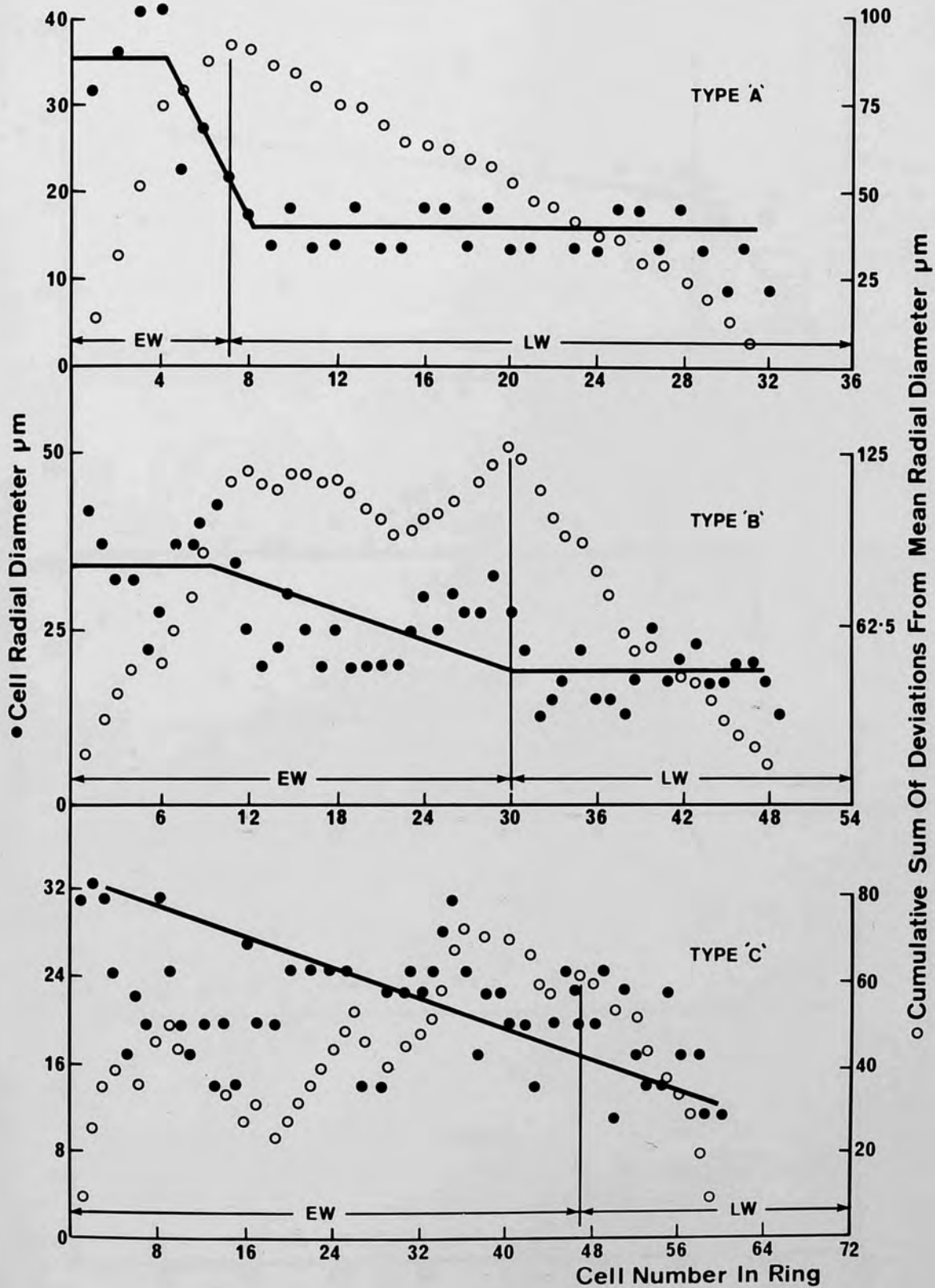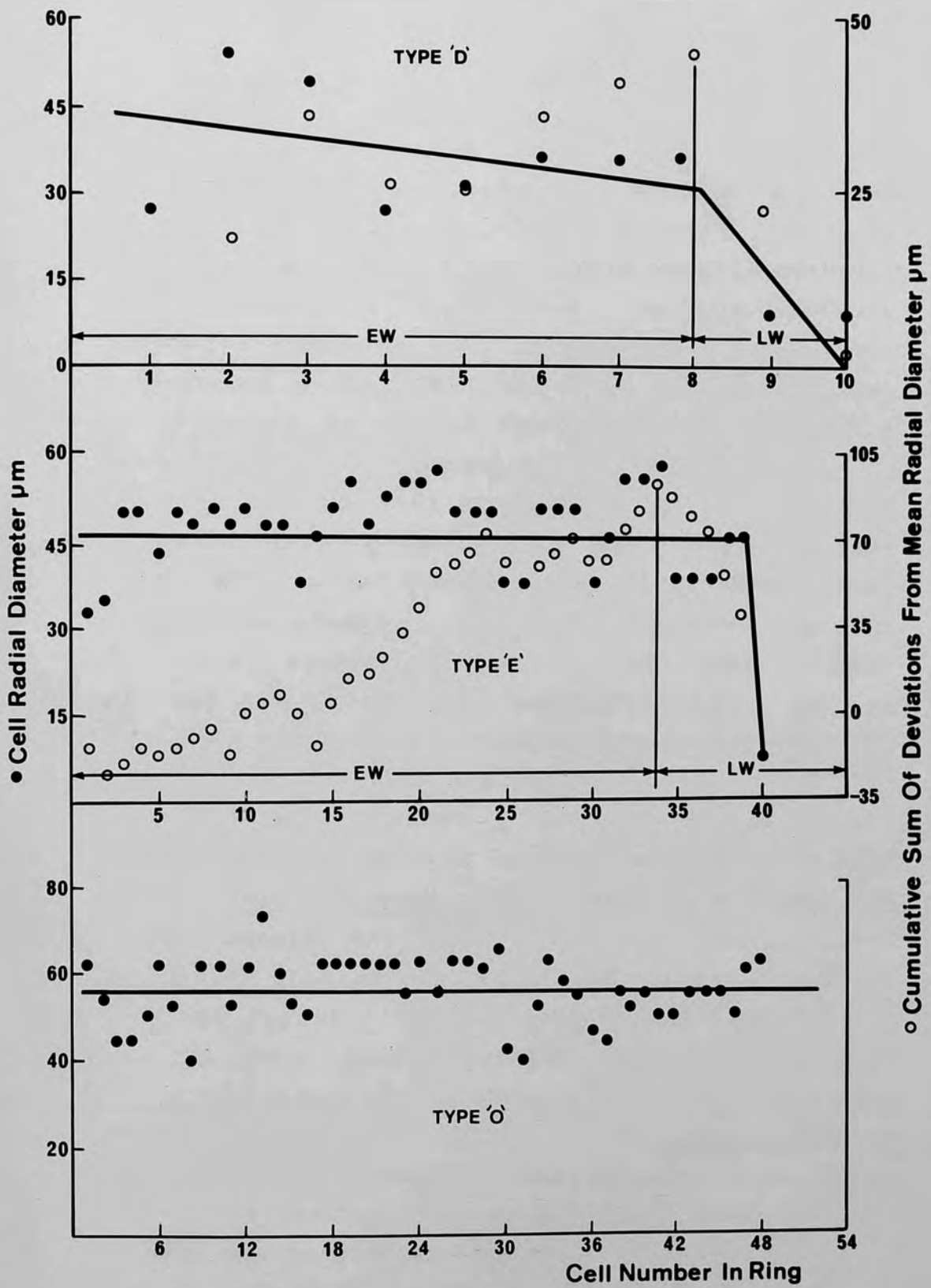
4. THE EFFECTS OF TEMPERATURE

(a) Frost effects

One of the more obvious and direct effects of temperature on wood growth manifests itself as a 'frost ring' (Bailey, 1925). Such a ring consists in part of crumpled tracheids and in part of crushed undifferentiated centripetal derivatives of the cambium. In this zone the rays are laterally displaced and inflated by an enlargement of their constituent cells. When the frost is over a normal equilibrium of forces is not at once restored owing to a more or less permanent deformation of the tissues. The abnormal radial and tangential stresses in the cambial zone are still present, causing enlargement and division of the surviving cells which crowd towards areas of lessened radial and tangential resistance. Thus the fissures in the compression zone become occluded, the rays expand tangentially and the intervening cells frequently tend to differentiate into an irregular short-celled parenchyma. As growth continues, the stresses are equalised and in the rest of the ring, the cells assume a normal form and radial seriation provided that there is no further frost. In some species, e.g. Abies balsamea (L.) Mill., a ring of 'traumatic resin canals' may form.

Whereas Bailey studied the results of natural frosts on trees, Glerum and Farrar (1966) carried out an experimental investigation in which they subjected seedlings of Pinus strobus L., P. resinosa, P. banksiana Lamb.. Picea glauca (Moench) Voss. P. mariana (Mill.) B.S.P. and Larix laricina (Du Roi) K. Koch to freezing conditions. From their observations on the damaged tissues they were able to show that frost rings can be divided into two parts:

1. an inner part composed of cells killed by the frost and
2. an outer part formed by the cells that develop abnormally after the frost.

Those of the inner part are dead cells of the cambial zone, chiefly xylem mother cells and immature tracheids in various stages of differentiation. Of the latter, those which had partially lignified retained their shape but the unlignified ones and the xylem mother cells collapse completely. One day after frost treatment there were about three surviving cells in the cambial zone. About six days later these cells had proliferated and had produced the abnormal cells as described previously by Bailey. After fourteen days the abnormal cells were maturing and the cambial zone had become much more recognizable again. Twenty days after the frost normal growth had resumed.

Sometimes the effect of low temperatures early in the growing season may not be so severe that an actual frost ring is produced but there may nevertheless be some observable effect. Fletcher (1975) reported that in his work on European oaks he could detect the effects of, historically known, severe winters and cold springs during the period 1428-1450. In these years the oaks produced growth rings with exceptionally small earlywood vessels, a feature readily detectable in view of the fact that in oak these vessels are usually extremely large.

(b) Directional effects

Another rather direct way in which temperature may affect wood growth was first reported by Hartig (1885) who found that cambial activity in Picea sp. growing in Europe started earlier on the southern, warmer, side of the trunk in spring. Chalk (1927) found that in Fraxinus excelsior L. growing near Oxford the south side of the trunk had cambial activity before it had started on the north side. Helms (1970) gave some figures (Table 1) which show the asymmetric distribution of solar radiation received by Pinus ponderosa Lars. trees growing in the Sierra Nevada. U.S.A.. latitude 37°N. Leikola (1969) has shown by installing thermometers

TABLE I

Percentage of above-canopy radiation load reaching different
levels within the Pinus ponderosa forest canopy at different
sides of the tree's crown. Each value was the mean of 5
readings (after Helms, 1970).

ASPECT

HEIGHT (m)	NORTH	SOUTH	EAST	WEST
23	31 ± 2	51 ± 2	42 ± 5	45 ± 4
18	25 ± 3	34 ± 2	32 ± 5	28 ± 6
12	20 ± 5	21 ± 6	22 ± 5	25 ± 4
1	18 ± 25	30 ± 21	25 ± 18	33 ± 27

into the cambial layer of specimens of <u>Pinus sylvestris</u> grown at 61°N in Finland. that the south side of such trees may be 4°C warmer at noon than the north side. His observations spanned the period from April 24th to August 31st.

It has long been thought that such effects lead to corresponding asymmetries in the wood of the trunks of the trees. It has been said that in the temperate regions of the world it is possible to judge from the eccentricity of a cross-section of a tree trunk which side was directed towards the North Pole. Kraus (1899) reviews such statements made over the last 900 years. In order to test their validity he examined the trunks of a number of trees, both angiospermous and coniferous, at Wurzburg. Germany. He found a somewhat confusing situation with no clear pattern of general agreeement with a North-South orientation. However, in spite of what he thought was a total refutation of earlier claims, it still remains possible that in some situations asymmetries in tree trunks may occur having a North-South orientation. and a temperature/radiation causality.

This was actually demonstrated by Liese and Dadswell (1959) who measured fibre and tracheid lengths in the wood of several species of trees (angiospermous and coniferous) in the Northern and Southern Hemispheres. Two were located only 7° south of the equator in Indonesia. Without exception all trees had shorter fibres (or tracheids) on the side of the trunk that faced towards the sun. that is to say the south side in the Northern Hemisphere and vice-versa. Using this technique the authors claimed that they could orientate a disc of wood cut from any of the trunks of their trees.

The possibility of deducing palaeopole positions from in situ stumps of fossil trees has attracted the interest of geologists. Krystofovich (1932) suggested that this should be exploited wherever possible. and to this end Kossovich

TABLE II

Number of vertical resin ducts in some fir trunks per mm^2 of
cross-section (after Mayr. 1893).

	OUTER ANNUAL RINGS		INNER ANNUAL RINGS	
	S	N	S	N
Lower part of trunk	150	62	61	10
Middle part of trunk	105	80	37	35
Upper part of trunk	62	60	–	–

(1935) in a preliminary study on living <u>Pinus</u> sp. attempted to find what features in the trunks seemed consistent enough to use in polar orientation. He concluded that the following features on the southern side would be usable: 1. The larger number of 'false rings'; 2. The occurrence of 2% more earlywood in the rings; 3. The earlywood tracheids tended to be larger; 4. The larger amount of latewood. He cautioned, though, that only the first 30 rings in the life of the tree should be used as these tended to be most influenced by the asymmetry of the environment while the young tree still had a relatively thin bark. He also cited some work by Mayr (1893) who measured the number of resin canals per square millimetre of cross-section area of cut trunks of fir trees (Table II). Not only are the numbers of resin canals obviously larger in the southern part of the cross-section of the trunk but this could also be observed qualitatively by the extra amount of resin seeping from the southern side of the cross-section.

Krames (1952) measured the radii of a number of trunks of oak and spruce near Wittlich, Germany, and found that both species had larger radii towards the North. One cannot accept, however, his explanation for the phenomenon as being due to the trees leaning towards the south as a result of crown asymmetry; the latter was believed to result from a preferential growth of foliage on the sunnier side of the tree. Since reaction wood is formed by conifers on the opposite sides of their trunks as compared with those of the angiosperms (Creber, 1975; Robards, 1969), the same eccentricity could not be caused by the sort of anatomical difference demonstrated by Liese and Dadswell (1959) which affected both types of tree on the same side. Krames (1956) went on to study the in situ stumps of fossil trees in two opencast lignite mines near Cologne. He claimed that the eccentricity of their trunks showed that the Miocene North (rotation) Pole was several degrees east of its present position.

Smirnoff and Connelly (1980) described some petrified stumps of Tertiary fossil trees at Kujulik Bay and Unga Island, Alaska Peninsula. The site geology indicates that these sequoias had been growing on flat land but their growth ring patterns are asymmetric with each ring being thicker on the sides of the trunks which was towards palaeosouth, as determined by palaeomagnetic studies. The authors felt that the asymmetry of the trunks supported the palaeomagnetic evidence. The eccentricity in this case was towards the South, in conflict with Krames' results but in agreement with Kossovich and also with a study of redwood tree stumps near Crescent City, California (Smirnoff and Connelly, 1980). Their paper provoked a sharp reply from Shroder and Schwarzbach (1981) who thought that there were many other possible explanations for the asymmetry of the stumps. The matter is at the moment not resolved. However, there seems to be enough evidence to suggest that North-South differences may be produced in tree trunks although the nature of its cause, and its consistency in occurrence still require further investigation.

(c)   Growing season

Although the primary trigger for budbreak is photoperiodic (Daubenmire, 1949), very little further growth will take place if the ambient temperature remains too low (Priestley, 1930). Denne (1976b) found in Picea abies that the first tracheids began to differentiate at the moment when the first scale leaf primordia were produced at the shoot apex. So that although the link between the apex and the cambium is a hormonal one, the date at which activity commences will almost certainly depend on the ambient temperature. This clearly emerged in a study by Ermich (1963) of firs and spruces growing at 1030 m on Mt. Nosal in the Tatra Mountains of Poland. He was able to show that cambial activity in the same trees commenced on different

dates in successive years. For example in a specimen of Abies alba (Mill.) it was found that cambial activity in 1957 started on the 21st May whereas in the same tree two years later it was already under way on the 11th of the month. Examination of the temperature records for that locality shows that in 1957 the mean daily temperatures for May were several degrees lower than those of 1959. A consequence of this was a growing season in 1957 at least 10 days shorter than that of 1959, three months as against three months ten days. Leikola (1969), working in Finland on Pinus sylvestris grown at $61^{O}N$ found that deviations of $0.5^{O}C$ in the April-May mean temperatures caused corresponding 1-2 day shifts of the date of the start of cambial activity. In this locality, the Metsa-Saramaki Forest, the onset of diameter growth varied from May 16th to May 25th.

However, when he came to study the cessation of cambial activity at the end of the season he found a different situation. He concluded that the influence of environmental temperature here was far less potent and it seemed to him that cambial activity ceased as a result of an endogenous factor. An earlier worker, (Brown, 1912, 1915) had already noted in his studies on Pinus rigida Mill. and P. strobus that cessation of the season's growth was not temperature dependent. In a more recent study, (Denne, 1976a) it was again noted that the duration of wood production seemed independent of temperature and also shoot activity. That is to say, wood production was found to cease at a much higher temperature than was necessary for its initiation. On the other hand a longer, more favourable growing season will definitely increase the amount of latewood. This was established experimentally by Larson (1967) in studies on Pinus resinosa and appears to be due to the fact that whereas earlywood development depends upon stored reserves, latewood is dependent upon current assimilates which will be available for longer in an extended growing season.

Mikola (1962) in a study of tree growth in Northern Finland, found further evidence of the importance of the length of the growing season. However, in such high latitudes radial growth ceases about the middle of August and hence extra length to the season can only come from an early start. In such years he found that there was more latewood produced in the rings, since the periods of earlywood formation were constant from year to year. The correlation of latewood growth and environmental temperature seemed to be one in which the number of individual days with maxima of $19^{\circ}C$ or more were of greater importance than periods of higher than average temperatures. There was also a lag effect, too. in which a very narrow ring tended to arise in the year after one with a poor growing season which provided little in reserve for the initial growth of earlywood in the next season (Creber, 1977; Fritts. 1976). Because of the large variation in conditions from year to year there was a correspondingly high percentage variation in the amount of latewood in the rings. The control imposed upon the trees by temperature is such that the timberline is more or less coincident with the $10^{\circ}C$ isotherm of the mean temperature of the warmest month in the year.

Leikola (1969) also found that the widest rings, as measured by dendrographs attached to the trees, were produced by his specimens of Pinus sylvestris in the years when the growing seasons were longest. He also established that at this latitude in Finland ($61^{\circ}N$). there was a marked difference in the growing season between the pines and the birches (Betula pubescens Ehrl.). Whereas the former showed diameter growth from about mid-May to mid-August, the birches started about the 10th June and ceased in late July. This is presumably a reflection of the fact that the birches are deciduous. With a totally new set of leaves. photosynthetic efficiency would be high and sufficient photosynthate could be produced in a relatively short time.

Support for both Mikola's and Leikola's work was

furnished by Millar (1980) who studied the growth of <u>Betula</u> <u>pubescens</u> ssp. <u>tortuosa</u> (Ledeb.) Nyman in Northern Finland at latitude 69°N. The area varied from 183m to 255m above sea level; the lowest monthly average minimum temperature was -18°C in January. whilst the highest average maximum temperature was 18.2°C in July. In the severe temperature regime the amounts of annual growth were very small, ranging from 0.20 mm yr^{-1} to 0.64 mm yr^{-1}. The former was in a tree that had taken 88 years to produce 48 mm diameter of wood whilst the latter had 87 mm diameter of wood after 68 years.

It is apparently not only daytime maximum temperatures that are important; Kramer (1957) found that lower night temperatures were influential as well. By maintaining a number of <u>Pinus taeda</u> L. seedlings at a series of different day and night temperatures he showed that with a 30°C day temperature. height growth was increased 11% per degree for each decrease of 1°C from 23° to 17°C in the night temperature. From these results he claimed to be able to explain a curious feature in the distribution of <u>P. taeda</u> which occurs from the Gulf Coast and Northern Florida to Southern Tennessee. and in the Coastal Plain. to Southern New Jersey. Hitherto there was no explanation for its southern limits nor for the fact that foresters claimed that the species made its best growth on the Virginia-North Carolina line. near the northern edge of its range; he felt that the lower night temperatures in the northern part of the range provided a satisfactory explanation for its better growth there. A similar example is provided by some work done in Zimbabwe by Barnes et al. (1977) on <u>Pinus caribaea</u> Morelet. It was found that the radial growth was markedly different on two of their growth sites; the only factor by which the two sites differed was in their monthly average temperatures which consistently, month by month were 14.0°C and 18°C. It was concluded that this difference was critical for the species which produced distinctly contrasting growth at the two sites.

Nicholls and Wright (1976) studied the growth of Pinus radiata D. Don on a number of sites in Victoria. Australia. using two parameters to define the length of the growing season: 1. A minimum ambient temperature of 9°C and 2. A minimum water tension in the soil of 4 bars. In this way they were able to estimate the number of growth days in the season. It was found that the percentage of latewood. determined by the Nicholls and Brown (1971) method, was positively correlated (r = 0.72) with the length of the growing season as was ringwidth itself (r = 0.87). Wodzicki (1971) contributed to this area by showing that there was a strong correlation (r = 0.97) of temperature with the rates of cell maturation and wall thickness in Pinus sylvestris; thus a wider zone of latewood formed when higher temperatures prevailed in the later part of the season, providing that water supply was not limiting. He also showed that the rate of wall formation dropped to a very low figure at 10°C which supplements Mikola's observation on the timberline in Northern Scandinavia. Wodzicki's findings have since been confirmed by Smith et al. (1977) in their studies on the effects of fertiliser treatment and environmental factors on Pinus nigra var. maritima (Ait.) Melv. They found that the environmental factors were at least as important, and in some cases more so. than the fertiliser treatment. Percentage of latewood was positively correlated with both rainfall and temperature during the growing season. A particularly direct effect of temperature on tree productivity was demonstrated by Brett (1983) in the growth of a specimen of Ailanthus altissima (Mill.) Swingl. in St. James' Park, London. The difference in mean June/July temperatures of the years 1859 and 1860 was about 4.5°C and the difference in ring width was 4.3mm. In London 1859 had one of the hottest summers on record whilst 1860 was one of the coldest.

Environmental temperatures may have effects other than those described above; for example, Gustafson (1938) showed

that red pine (<u>Pinus resinosa</u>) seedlings required freezing
winter temperatures to break dormancy in the following
spring, otherwise no new growth took place. The ambient
temperature may also control a subtle balance between the
processes of respiration and photosynthesis. Decker (1944)
showed that the optimum temperature for photosynthesis is
lower than that for respiration. He further went on to show
that over a range of temperatures from $20^{\circ}C$ to $40^{\circ}C$ the
ratio of the rates of photosynthesis and respiration changed
in the following way:- At $20^{\circ}C$ it was 13: 1. at $30^{\circ}C$ 6.8:1
and at $40^{\circ}C$ it had fallen to 3:1. This effect is thought to
be the explanation for the poorer growth of trees in
habitats with higher night temperatures. for example those
previously described by Kramer (1957). Denne (1971)
reported the results of some experiments in which she grew
<u>Pinus sylvestris</u> seedlings in photoperiodically long days
with a range of day/night temperatures: $27.5/20^{\circ}C$. $22.5/15^{\circ}C$
and $17.5/10^{\circ}C$. In her review of previous work she points
out that van Buijtenen (1958) and Richardson (1964) had both
shown in several conifer species that temperature and wall
thickness in the tracheids were inversely correlated. The
suggested explanation being a direct relation between
substrate availability and wall thickness; this was
supported by the greater effect of higher night temperatures
(Richardson, 1964; Richardson and Dinwoodie, 1960) resulting
in the respiration of substrate at an increased rate. The
results of Denne's experiments showed that although tracheid
dimensions showed some correlation with temperature the
effects were not very marked. A $10^{\circ}C$ difference in
temperature (i.e. from $17.5^{\circ}C$ to $27.5^{\circ}C$) produced some
increase in tracheid diameter but it was only of the order
of 10%. An inbuilt regulatory system was evident. for while
a rise in temperature increased the rates of cell expansion
and wall thickening. this was offset by a reduction in the
duration of both processes. Thus temperature was not seen
as a major factor in controlling the seasonal variation in

tracheid dimensions; the other factors, water supply and photoperiod will be dealt with in later sections.

(d) Altitude

One of the most potent controls on environmental temperature is the elevation of the land above sea level. A number of studies have been carried out to investigate the effects of altitude on tree growth; in one of these. Daubenmire (1946) studied the differences in growth of a number of conifer species on Thatuna Ridge in the Rocky Mountains 12 km north west of Moscow. Idaho. The ridge was 1600 m high and the species were distributed from top to bottom so that he was able to study the behaviour of each species through the altitude range. The north and south facing slopes of the ridge were studied separately so that the effects of aspect could be taken into account.

He found that Pinus ponderosa growth rings were 1 mm wider at 838 m as compared with 1065 m, a difference in altitude of only 227 m. At 1470 m Larix occidentalis Nutt. only produced growth rings 0.3 mm wide whilst at 987 m they were in excess of 2 mm. In an earlier study on P. ponderosa in the Sierra Nevada, Fowells (1941) obtained some very interesting results showing the different starting dates for radial growth and the lengths of the growing periods at different altitudes (Table III).

TABLE III

Starting dates for cambial activity and lengths of growing season for _Pinus ponderosa_ at different altitudes in the Sierra Nevada (after Fowells, 1941).

Altitude	600m	1000m	1330m	1660m	2000m
Starting dates	Feb. 17	Feb. 25	Mar. 11	Mar. 23	Apr. 17
Season lengths (days)	241	198	183	177	143

Productivity is also limited at high altitudes as was demonstrated by Oswald (1969) who found that in 75-year-old stands of _Picea abies_ in the Central Massif. France. at about 1200 m elevation the annual timber increment was 12 m^3 ha^{-1}. Above this level there was a rapid fall-off in volume increment so that at the 1650 m timberline it was reduced to 1.2 m^3 ha^{-1}. Most of this reduction was attributable to the much shorter growing season at the timberline.

(e) Effects of temperature upon photosynthesis

Pisek et al. (1969) showed that in specimens of _Picea abies_, _Larix decidua_ Mill. and _Betula verrucosa_ Ehrh. from the timberline in the Austrian Alps, the optimum temperature for photosynthesis was $3^\circ C$ lower than for specimens growing on the valley floor. In that up to 45% of the carbohydrate production of a tree may go into the wood (Kozlowski. 1962) any factor that affects this process is clearly of importance. Furthermore, it appears that the temperature giving optimum photosynthetic productivity varies between

different populations of a species, and is genetically controlled. As might be expected the optimum correlates closely with the temperature regime to which the parent population was adapted.

This relationship is demonstrated by Fryer and Ledig (1972) in their work on <u>Abies balsamea</u>. They collected seeds from trees growing along an elevational gradient (731, 853, 1158, 1311, 1463 m) on a south east slope in the White Mountains of New Hampshire. They found that the photosynthetic temperature optima of the seedlings decreased with increasing elevation of the seed source. The change in temperature optimum with elevation was similar to the rate of fall-off of air temperature with altitude, suggesting a precise adaptation to temperature through natural selection.

That this effect is not confined to the conifers was illustrated by Slatyer and Ferrar (1977) who worked on <u>Eucalyptus pauciflora</u> Sieb. ex Spreng in New South Wales. They collected seed at elevations of 915, 1215 and 1770 m from sites 40 km from one another. The photosynthetic response of the seedlings from lowest-elevation, warmest site showed the highest temperature optimum and significantly higher rates of net photosynthesis at the highest growth temperature, $33^{\circ}C$. In a corresponding way the seedlings from the highest-elevation, coldest site showed themselves to be adapted to the conditions there. In addition to such differences in physiology this species, ranging as it does from valley bottoms to alpine timberline, exhibits morphological differences in a continuous fashion. Because of these features it is suggested that such variants should not be given different specific or varietal names but should instead be regarded as populations of a single species distributed along a cline.

Slatyer and Morrow (1977) extended this work on <u>Eucalyptus</u> by showing that not only are the ecotypes adapted to the appropriate altitudinal temperatures but that all such ecotypes may change their optima during the course of

the year. They found that the optimum temperature for photosynthesis at any given moment was closely correlated with both the longer term mean maximum temperature and the mean maximum of the 10 days prior to the date of measurement. Thus there was a long-term adaptation of the photosynthetic apparatus of each population to the general temperature regime at each site, combined with a short-term acclimation to the prevailing seasonal temperature.

It has to be said that not all studies which search for altitudinal ecotypes in tree species are successful. Townsend et al. (1972) studied Pinus monticola Dougl., chosen because this species occurs in Idaho over a broad elevational belt from about 330 m to 2000 m in irregular, often attenuated stands following moister stream bottoms, lower benches and flats and northerly slopes. Thus there seemed to be the opportunity for selective forces to act upon populations separated by relatively short distances. The existence of local ecotypes had been reported previously by Squillace and Bingham (1958). Townsend et al. studied two physiological aspects of the species, rates of photosynthesis and monoterpene distribution. The latter only showed differences between widely separated areas unrelated to elevation or latitude. Although their seed sampling ranged from 500 m to 1760 m in altitude the latter did not appear to determine photosynthetic efficiency or compensation point. It would appear that some tree species can make adequate growth and be sufficiently competitive without becoming highly adapted to their own local site conditions. In this way they avoid the penalty of becoming very closely attuned to a particular altitude.

An example of a study of the effects of low temperatures on a single species was provided by the work of Neilson et al. (1972) who worked on Picea sitchensis (Bong.) Carr. They found that there is not a simple relationship with temperature but that much depends on the environmental history of the tree. They found that the optimum

temperature for photosynthesis in Picea sitchensis varied from $10^{\circ}C$ to $22^{\circ}C$ which is also the case for other species of Picea such as P. abies and P. glauca. There were very marked seasonal changes in the response of net photosynthesis to temperature. The new shoots which elongate from the bud in June possessed some frost hardiness in July and August but lost this completely in September and October and at the same time there was a rise in the optimum temperature for photosynthesis to a peak of $22^{\circ}C$. During this period when there was no frost hardiness and there was a high optimum temperature for photosynthesis the shoots also possessed a high temperature stress resistance. This developed in August with the higher leaf temperatures and leaf-air vapour pressure differences.

In late October and early November, at a time when the frequency and severity of night frosts increased substantially, hardiness increased very rapidly over a period of 2-4 weeks. Together with this went a sharp decline in the optimum temperature for net photosynthesis which continued gradually throughout the winter. The temperature effect on photosynthesis in Abies alba is similar in all respects to those described above with the further point that it appears to be resistant to even lower temperatures than Picea sitchensis. This is seen to have interesting connections with the Central European, montane distribution of Abies alba with much greater temperature extremes, whereas Picea sitchensis has a much more coastal distribution.

Vowinckel et al. (1975) studied Picea mariana (Mill.)B.S.P. in sub-arctic conditions at $55^{\circ}N$ at Schefferville, Quebec Province. They found that the onset and cutoff of photosynthesis was entirely controlled by temperature and was independent of photoperiod. The temperature optimum for photosynthesis lay between $13^{\circ}C$ and $15^{\circ}C$ indicating a physiological adaptation to the cool summers and severe winters of the subarctic tree zone.

Furthermore they found that 30% of the maximum rate for photosynthesis could occur at 0°C.

A number of authors have shown that photosynthesis may proceed in conifers at low temperatures which in certain cases may enable them to make significant contributions to their dry weight in winter. Ledig and Botkin (1974) of the Yale School of Forestry, Connecticut grew seedlings of Larix decidua in pots outside the laboratory and they observed during the mild winter of 1972-3 that some retained some of their leaves and had positive rates of CO_2 uptake at 3°C. Indeed, the rate was greater than that measured when the ambient temperature later in the year was 15°C. indicating acclimation to low temperatures. In a part of the U.S.A. where mild winter temperatures are common, Helms (1965) studied Douglas-firs growing in Washington State at an altitude of 300 m, 96 km south of Seattle. This region enjoys an equable climate with average temperatures of 5°C in January and February and Helms found that trees carried out 25% of their annual photosynthesis during the winter months. This could be particularly important if photosynthesis was reduced during summer drought periods. Also in Douglas-fir, Pharis et al. (1970) found that photosynthesis even occurred at -4°C.

In a high alpine site at 1940 m above Innsbruck in Austria, Tranquillini (1955) obtained some comparable results for Pinus cembra L. He showed that CO_2 uptake could take place at -5°C and the annual optimum temperature was between 10° and 15°C. whilst it could proceed up to 35°C. a range altogether of 40°C. Since needle water begins to freeze at -4°C (Tranquillini and Holzer, 1958) the minimum temperature compensation point for photosynthesis is most probably dependent on ice formation and the accompanying dehydration of the protoplasm (Pisek et al., 1967). Leaves of trees at timberline show a slight but distinctly lower temperature minimum for photosynthesis than leaves of similar age and development in the valley. In larch needles

(<u>Larix decidua</u>) taken from trees at 900 m and 1900 m in late summer it was found to be 0.5°C (Pisek et al., 1967). Even this minor shift in the temperature curve is of considerable advantage to trees at high altitude sites where slight summer frosts are frequent (Tranquillini and Holzer, 1958). Adaptation of photosynthesis to cool climates is largely a labile process. If plant individuals of the same species and origin are maintained for several weeks at both high and low temperatures, then plants are produced with correspondingly higher and lower temperature optima (Mooney and West, 1964). <u>Pinus aristata</u> Engelm. plants brought down from the timberline, where the temperature optimum lies between 10° and 15°C. to Los Angeles increased their temperature optimum for photosynthesis to 20°C and respiration was at the same time drastically reduced (Mooney et al., 1966).

Pointing out that the polar and alpine timberlines have a number of similar controlling factors Tranquillini (1979) gives some interesting figures for the correlations of these timberlines with temperature. The polar timberline correlates with sites where the annual sum of those daily mean air temperatures which exceed 10°C. totals between 600 and 700°C. The timberline for alpine situations correlates with sites where the total lies between 200 and 300°C. However, if leaf temperatures are used, both timberlines lie where the total attains about 800°C. It appears that cooler mountain air temperatures at alpine timberlines are thus compensated by marked increases in leaf temperature above ambient air temperature as a result of greater radiation intensities than at the polar timberline.

In a very unusual study by Müller (1928) carried out on Disco Island, off the west coast of Greenland in latitude 69°N he was able to show that <u>Salix glauca</u> L. could carry out net assimilation throughout almost all of the midsummer polar night hours. He found the compensation point for this species at 0°C lay at 0.009 J cm^{-2} min^{-1} whilst at midnight

from 1st July to 18th July the light intensity is 0.013 J cm^{-2} min^{-1}. However if the nights were warmer it is possible that no net assimilation could take place as the relation between temperature and photosynthesis was such that although at very low light intensities the optimum was at 0°C, at 10°C it was 0.06 J cm^{-2} min^{-1} and at 20°C it was 0.16 J cm^{-2} min^{-1}. Since the light intensity exceeded this figure for the dates quoted above from 04.00 hours until 20.00 hours it is obvious that the trees could carry out assimilation for at least 16 hours in the day.

These findings of Müller and those described earlier in this section have considerable relevance to the study of growth rings in fossil wood. This is especially so because trees were able to grow both in the Permian and in the Mesozoic at much higher latitudes than is possible at the present day (Sections 11 & 12). Thus for comparison it is very useful to have the results of research on tree growth at high latitudes and also, because of the similar factors involved, tree growth at high altitude. Fig. 5 shows the relationships of ambient temperature to other factors involved in wood growth, described in other Sections.
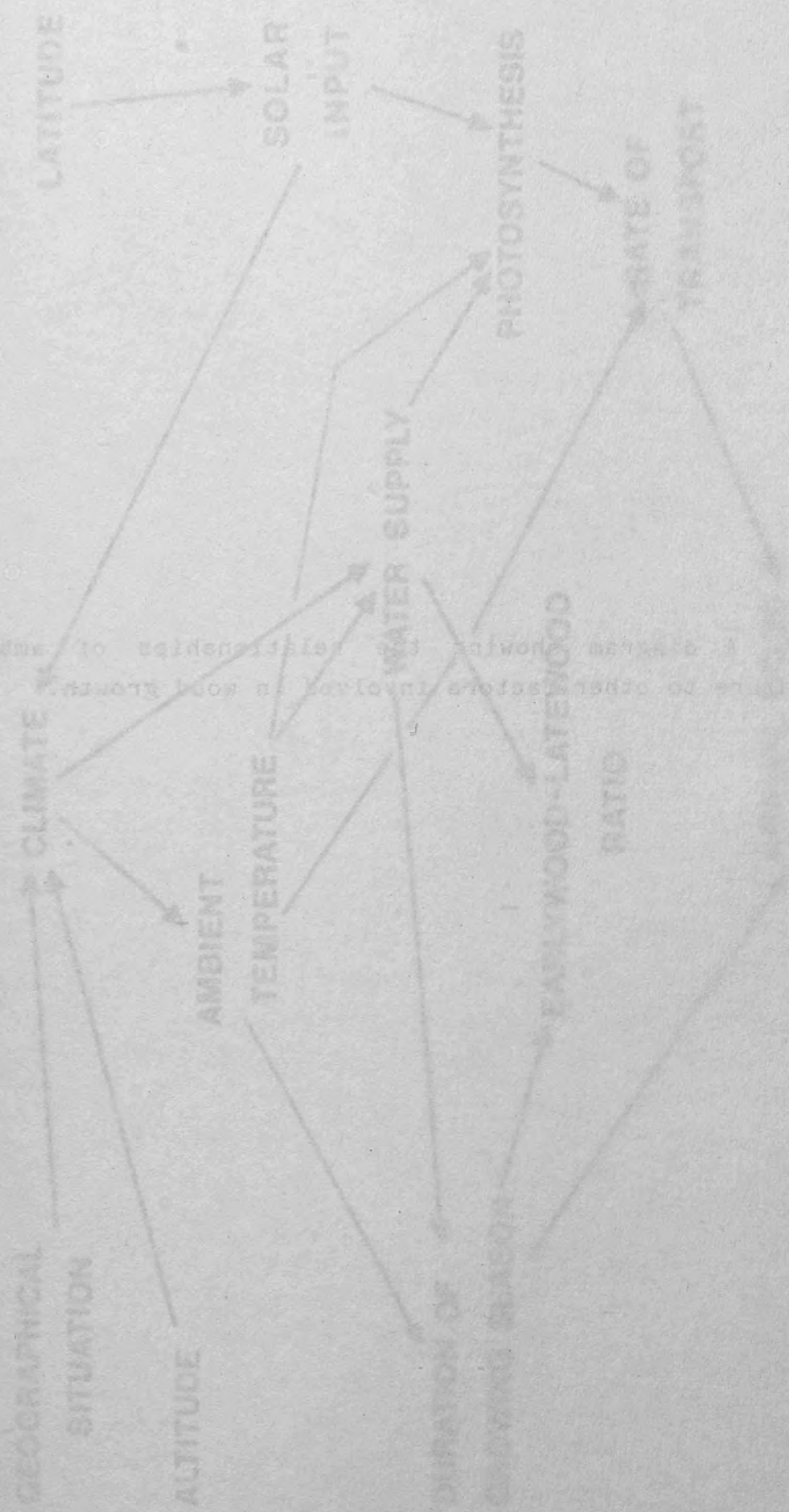
Figure ... A diagram showing the relationships of ambient conditions to other reactions involved in wood growth.

Fig. 5. A diagram showing the relationships of ambient
temperature to other factors involved in wood growth.
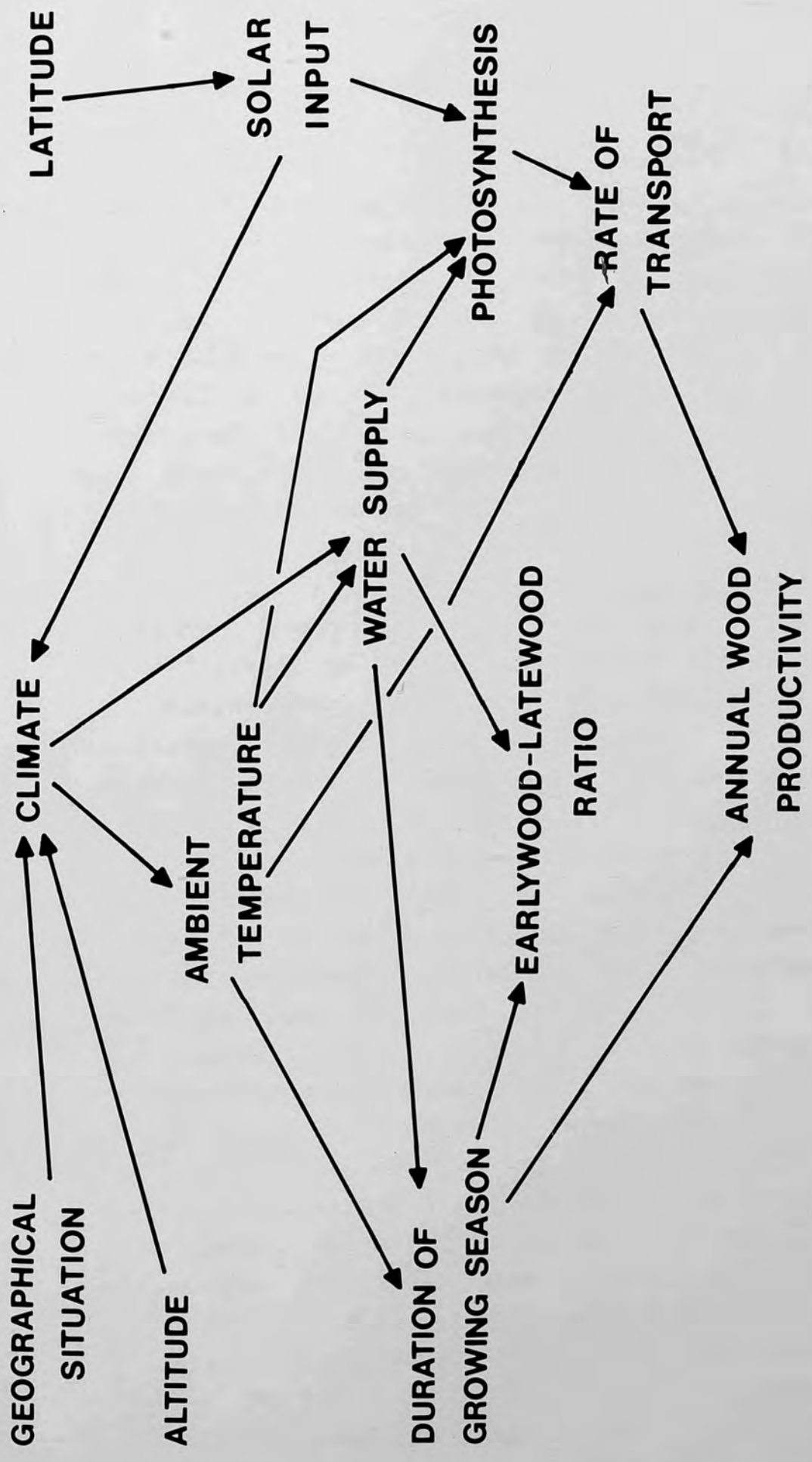
5. THE RELATIONSHIP OF PHOTOSYNTHESIS TO XYLEM GROWTH

(a) The use of photosynthate

The photosynthate produced in the tree's leaves becomes apportioned between the following: 1. Stem elongation; 2. Stem thickening; 3. Root growth; 4. Growth of new leaves and fruits or cones; 5. Respiration. In forestry studies the formation of wood in 1, 2 and 3 is variously quoted as 36% (Baker, 1950), 20 to 45% (Kozlowski, 1962) and 38% (Promnitz, 1975) of the total seasonal production of photosynthate. These relatively high figures indicate the importance of photosynthesis in the growth of secondary xylem.

By supplying $^{14}CO_2$ to 4-year-old Pinus resinosa trees, Gordon and Larson (1968) were able to measure the photosynthetic efficiency of the leaves, and to trace the movement of photosynthate. They found that the rate of production of photosynthate per gram of dry weight of leaf tissue was at a maximum in the current year's leaves at the time when they were starting to elongate. Simultaneously the translocation of ^{14}C from old to new leaves was at a maximum. The new leaves retained their high efficiency to the end of the period of rapid elongation when they were also translocating much greater quantities of ^{14}C to other parts of the plant than in their later activity. In particular the amount going to the stem was greatly increased at this stage when thick-walled xylem cells were first observed in the products of the cambium. The authors felt that this study indicated that the onset of latewood production is correlated with the maturation of the current year's leaves. Since there is a lesser demand for photosynthate in the new shoot and a high rate of photosynthesis in the whole plant at the time of new leaf maturity, a sharply increased amount of photosynthate becomes available for wall synthesis by the cambial derivatives. They conclude that the formation of the

thick-walled cells of latewood is promoted by the plentiful supply of photosynthate.

Not all workers in this field agree with this view. Skene (1969) showed in his study of tracheid development in Pinus radiata that the volume of wall material of an earlywood tracheid ranged from 8.2 to 6.2 x 10^{-3} mm^3 whilst that of a latewood one was from 8.9 to 6.9 x 10^{-3} mm^3. Thus an earlywood tracheid might actually have a greater volume of wall material than one from the lower end of the latewood range. He found, too, that in the later part of the season, tracheids took much longer to mature and there was a much reduced rate of deposition of cell wall material. Similarly Denne (1976a) in her studies on Picea sitchensis doubts that latewood formation is initiated only by availability of photosynthate. She suggests that it may be due to the effect of the increased amounts of substrate on growth regulator production. She found that the increase in wall thickness in the latewood tracheids could be due to a much increased period of differentiation; an improvement in substrate availability in her experiments speeded up the rate of differentiation such that the tracheids achieved maturity (and the contents died), with a smaller wall thickness. It would appear from the conflict between Gordon and Larson (1968) and Skene (1969) and Denne (1976a) that a complex of factors is involved in determining the onset of latewood production and also the degree of wall thickening that eventually results. This was illustrated by Larson (1969) who was able to show that by suitable treatments on young Pinus resinosa plants tracheid diameter and wall thickness could be altered independently for limited periods by appropriate growth control. It was possible to produce tracheids with: (a) large diameters and thick walls by maintaining both auxin synthesis and photosynthesis; (b) large diameters and thin walls by maintaining auxin synthesis but restricting photosynthesis; (c) narrow diameters and thick walls by restricting auxin synthesis but

maintaining photosynthesis; and (d) narrow diameters and thin walls by restricting both auxin synthesis and photosynthesis.

(b) Photosynthesis in leaves of different ages

Freeland (1952) investigated the rate of photosynthesis in the leaves of Pinus sylvestris, Pinus strobus, Pinus nigra Arnold, Pinus ponderosa, Abies concolor Lindl. and Gord. and Picea pungens. Engelm. In all cases he found that they declined from a maximum efficiency attained when fully elongated in their first year, to a level between 2/3 and 1/10 of that by their third year.

It is evident therefore that whilst the older leaves of an evergreen conifer such as Pinus sylvestris may still make a distinct contribution to the photosynthetic capacity of a tree, the new season's leaves are very important. This investigation also shows how a deciduous genus such as Larix obtains a good photosynthetic efficiency with a completely new set of leaves each year. The loss of efficiency in the older leaves of Pinus is apparently not due to a coating of epiphytes or dust since Freeland found that washing the older leaves made no significant improvement in their performance.

Further information on the relative merits of the deciduous and evergreen strategies is given by Tranquillini (1979). He compares the photosynthetic capacity of Larix decidua with that of Pinus cembra at the alpine timberline in the Gurglertal, Austria. There, the larch needles were only present for a season of 107 days compared with the 181 days during which conditions permitted P. cembra to carry on photosynthesis. However the daily CO_2-uptake rate in the larch needles was 143 mg g^{-1} dry weight, nearly double that for P. cembra needles which was 69 mg g^{-1} dry weight. In making this comparison it must be borne in mind that whilst the larch needles would all be newly produced that season

whereas at least some of the P. cembra needles would be 3 years old. In view of Freeland's (1952) work these would have a low photosynthetic efficiency. The larch's superior performance resulted from the better illumination of the needles in a more open crown and also from the fact that the proportion of unproductive foliage tissue was much less in the larch than in the pine. The mesophyllous character of the leaves of Larix with their lesser content of hypodermal fibres and thinner cuticle assists their photosynthetic efficency but, naturally, renders them incapable of surviving winters with hard frosts.

Larson (1964b), experimenting on 5-year-old Pinus resinosa plants, isolated the needles of different ages by covering entire age groups with black plastic bags. He found that when only the current year's new needles were exposed (and all others covered) there was a disproportionate concentration of wood growth in the apical part of the shoot and a reduction in the growth increase in the 2nd and 3rd year internodes, as compared with the controls. The greater part of the reduction was in the latewood. The concentration of growth in the upper part of the shoot was not bulbous as in a girdled stem but was evident as a strong, though uniform, taper from a maximum immediately above the shaded zone to the stem apex. Exposure of the 2nd year needles only, resulted in greater wood growth in the lower internodes with a reduced increment in the current year internode. In this, there was an earlier onset of latewood production which formed a larger percentage of the growth ring in that internode. When only the 3rd year needles were exposed, the greatest reduction in ring width increment occurred in the 2nd year internode with a lesser reduction in that of the current year. It appeared that most wood growth tended to occur in the internode with the exposed productive needles. In those internodes where the needles were covered, the active meristems seemed to act as sinks for assimilate produced elsewhere so that some

growth took place even though local materials were not available. Little latewood was formed however in the darkened internodes, presumably because the extra wall thickening needed materials in excess of the supply from nearby internodes. This work also demonstrated that cambial activity could continue in a darkened internode for 14 weeks and covered leaves could survive the same period and still retain the ability to turn green and resume photosynthesis.

The results of these experiments also supported previous worker's results (Craighead, 1940; Linzon, 1958; O'Neill, 1962) in that they emphasised the importance of the 2nd year needles. Removal of these had been shown to be very damaging to pine trees whereas their retention had enabled trees to withstand much other damage. Larson's work also showed that terminal extension growth is dependent almost exclusively on reserve materials whilst new needle extension depends less on reserves, with the remainder coming from current photosynthesis.

(c) Light intensity and photosynthesis

Kramer and Decker (1944) showed that the rate of photosynthesis at $30^{\circ}C$ in Pinus taeda increased from a light intensity of 0.09 J cm^{-2} min^{-1} up to 30.7 J cm^{-2} min^{-1} which was nearly full day sunlight. In contrast the rates in Quercus borealis maxima (Marsh) Ashe, Quercus alba L. and Cornus florida L. at the same temperature reached maxima at one third or less of full sunlight. The authors point out that at the low light intensities on the forest floors of all four of these species, pine seedlings would only be able to carry on photosynthesis at a much reduced rate and would not be able to survive. The seedlings of these angiosperm genera however would be able to establish themselves. In a later study Kramer and Clark (1946) showed that in contrast to the whole plants, single needles of P. taeda reached a maximum photosynthetic rate at about one third of full sunlight. They concluded that in this species the mutual

shading of needles in P. resinosa prevents each one from reaching its full potential and thus the plant must receive full sunlight in order to reach maximum photosynthesis. This effect being allegedly obviated in the angiosperm species studied, by their possession of a complicated leaf mosaic that minimises mutual shading of the leaves.

Vowinckel et al. (1975) also found a high light demand in Picea mariana growing at 560 m near Schefferville, in Quebec Province. The rate of photosynthesis increased continuously up to a maximum light intensity of 3.15 J cm^{-2} min^{-1}, with the compensation point at 0.1 J cm^{-2} min^{-1}. In contrast, Tranquillini (1955) found that in Pinus cembra, in the high alpine situation mentioned previously, maximum photosynthesis took place at only 0.84 J cm^{-2} min^{-1}, the compensation point being at 0.07 J cm^{-2} min^{-1}. Similar low light intensities were found to be adequate for photosynthesis in Douglas-firs grown in Washington State at 330 m (Helms, 1965). The compensation point was commonly as low as 0.003 J cm^{-2} min^{-1} and maximum rates of photosynthesis were attained at 0.24 J cm^{-2} min^{-1}. A typical daily rate of assimilation was about 13.5 mg CO_2 g^{-1} dry weight of leaf tissue; the greatest net photosynthesis in summer occurred under conditions of heavy morning fog followed by an overcast sky. The author considered that the beneficial effects of fog were probably associated with the creation of favourable moisture conditions in the foliage, with open stomata and plentiful gaseous exchange, and with a more efficient diffuse distribution of light. Further specific differences in the light saturation of leaves were provided by Clark (1961) who found 0.09 J cm^{-2} min^{-1} for Abies balsamea and 0.11 J cm^{-2} min^{-1} for Picea glauca. It is clear that no general quantitative statements can be made for photosynthetic capacity which may even vary between individual trees of the same species. For example, Helms (1965) found that a suppressed Douglas-fir might achieve an assimilation rate of 1.77 mg CO_2 g^{-1} dry weight (of leaf

tissue) hr^{-1} with only a light intensity of 0.09 J cm^{-2} min^{-1} whilst a dominant tree was achieving only 1.0 mg CO_2 g^{-1} dry weight hr^{-1} with an input of 0.9 J cm^{-2} min^{-1}.

(d) The end-product: wood formation

Helms (1970) measured the average net gain by photosynthesis in 4, 40 and 75-year-old <u>Pinus ponderosa</u> trees in a plantation in the Sierra Nevada (37°N). He estimated from the measurements that the three age groups were taking up an average of 33 mg CO_2 g^{-1} dry weight day^{-1}. Since six molecules of CO_2 when taken up result in the gain of one molecule of glucose, the CO_2 uptake figure has to be multiplied by a factor of 180/264 in order to estimate the actual gain in photosynthate. (The factor is the ratio of the molecular weight of glucose (180) to the combined molecular weights of 6 CO_2 molecules (264).) Using Kittredge's (1944) estimate of 10.25 x 10^6 g ha^{-1} for the total dry weight of foliage in a fully stocked stand of <u>Pinus ponderosa</u>, the daily production of photosynthate was calculated to be 225 kg ha^{-1} from which 12% was deducted for respiratory losses at night. The 198 kg ha^{-1} day^{-1} has an energy value of 0.32 MJ m^{-2} day^{-1} as compared with a daily light input of 21 MJ m^{-2} day^{-1}: this represents an efficiency of 1.5%. By such methods various estimates have been made of the quantity of dry weight of plant material produced by forests; these are shown in TABLE IV. It is interesting to note that Rabinowitch (1951) cites 1% as the amount of the total incident solar energy that is effectively used by forests.

Although there is some variation in these estimates, the figures are in fairly close agreement; it is seen that forests make a very important contribution to the global conversion of solar energy into dry weight of organic matter. The lower figures of Hall reflect that author's interest in the use of biomass as fuel and in using only the

wood of the trunk and larger branches the remainder of the tree's products are not included in the efficiency calculation.

TABLE IV

Percentage efficiencies of various tree species in utilising light energy.

Authors	Forest type or Tree species	Dry matter production	% Efficiency
Ovington (1961)	Pinus sylvestris	19.9×10^6 g ha^{-1} yr^{-1}	1.0%
Blackman & Black (1959)	Fagus sylvatica L.	23.5×10^6 g ha^{-1} yr^{-1}	1.5%
Helms (1970)	Pinus ponderosa	198×10^3 g ha^{-1} day^{-1}	1.5%
Miller (1955)	Pinus contorta Dougl.	15×10^6 g ha^{-1} yr^{-1}	1.0%
Hall (1978)	Evergreen forest	22×10^6 g ha^{-1} yr^{-1}	0.8%
Hall (1978)	Deciduous forest	15×10^6 g ha^{-1} yr^{-1}	0.6%

These studies on photosynthesis and wood production play an important part in the interpretation of fossil wood growth rings, particularly those from high latitudes (Sections 11 and 12). With a knowledge of the spacing of trees and their mean anual ring width, their wood production implies a certain minimum light input. Also, the research on photosynthesis in the depths of tree crowns gives information on the use of light when the latter is at a low intensity.

6. PHOTOPERIODISM AND WOOD GROWTH

(a) Photoperiodic control of shoot extension and cambial growth

Although photoperiodic effects are principally studied in connection with the flowering of angiospermous plants, they also influence the growth of the vegetative parts. Kramer (1936) and Downs and Borthwick (1956) review early work on woody plants which was mainly directed at the processes of establishment and breaking of dormancy. Gustafson (1938) noted that 3-year-old Pinus resinosa plants made little growth in the summer if they had not been exposed to freezing conditions in the previous winter. However, this suppression of growth could be removed if the plants received a photoperiod of 16 hours. Wareing (1951b) showed that cambial growth in Pinus sylvestris could be prolonged into the autumn if long days were maintained with artificial light.

Wareing (1953) showed that in beech photoperiodic perception takes place in the young leaf primordia. When twigs, with their dormant buds covered, were exposed to continuous light it was found that the buds did not open. However, the buds did so when exposed to continuous light and also when their bud scales had been removed providing that the meristematic tissue was left intact. Measurements of light intensity showed that only about 0.7% of the incident light passed through the bud scales to the primordial tissue, but this was sufficient to cause a response. This work emphasises the importance of the direct effect of light on the primordial tissue rather than the bud scales.

Following Kramer's (1936) observation that Robinia pseudacacia L. showed marked photoperiodic response in shoot extension, Wareing and Roberts (1956) pursued the matter further. They found that if plants were first exposed to

short-day conditions to cause cessation of shoot extension, they never resumed cambial activity if the short days were continuously maintained. Cambial activity would only continue if the leaves were exposed to long-day conditions; bark-ringing experiments showed that the cambial stimulus, originating in the leaves, was transported in a basipetal direction in the stem. This maintenance of cambial acitvity under long-day conditions was not accompanied by any obvious bud-growth. Whilst extension growth in this species ceases in July or August, latewood formation continues for a considerable period whilst the natural daylength is still long. This suggested to the authors that the onset of dormancy of the cambium is due to the production of a growth inhibitor under long dark periods, rather than to reduced auxin production with short light periods.

Vaartaja (1959) studied 38 tree species, 23 conifers and 15 angiosperms, in order to establish their growth reaction to photoperiods of various lengths. He obtained seed from 82 documented sources so that both high and low latitude seed was obtained for each species. He found that seedlings derived from high latitude sources made substantial growth only when receiving long-day treatment and were much reduced if short-day treatment was applied. These variants he referred to as photoperiodic ecotypes. Summarising a long series of papers in this field he further showed (1962) that there was a tendency for certain more northerly genera, such as Betula, Picea and Larix to possess both an endogenous rhythm and a photoperiodic response which could overcome the rhythm. On the other hand, genera with a less northerly distribution, Quercus, Pinus and Tsuga, tend to have a much weaker photoperiodic response which cannot overrule the endogenous control. He felt that this showed adaptation to the need for the more northerly genera to make as much use as possible of the light available in the long summer days. It may be said too that a day-length controlled strategy could be considered much more

advantageous to high latitude trees than to those in low latitudes. For the latter, an adequate growing season will almost certainly occur every year. In his experiments he ensured that the long-day treatment did not involve a substantially greater light energy input than was applied in the short-day regime. The extra daylength for the long-day treatment was achieved with an illumination of only 5% of the full daylight intensity.

It must not be thought however that trees will only respond to photoperiodic situations with markedly different lengths of day and night. Njoku (1963, 1964) showed that in Nigeria a number of tropical tree species may show a photoperiodic response even though the annual variation in daylight may only be between 11.5h and 12.5h per day.

More recently the phenomenon of photoperiodic ecotypes has been reviewed by Vince-Prue (1975) and Salisbury (1981). Some interesting data were obtained by Håbjørg (1978) who studied ecotypes of various Scandinavian trees and shrubs. Plants collected near Århus (56°N) had a critical daylength for shoot elongation of 14-16 h; plants collected at Trondheim (63°N), 16-18 h; and at Alta (70°N), 20-24 h. There was also an altitude effect, with longer critical days being observed in plants from higher altitudes, apparently adapting them to begin growth later in the spring.

(b) Production of 'false rings'

Larson (1962) showed that when young Pinus resinosa plants were grown under a long-day:short-day:long-day regime they produced a 'false ring' of small diameter tracheids in the wood corresponding to the short photoperiod. In this case a growth correlation was demonstrated because needle elongation was suppressed during the short photoperiod and it resumed when the long photoperiod recommenced. In this work Larson also independently exposed the buds and needles to different photoperiods. Long days promoted needle

elongation and large diameter tracheids formed in the wood whilst short days stopped needle elongation. The response on photoperiod varied with the stage of plant development; during active extension growth the apical meristem exerted a powerful influence on tracheid diameter but this was then taken over by the developing needles when extension growth ceased. The author concluded that the photoperiodic effect on the wood was indirect and was mediated by auxin production in the buds and leaves.

(c) Production of growth inhibitors

In a study in which he was able to detect by bioassay both growth inhibitors and promoters, Wodzicki (1964) subjected one-year-old Larix decidua plants to three different treatments. Two sets received continuous light but one of them (C.L.H.) had 16 of the 24 hours at a high light intensity ($0.3J \ cm^{-2} \ min^{-1}$); the other (C.L.L) had 12 hours at a very low light intensity. The third set (S.D.) was put on short days. Both the C.L.L. and the S.D. sets accumulated inhibitors in the cortical tissues and thick-walled tracheids were formed in their wood. In contrast the C.L.L. set produced thin-walled tracheids and did not accumulate inhibitors. Accumulation of inhibitors after 14 S.D.. or the C.L.L. treatment was equally high in the cortex of both sets, but there was still significantly less inhibitor in the apices of the latter group. On the other hand S.D.-treated plants transferred to C.L.H. conditions showed, after 14 days, an increase in promoters and a decrease in inhibitors in the cortical tissues but not in the apices. These results showed that the changes in growth substances occurred before the changes in the apices, indicating that the accumulation of growth substances, particularly inhibitors, was independent of the shoot apex.

(d) Photoperiodism and photosynthesis

Bamberg et al. (1967) carried out some experiments to establish whether the decrease in photosynthetic rate during the winter in alpine Pinus cembra was solely temperature controlled or whether there was also a photoperiodic factor at work. They also sought to assess the strength of an endogenous annual rhythm. Measurements of photosynthetic rate were taken through the winter from trees at 2000 m under natural conditions of daylength and temperature. The experimental plants were kept in a greenhouse, also at 2000 m at an average temperature of 15°C. Half of them received natural daylength whilst the remainder received a 12-hour photoperiod. After mid-January, 15 of the greenhouse plants were reduced to an 8-hour photoperiod. It was found that the photosynthetic rate of the trees under natural conditions reached zero in mid-November and remained there until mid-March. The daily maximum ambient temperature for this period was almost always below 0°C and the minima ranged from -10°C to -20°C. At the much higher temperature in the greenhouse the plants maintained photosynthesis throughout the winter but all three groups showed a gradual decline until January when the rate started to rise again. There was little difference between the groups receiving 8 and 12-hour photoperiods. These results seem to indicate that an endogenous rhythm was operating which could not be overridden by maintaining a 12-hour photoperiod throughout the winter. However the authors point out that the experiment was started in October, by which time the natural decline in daylength may already have triggered the reduction in photosynthetic rate.

Denne and Smith (1971) subjected seedlings of Picea sitchensis and Pinus sylvestris to a variety of photoperiodic situations. They found, as had previous workers, that short-day treatment caused an increase in tracheid wall thickness and the cessation of cambial activity; but what was surprising was that long-day

treatment produced a sharp drop in the rate of CO_2 uptake. One would have thought that the continued growth in long days would have led to a rise in demand for photosynthate. It would seem that the extended period for photosynthesis in the long-days was very beneficial and the leaves were seen to have a very high starch content. The presence of the latter would then set up a back reaction to photosynthesis and slow the rate down. Denne and Smith also noticed lags between the times of change of photoperiod and the reaction in the cambial zone. Whereas a change affected the rate of wall development in the next tracheid to begin thickening, its effect on radial diameter was delayed for a few days, the second or third tracheid to begin expansion after a change of photoperiod was clearly larger than its predecessors.

(e) Photoperiodism and dormancy

As stated previously, Wareing and Roberts (1956) showed that cambial dormancy could be induced photoperiodically; however, Denne (1974) showed that daylength could not be the sole factor. She showed that the onset of dormancy in Picea sitchensis varied with the light intensity. She was also able to show that the same was true for Picea abies (1976b). shoots of which stopped wood production shortly after they were artificially shaded. Daylength may, in certain circumstances, have no effect at all on the onset of dormancy, particularly if there is a strong endogenous rhythm operating. Liphschitz, Lev-Yadun and Waisel (1981) showed that in Cupressus sempervirens L. growing in Tel Aviv, Israel, experimental changes in day-length did not alter the annual growth rhythm which was locked on to an extremely seasonal climate. In Israel, the onset of cambial activity in Cupressus sempervirens takes place in October, following a flush of extension growth when the average temperature falls and there is a better water supply.

Cambial dormancy sets in at the beginning of the hot, dry summer. Variations in the water supply during the growing season may produce 'false rings' in the wood near the growing apex. The authors demonstrated, however, that the roots of these trees did not have 'false rings' and they suggest therefore that such roots might be used in dendrochronological studies. Glock (1951), Schulman(1951) and Glock et al. (1960) in the past had all abandoned Cupressus in their dendrochronological work on account of its tendency to produce 'false rings' in its trunk wood.

Studies in photoperiodism as outlined in this section have provided information that has been very helpful in interpreting the significance of the world-wide distribution of fossil wood particularly that in very high latitudes (Sections 11 and 12).

7. THE INFLUENCE OF PLANT GROWTH REGULATORS

(a) Early work

The results of the earliest workers in this field seemed to show that the initiation of cambial activity after a period of dormancy is dependent upon the presence of expanding buds and hence on their production of plant growth regulators. Those who presented such an opinion included Antevs (1917), Coster (1927-28), Priestley (1930) and Kienholz (1934). Wareing (1951a) summarised what at that time appeared to be the relevant evidence as follows: 1. There is, in general, a close correlation between the time of bud-break and the initiation of cambial activity; 2. In many woody species the initiation starts immediately below the buds and then spreads in a basipetal direction down the branches and trunk; 3. If shoots of various woody species are disbudded, then usually no cambial activity occurs in the treated shoots; 4. If a ring of bark is removed from a shoot, there is no cambial activity below the ring. The full significance of the relationship became apparent when it was shown that developing buds produce much auxin (Zimmermann, 1936). In the following year Avery et al. (1937), working on Aesculus hippocastanum L. and Pyrus malus L. var. McIntosh, showed that the flow of auxin (IAA) down the shoot from the terminal buds was paralleled by the onset of cambial activity which also progressed basipetally. The latter was seen to be highly significant since it is characteristic that IAA normally moves only in this direction. Furthermore Söding (1936) and Reinders-Gouwentak (1941) showed that it was possible to induce cambial division in disbudded twigs of poplar and other woody species by applying synthetic IAA to them. Thus became established the theory that IAA produced in the young growing leaves and expanding buds passes down the stem stimulating cambial activity as it goes.

(b) The present situation

Whilst the early work seemed to present a clear case for IAA alone, derived from new shoot growth, as the initiator of cambial activity at the onset of the growing season, serious difficulties now appear. In recent determinations of IAA movement rates the following results have been obtained: Fraxinus americana L., 13mm hr^{-1} (Hollis & Tepper, 1971); Zea mais L. coloeptile, 12mm hr^{-1} (Goldsmith, 1977); Abies balsamea, 9-10mm hr^{-1} (Little, 1981). It is evident from such figures that a considerable period of time would elapse before IAA reached stump level in a tree with its lowest lateral branch 50m above ground. Furthermore, Little (1981) found that the rate of transport was similar in resting and active cambia which led him to the belief that there was not a close connection between the transport system and the changes associated with cambial reactivation. There are, too, the results of Zajaczkowski (1973) and Wodzicki and Wodzicki (1973) in their work on Pinus sylvestris; they were unable to demonstrate any especially high concentration of IAA at the onset of cambial activity nor did there appear to be any noticeable decline during the growing season.

Savidge and Wareing (1981a), in the course of a major review of plant growth regulators in xylem differentiation, presented new evidence demonstrating that the conifer cambium may reactivate purely on a rise in temperature. They applied electric heat tape to the main stems of specimens of Pinus contorta, 5 and 10 years old, which had been transferred in early January from out-door winter conditions to a refrigerated growth room maintained at 6-8°C. They found after 4 weeks heat treatment that the cambium had reactivated in the region heated by the tape where some mature leaves were present nearby.

In contrast to the conifers there seems to be a closer connection between the onset of cambial activity and IAA levels in dicotyledonous trees. Avery et al. (1937) found

that in the diffuse-porous Aesculus and Pyrus, IAA levels
are high during active extension growth of the shoots when
cambial reactivation also occurs. It is a characteristic of
diffuse-porous species that the onset of cambial activity
spreads only slowly down their trunks, reaching their bases
several weeks after it is first observed in the twigs
(Wareing, 1958; Savidge and Wareing, 1981a).

In ring-porous species, however, cambial activity
starts at a very early stage of bud-break and spreads
extremely rapidly down the branches and trunk. Very slight
bud development is capable of stimulating widespread cambial
activity and the difference between ring-porous and
diffuse-porous species lies in the degree of development of
the buds required to stimulate cambial division. When
debudding experiments are carried out on ring-porous species
some earlywood is formed but the vessels produced can always
be traced back to the adventitious buds formed from callus
at the wound sites. In diffuse-porous species such
adventitious buds do not cause appreciable cambial activity
(Wareing, 1951a).

In a later study, Digby and Wareing (1966) extracted a
substance with IAA activity from the cambial tissues of a
ring-porous tree (Ulmus glabra Huds.) and a diffuse-porous
one (Populus trichocarpa Torr. and Gray). As the substance
had a different Rf position (0.2-0.3) on the chromatogram
from IAA (0.3-0.4) but had similar properties otherwise, it
was assumed to be a precursor to IAA. The substance was
found to be present at each of the tree stem heights sampled
in the ring-porous species prior to bud swelling; it
remained in significant amounts at budbreak and for three
weeks afterwards. On the other hand, in the diffuse-porous
tree no IAA activity could be found prior to budbreak; it
was only after the latter that it appeared and three weeks
later it was present at all three of the stem sampling
levels. Their interpretation of these findings was that in
the diffuse-porous tree the primary source of IAA was in the

expanding buds while in the ring-porous one a precursor is present at all levels and is rapidly converted simultaneously to IAA.

Now that the older, rather simplistic, theory of cambial reactivation by direct action of IAA is in doubt, attention is being focussed upon other agencies which may lead to its reactivation and also promote its spread down the trunk. Little and Wareing (1981) suggest that the cambial protoplast may change in its sensitivity to IAA so that a resting state in the autumn results from an inability to respond to IAA. The rest state turns to a quiescent one during the winter as a result of chilling and the protoplasts regain their ability to respond to IAA. Membrane changes passing down the cambium have also been invoked (Berlyn, 1982) as a means whereby cambial reactivation might take place sequentially down the trunk. The potential rate of such a process would be adequate to explain the rapid spread of cambial reactivation down the trunks of conifers and ring-porous trees.

(c) The maintenance of cambial activity

Once initiated, cambial activity continues through the growing season until the next period of dormancy and thus a growth ring is formed. Considerable attention had been paid to the possible factors that might be responsible for the continued activity of the cambium. It was noted by Priestley (1930) that the very large earlywood vessels in Fraxinus are only formed as long as there is extension growth of the shoots, after its cessation only the narrow latewood vessels are formed. This effect has been seen, too, in other ring-porous genera such as Ulmus and Robinia (Digby and Wareing, 1966). In Pinus sylvestris, growing near Leeds, Yorkshire, Wight (1933) found that extension growth of the shoots ceased in June but cambial activity continued until October. As a contrast, in diffuse-porous

trees cambial activity ceases at the end of the period of extension growth (Avery et al., 1937; Digby and Wareing. 1966). Some work has been done on the possible role of leaves in the process of maintaining the activity. A connection between shoot extension and needle growth was noted by Larson (1963) who pointed out that needle elongation only proceeds when terminal growth ceases and a new bud is being formed. Thus the growth of the needles takes over just when the extension of the shoot ceases. Larson was able to show that depression of needle extension by drought led to reduced amounts of IAA being produced by the leaves. Larson (1964a) showed that in Pinus resinosa earlywood continues to form, particularly in the upper stem parts, during the period of active needle elongation following terminal extension growth. Whilst it is possible to show such general connections between leaf growth and cambial activity, attempts to show the precise nature of the relationships involved have not been very successful. Denne (1976b) embarked on an investigation to see if the duration of wood production was related to the duration of primordial initiation at the shoot apex, and secondly to see if the seasonal change from early to latewood was coincident with the change from production of scales to foliage leaves. Cambial activity, shoot elongation and initiation of primordia were compared in two conifer species (Picea abies and Pseudotsuga menziesii), in two ring-porous hardwoods (Quercus robur L. and Fraxinus excelsior) and in one diffuse-porous hardwood (Fagus sylvatica). In the ring-porous hardwoods the rapid decline in vessel diameter coincided with the cessation of shoot elongation, but in the other three species the diameter of the xylem elements declined steadily from the onset of cambial activity. In the two conifers leaf initiation in the developing terminal bud continued at a rapid rate for several weeks after cambial activity had ceased, as it did also in the three hardwoods. The decline in the diameter of the xylem

elements being produced in all of the species was not consistently related to the change from the initiation of bud scales to foliage leaves.

A very important contribution to this matter comes from the work of Savidge and Wareing (1981b) who have demonstrated the existence of an unidentified tracheid-differentiation factor in the needles of Pinus contorta. From earlier work (Wareing et al.. 1964) it was known that the conifer vascular cambium is less responsive to applications of exogenous IAA than is the hardwood cambium and hence it has seemed profitable to search for other factors. For the experiments Savidge and Wareing used 1, 2 and 3-year-old cuttings from which all but single foliated short shoots had been removed. They found that these single short shoots could cause the differentiation of tracheids from the cambial zone whereas IAA could not do so. The latter could only stimulate cell division and expansion in the cambial zone. Endogenous IAA (estimated by mass spectroscopy) was found in the cambial zone at all seasons of the year, the highest concentrations in winter being near the crown base; examination of the spring pattern of cambial reactivation showed the first cambial division to occur at those positions where there was most IAA. Although cell division and radial expansion of the derivatives progressed to an advanced stage at the crown base in spring, the first new tracheid differentiation commenced in foliated regions at the top of the crown and from there progressed basipetally. They felt that this constituted strong evidence for the separate regulation of cambial division and tracheid differentiation.

(d) Quantitative studies on IAA

After the demonstrations by the earlier workers that IAA and other plant growth regulators were involved in the control of wood growth. attempts were made to establish

their role more precisely. Larson (1960) set up a series of experiments on seedlings of Pinus resinosa to test the hypothesis that the transition to latewood formation could be correlated with the cessation of terminal elongation and the setting of new buds through an IAA mediated system. He found that decapitation of the shoot induced the formation of latewood; this could be reversed by the application of 100μg of IAA to the decapitated stem tip and the production of earlywood was resumed. It was also found that application of 50μg of IAA produced a smaller effect thus simulating the creation of a 'false ring' by a second flush of shoot growth. With the lesser amount of IAA, the resumed formation of earlywood was only induced close to the site of application, the 'false ring' being also evident only in the uppermost part of the shoot.

Following Larson's (1960) work a number of workers pursued further the extraction and bioassy of IAA. Typical of the studies at this time was that of Shepherd and Rowan (1967) who obtained cambial tissue from various parts of the trunks of mature specimens of Pinus radiata. They found the IAA concentration to be greater at the top of the trunk in the latter part of the winter and in the mid and lower trunk in mid-spring, consistent, as they said, with IAA moving down the trunk as spring progressed. To offset the criticism by Whitmore and Zahner (1964) that IAA may be formed from tryptophan by oxidation whilst carrying out methanol extractions of the tissue, Shepherd and Rowan added (^{14}C) tryptophan to methanol and found that all of their assayed IAA was only that originally present in the samples of cambial tissue. Studies on samples of IAA from conifers have been complicated by reports such as those by Wodzicki (1968) and Wodzicki and Wodzicki (1973) which indicated that the IAA had different physical characteristics from samples obtained from other sources. It has been suggested that it is very difficult to separate out the IAA from the many resinous substances in conifer tissue and that these may

mask to some extent the characteristic properties of the IAA.

(e) Synergistic effects

Wareing, Hanney and Digby (1964) carried out experiments in which both IAA and gibberellic acid (GA_3) were applied to disbudded twigs. On later examination it was found that a wide zone of new xylem had formed in them. It was established that these two substances (IAA and GA_3) operated synergistically; GA_3 applied on its own stimulated cambial division but the resulting cells did not differentiate into xylem tissue. Conversely, the application of IAA caused only a small stimulation of cambial division but the cells so produced differentiated fully into xylem. Balatinecz and Kennedy (1968), in their work on Larix decidua, isolated 5-hydroxy-IAA, IAA and a phenolic growth inhibitor. During earlywood formation there was a higher concentration of the indolic substance in the phloem and cambial zones whereas the IAA and GA_3, applied with IAA, had a stimulatory effect on the cambium of decapitated specimens of Pinus sylvestris grown in a forest situation. In the angiosperms, Doley and Leyton (1968) showed that in Fraxinus excelsior GA_3 increased the rate of vessel differentiation and acted synergistically with IAA in maintaining cambial activity which was reduced if either one were withdrawn.

Beside the effects of GA_3, the cambial response to IAA may be modified by growth inhibitors such as 2, 3, 5-tri-iodobenzoic acid (Cronshaw and Morey, 1965; Kennedy and Farrar, 1965). Much other experimental work has been carried out on tree species and has been reviewed by Roberts (1976), Denne and Wilson (1977), Shininger (1979) and Savidge and Wareing (1981a). The latter examine the possible involvement of other plant growth regulators such as abscisic acid (ABA) but none seem to have such definite

effects on cambial activity as IAA and GA_3.

It is becoming increasingly clear that the normal functioning of the cambium involves both plant growth regulators and other substances and the conflicting results of some of the workers may be due to an excessive concentration upon only one of them. Robards et al. (1969), working on debudded stem segments of Salix fragilis L., found that a simultaneous treatment of IAA, kinetin, GA_3 and sucrose induced more than twice as much cytodifferentiation and nearly fifty per cent more cell production as compared with control segments. More recently, Philipson and Coutts (1980) have shown that IAA and 6 benzylaminopurine (BAP) when applied to Picea sitchensis seedlings stimulated radial growth in the stems but not in the roots. The application of BAP alone altered the derivatives produced by the vascular cambium both in the stems and roots such that large multiseriate rays were produced leading to an overall increase in the proportion of ray tissue.

Others who have studied the interplay of plant growth regulators and other factors include Torrey et al. (1971). Their suggestions for the possible involvement of plant growth regulators and other substances in the origin, enlargement and differentiation of xylem cells are summarised in Table V.

TABLE V

Developmental stages in xylem element formation (after Torrey et al..
1971).
Zones as in Fig. 1.

STAGE	CYTOLOGICAL AND BIOCHEMICAL EVENTS	POSSIBLE HORMONAL OR CHEMICAL CONTROLS
Cambial zone	Critical cell division Gene activation	Cytokinin. auxin and gibberellins in the regulation of cell division. Hormonal activation of genes?
Cell enlarging zone	DNA synthesis (endo-mitotic reduplication)	Auxin-cytokinin regulation?
	Protein synthesis	Cytokinin regulation of protein synthesis
	Synthesis of primary cell wall materials	Auxin regulation of cell enlargement
	Determination of future secondary wall pattern	Gibberellins may influence the wall pattern-determining mechanism
Wall thickening zone	Synthesis and deposition of cellulose and hemicellulose	Sucrose may affect the synthesis of sugar nucleotides. Auxin may regulate hemicellulose synthesis
	Synthesis and deposition of lignin	Both auxin and cytokinin may regulate lignification
Wall lysis (vessels) and cell autolysis in maturation zone	Rupture of lysosomes	Autocatalytic
	Lysis of portions of the primary wall. cytoplasm and nucleus	Feedback stimulation from autolytic products?

However in spite of the volume of effort involved it has to be said that the precise role of plant growth regulators in cambial activity is still far from clear. Savidge and Wareing (1981a) say that "the information gathered so far seems to raise more problems than it solves". Nevertheless, if one has to give an opinion at the present moment as to what appears to be the most likely outcome of the studies in this field it would certainly seem that trees develop an endogenous rhythm which operates on an annual cycle. In the temperate and higher latitudes this becomes locked on to the annual temperature and photoperiodic cycles. Even at very low latitudes, as described in the section on photoperiodism, there is a slight annual cyclic variation in daylength which trees are known to perceive. As far as the cambium is concerned, the annual endogenous rhythm seems to be one involving a change in the characteristics of the cell membrane or other organelles such that the cells have a variable response to plant growth regulators. The latter cause activity in the cambium in that part of the year which is the most favourable for plant growth.

(f) The kinetics of cell differentiation

Under the influence of various plant growth regulators, xylem initials are cut off from the cambial initial and, possibly after further divisions, these cells expand, undergo wall thickening and unless parenchymatous, mature into lignified tracheids, vessels or fibres (Fig. 1). The period of time required for these processes has been studied in Pinus radiata (Skene, 1969), Tsuga canadensis (L.) Carr. (Skene, 1972), Pinus banksiana (Kennedy and Farrar, 1965), Pinus resinosa (Whitmore and Zahner, 1966) and Pinus sylvestris (Wodzicki, 1971). In these studies the periods required for the various processes to be completed varied widely, but as Skene (1969) points out, comparisons are

probably not very profitable owing to the differences in the species and ages of the trees, in the climates and latitude and in the methods used. However in all cases the times involved are measured in weeks rather than days and, as Roberts (1976) comments, it seems remarkable that such long periods are required compared to the rapidity with which the same events take place in cultured explants.

Denne and Wilson (1977) investigated the role of IAA in influencing the final dimensions of tracheids in the wood of Picea abies and Picea sitchensis. Their work was prompted by the fact that the role of IAA was still very unclear; whereas the increase in wall thickness from early to latewood had been attributed to the increase in substrate availability associated with the cessation of shoot growth (Gordon and Larson, 1968; Larson 1964a), other work seemed to show that the increase might be due to the formation of an inhibitor (Wodzicki, 1964). Since the actual increase in wall thickness is proportional to the time that the developing cells spend in the wall-thickening phase of the whole process of differentiation (Denne, 1972; Skene, 1972; Wodzicki, 1971) it seemed worthwhile to examine the possible effects of IAA on the rate of duration of differentiation. Denne and Wilson found that with active, intact shoots, exogenous IAA increased the rate of tracheid production, the tracheid diameter and wall thickness as compared with control shoots. As the increase in wall thickness was associated with an increase in the number of cells in the wall-thickening zone (Fig. 1), it would appear that the IAA had increased the duration of the process and had delayed the senescence of the cells. Also in their investigations they found that the cambium became dormant when the Picea abies shoots were debudded; from this they concluded that endogenous IAA could not originate from differentiating xylem elements as had been suggested by Sheldrake and Northcote (1968). Dormancy occurred both in the presence and absence of the current leaves, indicating that continued

cambial activity depended on the IAA coming from the buds. However, other work has shown no clear association between the cambial activity and the duration of leaf initiation in the buds of P. abies (Denne, 1976b). Similarly, Wareing and Roberts (1956) showed that cambial activity continued after bud abortion in Robinia pseudacacia.

A study of plant growth regulators as outlined in this section indicates their involvement in growth ring formation. Unfortunately almost every investigation seems to produce at least some results that conflict with those of previous workers. It would appear that much future work will be required before their exact role is fully explained. Unfortunately, too, attempts to study their evolution through geological time are hindered by the fact that the earliest trees are mostly only recorded from tropical palaeolatitudes (Section 11). In such latitudes trees may grow uninterruptedly without forming growth rings in their wood.

8. THE EFFECTS OF WATER SUPPLY

Water supply is one of the most potent factors in the control of tree growth; the net annual production of forests may range from about 30 t ha^{-1} y^{-1} in wet localities to very small amounts where water is scarce (Kozlowski, 1982). As much as 90% of the annual variation in xylem increment may be attributable to water deficits in arid regions and up to 80% in wet localities (Zahner, 1968). Much of the variation that dendrochronologists rely upon in tree-ring studies depends on the differences in annual rainfall in successive years (Creber, 1977; Fritts, 1976).

(a) 'False rings' and drought

A period of drought hinders the increase in radial diameter of cells in the cell expansion zone (Fig. 1); if the drought is followed by a period of rainfall, larger cells will again develop, and the effect seen in the wood is known as a 'false ring'. In general, earlywood is less likely to be affected by drought than latewood since it forms when the tree is drawing upon stored moisture in the soil in the early part of the growing season. However, should a prolonged drought take place during earlywood formation, especially if the previous winter was dry, there will be a premature transition to latewood formation and there will also be much less latewood formed that season (Voegeli and Reinhart, 1956). If the drought is very severe, a ring may not be formed at all (Gassner and Christiansen-Weniger, 1942; Glock, 1937). 'False rings' in fossil wood have been figured by Barber (1898, Figs. 1-4) and Creber (1972, Plate 131, Fig. 4).

(b) Interactions between water supply and plant growth regulators

Although the more obvious cause of such 'false rings' in wood would seem to be lack of water for cell vacuolation during the expansion phase of tracheid development (Priestley, 1930; Priestley and Scott, 1936). it is now thought more probably that the temporary cessation of terminal shoot elongation, leading to a decrease in auxin supply, may be the actual control factor involved. In an attempt to demonstrate this effect, Larson (1963), working in Wisconsin, subjected 5-year-old Pinus resinosa trees, grown in pots, to artificial drought periods. Terminal growth in that species takes place by rapid internode extension with only limited growth of the needle primordia. When shoot extension ceases, the needles gradually elongate and a new terminal bud is formed.

All of the artificial drought treatments were carried out during the period of active needle extension. He found that a single 3-week drought resulted in the formation of a 'false ring' and two separate such periods produced two distinct 'false rings'. The formation of these 'false rings' was positively correlated with decreased needle elongation during the drought periods and reduced IAA synthesis was demonstrated by bioassay. The increase in tracheid radial diameter which would normally have resulted from a renewed water supply after drought could be prevented by inhibiting the recovery in needle elongation and thus stopping the renewal of the IAA supply. He was thus able to show conclusively that the influence of the drought was directly on the growth of the needles and only indirectly on tracheid diameter through the mediation of IAA.

Plant growth regulating substances may not be able to cause the expansion of cells if cell turgor falls during a water deficit (Zahner, 1968). Growth regulators must be able to move basipetally; severe reduction in cambial activity below phloem blocks has been demonstrated in Populus tremuloides Michx. (Evert and Kozlowski, 1967). Acer saccharum Marsh. (Evert et al., 1972) and Pinus sylvestris (Wodzicki and Wodzicki, 1973).

(c)   Needle elongation and artificial irrigation

That the soil moisture stress has a direct effect on shoot development was clearly demonstrated by Lotan and Zahner (1963) who subjected 2 sets of 20-year-old Pinus resinosa trees, in Michigan, to contrasting drought and irrigation treatments. Bud formation and cessation of shoot elongation were not influenced by soil moisture treatment since both groups set terminal buds and ceased elongation at almost exactly the same time in mid-July. However, main stem shoots on the irrigated trees elongated 40% more than those on drought treatment whereas those at the base of the crown showed no difference in elongation. Needle elongation was also increased by 40% and the period of elongation was extended into September but the dry trees ceased elongation in mid-August. The shorter needles on the drought-treated trees represent an effect that has longer term implications; for these smaller needles did not elongate the following year and thus they had a reduced photosynthetic capacity for the 2-3 years that they persisted. A drought may therefore affect more than the current year's growth of wood. Considerable controversy has arisen in the past over whether or not conifer leaves grow in length after the first year. Kraus (1883) maintained that they did, while Meissner (1894) insisted that they did not. Honda (1896), working with Pinus longifolia Roxb. in Japan, found that the needles did not grow in length the second year. Lodewick (1931) found increased length during the second year of the needles of P. palustris Mill. Kienholz (1934), however, found no further growth whatsoever in the needles of both P. resinosa and P. strobus with a variety of treatments including partial defoliation. He concluded that in view of the conflicting results of previous workers that elongation in the second year may be a matter of specific difference and geographical location with loss of other leaves having an important effect. It is interesting to see that Lotan and Zahner also found no

TABLE VI

Data from rings in an irrigated tree and in a drought-treated tree. in both cases samples were taken from two places in the trunk. The rings were divided into earlywood and Mork latewood and the number of cells in each zone was counted and their total radial diameter was measured. Data from Zahner et al. (1964).

IRRIGATED TREE

UPPER BOLE		LOWER BOLE	
EARLYWOOD	LATEWOOD	EARLYWOOD	LATEWOOD
160 cells	23 cells	130 cells	30 cells
5.98 mm	0.52 mm	5.13 mm	0.77 mm

DROUGHT-TREATED TREE

UPPER BOLE		LOWER BOLE	
EARLYWOOD	LATEWOOD	EARLYWOOD	LATEWOOD
110 cells	16 cells	80 cells	19 cells
3.5 mm	0.30 mm	2.61 mm	0.39 mm

elongation in the leaves of P. resinosa.

Zahner et al. (1964) extended their investigations on P. resinosa by detailed observations on the wood structure of further specimens given similar treatment. They found that in an irrigated tree the growth ring for that year in the lower trunk was about twice the width of the equivalent one in a drought-treated tree. In the upper trunk the extra growth was about 50% (Table VI), these growth rings showing the positional effect mentioned above. The outstanding result of this study was seen in the difference between the two groups of trees in the amount of latewood formed. In the irrigated trees formation of tracheids with smaller radial diameters did not take place until cambial activity has almost ceased in late September, so that only about 6 cells of latewood formed. Whereas trees in the drought treatment were producing flattened tracheids towards the end of July and they produced more than twice the amount of latewood as did the irrigated trees.

In a comprehensive review of the effects of moisture stress on wood growth Zahner (1963) produced a very useful set of specimen growth rings in which events during the growing season are shown recorded in the wood structure. Many of the effects so far described may be seen in these specimen rings (Table VII). In a later review, Zahner (1968) took the opportunity to point out that the results of Larson (1963) may only have relevance in very young trees. He and Whitmore (Whitmore and Zahner, 1966) found that extractable IAA in the cambial region of 20-year-old P. resinosa trees remained high in the main stem throughout a drought period that severely curtailed shoot and needle elongation and radial growth. They found IAA content to be highly variable during the period of most active growth, becoming more uniform as shoot activity ceased but found no significant difference in IAA levels between trees under drought and those irrigated. Further mention will be made about such discrepancies in IAA studies in trees and at the

Table VII. Some examples of data from tree rings formed under various environmental water conditions. (Data from Zahner, 1963.)

WATER SUPPLY DURING THE GROWING SEASON	RING WIDTH	PERCENTAGE OF LATEWOOD UPPER BOLE	LOWER BO[LE]
Average throughout the season	Average	15%	35%
Higher than average throughout the season	Wide	5%	10%
Average early in the season, drought in the later part	Narrow	15%	10%
Brief drought in early part of season, higher than average later	Wider than average with 'false ring' in earlywood in upper bole only	10% (including 'false ring')	55%
Longer drought in early part of season, higher than average later	Slightly wider than average with very pronounced 'false ring' in earlywood throughout the tree	20% (including 'false ring')	35% (including 'false ring')

moment no reconciliations seem to have developed.

Pursuing these studies on the effects of water supply on tree growth in a chronological order one finds accounts of research in various other parts of the world. Polge and Keller (1968) investigated the wood of 28-year-old specimens of Pinus sylvestris grown under different conditions of water supply, in the Arboretum d'Amance, Eastern France. A group of 32 trees were chosen for the experiment and they were divided into 16 pairs of equal status in the stand. One of each pair acted as a control whilst the roots of the other were enclosed by a basin-like structure and an extra 500 l of water was supplied to it with no possibility of seepage to the control. Using the X-ray technique described above (Polge, 1966), Polge and Keller were able to obtain figures for the amount of wood formed in a ring of each of 6 densities ranging from 450 g cm^{-3} to 700 g cm^{-3} in steps of 50 g cm^{-3}. They found that there was an increase in the amounts of the lower densities (earlywood) but not of the higher ones (latewood) in the irrigated trees. The fact that this latter result was not found by Nicholls (1971) in his study on Pinus radiata indicates that there are interspecific differences in responses to environmental effects. He investigated the effects of irrigation on 3 stands of trees 34, 49 and 12 years old, growing at 550 m above sea level on Mount Crawford, 40 km north-east of Adelaide. In those trees which received irrigation to the extent of the equivalent of 25 mm of rain per week there was an increase of ring width of about 80% but, unlike Polge and Keller's result he found that there was also an increase of latewood of 10%. An additional fact that arose from this study was that he found the irrigation to have little effect when there was also a high ambient temperature and also therefore a high evaporation rate. It seemed that the tracheids could not transport water sufficiently rapidly to the crown. Continuing with the work on P. radiata, McKinnell and Shepherd (1971) found that in trees grown in

Victoria, although there was a positive correlation of tracheid diameter with soil water supply during most of the growing season, there was no return to earlywood production after a drought if the transition to latewood had already been made. It seemed to the authors that some factor other than plentiful water supply determined the type of wood produced at such a time.

Nicholls and Waring (1977) reported results from a long-term study carried out on a stand of P. radiata, planted in 1945, 5 km west of Canberra and 550 m above sea level. They had 3 treatment regimes: 1, partial droughting; 2, normal rainfall and 3, irrigation equivalent to 12.5 mm of rain per week. As had been found by previous workers, irrigation caused an increase in ring width but it was only 18% more. Whereas Nicholls (1971) had shown that irrigation increased the proportion of latewood, in this study the small increase in ring width was shared more evenly between early and latewood. On the other hand droughting certainly increased the proportion of latewood. a result later confirmed by Nicholls et al. (1974). It seemed that the drought took its toll more in the earlier than in the later part of the season.

The results of these irrigation experiments are reinforced by observations on natural stands. Paul and Marts (1954) showed that in the deep sandy soils of the Choctawhatchee National Forest, the water supply in the later part of the season was strongly positively correlated with latewood formation. Harris (1955), in his observations on Pinus sylvestris growing in East Anglia, distinguished 5 latewood types with different degrees of sharpness of boundary between early and latewood. A very sharp boundary was caused by water shortage at the end of earlywood formation.

Reference has already been made to studies on Pinus caribaea and they make a further contribution in this section. Barnes et al. (1977) observed the differences in

wood growth in this species on 5 sites in Zimbabwe where, apparently, latewood production does not take place every year. Whereas many tree species start forming latewood when the ambient temperature falls, P. caribaea continues to form earlywood even though the rate of shoot extension and hence auxin production has fallen to a low value. The only proviso is that the water supply must continue to be adequate, which suggests that in this species water stress rather than low IAA levels may be the more important factor in controlling tracheid radial diameter. In species such as P. resinosa and P. banksiana there is no return to active shoot elongation if late season wet periods occur and diameter growth resulting from such rainfall is made up of latewood with no reversion to earlywood production (Zahner and Oliver, 1962). A high percentage of latewood in P. taeda on certain sites in Illinois has been attributed to moisture being available for extended production of latewood during the growing season. P. caribaea appears not to follow this pattern; if it did one would have expected much latewood in those sites in Zimbabwe where plentiful moisture was more or less continually available. Barnes et al. suggest that the difference could be due to the less rigid genetic control of shoot growth which may allow reversion to earlywood formation with late summer rain.

Fraser (1956) not only correlated wood growth with ambient temperatures but also with water supply. Excessive rainfall tended to reduce wood growth in Betula lutea Michx. because of waterlogging of the soil. There appeared to be an optimum level of water supply, enough to ensure maximum growth but not so much as to be a limitation.

(d)   Carlquist's wood anatomy indices

Carlquist (1977) has developed the concept of indices of 'vulnerability' (V) and 'mesomorphy' (M) in order to show the relation between wood anatomy and environmental factors,

particularly water supply. In this connection 'vulnerability' refers to the possibility of cavitation occurring in large vessels. V is calculated by dividing the mean vessel (or tracheid) diameter by the number of vessels (or tracheids) per square millimetre. A low value of V could be interpreted in terms of a greater 'redundancy' of vessels; the more numerous the latter, the less is the chance that water conduction would be seriously impaired by air embolisms formed in a number of vessels under water stress. M is derived by mulitplying V by the mean vessel (or tracheid) length in the wood. Values of V between 1.0 and 2.5 indicate 'redundancy' of vessels and greater safety under conditions of water stress. Mesophytes have values of M greater than 200 whilst those of xerophytes are about 75 or less. Working in south-western Australia he found good correlations between V and M and the environmental water supply. V and M indices for conifers show that their xylem is ideally adapted to water stress conditions. They clearly have a considerable 'redundancy' and, in addition, air embolisms that occur are localised in individual cells whereas in angiosperms they may spread down entire vessels.

In this section the tree's water supply has been shown to be a very potent factor influencing the growth of wood. In examining the rings in fossil wood, therefore, it is possible to say with some confidence that wider ring widths are positive indicators of rainfall. As a case in point, the Kimmeridgian wood of the East Sutherland coast exhibits growth rings up to 9mm in width (Creber, 1972; Section 12, Table XI; Appendix I, Nos 90-92). In contrast, the Purbeck Fossil Forest (Francis, 1983; Section 12, Table XI; Appendix I, No. 89) is shown from geological evidence to have existed in an arid environment with the trees only forming rings about 1mm in width. As further indicators of water supply difficulties, the wood of the Purbeck Forest trees contains many 'false rings'. Clearly the annual water supply to the trees in these two localities was very different.

9. INHERITABLE VARIATION

Not all of the variation shown by samples from a single species owes its origin to physiological or environmental causes. The considerable attention paid by foresters to inheritable variation in wood characteristics is an indication of the amount of variability which is available for selection and which may be directed towards the production of a favoured type of wood.

(a) Inheritance of wood properties

A number of authors have listed wood characters with reference to the relative degree with which they may be inherited (van Buijtenen, 1962; Dadswell and Wardrop. 1960; Schreiner, 1958). Zobel (1964) warns however that these need very cautious interpretation since the inheritance has to be expressed in unambiguous terms. Only in this way can an estimate be made of the possible gain if a certain breeding procedure were to be applied to a given species growing under closely defined conditions. Part of the problem is that a feature of wood such as specific gravity is itself made up of smaller features such as cell diameter, cell wall thickness and the ratio of earlywood to latewood. For example Goggans (1962) found that cell diameter in earlywood and wall thickness in latewood in Pinus taeda were strongly inherited whilst cell diameter of latewood and earlywood specific gravity showed the lowest genetic control of all of the characters examined. Nevertheless it is possible to select for enhanced specific gravity in growing timber. Zobel (1964), reporting some results of breeding experiments on Pinus taeda in North Carolina, found that selection had increased the standard cord weight of the timber by about 34 kg. These results are supported by other studies on Pinus taeda (Brown and Klein, 1961; van Buijtenen, 1962; Zobel and Rhodes, 1957). Variations in

tracheid length and wood specific gravity were analysed by McKimmy and Nicholas (1971) in 50-year-old Douglas-fir trees that represented progeny from five half-sib populations each from a single parent tree. It was found that progeny from one parent had the longest tracheid length in three different plantations and the progeny from another had the shortest. The results as regards specific gravity were not so clear cut; no single parent had either the highest or the lowest value in all plantations.

Studies on broad-leaved species include those of Boyce and Kaeiser (1961) who showed that fibre length was inherited in Populus deltoides Bartr.; Cech et al. (1960) found specific gravity to be a heritable character in Populus trichocarpa. A more recent study is that of Longman et al. (1979) who investigated clones of Terminalia superba Engl. and Diels. The clones were in the form of groups of rooted cuttings obtained from single selected trees derived from seed-lots of known provenance. Although a tropical genus, it was known from earlier work (Longman, 1969, 1978) that it was sensitive to photoperiod and night temperature. Four juvenile clones were used, originating from the same seed-lot but selected for their variability in branching. They were grown in growth cabinets and received factorial combinations of two photoperiods (12 and 14 h) and two night temperatures (23°C and 30°C).

Highly significant clonal differences were found in most of the characteristics measured. Mean numbers of branches per tree showed the greatest contrast, with more than five times as many branches in one clone as compared with the clone that had the least. Main-stem leaf areas, sample stem dry weights, total xylem widths and numbers of fibres and parenchyma cells all differed by a factor of at least x2 among the clones, while there were no significant genetic effects on height, total leaf dry weight or diameters of xylem cells. It was the clone that produced the most foliage and dry weight that also had the greatest

amount of new wood due chiefly to the extra numbers of xylem cells produced. Diameters of fibre and parenchyma cells differed among the clones but not very widely. One clone produced the fewest, but also the largest. xylem cells and also had a large total leaf area. Vessel diameters, on the other hand, tended to be larger when many xylem cells were produced. There was a 10% variation between clones in mean fibre wall thickness.

These substantial clonal differences were demonstrated. without significant interaction with the environment, across the four regimes used in this experiment. Similar large inherent differences between clones have been found in shoot growth, apical dominance and rooting ability in another West African timber tree, Triplochiton scleroxylon K. Schum. (Leakey et al., 1975; Longman, 1978). The implications are that even a small number of seedlings derived from a single seed-lot may contain widely differing genotypes, and that significant improvement by clonal selection has distinct potential. It is desirable however that the criteria for selection should only be determined after field trials of a large number of clones, derived from the entire range of the species, in a variety of sites and competitive situations. These authors report that such field experiments are already in progress with both of the tree species studied so far.

(b) Maintenance of wood characteristics through vegetative
      reproduction

With the growing interest in establishing clonal plantations of forest trees some studies have been carried out to investigate the characteristics of vegetatively reproduced trees as compared with those of seedling origin. Nicholls and Brown (1971) carried out an investigation to compare the wood characteristics of the ortets (the donor trees) with those of the ramets (the cuttings), the experimental material being Pinus radiata, grown in

Australia. They found that the ramets exhibited longer tracheids, larger spiral grain angles and lower specific gravity than the ortets. These differences were attributed to the effects of both topophysis and cyclophysis. Cuttings or grafts are said to show topophysis when they retain the characters of that part of the shoot (i.e. position on the tree) from which they arise, and cyclophysis when they preserve the characters associated with the age of the shoot from which they originate.

This study was followed by one in which there was a greater attempt to control variable parameters such as geographical separation of the ortets and ramets and the different physiological age of wood in the two groups (Nicholls et al., 1974). Whilst the results in general confirmed those of the earlier study, it was possible to be more definite in concluding that the differences in the wood were due to the effects of cyclophysis. Nicholls et al. (1976) pursued the matter still further by much more detailed experimental technique. The ortets were sampled at two heights in the tree, first and second stage ramets were studied and ortets of two different ages were used as source material. It was found that variation in spiral grain angle only appeared when the ramets were taken from older ortets; from younger ortets the ramets did not exhibit such differences. Tracheid length was larger in the ramets but the difference tended to diminish in the later growth rings. Again, no difference was observable if very young ortets were used. These experiments emphasise the great attention that must be paid to the source material that is used for building up clonal stocks in forestry.

The genetic studies in this section serve as a reminder of the variability inherent in the wood production process in trees. That commercial timber growers find it worthwhile to set up breeding programmes testifies to the magnitude of the possible variability. In interpreting the characters of fossil wood, it has to be borne in mind therefore that even

in one monospecific assemblage there is likely to be variation due to this non-environmental factor. It remains true however that in practice this potential for variability rarely seems to be a problem when fossil wood is being examined for the influence of climatic factors. In very many of the sites where fossil wood is found, the climatic factors seem to have been acting so forcefully that they were the dominant influence on tree growth. As regards the inheritance of characters through vegetative reproduction. it is worth remarking that as a species <u>Sequoia sempervirens</u> may perpetuate itself in this way from lateral suckers. Thus in such forests clonal groups may arise.

10.   THE EFFECT OF GRAVITY

Wood that is formed under the effects of a transverse or oblique gravitational force, and which shows some discernible response to it, is known as reaction wood. This is of normal occurrence in lateral branches which grow more or less at right-angles to the line of action of the force of gravity; it occurs also in trunks which have become displaced from the vertical. The reaction wood of angiospermous trees, known as tension wood, forms along the upper sides of trunks and branches while in gymnosperms it forms on the lower sides of trunks and branches and is called compression wood. This process has been the subject of several recent reviews (Creber, 1975; Robards, 1969; Westing, 1965, 1968) and only work not covered there is considered.

(a)   Mechanical stresses

Much recent work has been directed towards a fuller understanding of all of the mechanical stresses set up in a tree as it maintains an upright position and supports its canopy. With the aid of strain-gauges the longitudinal strains were measured by Trenard and Guéneau (1975) at a height of 1.3 m at 5 points around the stems of 76 specimens of <u>Fagus sylvatica</u> from different provenances. Subsequent examinations of cross-sections of their trunks revealed that tension wood was common and present in at least one sector in 65 of the trees, persisting from the centre to the outermost ring. A high degree of correlation was found between the presence of tension wood and the locations of strains. In a similar study by Sasaki et al. (1978), surface stresses were measured in both the longitudinal and tangential directions at various heights on the trunks of trees of 13 species and at different times of the year. The highest values were found in areas where reaction wood had

formed; in general, higher values were encountered in the hardwood species as compared with softwoods. The implications of reaction wood to the timber industry is illustrated by a technical publication (Princes Risborough, 1972) giving details of the serious damage that may be done to timber by the abnormal longitudinal shrinkage that takes place in areas of reaction wood.

Archer and Wilson (1970, 1973) constructed mathematical models predicting the distribution of strains in the tilted leaders of specimens of Pinus strobus, 3.5 m tall growing near Amherst, Massachusetts. They achieved a notably close agreement between their models and the actual distribution of compression wood in the cross-sections of their experimental leaders. Archer and Wilson concluded that compression wood formation was a remarkably sensitive physiological-mechanical response to a gravitational stimulus. The system that regulates the location of compression wood appears to act as a complex switch to changes in the magnitude of the gravitational force acting as the geotropic stimulus; there is not merely a simple formation of compression wood on the under side of a stem under all conditions. As the compression wood response continues, the stem thickens due to compression and normal wood formation, and the curvature changes from the elongation strains of the compression wood. Thus, all of the mechanical parameters that determine the amount of inertia and resistance to bending by compression wood action are changing at the same time that the geotropic stimulus and the strains at the outside of the stem change.

Boyd (1973) is of the opinion that the forces that develop in compression wood could arise from the process of lignification. He points out that in gymnosperms, compression wood is stronger in comparison with normal wood by about 30%, the cell walls are about twice the thickness of earlywood cells and approach that of latewood, this type of wood also contains about 28% more lignin than normal

wood. He shows that compression wood cells are capable of generating an expansive force with a compressive-stress equivalent of about 10 MPa (Mega Pascals). In the part of the trunk of a leaning gymnospermous tree subject to corrective bending, normal wood develops on the sides parallel to the plane of lean and also on the side opposite to the compression wood; each has a natural tendency to contract in length during differentiation. The tissues to the sides confer a mutually balanced stiffening against external forces transverse to the lean while those at the upper face tend to pull the tree back towards the vertical. Thus 'the action of compression wood alone does not counteract the bending moment; the effective restoring moment is developed jointly by the tendency for expansion in the compression wood and contraction of the normal wood on the upper side.

This work and similar studies by McMahon (1975) are typical of the school of thought that believes it is not gravity per se that causes reaction wood to form, but rather that the stresses are the causative agents set up in the tree by the force of gravity. Boyd (1977) analysed all of the results of many previous experimenters in this field who had interpreted them in terms of direct gravitational response and auxin redistribution. He came to the conclusion that they can all be explained instead by the effects of stresses set up in the trunks and branches of the trees. He pointed out, for example, that in Robards' experiments (1965) involving looped willow shoots some tension wood was developed in the vertical segments of the loops as well as in the upper and lower portions.

(b) The involvement of IAA

It is difficult to reconcile Boyd's view that IAA is not involved in the stimulation of reaction wood with the results of workers such as Blum (1971). He found that

application of IAA to straight stems of <u>Picea abies</u> caused the formation of compression wood below the place of application. Kinetin alone, gibberellin, cane sugar solution, coniferin solution or inhibitors (e.g. TIBA. 2.3. 5-Triiodobenzoic acid), or the application of mechanical pressure or tension did not have this effect. but girdling and strangulation did. IAA applied to straight stems of <u>Populus tremula</u> L. and <u>P. alba</u> L. caused tension wood to form on the opposite sides of the stem or, if applied to two opposing sides, it formed laterally. Gibberellin and kinetin did not cause tension wood to form but TIBA increased tension wood formation when applied to the upper side of branches, and inhibited its formation on the upper side when applied to the lower. Blum concluded from these results that compression wood forms when the absolute content of growth substances in the cambium exceeds a threshold value, while tension wood formation depends upon a concentration gradient of growth substances.

Some work has also been done on the use of morphactins, which interfere with the movement of IAA. Phelps et al. (1974) studied stems of <u>Pinus sylvestris</u> and <u>Picea abies</u> after treatment with 2-chloro-9-hydroxy-fluorene-9 carboxylic acid and they found compression wood had developed at and above the treated regions. They interpret the effect as being due to accumulation of IAA hindered in its basipetal movement by the morphactin. Smolinski et al. (1974) found that they could suppress the formation of tension wood in bent shoots of <u>Aesculus hippocastanum</u> by treatment with morphactin 3456.

(c) <u>Miscellaneous wood growth phenomena</u>

The remaining work does not fit into any particular category but each item has some features of botanical interest. For example, Burdon (1975) showed that different genotypes of <u>Pinus radiata</u> differed markedly in their

tendency to form compression wood at the same angle of lean from the vertical. Again, this result rather seems to imply that all cannot be explained in terms of the mechanical stresses in a tree since two similar trees would be expected to react in exactly the same way if their mechanical requirements for support are identical. Some work of importance to foresters was done by Barger and Ffolliott (1976) who studied Pinus ponderosa in virgin stands, thinned young growth and old growth near Flagstaff. Arizona. After examining 103 trees for the presence of compression wood they came to the conclusion that greatly increased growth in the released trees after thinning and selective felling may substantially increase the development of compression wood. They advise that the residual trees remaining after thinning should not have any tendency to lean and that this should be borne in mind in preparing guidelines in forestry techniques.

An interesting study by Timell (1978) on Ginkgo biloba L. has shown that the compression wood of this species differs from the more recently evolved gymnosperms in the more angular outline, thinner walls and lack of helical cavities in the walls of the tracheids. The author suggsts that such helical cavities developed later in the evolution of compression wood as they are also absent from the Taxales and Araucariales. He goes on to suggest that since the ancestry of Ginkgo is traceable to the Upper Devonian, compression wood may have always been essential for the conifers to develop the arborescent habit.

A bizarre effect was described by Marchenko (1974, 1975) in the interaction of birch and pine trees when grown in mixed plantations. The effect of the birch trees upon the pines was assessed by measuring the angles of the needles on the leading shoots of the pines. When the pines are outside the influence of the birches, the needles on opposite sides of the leader are symmetrically disposed at the same angle relative to the shoot axis; with increasing

proximity to the birches, the needles on the side of the leader nearest to the birches close up to form a narrower angle with the shoot axis, while the needles on the opposite side move in the opposite direction. Investigation of these effects led to the discovery of ultra-violet radiation by the birches which could be prevented by interposing glass shields between the birches and pines. A further effect was that under the influence of this radiation, reaction wood was produced not only in the expected sites in the branches but also in the vertical leaders on the sides away from birches.

Studies outlined in this section on the effect of gravity on the growth of wood indicate how widespread is the development of reaction wood. Although, naturally, it is more common in branch wood it is also not rare in trunks. Seen from the point of view of an investigator attempting to assign a fossil wood specimen to a particular part of a tree, the occurrence of reaction wood poses a problem. However, it can at once be said that the specimen is not a root since reaction wood does not occur in roots. To decide whether it is a piece of a trunk or a branch needs a little more consideration. If the rings have a small radius of curvature and the rings become substantially larger where the reaction wood is developed then a branch is indicated (Creber 1975, Fig. 6). On the other hand if the rings have a radius of curvature that is large and if the reaction wood is not developed right across the specimen then it is likely that it is from a trunk. In many, though obviously not all, trunks reaction wood ceases to be developed when an upright condition has been fully restored whereas branches tend to be experiencing the force of gravity transversely throughout their lives and will thus be producing reaction wood every year.

11. THE INTERPRETATION OF FEATURES OF WOOD GROWTH IN THE PALAEOZOIC

(a) The earliest fossil wood. Upper Devonian

The first occurrences of fossil wood are in the Upper Devonian about 370 my BP. Although the earliest land plants had only become established during this geological period, species evolved relatively soon which attained the stature of large trees 1m in diameter at the bases of their trunks. Details of the occurrences are shown in Table VIII. In a number of cases growth rings are absent (Type 'O'). When present (Type 'E') they are often very wide (e.g. 14mm) and may occur in very irregular sequences. Furthermore there is evidence that some of the ring boundaries do not entirely encircle the trunks. The indications are therefore that the trees grew in situations where conditions for growth were favourable in a climate which had little or no seasonality; the ring boundaries being caused by temporary cessations of cell expansion (Fig. 1) which do not necessarily take place around the entire circumference of the trunk.

When we come to examine the palaeopositions of their growth sites, as determined by the palaeomagnetic evidence, we find that these were either virtually on the Upper Devonian equator or at least within the tropical belt of those times. Hence there would appear to be no conflict between what we see in the wood of these trees and the palaeomagnetically determined positions of their growth sites. It is an unfortunate fact that at the moment no fossil wood is recorded from the higher latitudes of the Upper Devonian and thus we are not in a position to say whether or not these early tree species ever grew in higher latitudes.

It was suggested by Antevs (1925, 1953) that these early trees had not evolved a mechanism for producing growth rings. We can now see that his proposition is not so persuasive as it was in the days before continental drift

TABLE VIII   UPPER DEVONIAN FOSSIL WOOD

GENUS	LOCALITY	PALAEOLATITUDE	RING TYPE	AUTHORS
Callixylon	Indiana	19°S	'E'	Elkins & Wieland. 1914
Callixylon	Indiana	19°S	'E'	Arnold. 1931
Callixylon	New York State	17°S	'E'	Hylander. 1922
Callixylon	New York State	17°S	'E'	Arnold. 1930
Callixylon	New York State	17°S	'E'	Beck. 1953
Callixylon	Donetz Basin	3°N	'O'	Zalessky. 1909. 1911
Callixylon	New York State	17°S	'E'	Matten & Banks. 1967
Sphenoxylon	Spitzbergen	20°N	'O'	Høeg. 1942
Indet. gymnosperm wood				

became established dogma. In the light of our present knowledge of plant growth regulators (Section 8) one might perhaps argue that in the Upper Devonian there was not the complex of growth regulators that exist in present day trees but it is difficult to conceive of a plant structure as large as a tree being able to co-ordinate its internal activities without them. Also, as we go on to consider the Carboniferous Period there appear a number of instances of fossil wood with growth rings (Table IX). It seems more likely therefore that where growth rings are not present in Palaeozoic wood, the climatic conditions were such as to maintain growth continually throughout each year.

(b)   The Carboniferous Period

A considerable variety of large stems without rings are known from growth sites ranging from Kansas eastwards across the Mid-West of the United States, and from Western Europe through to the Donetz Basin in Russia. Furthermore this lack of growth rings is a feature not only of gymnosperm woods but also of lycopods, articulates and seed-ferns. Details of some occurrences of fossil wood in the Carboniferous are shown in Table IX.

Again, the circumstances are similar to those of the Upper Devonian in that the occurrences are all within 20° of the Carboniferous palaeo-equator. The growth rings are mostly faint (Type 'E') or absent (Type 'O'). which seems quite consistent with the trees having grown in very low latitudes. The formation of faint rings was probably due to minor fluctuations in the water supply (Section 9).

(c)   The Permian Period

As in the Carboniferous, many Permian fossil woods in Western Europe and North America lack growth rings. Frentzen (1931) remarked upon their absence from Western

TABLE IX   CARBONIFEROUS FOSSIL WOOD

GENUS	LOCALITY	PALAEOLATITUDE	RING TYPE	AUTHORS
Pitus	Southern Scotland	2°S	'O'	Long, 1979
Callixylon	Oklahoma	18°S	'E'	Arnold, 1934
Callixylon	Kentucky	17°S	'E'	Hoskins & Cross, 1951
Eristophyton	Southern Scotland	2°S	'D'	Absalom, 1931
Eristophyton	Southern Scotland	2°S	'E'	Lacey, 1953
Dadoxylon	Oklahoma	18°S	'O'	Wilson, 1963
Dadoxylon	Ohio	11°S	'O'	Arnold, 1947
Dadoxylon (Cordaites)	Oklahoma	18°S	'E'	Jensen, 1982
Cordaites	Oklahoma	18°S	'E'	Goldring, 1921
Cordaites	Oklahoma	18°S	'O'	Tynan, 1959
Cordaites	Kansas	16°S	'E'	Arnold, 1947

European specimens and Holden (1913) described a specimen of Tylodendron from Eastern Canada which was, typically, without rings (Table X). On the other hand, Lemoigne and Tyroff (1967) and Schweitzer (1968) have described occurrences of very weakly developed rings (Type 'E') in some German specimens but these are regarded as exceptional and reported for that reason.

In Permian times Western Europe and North America were spread across tropical palaeolatitudes. Thus the almost total absence of rings is consistent with this situation. However, parts of the Western USSR were outside the tropical zone and it is of interest that Permian woods from the Kuznetsk Basin (palaeolatitude $29°N$) show growth rings (Lepekhina, 1972). A large number of specimens were described by Lepekhina, most of which belonged to species of Araucarioxylon with growth rings of Types 'D' and 'E'. As indicated previously (Section 3). from the characters of the wood and the morphology of entire trunks there is a considerable affinity with the modern genus Araucaria and it is perfectly possible that the earlywood/latewood ratio is a genetic character of the wood production process which does not have any particular significance. Not all rings were of the araucarian type; some species of Eristophyton had rings of Types 'A' and 'B' as did a few of Araucarioxylon (A. humiliradiale Lepekhina and A. originale Lepekhina). It is noticeable, though, that these are not scattered at random in the region but are localised in small areas and at particular horizons.

It seems likely therefore that those specimens with more latewood in the growth rings were exhibiting either a different generic response (e.g. Eristophyton) or a specific variation (e.g. A. humiliradiale and A. originale). It can be concluded therefore that although the earlywood-latewood ratio cannot be much utilised in these specimens the development of growth rings in the woods of the Kuznetsk Basin is quite compatible with the palaeolatitude of the

TABLE X   PERMIAN FOSSIL WOOD

SPECIES	LOCALITY	PALAEOLATITUDE	RING TYPE	MAXIMUM RING WIDTH	AUTHORS
Araucarioxylon spp.	Kuznetsk Basin. USSR	29°N	D and E	no data	Lepekhina. 1972
A. humiliradiale and	Kuznetsk Basin. USSR	29°N	C	no data	Lepekhina. 1972
A. originale	Kuznetsk Basin. USSR	29°N	C	no data	Lepekhina. 1972
Eristophyton zalesskyi Lepekhina	Kuznetsk Basin.	29°N	A/B	no data	Lepekhina. 1972
Not assigned	Upper Rhine district. West Germany	app.13°N	E	no data	Schweitzer. 1968
Lebachia piniformis (Schlotheim) Florin	Nahe Basin West Germany	app.11°N	E	no data	Lemoigne and Tyroff, 1967

TABLE X   PERMIAN FOSSIL WOOD

SPECIES	AUTHORS	LOCALITY	PALAEOLATITUDE	RING TYPE	MAXIMUM RING WIDTH
Tylodendron sp.	Holden. 1913	Prince Edward Island Eastern Canada	3°S	O	no rings
Palaeospiroxylon heterocellularis Prasad and Chandra	Prasad and Chandra. 1980	Bengal. India	39°S (Upper Permian)	D	9mm
Podocarpoxylon sp.	Leistikow and Creber, Ms	Bagé, S. Brazil	41°S	E	8.5mm
Various genera	Kräusel and Range. 1928	Reuning's Fossil Forest Franzfontein. S.W. Africa	42°S	D	4.5mm
Dadoxylon bakeri Seward and Walton	Seward and Walton. 1923	Falkland Islands	55°S	A/B	9mm
Dadoxylon indicum Holden	Holden. 1917	Bengal. India	62°S (Lower Permian)	C/D	10mm
D. bengalense Holden	Holden. 1917	Bengal. India	62°S	C/D	10mm
Various genera	Maheshwari. 1972	Transantarctic Mountains.	70°S	D	10mm

area in which they grew which is likely to have had some seasonality of climate at 29°N.

Although Western Europe and North America were in the Permian tropics. Gondwanaland to the south was in much higher latitudes extending to the South Pole. Significantly Gondwana fossil woods invariably have growth rings. Again, as in the north these are almost exclusively of Types 'D' and 'E' and the woods are classified in such genera as Araucarioxylon and Podocarpoxylon. Thus they are not of value for deductions from the earlywood-latewood ratio but their ring widths (up to 10mm) indicate vigorous growth well into very high latitudes as was the case in the Mesozoic. A substantial difference from the latter, however, arises from the occurrence of a major glaciation period in Gondwana (Frakes, 1979) at about the Permo-Carboniferous boundary. The exact dating of rocks bearing the fossil wood therefore becomes very critical. Clearly the growth of the trees must post-date the glaciation but because there was a relatively large drift of the Antarctic plate during the Permian (about 21° in 40 my) it is not possible on the evidence presently available to state very accurately how near to the South Pole tree growth actually took place. In Table X. 70°S is suggested as a possible latitude of growth but it has to be borne in mind that it might have been at an even higher latitude.

At all events. tree growth certainly took place at a much higher southern latitude than is the case at the present day (Fig. 6). From our study of the Mesozoic, there would seem to be no inherent barrier to tree growth at high latitudes but as yet we do not have a detailed account of an in situ Permian fossil forest such as Jefferson (1982) provided for the Lower Cretaceous. We have no evidence therefore as to the spacing of the trees which might impose limiting factors on the availability of light. However, such evidence as is available leaves no doubt that tree productivity was of a high order with wide rings commonly

occurring (Table X; Maheshwari, 1972). Doumani and Long
(1962) report the existence of trunks up to 8m long and 60cm
in diameter which would support the view that if they were
not exactly in situ trees they are not likely to have been
drifted far. Much therefore depends on future geological
exploration designed to establish more precisely the age of
the Permian fossil forests.

12. WOOD GROWTH IN THE MESOZOIC

(a) Ring characters

Fig. 6 illustrates the distribution of selected records of fossil wood from the Jurassic, Cretaceous and Early Tertiary (Table XI). It is seen that there is a very broad zone from about $32^{O}N$ to $32^{O}S$ in which the wood specimens are either without rings or have only very weakly defined ones (Ring Types 'D' and 'E'). Thus the indications are that for a long period in the second half of the Mesozoic, the lower latitudes generally experienced a climate which permitted more or less continuous tree growth. Those trees that produced faint rings might have done so as a result of a photoperiodic mechanism coupled to an annual leaf-flushing period. Njoku (1963, 1964) demonstrated that tropical trees at the present day may perceive very small differences in daylength. One may also cite the case of Taxodium which even when growing virtually in the tropics at $25^{O}N$ in Southern Florida, has an annual leaf-flush and leaf-fall and produces rings in its wood.

(b) Temperature and light

What is remarkable about the higher latitudes is that trees were apparently able to grow much nearer to the poles than is possible now. At present coniferous forest does not extend more than a few degrees within the Arctic Circle (Fig. 7, Table XII). The data obtained from high latitudes at the present day emphasises the very small amount of radial growth that is made by woody stems. In terms of actual productivity, Elkington and Jones (1974) showed that Betula pubescens s. lat. in south-west Greenland ($61^{O}N$) achieved only 25% of that produced by Betula in England (Ovington and Madgwick, 1959). In general it is thought that the severe limitation of tree growth in high latitudes is due to the very low mean annual temperatures prevailing
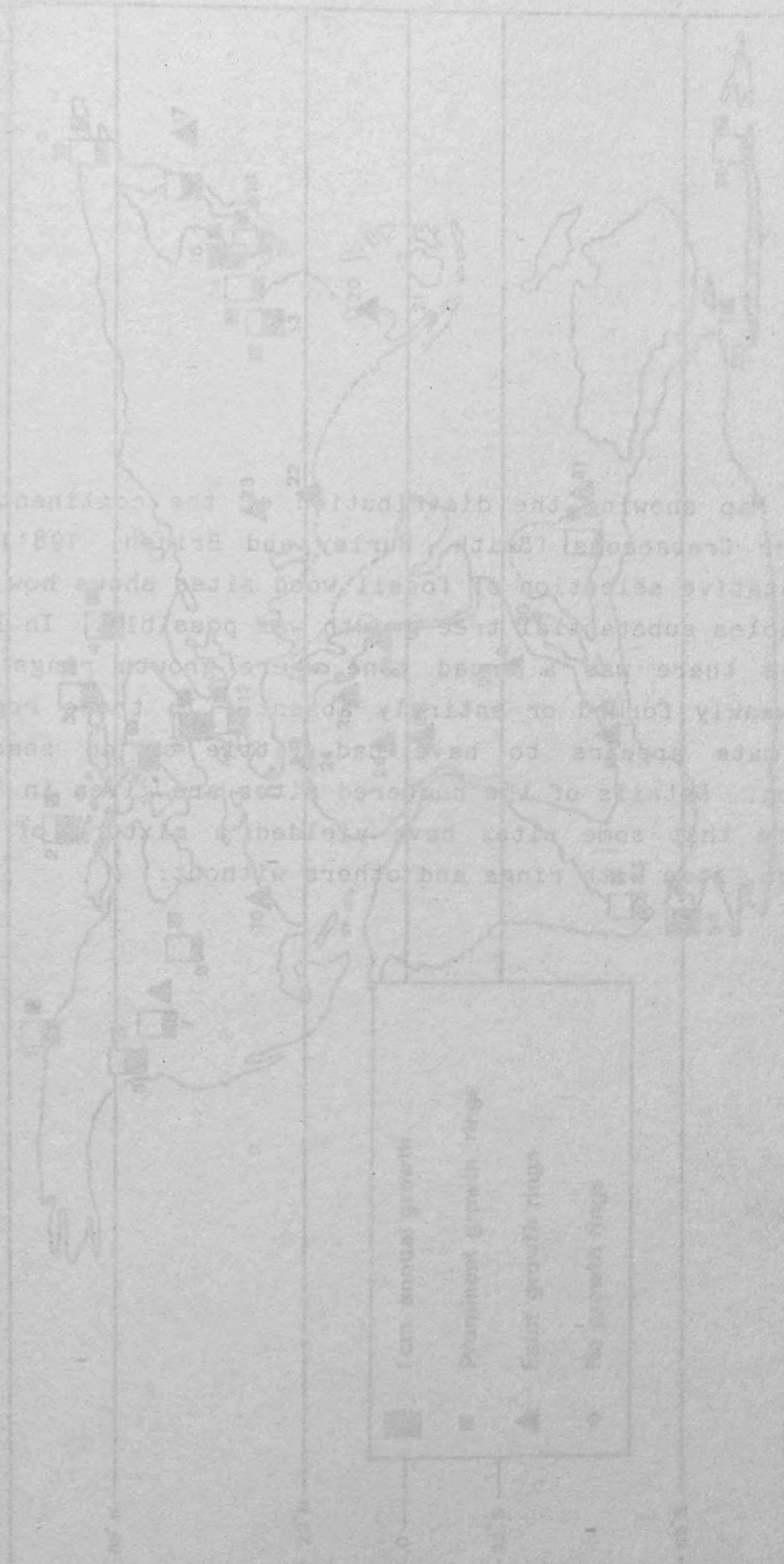
Fig. 6. Map showing the distribution of the continents in the Lower Cretaceous (Smith, Hurley and Briden, 1981). A representative selection of fossil wood sites shows how near to the poles substantial tree growth was possible. In lower latitudes there was a broad zone where growth rings were either weakly formed or entirely absent. In these regions the climate appears to have had little or no seasonal variation. Details of the numbered sites are given in Table XI. Note that some sites have yielded a mixture of wood specimens, some with rings and others without.

1cm annual growth

Prominent growth rings

Faint growth rings

No growth rings

66° N

23° N

0

23° S

66° S
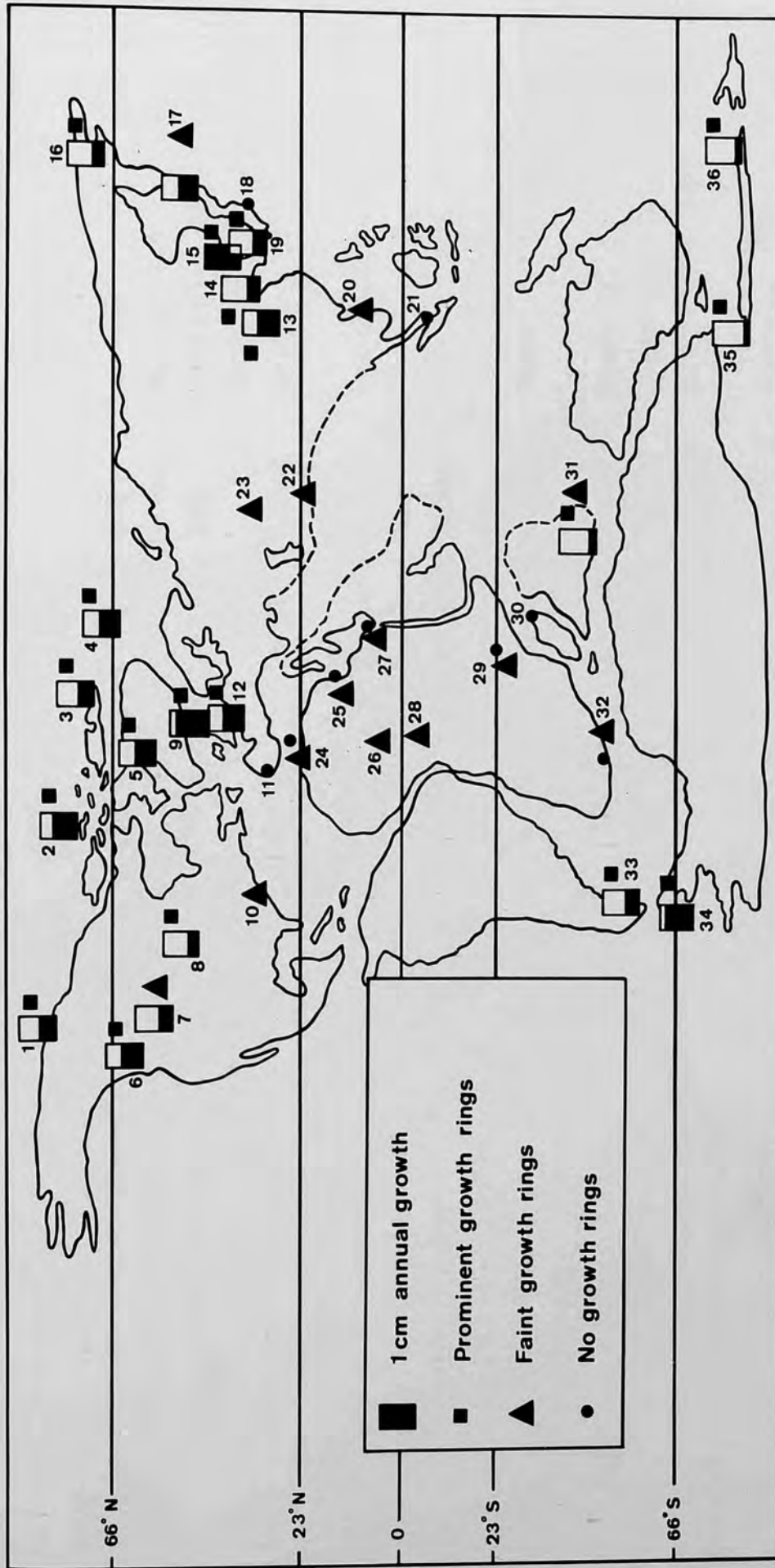
Table XI. Jurassic. Cretaceous and Early Tertiary fossil woods plotted on Figure 6.

NOS. IN APPENDIX I	LOCALITY	SITE ON MAP	PALAEO-LATITUDE	RING DETAILS	REFERENCE
1/2	Northern Alaska	1	80°N	Largest:4mm	Arnold. 1952
6/7	Amund Ringnes Island	2	75°N	Largest:6.5mm	Bannan and Fry. 1957
34	Ellesmere Island	3	74°N	Largest:3mm	Christie. 1964
					Bradley,1982 (pers. comm.)
3	Spitzbergen.	4	61°N	Largest:4.4mm	Gothan. 1907
64/65	King Charles Land Hare Island. West Greenland	5	62°N	Largest:5.4mm	Not published
88	Chilko Lake. British Columbia	6	59°N	Largest:5.6mm	Fry. 1958
68	Rosedale, Alberta. Canada	7	51°N	Largest:1.8mm	Ramanujam & Stewart. 1969
8	Dakota. U.S.A.	8	48°N	Largest:1.25mm	Read. 1932
90/91/92	East Sutherland	9	43°N	Largest:9mm	Creber, 1972
95	North Carolina. U.S.A	10	28°N	Faint	Boeshore & Gray, 1936
30	South Portugal	11	31°N	Absent	Boureau. 1949
89	Dorset	12	36°N	Largest:3.7mm	Francis. 1983
80	Hopeh. China	13	37°N	Largest:5.0mm	Chang. 1929
57	Liaotung. Manchuria	14	35°N	Largest:2.5mm	Shimakura. 1937

167

Table XI. Jurassic, Cretaceous and Early Tertiary fossil woods plotted on Figure 6.

Ref. Nos.	Locality	No.	Lat.	Growth rings	Author
71	Pyong-Yang. N Korea	15	43°N	Largest:13mm	Shimakura. 1936
103	Koryak, USSR	16	72°N	Largest:30mm	Shilkina. 1963
58/59	South Sakhalin, Japan	17	56°N	Largest:3.7mm	Shimakura. 1937
60/61/62	Chiba, Japan	18	36°N	Absent	Nishida, 1973
72	Koti-ken, Japan	19	36°N	Largest:3.0mm	Shimakura. 1936
83	Nong-son, Vietnam	20	28°N	Faint	Boureau. 1950
116	Changwat Kalasin, Thailand	20	28°N	Faint	Asama, 1982
97	(illegible)		(illegible)	(illegible)	(illegible)
32	Soegi Island, Indonesia	21	21°N	Absent	Roggeveen, 1932
104	Afganistan	22	22°N	Faint	Sitholey 1940
31	Uzbekistan, USSR	23	32°N	Faint	Khudayberdyev. 1962
23/24	Morocco	24	24°N	Faint or Absent	Boureau, 1951
26	Tripolitania	25	13°N	Faint or Absent	Negri, 1914
19/20/21	Niger	26	2°N	Faint	Williams, 1930
27	Cairo	27	5°N	Faint or Absent	Unger, 1859
28	Tchad	28	7°S	Faint	Boureau. 1952
22	Tanzania	29	28°S	Faint or Absent	Potonié, 1902
25	Madagascar	30	31°S	Absent	Fliche. 1900
39/42/43	Bihar, India	31	40°S	Largest:1.2mm	Kräusel & Jain, 1963

Table XI. Jurassic, Cretaceous and Early Tertiary fossil woods plotted on Figure 6.

	Locality		Latitude	Rings	Author
76/77/78	East Pondo Land, South Africa	32	48°S	Faint or Absent	Mädel, 1960
98/99					Schultze-Motel, 1966
81	Santa Cruz	33	53°S	Largest:2.5mm	Calder, 1953
87	Alexander Island, Antarctica	34	70°S	Largest:9mm	Jefferson, 1982 (and pers. comm.)
115	New Zealand, South Island	35	70°S	Largest:1.1mm	Pole, 1982
11	New Zealand, South Island	36	67°S	Largest:1mm	Stopes, 1916

there now. In other words the high latitude timberline has
many features in common with the alpine timberline as
described earlier (Section 4d). That solar energy is not a
limiting factor is evident from Table XIII; the long days of
the arctic polar summer ensure that not only is the daily
rate adequate but also the total for the whole season is
sufficient. In Antarctica the following data have been
collected:

LOCALITY	LIGHT ENERGY	AUTHORS
The base 'Southice' (81.9°S) on the 1955-8 Trans-Polar Expedition	3664 MJ m^{-2} yr^{-1}	La Grange, 1963
Halley Bay (75°S)	3452 MJ m^{-2} yr^{-1}	Farman and Hamilton, 1978

These figures may be compared with that of Ovington
(1961) for Thetford, East Anglia where 3212 MJ m^{-2} yr^{-1} was
recorded. In this comparison there would appear to be no
growth-limiting shortage of sunlight near the South Pole.

With Vaartaja's (1959, 1962) work in mind (Section 6a)
we have the possibility that these high latitudes might well
have been inhabited by photoperiodic ecotypes very much
suited to the long polar summer days. This point is further
emphasised by Monteith (1965) in his mathematical modelling
of photosynthetic rates. He shows that the daily rate of
photosynthesis is almost the same in an equatorial climate
with 12h daylight and solar input of 21 MJ m^{-2} d^{-1} as it is
in a cloudy temperate climate with a 16h daylength and input
of 12.6 m^{-2} d^{-1}. This is due to the fact that the extra
light input in the tropics cannot be utilised by leaves
already light-saturated.

If light is not limiting then the ambient temperature
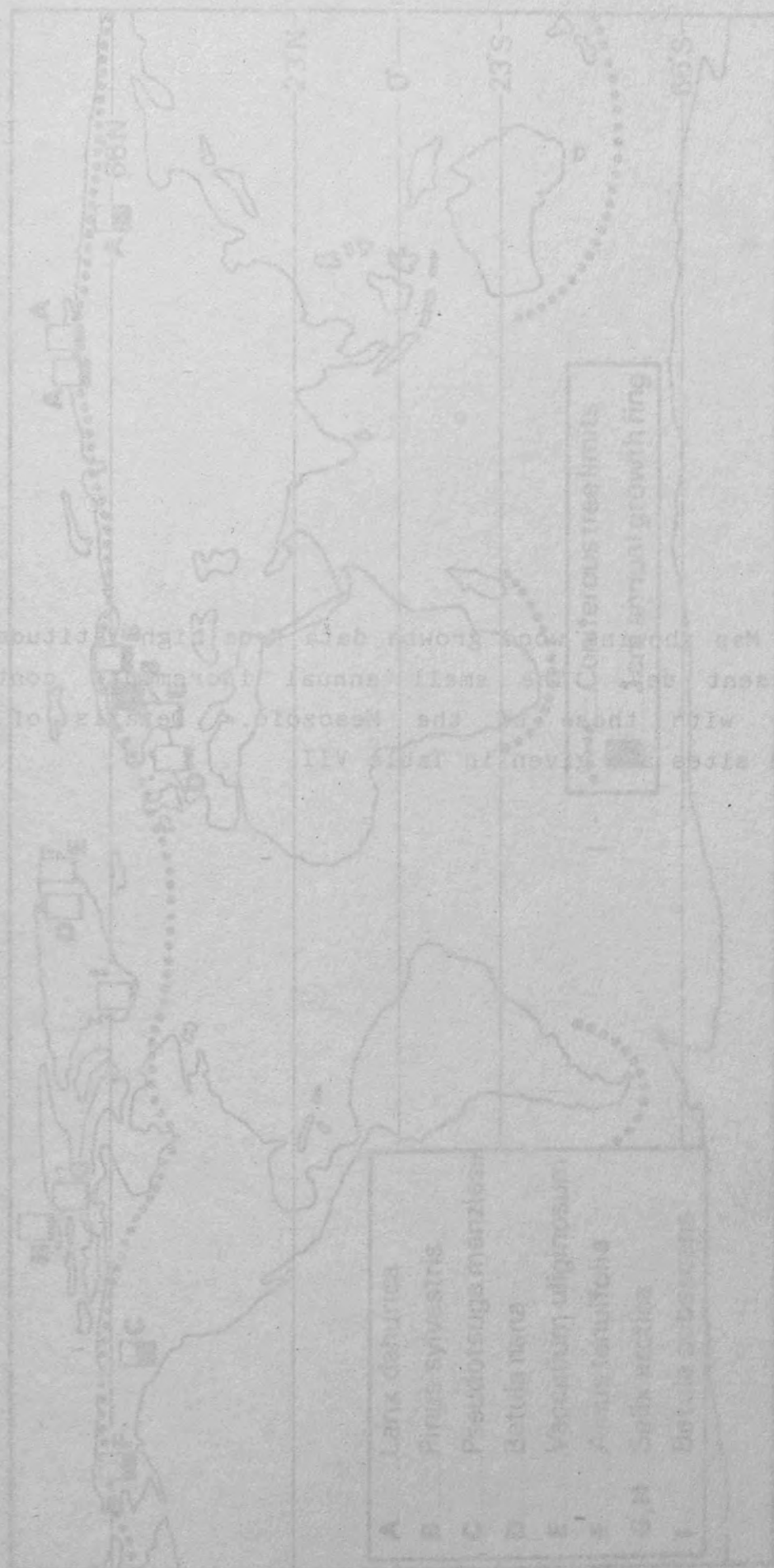
Fig. 1. Map showing above ground dry weight and height values at the present and the small annual increments contrasted through with those in the Mesozoic. Estimates of the latitudes given in Table VII.

Legend (growth ring box):
Coniferous tree limits
—— Recent annual growth ring

A   Larix decidua
B   Pinus sylvestris
C   Pseudotsuga menziesii
D   Betula nana
E   Vaccinium uliginosum
F   Alnus fruticosa
G, H   Salix herbacea
I   Empetrum sp. / Dryas sp.

Fig. 7. Map showing wood growth data from high latitudes at the present day. The small annual increments contrast strongly with those of the Mesozoic. Details of the lettered sites are given in Table VII.

A	Larix dahurica
B	Pinus sylvestris
C	Pseudotsuga menziesii
D	Betula nana
E	Vaccinium uliginosum
F	Alnus tenuifolia
G,H	Salix arctica
I	Betula pubescens

Coniferous tree limits
1cm annual growth ring

23'N
0'
23'S
66'S
66'N
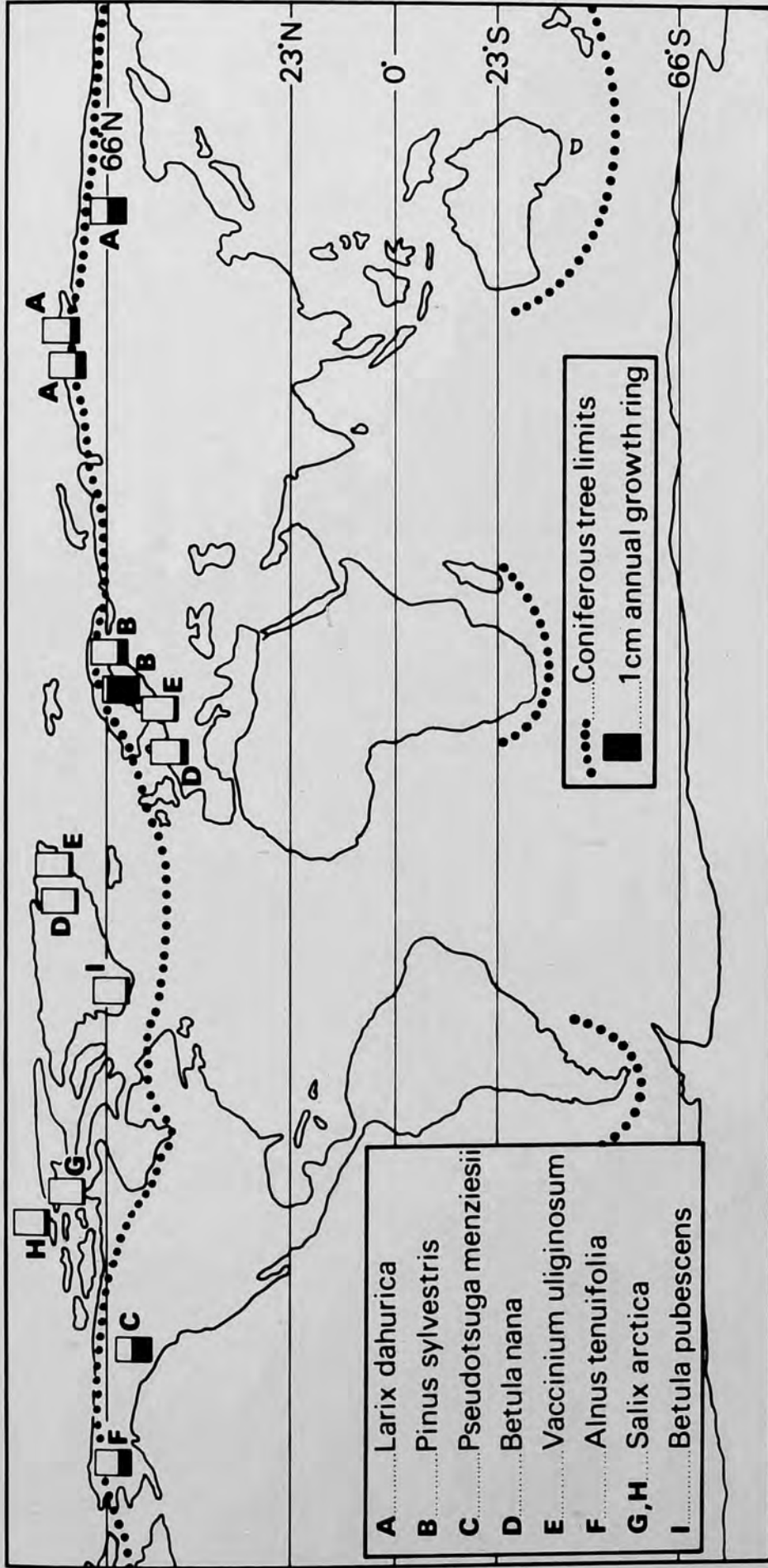
TABLE XII. Recent ring width data from high latitudes plotted on Figure 7.

SPECIES	MAP SITE	WIDEST RING (mm)	LOCALITY	LATITUDE (°N)
Larix dahurica Trautvetter	A	2.0	River Novaja	72
"	A	1.9	River Boganida	71
"	A	5.0	Between Amginsk and the River Aldan	60
Pinus sylvestris	B	2.1	Leningrad	60
"	B	9.0	Estonia	59
Pseudotsuga menziesii	C	5.0	British Columbia	55
		AVERAGE RING WIDTH		
Betula nana L.	D	0.14	Kaiser Franz Joseph's Fjord, East Greenland	73
"	D	1.6	Wurzburg. Germany	48
Vaccinium uliginosum L.	E	0.032	Kaiser Franz Joseph's Fjord. East Greenland	73
"	E	0.7	Erlanger. Germany	49
Alnus tenuifolia Nutt.	F	2.7	Glacier Bay. Alaska	59
Salix arctica Pall.	G	0.07	Cornwallis Island	75
"	H	0.2	Axel Heiberg Island	79
Betula pubescens Ehrh.	I	0.5	S.W. Greenland	61

The above data were obtained from: Middendorf. 1867 (A&B); British Columbia Forest Service. 1947 (C); Kraus. 1874 (D&E); Cooper. 1931 (F); Warren Wilson. 1964 (G); Beschel and Webb. 1963 (H); Elkington and Jones. 1974 (I).

Table XIII.   Solar radiation in high latitudes; daily rate
in June.

LOCATION	LATITUDE (^{O}N)	MEAN JUNE TEMPERATURE (^{O}C)	SOLAR RADIATION RATE (MJ M^{-2} DAY $^{-1}$)
Abisko, Sweden	68	6.3	19.7
Umiat, Alaska	69	8.5	17.2
Resolute, Cornwallis Island	75	4.0	27.8
Greenharbour, Spitzbergen	78	2.4	22.9
Sveanor, Spitzbergen	80	2.1	24.4
Lower latitude site for comparison.			
Washington, D.C.	39	23.7	31.5

It should be noted that the receipt of solar radiation per
day at all latitudes above the Arctic Circle is enhanced by
the fact that there is sunlight throughout 24 hours.   The
daily radiation rate is given because annual rate data are
not available.

certainly is. Examination of Table XIII shows how low the temperatures are in the Arctic summer. Warren Wilson (1964), who has made an extensive study of plant growth in the Arctic takes the view that the low temperatures limit those metabolic processes involved in the transport and use of photosynthate very much more than it does photosynthesis itself. Thus assimilates accumulate and their concentration in the leaves rises to a level which depresses assimilation to a rate which roughly balances their rate of use; thus plant growth is effectively depressed.

There is an experimental basis for the suppression of assimilation by the accumulation of substrate. Kurssanow (1933) showed that sugar-feeding of leaves depressed the rate of assimilation. He also showed that girdling a leaf caused accumulation of sugars and starch which was followed by an increase in the respiration rate and a decrease in assimilation. Hatch and Glasziou (1963) have demonstrated experimentally that in sugar cane any decrease in temperature in the range 18-34°C leads to a decrease in stem elongation and an increase in sugar accumulation. The latter resulted from a temperature-controlled change in enzyme activity. Russell (1940) and Warren Wilson (1966) have shown that the sugar concentration in the leaves of such arctic plants as Ranunculus glacialis L., Oxyria digyna (L.) Hill and Salix herbacea L. is from twice to four times the concentration of comparable leaves of plants of warmer climates. Mooney and Billings (1961) found sugar concentrations in Oxyria roots in Alaska five times as high as in a temperate greenhouse. That the low temperatures would directly limit photosynthesis to the same extent as other plant processes would seem very unlikely in view of the previously mentioned studies (Section 4e) on the process which show that it may take place at 0°C. It would appear therefore that tree growth at high latitudes in the Cretaceous would have been possible from the point of view of the supply of light energy. Higher ambient temperatures

would have been necessary and there is very good evidence from isotope studies of the shells of marine organisms (Kennett, 1977) in deep sea oozes that the surface waters around Antarctica at the end of the Cretaceous were of the order of 20°C. Clearly ambient temperatures of this magnitude would have permitted abundant tree growth on the nearby land.

(c) Productivity

However, having shown that the total annual solar input at high latitudes is adequate for tree growth it is also necessary to show that the crowns of the trees would have been able to intercept it sufficiently well. For this to happen the trees must be spaced fairly widely apart and must have appropriate crown shapes. One of the most detailed description of a fossil forest in high latitudes is that of Jefferson (1982) on Alexander Island (palaeolatitude 70°S). In one continuous geological exposure there were 31 gymnosperm tree stumps in an area of 550 m^2; a density of 1 tree per 17 m^2. In forestry terms, these are rather widely spaced at 563 trees ha^{-1} since comparable trees are capable of growing at a density of 900 trees ha^{-1}. In order to estimate the area of crown that may be presented to the incoming radiation, the formula of Jahnke and Lawrence (1965) is used to calculate areas of interception of conically shaped trees of a range of dimensions and a range of angles of solar elevation. The authors point out that for interception of solar radiation at low angles of elevation, a cone whose height is much greater than the basal radius has the best characteristics (Fig. 8). It has been noted too that spruce-fir forests have extremely low albedos at low angles of sunlight (Dickinson, 1983). A low-angle solar beam penetrates well into the conical crowns and since much of the back-scattering of reflected light is downwardly directed, it tends to be absorbed by nearby trees

on their otherwise shaded sides. Therefore the architecture of such forests very nearly maximises the possible trapping of solar radiation from low-angle sunlight. It is perhaps very significant that trees of the conical growth habit so successfully form forests at high latitudes.

Conical crowns of height 17m and basal radius 1.6m could have been borne by Jefferson's trees without the lower branches being in contact. Such cones have light-intercepting areas at low solar angles of about 25 m^2. Obviously some allowance for shading must be made but it has to be pointed out that in midsummer at latitude 70° the sun travels through 360° and reaches an angle of 43.5° above the horizon at midday. For two months in the summer it only just touches the horizon at midnight and still reaches 40° at midday. With an effective surface area of 25 m^2 the tree could intercept over 80,000 MJ of direct radiation during the illuminated part of the year. With a total conical surface area of 86 m^2 the tree would be well placed to receive diffuse radiation which, as Monteith (1973) points out. may be up to 25% of incoming radiation even on a cloudless day. Figs. 9 and 10 illustrate the formation of shadows in Jefferson's forest.

Jefferson (1982) stated that the average ring width for his trees was 2.5mm which for one tree would represent about 7.8kg of wood with an energy content of about 164 MJ. With a potential light energy flux of 80,000 MJ for the year, the 164 MJ required for wood production only represents 0.2% of the total rather than 0.4% according to Ovington (1961) and Kozlowski (1962) as stated previously (Section 5a). Thus it would seem perfectly possible for these trees to have grown at 70°S. Having seen also that some conifer foliage at the present day is capable of carrying out photosynthesis at extremely lowlight intensities one feels that there would have been no shortage of photosynthate; Müller's (1928) work on Disco Island also seems particularly relevant here (Section 5c). With a production of 7.8kg of wood in trees

Fig. 8. A family of curves showing the effective surface areas for absorption of solar radiation of conical tree crowns of three different ratios of height to basal radius. Note that for low angles of solar altitude (elevation) a tall conical tree crown intercepts disproportionately more light than a crown of the same basal radius but lesser height. With sunlight approaching the vertical (as in the tropics) the effective area of light absorption is 3.14 m^2 (πr^2) for all three cones regardless of height; h, height; r, radius. (After Jahnke and Lawrence, 1965).

Effective tree crown area intercepting sunlight (m²)

Solar altitude (elevation of sun above horizon)

h=8, r=1

h=4, r=1

h=2, r=1
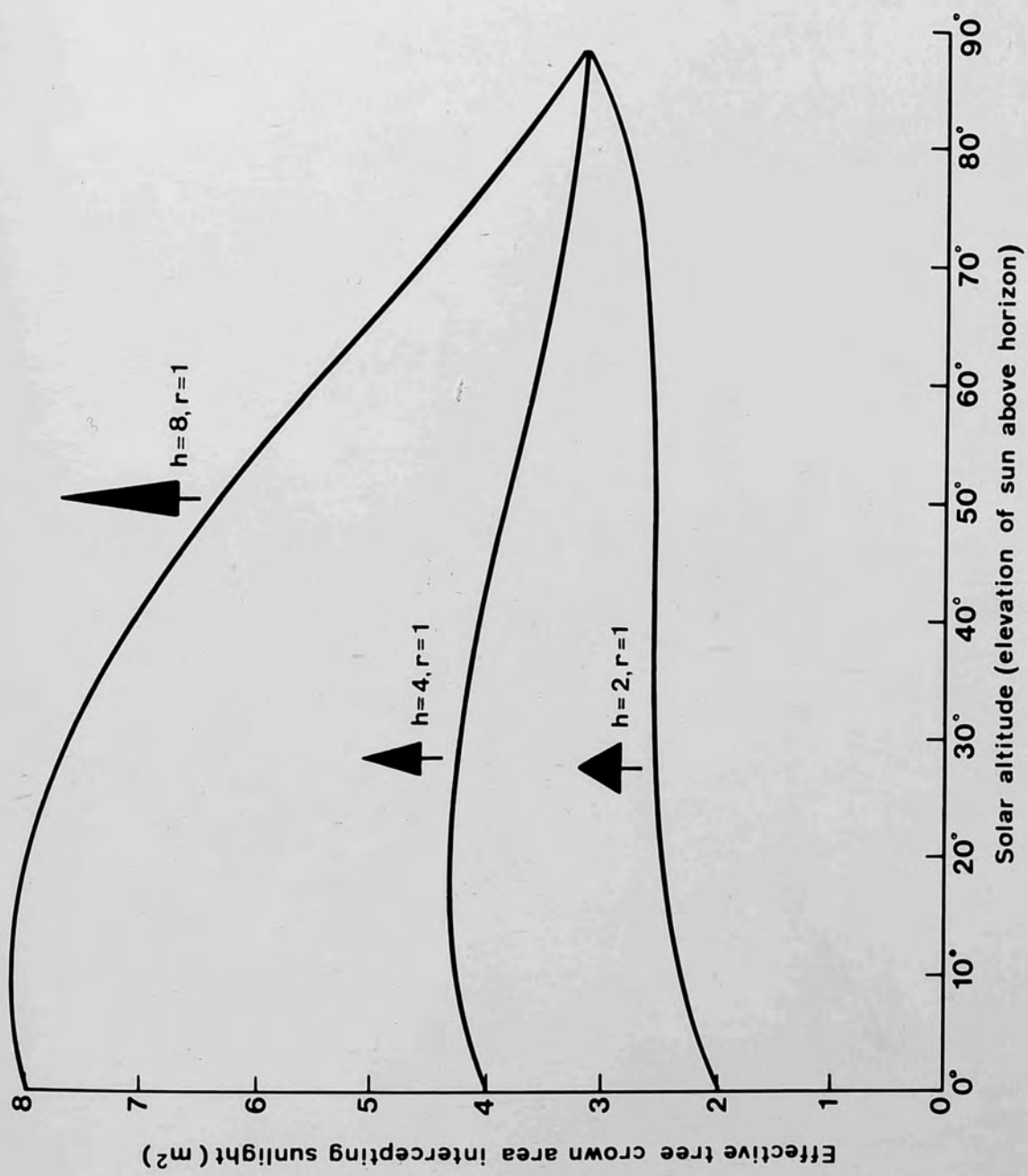
Fig. 9. (a) The formation of a shadow by a tree 20m high with the sun at 40° above the horizon. (b) The shadow as seen in plan view. (c). (d) and (e).* The gradation to lighter grey in the shadows is used to indicate that the shadow line is approaching ground level. Scale: 1cm = 4m.

* Shadows produced with the sun at 35°, 19° and 1° above the horizon respectively.

a

40°

b

24 m

c

29 m

d

58 m

e

1146 m
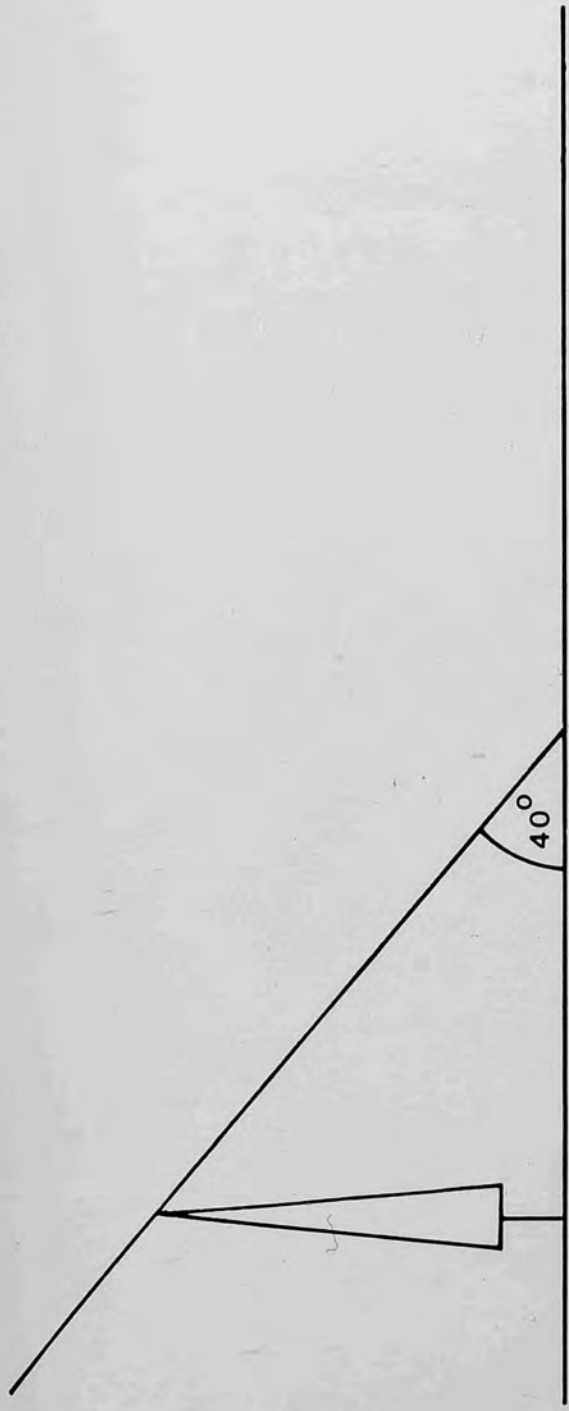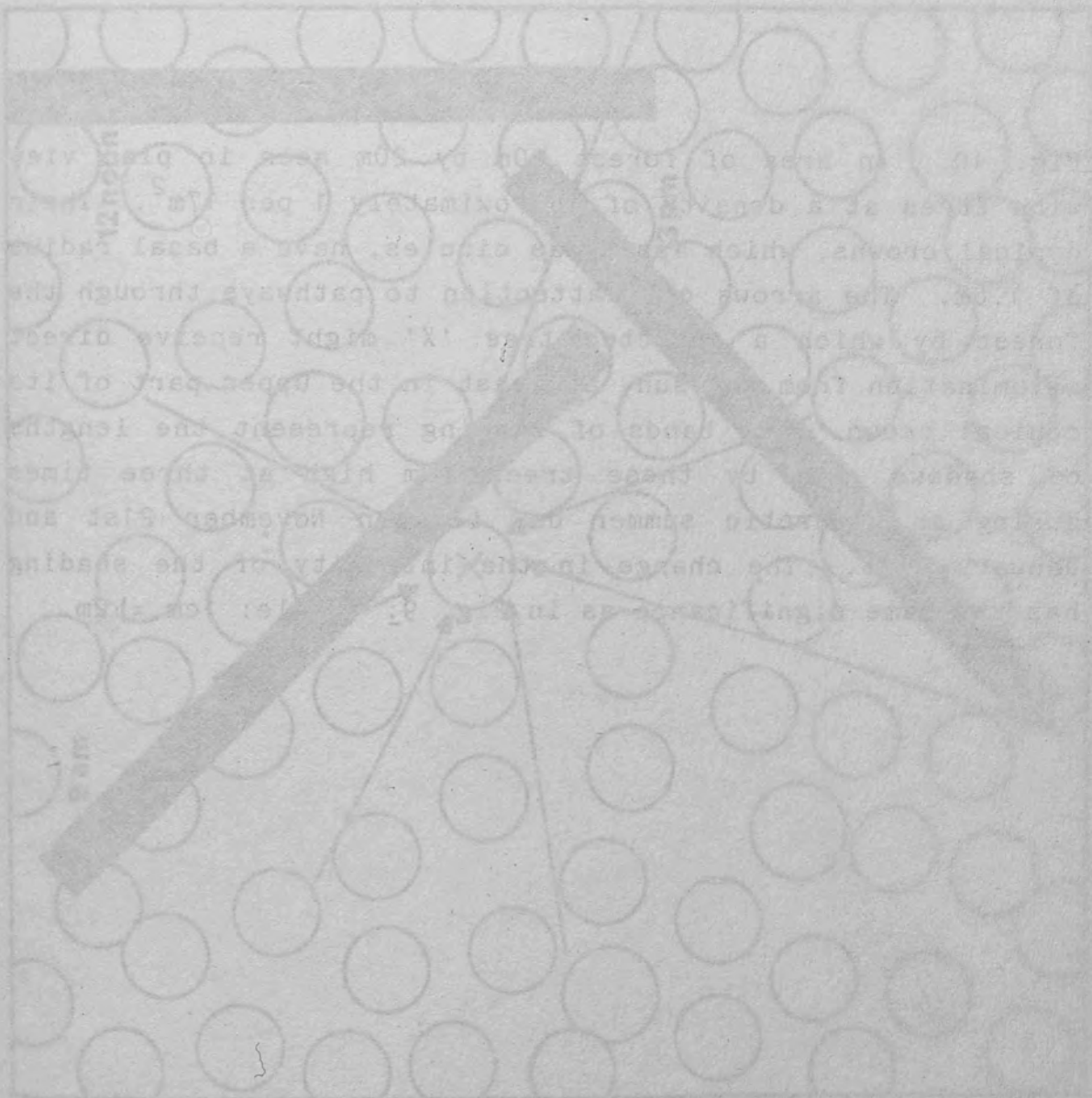
Fig. 10.   An area of forest 20m by 20m seen in plan view
with trees at a density of approximately 1 per $17m^2$.   Their
conical crowns, which appear as circles, have a basal radius
of 1.6m.   The arrows call attention to pathways through the
forest by which a selected tree 'X' might receive direct
illumination from the sun, at least in the upper part of its
conical crown.   The bands of shading represent the lengths
of shadows cast by these trees 20m high at three times
during an antarctic summer day between November 21st and
January 21st.   The change in the intensity of the shading
has the same significance as in Fig. 9.   Scale: 1cm =1·5m.
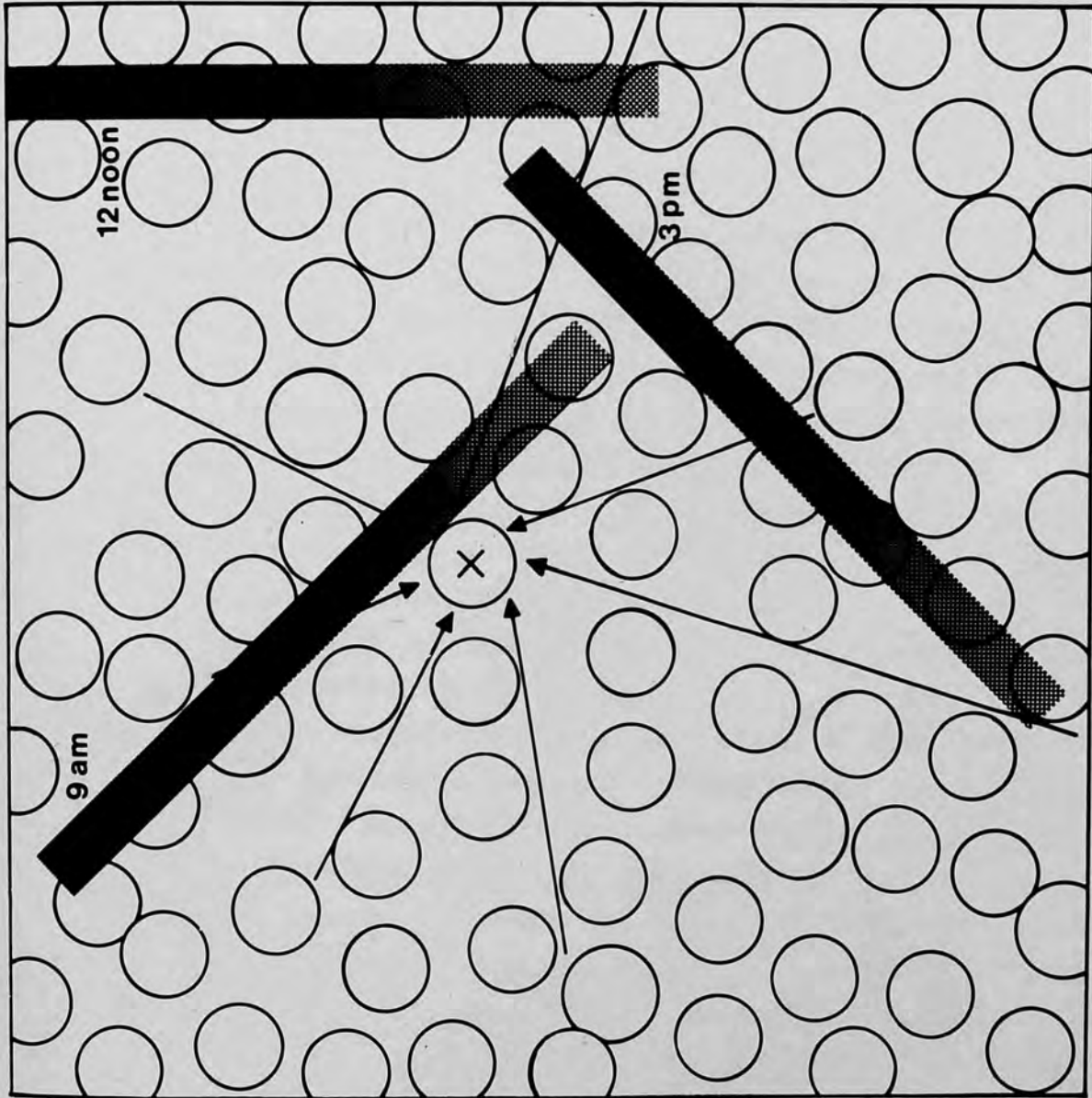
12 noon

3 pm

9 am

spaced one per $17m^2$ this represents an annual timber increment of 0.46kg m^{-2} of forest. A temperate coniferous forest at the present day may be producing over 1kg m^{-2}, so that a productivity of 0.46kg m^{-2} would appear quite possible in the Antarctic light regime, providing the ambient temperature was suitable.

(d) Growing season

Although necessarily the growing season in very high latitudes is relatively short, there is evidence that it could certainly have been adequate in the past. Ford et al. (1978) showed that in Sitka spruce, xylem mother cells were produced by the cambial initial in a file of cells at the rate of 4 per day when the light energy input was 22.5 MJ m^{-2} day^{-1}. At very high latitudes the light input is of this order for 3 months at least. Thus 360 cells of, say, 40μm radial diameter could be formed with a total width of 14.56 mm; this rate of production is clearly adequate to form ring widths normally encountered.

Even though relatively long periods are available to temperate trees for their seasonal growth, many do not use them to the full. Kramer (1943) showed that Pinus resinosa only requires 140 days and Abies balsamea and Pinus strobus complete their seasonal growth in 120 days. In very high latitudes the duration of the adequately illuminated part of the year could well have been sufficient. This is emphasised by Gosz et al. (1978) who show that an entire temperate, deciduous forest ecosystem is in fact supported on only that quantity of light energy that falls on the trees in the few months that they are in leaf. Whereas 5267 MJ m^{-2} are received in a year, the trees are only in a position to absorb 2016 MJ m^{-2} during the summer. This quantity is substantially less than that received within the Arctic and Antarctic during a polar summer.

(e) The Cretaceous climate

That the Cretaceous climate was very different from that of the present day is clear from much geological and palaeontological evidence. In fact it may have been an ice-free world (Barron, Thompson and Schneider, 1981) with the North and South 21°C isotherms displaced 5-15° poleward of their positions now, at least along continental margins. Efforts to simulate such a climate show that 40% of the difference in absorbed solar energy can be explained by differences in the distribution of the continents due to continental drift (Barron, Thompson and Schneider, 1981). However, difficulties remain in providing a full explanation of the way in which the Cretaceous world climate was established and was apparently maintained for a long period of geological time (Barron, 1983).

One interesting feature that emerged from the mid-Cretaceous climatic modelling carried out by Barron and Washington (1982) was that the climate of continental margins was likely to have been very seasonal. Whether true for the Lower Cretaceous and the Upper Jurassic would have to be established by climatic modelling for those periods by it may be significant that the Upper Jurassic woods of East Sutherland (43°N, Appendix 1, Nos. 90-92, Creber, 1972). the Upper Jurassic Purbeck Fossil Forest (36°N, No. 89, Francis, 1983) and Jefferson's Lower Cretaceous Fossil Forest on Alexander Island, Antarctica (70°S, No. 87, Jefferson, 1982) all indicate to different extents a moderate to high seasonality, with marked differences from year to year in the climate in the marginal sites in which they grew.

13. LITERATURE CITED

Absalom, R.G. 1931. Calamopitys (Eristophyton) beinertiana (Goeppert) containing annual rings. NWest. Nat. 6: 70-74.

Antevs, E. 1917. Jahresringe der Holzgewächse und die Bedeutung derselben als klimatischer Indikator. Progr. Rei Bot. 5: 285-386.

Antevs. E. 1925. The climatologic singificance of annual rings in fossil woods. Amer. J. Sci. 5th Ser., 9: 296-302.

Antevs. E. 1953. Tree rings and seasons in past geological eras. Tree-Ring Bull. 20: 17-19.

Archer, R.R. and B.F. Wilson. 1970. Mechanics of the compression wood response. I. Preliminary analyses. Plant Physiol. (Lancaster) 46: 550-556.

_____ 1973. Mechanics of the compression wood response. II. On the location. action. and distribution of compression wood formation. Plant Physiol. (Lancaster) 51: 777-782.

Arnold, C.A. 1930. The genus Callixylon from the Upper Devonian of central and western New York. Pap. Mich. Acad. Sci. 11: 1-50.

Arnold, C.A. 1931. On Callixylon newberryi (Dawkins) Elkins et Wieland. Mich. Univ, Mus. Palaeont. Contr., 3: 207-232.

Arnold, C.A. 1934. Callixylon whiteanum sp. nov.. from the Woodford Chert of Oklahoma. Bot. Gaz. 96: 180-185.

Arnold, C.A. 1947. An introduction to paleobotany. McGraw Hill Book Co., New York.

Arnold, C.A. 1952. Silicified plant remains from the Mesozoic and Tertiary of Western North America II. Some fossil woods from Northern Alaska. Pap. Mich. Acad. Sci. 38: 9-20.

Asama, K. 1982. Contributions to the geology and palaeontology of south-east Asia. CCXXII: Araucarioxylon from Khorat, Thailand. Geol. Pal. Southeast Asia 23: 57-64.

Avery, G.S., P.R. Burkholder and H.B. Creighton, 1937. Production and distribution of growth hormone in shoots of Aesculus and Malus, and its probable role in stimulating cambial activity. Amer. J. Bot. 24: 51-58.

Bailey, I.W. 1925. The spruce budworm biocoenose. 1. Frost rings as indicators of the chronology of specific biological events. Bot. Gaz. (Crawfordsville) 80: 93-101.

_____ and A.F. Faull. 1934. The cambium and its derivative tissues. No. IX. Structural variability in the redwood, Sequoia sempervirens, and its significance in the identification of fossil woods. J. Arnold Arbot. 15: 233-252.

Baker, F.S. 1950. Principles of silviculture. McGraw-Hill Book Co., NY.

Balatinecz, J.J. and R.W. Kennedy. 1967. Mechanism of earlywood-latewood differentiation. Tech. Assoc. Pulp and Paper Ind. 51: 414-422.

Bamberg, S., W. Schwarz and W. Tranquillini. 1967. Influence of daylength on the photosynthetic capacity of stone pine (Pinus cembra L.). Ecology 48: 264-269.

Bannan, M.W. 1962. The vascular cambium and tree-ring development. Pages 3-21 in T.T. Kozlowski (ed.) Tree growth. Ronald Press, NY.

Bannan, M.W. and W.L. Fry, 1957. Three Cretaceous woods from the Canadian Arctic. Can. J. Bot. 35: 327-337.

Barber, C.A. 1898. Cupressinoxylon vectense: a fossil conifer from the Lower Greensand of Shanklin, in the Isle of Wight. Ann. Bot. (London) 12: 329-361.

Barger, R.L. and P.F. Ffolliott. 1976. Factors affecting occurrence of compression wood in individual Ponderosa Pine trees. Wood Sci. 8: 201-208.

Barnes, R.D., J.J. Woodend, M.A. Schweppenhauser and L.J.
    Mullin. 1977. Variation in diameter growth and wood
    density in six-year-old provenance trials of Pinus
    caribaea Morelet on five sites in Rhodesia. Silvae
    Genet. 26: 163-167.

Barron. E.J. 1983. A warm, equable Cretaceous: the nature of
    the problem. Earth-Science Rev. 19: 305-338.

Barron, E.J.. S.L. Thompson and S.H. Schneider. 1981. An
    ice-free Cretaceous? Results from climate model
    simulations. Science 212: 501-508.

Barron, E.J. and W.M. Washington. 1982. Cretaceous climate:
    A comparison of atmospheric simulations with the geologic
    record. Palaeogeogr., Palaeoclimatol., Palaeoecol. 40:
    103-133.

Beck, C.B. 1953. A new root species of Callixylon. Amer. J.
    Bot. 40: 226-233.

Berlyn, G.P. 1982. Morphogenetic factors in wood formation
    and differentiation. Pages 123-150 in P. Baas (ed.).
    New perspectives in wood anatomy. Nijhoff-Junk, The
    Hague.

Beschel, R.E. and D. Webb. 1963. Growth ring studies on
    Arctic Willows. Pages 189-198 in F Muller (ed.). Axel
    Heiberg Island, Preliminary Report 1961-2. McGill
    University, Montreal.

Blackman, G.E. and J.N. Black. 1959. Physiological and
    ecological studies in the analysis of plant environment.
    XII. The role of the light factor in limiting growth.
    Ann. Bot. (London) 23: 137-145.

Blum, W. 1971. Experimental induction of reaction-wood
    formation in spruce and poplar. Ber. Schweiz. Bot. Ges.
    80: 225-251.

Boeshore, I. and W.D. Gray. 1936. An Upper Cretaceous wood:
    Torreya antiqua. Amer. J. Bot. 23: 524-8.

Boureau, E. 1949. Dadoxylon (Araucarioxylon) teixeirae n.
    sp. Bois fossile du Jurassique supérieur portugais.
    Comunções Servs. geol. Port. 29: 187-194.

Boureau, E. 1950. Contribution à l'étude paléoxylogique de l'Indochine. Bull. Serv. géol. Indochine 29:1-13.

Boureau, E. 1951. Étude paléoxylologie de l'Afrique du Nord (1): Presence de Dadoxylon (Araucarioxylon) teixeirae Boureau dans le Haut Atlas de Maroc. Notes Mem. Serv. Mines Carte géol. Maroc. 4: 123-133.

Boureau, E. 1952. Étude des fossiles du Territoire du Tchad: 1. Protopodocarpoxylon rochii n. sp. Bois fossile mésozoïque. Bull. Mus. Hist. nat. Paris. 2° Série 24: 223-232.

Boyce. S.G. and M. Kaeiser. 1961. Environment and genetic variability in the length of fibers of eastern cottonwood. Tech. Assoc. Pulp and Paper Ind. (TAPPI) 44: 363-366.

Boyd, J.D. 1973. Compression wood force generation and functional mechanics. New Zealand J. Forest. Sci. 3: 240-258.

_____ 1977. Basic cause of differentiation of tension wood and compression wood. Austral. Forest Res. 7: 121-143.

Brett, D.W. 1983. Records of temperature and drought in London's park trees. Arbor. Journal 7: 63-71.

British Columbia Forest Sevice 1947. Yield Data. B.C. For. Service.

Brown, C.L. and J. Klein. 1961. Observations on inheritance of wood specific gravity in seedling progeny of loblolly pine. J. Forest (Washington) 59: 898-899.

Brown H.P. 1912. Growth studies in forest trees. I. Pinus rigida Bot. Gaz. (Crawfordsville) 54: 386-403.

_____ 1915. Growth studies in forest trees. II. Pinus strobus. Bot. Gaz. (Crawfordsville) 59: 197-241.

van Buijtenen. J.P. 1958. Experimental control of environmental factors and their effect upon some aspects of wood anatomy in loblolly pine. Tech. Assoc. Pulp and Paper Ind. (TAPPI) 41: 175-178.

_____ 1962. Heritability estimates of wood density in loblolly pine. Tech. Assoc. Pulp and Paper Ind. (TAPPI) 45: 602-605.

Burdon, R.D. 1975. Compression wood in Pinus radiata clones on four different sites. New Zealand J. Forest. Sci. 5: 152-164.

Calder, M.G. 1953. A coniferous petrified forest in Patagonia. Bull. Brit. Mus. (N.H.) Geology 2: 99-138.

Carlquist, S. 1977. Ecological factors in wood evolution: a floristic approach. Amer. J. Bot. 64: 887-896.

Cech, M.Y., R.W. Kennedy and J.H.G. Smith. 1960. Variation in some quality attributes of one-year-old black cottonwood. Tech. Assoc. Pulp and Paper Ind. (TAPPI) 43: 857-858.

Chalk, L. 1927. The growth of the wood of ash (Fraxinus excelsior L. and F. oxycarpa Willd.) and Douglas Fir (Pseudotsuga douglasii Carr.) Quart. J. Forest. 21: 102-122.

_____ 1930. The formation of spring and summer wood in ash and Douglas-fir. Oxford Univ. Forestry Memoir No. 10.

Chang, C.Y. 1929. A new Xenoxylon from North China. Bull geol. Soc. China. 8: 243-251.

Christie, R.L. 1964. Geological reconnaissance of northeastern Ellesmere Island, District of Franklin. Bull. geol. Surv. Can. Memoir 331, 1-77.

Clark, J. 1961. Photosynthesis and respiration in white spruce and balsam fir. Tech. Publ. N.Y. St. Coll. For. No. 58. Syracuse, NY.

Cooper, W.S. 1931. A third expedition to Glacier Bay. Alaska. Ecology, 12: 61-95.

Coster, C. 1927-1928. Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. Ann. Jard. Bot. Buitenzorg 37: 49-160: 38; 1-114.

Cown, D.J. and M.L. Parker. 1979. Densitometric analysis of wood from five Douglas-fir provenances. Silvae Genet. 28: 48-53.

Craighead, F.C. 1940. Some effects of artificial defoliation on pine and larch. J. Forest (Washington) 38: 885-888.

Creber, G.T. 1972. Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham sands of Norfolk. Palaeontology, 15: 655-661.

_____ 1975. The effect of gravity and the earth's rotation on the growth of wood. Pages 75-87 in G.D. Rosenberg and S.K. Runcorn (eds.). Growth rhythms and history of the earth's rotation. John Wiley, London.

_____ 1977. Tree rings: a natural data-storage system. Biol. Rev. Cambridge Philos. Soc. 52: 349-383.

Cronshaw, J. and P.R. Morey. 1965. Induction of tension wood by 2,3,5-tri-iodobenzoic acid. Nature 205: 816-818.

Dadswell, H.E. and A.B. Wardrop. 1960. Some aspects of wood anatomy in relation to pulping quality and to tree breeding. J. Aust. Pulp and Paper Ind. Tech. Assoc. (APPITA) 13: 161-173.

Daubenmire, R.F. 1946. Radial growth of trees at different altitudes. Bot. Gaz. (Crawfordsville) 107: 462-467.

_____ 1949. Relation of temperature and daylength to the inception of tree growth in spring. Bot. Gaz. (Crawfordsville) 110: 464-475.

Decker, J.P. 1944. Effect of temperature on photosynthesis and respiration in red and loblolly pines. Plant Physiol. (Lancaster) 19: 679-688.

Denne, M.P. 1971. Temperature and tracheid development in Pinus sylvestris seedlings. Journ. Exp. Bot. 22: 362-370.

_____ 1972. A comparison of root- and shoot-wood development in conifer seedlings. Ann. Bot. (London) 36: 579-587.

_____ 1974. Effects of light intensity on tracheid dimensions in Pinus sitchensis. Ann. Bot. (London) 38: 337-345.

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

_____ 1976b. Wood production and structure in relation to bud activity in some softwood and hardwood species. Pages 204-221 in P. Baas, A.J. Bolton and D.M. Catling (eds.). Wood structure in biological and technological research. Leiden Botanical Series. Leiden Univ. Press, Dordrecht.

_____ and R.S. Dodd, 1981. The environmental control of wood development. Pages 236-255 in J.R. Barnett (ed.). Xylem cell development. Castle House Publ. Tunbridge Wells.

_____ and C.J. Smith. 1971. Daylength effects on growth, tracheid development and photosynthesis in seedlings of Picea sitchensis and Pinus sylvestris. J. Exp. Bot. 22: 347-361.

_____ and J.E. Wilson. 1977. Some quantitative effects of indoleacetic acid on the wood production and tracheid dimensions of Picea. Planta 134: 223-228.

Dickinson, R.E. 1983. Land surfaces and climate - Surface albedos and energy balance. Pages 305-353 in B.Saltzman (ed.). Theory of Climate, Advances in Geophysics, Vol. 25. Academic Press, New York.

Digby, J. and P.F. Wareing. 1966. The relationship between endogenous hormone levels in the plant and seasonal aspects of cambial activity. Ann. Bot. (London) 30: 607-622.

Dinwoodie, J.M. 1963. Variation in tracheid length in Picea sitchensis Carr. Forest Products Research. Special Report No. 16.

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

Doumani, G.A. and W.E. Long, 1962. The ancient life of the antarctic. Scient. Am. 207(3): 168-184.

Downs, R.J. and H.A. Borthwick. 1956. Effects of photoperiod on growth of trees. Bot. Gaz. (Crawfordsville) 117: 310-326.

Duke, N.C., W.R. Birch and W.T. Williams. 1981. Growth rings and rainfall correlations in a Mangrove tree of the Genus Diospyros (Ebenaceae). Austral. J. Bot. 29: 135-142.

Elkington, T.T. and B.M.G. Jones, (1974). Biomass and primary productivity of birch (Betula pubescens s. lat.) in south-west Greenland. J.Ecol. 62: 821-830.

Elkins, M.G. and G.R. Wieland, 1914. Cordaitean wood from the Indiana black shale. Am. J. Sci. 38: 65-78.

Elliott, G.K. 1970. Wood density in conifers. Technical Communication No. 8, Commonwealth Forestry Bureau, Oxford, England.

Ermich, K. 1963. The inception and the end of the annual tree ring formation in Fagus silvatica L., Abies alba Mill. and Picea excelsa L.K. in the Tatra Mountains. Ekol. Polska. Ser. A 11: 311-336.

Evert, R.F. and T.T. Kozlowski. 1967. Effect of isolation of bark on cambial activity and development of xylem and phloem in trembling aspen. Amer. J. Bot. 54: 1045-1055.

_____ and J.D. Davis. 1972. Influence of phloem blockage on cambial growth of Acer saccharum. Amer. J. Bot. 69: 632-641.

Farman, J.C. and R.A. Hamilton, 1978. Measurements of radiation at the Argentine Islands and Halley Bay. 1963-72. Brit. Antarct. Surv. Scient. Rept. No. 99.

Fletcher, J.M. 1975. Relation of abnormal earlywood in oaks to dendrochronology and climatology. Nature 254: 506-507.

Fliche, P. 1900. Note sur un bois fossile de Madagascar.
    Bull. Soc. géol. Fr. 3° Série. 28: 470-472.

Ford, E.D., A.W. Robards, and M.D. Piney, (1978). Influence
    of environmental factors on cell production and
    differentiation in the early wood of Picea sitchensis.
    Ann. Bot. (LONDON) 42: 683-692.

Fowells, H.A. 1941. The period of seasonal growth of
    ponderosa pine and associated species. J. Forest.
    (Washington) 39: 601-608.

Frakes, L.A. 1979. Climates throughout geologic time.
    Elsevier, Amsterdam.

Francis, J.E. 1983. The dominant conifer of the Jurassic
    Purbeck Formation, England. Palaeontology. 26: 277-294.

Fraser, D.A. 1956. Ecological studies of forest trees at
    Chalk River, Ontario. Canada. II. Ecological conditions
    and radial increment. Ecology 37: 777-789.

Freeland, R.O. 1952. Effect of age of leaves upon the rate
    of photosynthesis in some conifers. Plant Physiol.
    (Lancaster) 27: 685-690.

Frentzen, K. 1931. Die palaeogeographische Bedeutung des
    Auftretens von Zuwachszonen (Jahresringen) bei Holzern
    der Sammelgattung Dadoxylon Endl. aus dem Carbon und dem
    Rotliegenden des Oberrheingebietes. Zentbl. Miner. Geol.
    Palaönt. Jr. 1931B: 617-624.

Fritts, H.C. 1962. The relation of growth ring widths in
    American beech and white oak to variations in climate.
    Tree-Ring Bull. 25: 2-10.

_____ 1976. Tree rings and climate, Academic Press, New
    York.

Fry, W.L. 1958. Petrified logs of Cupressinoxylon from the
    west shore of Chilko Lake, British Columbia. Geol. Surv.
    of Canada, Bulletin. 48: 11-14.

_____ and L. Chalk. 1957. Variation of density in the
    wood of Pinus patula grown in Kenya. Forestry (Oxford)
    30: 29-45.

Fryer, J.H. and F. T. Ledig. 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. Canad. J. Bot. 50: 1231-1235.

Gassner, G. and F. Christiansen-Weniger. 1942. Dendroklimatologische Untersuchungen über die Jahresringentwicklung der Kiefern in Anatolien. Nova Acta Leop. 12: 1-137.

Glerum, C. and J.L. Farrar. 1966. Frost rings in the stems of some coniferous species. Canad. J. Bot. 44: 879-886.

Glock, W.S. 1937. Principles and methods of tree-ring analysis. Carnegie Inst. Washington Publ. No. 486. Carnegie Inst. Washington.

_____ 1951. Cambial frost injuries and multiple growth layers at Lubbock, Texas. Ecology 32: 28-36.

_____, R.A. Studhalter and S.R. Agerter. 1960. Classification and multiplicity of growth layers in the branches of trees at the extreme lower forest border. Smithsonian Miscellaneous Collection, 140, Smithsonian Institution Publication Number 4421. Washington.

Goggans, J.F. 1962. The correlation, variation, and inheritance of wood properties in loblolly pine (Pinus taeda L.). Tech. Rept. 14, School of Forestry, North Carolina State College, Raleigh.

Goldring, W. 1921. Annual rings of growth in Carboniferous wood. Bot. Gaz. 72: 326-330.

Goldsmith, M.H.M. 1977. The polar transport of auxin. Ann. Rev. Plant Physiol. 28: 439-478.

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

Gosz, J.R., R.T. Holmes, G.E. Likens, and F.H. Bormann, 1978. The flow of energy in a forest ecosystem. Scient. Am. 238(3): 92-102.

Gothan, W. 1907. Die fossilen Hölzer von König Karls Land.
K. svenska Vetensk-Akad. Handl. 42: 1-41.

Gothan, W. 1911. Die Jahresringlosigkeit der paläozoischen
Baume und die Bedeutung dieser Erscheinung für die
Beurteilung des Klimas dieser Perioden. Naturw. Wschr..
N.F. 10: 1-13.

Green H.V. and J. Worrall. 1963. Wood quality studies. Part
1. Scanning microphotometer for automatically measuring
and recording certain wood characteristics. Pulp and
Paper Research Inst. of Canada, Tech. Rept. No. 331.

Gustafson, F.G. 1938. Influence of the length of day on the
dormancy of tree seedlings. Plant Physiol. (Lancaster)
13: 655-658.

Håbjørg, A. 1978. Photoperiodic ecotypes in Scandinavian
trees and shrubs. Norges Landbrukshogskole Meldinger 57:
2-20.

Hall, D.O. 1978. Solar energy through biology: could it be a
practical energy source? Pages 9-38 in H. Clijsters. M.
Van Poncke and R. Marcelle (eds.). Biological solar
energy conversion. Limburgs Universitair Centrum,
Netherlands.

Harris, E.H.M. 1955. The effect of rainfall on the late wood
of Scots pine and other conifers in East Anglia.
Forestry (Oxford) 28: 136-140.

Hartig, R. 1885. Holz der deutschen Nadelwaldbaume. Berlin.

Hatch. M.D. and K.T. Glasziou. 1963. Sugar accumulation
cycle in sugar cane. II. Relationship of invertase
activity to sugar content and growth rate in storage
tissue of plants grown in controlled environments. Plant
Physiol. (Lancaster) 38: 344-348.

Hejnowicz, A. and M. Tomaszewski. 1969. Growth regulators
and wood formation in Pinus sylvestris. Physiol. Pl.
(Copenhagen) 22: 984-992.

Helms, J.A. 1965. Diurnal and seasonal patterns of net
assimilation in Douglas-fir, Pseudotsuga menziesii
(Mirb.) Franco, as influenced by environment. Ecology
46: 698-708.

_____ 1970. Summer net photosynthesis of ponderosa
pine in its natural environment. Photosynthetica 4:
243-253.

Høeg, O.A. 1942. The Downtonian and Devonian Flora of
Spitzbergen. Norges Svalb. Ishavs-Undersok.. 83: 1-128.

Holden, R. 1913. Some fossil plants from Eastern Canada.
Ann. Bot. (London) 27: 243-255.

Holden, R. 1917. On the anatomy of two palaeozoic stems from
India. Ann. Bot. (London). 31: 315-326.

Hollis, C.A. and H.B. Tepper. 1971. Auxin transport within
intact dormant and active white ash shoots. Plant
Physiol. (Lancaster) 48: 146-149.

Honda, S. 1896. Besitzen die Kiefernadeln ein mehrjähriges
Wachstum? Imp. Univ. Coll. Agr. Bull. 2: 391-392.

Hoskins, J.T. and A.T. Cross, 1951. The structure and
classification of four plants from the New Albany shale.
Amer. Midl. Nat. 46: 684-716.

Hughes, N.F. 1976. The palaeobiology of angiosperm origins.
Cambridge University Press, Cambridge.

Hylander, C.J. 1922. A Mid-Devonian Callixylon. Am. J. Sci.
4: 315-321.

Jahnke. L.S. and D.B. Lawrence, 1965. Influence of
photosynthetic crown structure on potential productivity
of vegetation, based primarily on mathematical models.
Ecology 46: 319-326.

Jefferson, T.H. 1982. Fossil forests from the Lower
Cretaceous of Alexander Island, Antarctica.
Palaeontology 25: 681-708.

Jensen, K.N. 1982. Growth rings in Pennsylvanian fossil wood
found in Oklahoma. Okla. Geol. Notes, 42: 7-10.

Kennedy, R.W. and J.L. Farrar. 1965. Tracheid development
in tilted seedlings. Pages 419-453 in W.A. Côté Jr.
(ed.). Cellular ultra-structure of woody plants.
Syracuse Univ. Press, NY.

Kennett, J.P. 1977. Cenozoic evolution of antarctic
    glaciation, the circum-antarctic ocean, and their impact
    on global paleoceanography. J. geophys. Res. 82:
    3843-3860.

Khudayberdyev. R. 1962. Ginkgo wood from the Upper
    Cretaceous of south-west Kyzylkum. Dokl. Akad. Nauk USSR
    145: 422-424.

Kienholz. R. 1934. Leader, needle. cambial and root growth
    of certain conifers and their interrelations. Bot. Gaz.
    (Crawfordsville) 96: 73-92.

Kittredge, J. 1944. Estimation of the amount of foliage of
    trees and stands. J. Forest. (Washington) 42: 905-912.

Klem, G.G. 1957. The quality of Norway spruce (Picea abies)
    of Norwegian and German origin. Medd. Norske
    Skogforsøksv. 14: 285-315.

Klem, G.G., F Løschbrandt and O. Bade. 1945. Undersokelser av
    granwirke i forbindelse med slipe- og sulfitkokeforsok.
    Medd. Norske Skogforsøksv.   9: 1-127.

Knigge, W. and C. Koltzenburg. 1964. Bestimmung der
    Früholz-Spätholzgrenze in Nadelholzjahrringen mit Hilfe
    eines Teilchengrössen-Analysators. Holz als Roh- und
    Werkstoff 22: 249-254.

Koehler, A. 1938. Wood quality - a reflection of growth
    environment. J.Forest. (Washington) 36: 867-869.

Kossovich, N.L. 1935. On differences in the anatomical
    structure of the northern and southern sides in the wood
    of conifers. (English summary.) Bot. Zurn. SSSR 20:
    471-472.

Kozlowski, T.T. 1962. Photosynthesis. climate and tree
    growth. Pages 149-164 in T.T. Kozlowski (ed.). Tree
    Growth. Ronald Press, NY.

_____ 1982. Water supply and tree growth. Part I.
    Water deficits. Review article, Forest. Abstr. 43:
    57-95.

Kramer, P.J. 1936. Effect of variation in length of day on
    growth and dormancy of trees. Plant Physiol. (Lancaster)
    11: 127-137.

_____ 1943. Amount and duration of growth of various species of tree seedlings. Plant Physiol.. 18, 239-251.

_____ 1957. Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. Forest Sci. 3: 45-55.

_____ and W.S. Clark. 1946. A comparison of photosynthesis in individual and entire seedlings at various light intensities. Plant Physiol. (Lancaster) 22: 51-57.

_____ and J.P. Decker. 1944. Relation between light intensity and rate of photosynthesis in loblolly pine and certain hardwoods. Plant Physiol. (Lancaster) 19: 350-358.

_____ and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press. NY.

Krames, K. 1952. Geologischer Kompass. Pure and Applied Geophysics 22: 57-62.

_____ 1956. Stubbenuntersuchungen im Braunkohlentagebau der Grube Berrenrath. Braunkohle 8: 329-336.

Kraus. G. 1874. Einige Bemerkungen uber Alter Wachstumverhaltnisse ostgronlandischer Holzgewachse, in Die Zweite deutsche Nordpolarfahrt in den Jahren 1869 und 1870. 2. 1. Leipzig.

_____ 1883. Das mehrjahrige Wachsen der Kiefernadeln. Abh. Naturf. Ges. Halle 16: 361-372.

_____ 1899. Nord und Sud im Jahrring. Pages 130-136 in Festschrift zur Feier ihres funfzigjahrigen bestehens. Physikalisch-Medizinischen Gesellschaft. Wurzburg.

Kraus, J.F. and S.H. Spurr. 1961. Relationship of soil moisture to the springwood-summerwood transition in southern Michigan red pine. J. Forest. (Washington) 59: 510-511.

Kräusel, R. and K.P. Jain. 1963. New fossil coniferous woods from the Rajmahal Hills, Bihar, India. Palaeobotanist 12: 59-67.

Kräusel, R. and P. Range. 1928. Beitrage Zur Kenntniss der
    Karrooformation Deutsch-Sudwest Afrikas. Beitr. geol.
    Erforsch. dsch. Sch. Geb: 20: 1-55.

Krystofovich. A. 1932. Le bois fossiles comme indicateurs
    des points cardinaux dans le passé géologique et la
    theorie de Wegener. Bull. de l'Acad. des Sciences URSS.
    3.

Kurssanow, A.L. 1933. Uber den Einfluss der Kohlenhydrate
    auf den Tagesverlauf der Photosynthese. Planta 20:
    535-548.

Lacey, W.S. 1953. Scottish Lower Carboniferous plants:
    Eristophyton waltoni sp. nov. and Endoxylon zonatum
    (Kidston) Scott from Dunbartonshire. Ann. Bot. (London)
    17: 579-596.

La Grange, J.J. 1963. Trans-Antarctic Expedition 1955-58
    Scientific Report No. 13. Meteorology 1. Shackleton,
    Southice and the journey across Antarctica.
    Trans-Antarctic Expedition Committee.

Larson, P.R. 1957. Effect of environment on the percentage
    of summerwood and specific gravity of slash pine. Yale
    Univ. Sch. Forest. Bull. No. 63.

_____ 1960. A physiological consideration of the
    springwood-summerwood transition in red pine. Forest
    Sci. 6: 110-122.

_____ 1962. The indirect effect of photoperiod on
    tracheid diameter in Pinus resinosa. Amer. J. Bot. 49:
    132-137.

_____ 1963. The indirect effect of drought on tracheid
    diameter in Red Pine. Forest Sci. 9: 52-62.

_____ 1964a. Some indirect effects on wood formation.
    Pages 345-365 in M.H. Zimmermann (ed.). The formation of
    wood in forest trees. Academic Press, NY.

_____ 1964b. Contribution of different aged needles to
    growth and wood formation of young red pines. Forest
    Sci. 10: 224-238.

_____ 1967. Effects of temperature on the growth and wood formation of ten Pinus resinosa sources. Silvae Genet. 16: 58-65.

_____ 1969. Wood formation and the concept of wood quality. Bull. Yale Univ. School Forest. No. 74.

Leakey, R.R.B., V.R. Chapman and K.A. Longman. 1975. Studies on root initiation and bud growth in nine clones of Triplochiton scleroxylon K. Schum. Pages 86-92 in Proc. Symp. on variation and breeding systems of Triplochiton scleroxylon K. Schum. Forest Res. Inst. of Nigeria, Ibadan.

Ledig, F.T. and D.B. Botkin. 1974. Photosynthetic CO_2-uptake and the distribution of photosynthate as related to growth of Larch and Sycamore progenies. Silvae Genet. 23: 188-192.

Leikola, M. 1969. The influence of environmental factors on the diameter growth of young trees. Acta Forest. Fennica 92: 1-44.

Lemoigne, Y. and H. Tyroff, 1967. Caractères anatomiques d'un fragment de bois appartenant a l'èspèce Walchia (Lebachia) piniformis du Permien d'Allemagne. C. r. hebd. Séanc. Acad. Sci. Paris. 265: 595-597.

Lepekhina, V.G. 1972. Woods of palaeozoic pycnoxylic gymnosperms with special reference to North Eurasia representatives. Palaeontographica B 138, 44-106.

Liese, W. and H.E. Dadswell. 1959. Über den Einfluss der Himmelsrichtung auf die Länge von Holzfasern und Tracheiden. Holz als Roh- und Werkstoff 17: 421-427.

Linzon, S.N. 1958. The effect of artificial defoliation of various ages of leaves upon white pine growth. Forest. Chron. 34: 51-56.

Liphschitz, N., S. Lev-Yadun and Y. Waisel. 1981. The annual rhythm of activity of the lateral meristems (cambium and phellogen) in Cupressus sempervirens L. Ann. Bot. (London) 47: 485-496.

Little, C.H.A. and P.F. Wareing. 1981. Control of cambial
    activity and dormancy in Picea sitchensis by
    indol-3-ylacetic and abscisic acids. Canad. J. Bot. 59:
    1480-1492.

Little, C.H.A. 1981. Effect of cambial dormancy state on the
    transport of (1-^{14}C)indol-3-ylacetic acid in Abies
    balsamea shoots. Canad. J. Bot. 59: 342-348.

Lodewick, J.E. 1931. Some effects of irrigation and
    fertilisation of the size of longleaf pine needles.
    Forest Worker 7: 12-13.

Long, A.G. 1979. Observations on the Lower Carboniferous
    genus Pitus Witham. Trans. R. Soc. Edin. 70: 111-127.

Longman, K.A. 1969. The dormancy and survival of plants in
    the humid tropics. Symp. Soc. Expt. Biol. 23: 471-488.

_____ 1978. Control of shoot extension and dormancy:
    external and internal factors. Pages 465-495 in P.B.
    Tomlinson and M.H. Zimmermann (eds.). Tropical trees as
    living systems. Proc. 4th Cabot Symp.. Harvard Forest.
    Cambridge University Press, NY.

_____, R.R.B. Leakey and M.P. Denne. 1979. Genetic
    and environmental effects on shoot growth and xylem
    formation in a tropical tree. Ann. Bot. (London) 44:
    377-380.

Lotan, J.E. and R. Zahner. 1963. Shoot and needle responses
    of 20-year-old red pine to current soil moisture regimes.
    Forest Sci. 9: 497-506.

Mädel, E. 1960. Monimiaceen-Hölzer aus den oberkretazischen
    Umzamba-Schichten von Ost-Pondoland (S-Africa).
    Senckenbergiana Lethaea 41:331-391.

Maheshwari, H.K. 1972. Permian wood from Antarctica and
    revision of some Lower Gondwana wood taxa.
    Palaeontographica B, 138: 1-43.

Marchenko, I.S. 1974. Interaction of woody plants. Lesnoe
    Khozyaistvo 11: 37-45. (In Russian. Forest. Abstr. 1977,
    38, No. 3379.)

_____ 1975. The mutual effect of woody plants. Lesnoe
Khozyaistvo 12: 44-48. (In Russian. Forest. Abstr. 1977,
38, No. 3380).

Matten, L.C. and H.P. Banks, (1967). Relationship between
the Devonian progymnosperm genera Sphenoxylon and
Tetraxylopteris. Bull. Torrey Bot. Club 94: 321-323.

Mayr, H. 1893. Das Harz der deutschen Nadelwaldbäume.
Zeitschr. f. Forstund Jagd. 25: 313-324, 389-417,
565-593. 654-670.

McKimmy, M.D. and D.D. Nicholas. 1971. Genetic differences
in wood traits among half-century-old families of
Douglas-fir. Wood and Fiber 2: 347-355.

McKinnell, F. H. and K.R. Shepherd. 1971. The effect of
moisture availability on density variation within the
annual ring of Radiata pine. J. Inst. Wood Sci. 5:
25-29.

McMahon, T.A. 1975. The mechanical design of trees. Sci.
Am. 233(1): 93-102.

Meissner, R. 1894. Studien über das mehrjährige Wachstum der
Kiefernadeln. Bot. Zeitschr. 52: 55-82.

Middendorff, A.T.v. 1867. Die Gewächse Sibiriens, in Reise
in den äussersten Norden und Osten Sibiriens. 4, 1. St.
Petersburg.

Mikola, P. 1962. Temperature and tree growth near the
northern timber line. Pages 265-287 in T.T. Kozlowski
(ed.). Tree Growth. Ronald Press. NY.

Millar, A. 1980. Annual rings of birch (Betula pubescens
ssp. tortuosa (Ledeb) (Nijman)). climate and defoliation:
An exploratory study. Merlewood Research and Development
Paper No. 77, Merlewood Research Station,
Grange-over-Sands, England.

Miller, D.H. 1955. Snow cover and climate in the Sierra
Nevada, California. Univ. Calif. Publs. Geogr. 11:
1-218.

Monteith, J.L. 1965. Light distribution and photosynthesis
in field crops. Ann. Bot. (London) 29: 17-37.

_____ 1973. Principles of environmental physics. Edward Arnold, London.

Mooney, H.A. and W.D. Billings, 1961. Comparative physiological ecology of arctic and alpine populations of Oxyria digyna. Ecol. Mongr. 31: 1-29.

_____ and M. West. 1964. Photosynthetic acclimation of plants of diverse origin. Amer. J. Bot. 51: 825-827.

_____ and R. Brayton. 1966. Field measurements of the metabolic responses of bristlecone pine and big sagebrush in the White Mountains. Bot. Gaz. (Crawfordsville) 127: 105-113.

Mork, E. 1928. Der Qualität des Fichtenholzes unter besonderer Rucksichtnahme auf Shief- und Papierholz. Papierfabrikant 26: 741-747.

Müller, D. 1928. Die Kohlensäureassimilation bei arktischen Pflanzen und die Abhangigkeit der Assimilation von der Temperatur. Planta 6: 22-39.

Negri, G. 1914. Sopra alenni legni fossili del Gebel Tripolitano. Bull. Soc. Geol. Ital. 33: 321-344.

Neilson, R.E., M.M. Ludlow and P.G. Jarvis. 1972. Photosynthesis in Sitka spruce (Picea sitchensis (Bong.) Carr.). II Response to Temperature. J. Appl. Ecol. 9: 721-745.

Newman, I.V. 1956. Pattern in meristems of vascular plants. 1. Cell partition in living apices and in the cambial zone in relation to the concepts of initial cells and apical cells. Phytomorphology 6: 1-19.

Nicholls, J.W.P. 1971. The effect of environmental factors on wood characteristics. 1. The influence of irrigation on Pinus radiata from South Australia. Silvae Genet. 20: 26-33.

_____ and A.G.Brown. 1971. The ortet-ramet relationship in wood characteristics of Pinus radiata. J. Austr. Pulp and Paper Ind. Tech. Assoc. (APPITA) 25: 200-209.

_____ and L.A. Pederick. 1974. Wood characteristics of sexually and vegetatively reproduced *Pinus radiata*. Austral. J. Bot. 22: 19-27.

_____ C.K. Pawsey and A.G. Brown. 1976. Further studies on the ortet-ramet relationship in wood characteristics of *Pinus radiata*. Silvae Genet. 25: 73-79.

_____ and H.D. Waring. 1977. The effect of environmental factors on wood characteristics. IV. Irrigation and partial droughting of *Pinus radiata*. Silvae Genet. 26: 107-111.

_____ and J.P. Wright. 1976. The effect of environmental characters on wood characteristics. III. The influence of climate and site on young *Pinus radiata* material. Canad. J. For. Res. 6: 113-121.

Nishida, M. 1973. On some petrified plants from the Cretaceous of Choshi, Chiba Prefecture VI. Bot. Mag., Tokyo 86: 189-202.

Njoku. E. 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. J. Ecol., 51: 617-624.

Njoku, E. 1964. Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. J. Ecol., 52: 19-26.

O'Neil, L.C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamb.). Canad. J. Bot. 40: 273-280.

Orman, H.R. 1958. The physical and mechanical properties of New Zealand grown Douglas-fir. Part II. The mechanical properties of New Zealand grown Douglas-fir. New Zealand For. Serv. Tech. Paper No. 24: 41-86.

Oswald, H. 1969. Conditions forestières et potentialité de l'épicéa en haute ardèche. Ann. Sci. Forest. 26: 183-224.

Ovington, J.D. 1961. Some aspects of energy flow in plantations of *Pinus sylvestris* L. Ann. Bot. (London) 25: 12-20.

_____ and H.A.I. Madgwick. 1959. The growth and composition of natural stands of birch. 1. Dry-matter production. Pl. Soil 10: 271-283.

Paul. B.H. and R.O. Marts. 1954. Controlling the proportion of summerwood in Longleaf Pine. U.S.D.A. Forest Prod. Lab., Madison For. Serv.. Rept. No. 1988.

Pharis, R.P., H. Hellmers and E. Schuurmans. 1970. Effects of subfreezing temperatures on photosynthesis of evergreen conifers under controlled environment conditions. Photosynthetica 4: 273-279.

Phelps. J.E., M. Saniewski, M. Smolinski. J. Peniazek and E.A. McGinnes, Jr. 1974. A note on the structure of morphactin-induced wood in two coniferous species. Wood and Fiber 6: 13-17.

Philipson, J.J. and M.P. Coutts. 1980. Effects of growth hormone application on the secondary growth of roots and stems in Picea stichensis (Bong.) Carr. Ann. Bot. (London) 46: 747-755.

Pisek. A., W. Larcher and R. Unterholzner. 1967. Kardinale Temperatur-bereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verscheidener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier- und Frostschadensbereiche der Blatter. Flora B. 157: 239-264.

_____, W. Moser and I. Pack. 1969. Kardinale Temperatur-bereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. III. Temperaturabhängigkeit und optimaler Temperaturbereich der Netto-Photosynthese. Flora B. 158: 110-128.

Pole, M. 1982. The geology of Slope Point to Curio Bay. Unpublished Ms. Geology Department, Otago Unversity.

Polge, H. 1966. Établissement des courbes de variations de la densite du bois par exploration densitométrique de radiographies préleves a la tarière sur des arbres vivants. Applications dans les domaines technologique et physiologique. Thèse Docteur ès sciences appliquées. Ann. Sci. Forest. 23: 1-206.

_____ and R. Keller. 1968. Influence de
l'appraisionnement en eau sur la structure interne des
accroissements annuals. Ann. Sci. Forest. 25: 125-133.

Potonie, H. 1902. Fossile Hölzer aus der oberen Kreide
Deutsch-Ostafrikas, in Die Reisen der Bergassessors Dr.
Dantz in Deutsch-Ostafrika in den Jahren 1898-1900. Mitt.
aus den deutschen Schutzgebieten. Bd. 15 Heft 4: 227-230.

Prasad, M.N.B. and S. Chandra, 1980. Palaeospiroxylon - a
new gymnospermous wood from Raniganj coalfield, India.
Palaeobotanist 26: 230-236.

Priestley, J.H. 1930. Studies in the physiology of cambial
activity. III. The seasonal activity of the cambium.
New Phytol. 29: 316:354.

_____ and L.I. Scott. 1936. A note upon summer wood
production in the tree. Proc. Leeds Phil. Lit. Soc.
Science Section 3: 235-248.

Princes Risborough. 1972. Reaction Wood (Tension Wood and
Compression Wood). Technical Note No. 57, Princes
Risborough Lab., Build. Res. Estab., Princes Risb.
Bucks., England. H.M.S.O. London.

Promnitz, L.C. 1975. A photosynthate allocation model for
tree growth. Photosynthetica 9: 1-15.

Rabinowitch, E.I. 1951. Photosynthesis and related
processes. Vo. 2. Pt. 1. Spectroscopy and fluorescence
of photosynthetic pigments; kinetics of photosynthesis.
Wiley, NY.

Ramanujam, C.G.K. and W.N. Stewart. 1969. Fossil woods of
Taxodiaceae from the Edmonton Formation (Upper
Cretaceous) of Alberta. Canad. J. Bot. 47: 115-124.

Read, C.G. 1932. Pinoxylon dakotense from the Cretaceous of
the Black Hills. Bot. Gaz. 93: 173-189.

Reinders-Gouwentak, C.A. 1941. Cambial activity as dependent
on the presence of growth hormone and the non-resting
condition of stems. Proc. Ned. Akad. Weteusch. Amst. 44:
654-662.

Richardson, S.D. 1964.   The external environment and tracheid
    size in conifers.   Pages 367-388 in M.H. Zimmermann
    (ed.).   The formation of wood in forest trees.   Academic
    Press, NY.

_____ and J.M. Dinwoodie. '1960.   Studies on the
    physiology of xylem development.   Part I.   The effect of
    night temperature on tracheid size and wood density in
    conifers.   J. Inst. Wood Sci. 1: 3-13.

Robards. A.W. 1965.   Tension wood and eccentric growth in
    crack willow (Salix fragilis L.).   Ann. Bot. (London) 29:
    419-431.

_____ 1969.   The effect of gravity on the formation of
    wood.   Sci. Prog. (London) 57: 513-532.

_____, E. Davidson and P. Kidwai. 1969.   Short-term
    effects of some chemicals on cambial activity.   J. Exp.
    Bot. 20: 912-921.

Roberts, L.W. 1976.   Cytodifferentiation in plants:
    xylogenesis as a model system.   Cambridge Univ. Press,
    Cambridge and London.

Roggeveen, P.M. 1932.   Mesozoisches Koniferenholz
    (Protocupressinoxylon malayense n. sp.) ven der Insel
    Soegi in Riouw-Archipel, Niederländisch Ost-Indien.
    Proc. kon. Akad. Wetensch. Amsterdam 35: 580-4.

Russell, R.S. 1940.   Physiological and ecological studies on
    an arctic vegetation. III.   Observations on carbon
    assimilation, carbohydrate storage and stomatal movement
    in relation to the growth of plants on Jan Mayen Island.
    Journ. Ecology 28: 289-309.

Salisbury, F.B. 1981.   Responses to photoperiod.   Pages
    135-167 in O.L. Lange. P.S. Nobel, C.B. Osmond and H.
    Zeigler (eds.).   Physiological plant ecology I.
    Springer-Verlag, Berlin.

Sasaki, Y., T. Okyama and Y. Kikata.   1978.   The evolution
    process of the growth stress in the tree.   The surface
    stresses on the tree.   Mokusai Gakkaishi (J. Jap. Wood
    Res. Soc.) 24: 149-157.

Savidge, R.A. and P.F. Wareing. 1981a. Plant-growth
    regulators and the differentiation of vascular elements.
    Pages 192-235 in J.R. Barnett (ed.). Xylem cell
    development. Castle House Publ. Tunbridge Wells.
    _____ 1981b. A
    tracheid-differentiation factor from pine needles.
    Planta 153: 395-404.

Schreiner, E.J. 1958. Possibilities for genetic improvement
    in the utilisation potentials of forest trees. Silvae
    Genet. 7: 122-128.

Schulman, E. 1951. Tree-ring indices of rainfall.
    temperature and river flow. Pages 1024-1029 in Meteor.
    Soc. (eds.). Compendium of Meteorology. Meteor. Soc.
    Boston.

Schultze-Motel, J. 1966. Gymnospermen-Hölzer aus den
    oberkretazizchen Umzamba-Schichtem von Ost-Pondoland
    (S-Afrika). Senckenbergiana Lethaea 47: 279-337.

Schweitzer, H.-J. 1968. Die Flora des oberen perms in
    Mitteleuropa. Naturw. Rdsch., Braunschw. 21. 93-102.

Seward, A.C. and J. Walton, 1923. On fossil plants from the
    Falkland Islands. Q. Jl. geol. Soc. Lond. 79: 313-333.

Sheldrake, A.R. and D.H. Northcote. 1968. The production of
    auxin by tobacco internode tissues. New Phytol. 67:
    1-11.

Shepherd, K.R. and K.S. Rowan. 1967. Indoleacetic acid in
    cambial tissue of Radiata pine. Austral. J. Bio. Sci.
    20: 637-646.

Shilkina, I.A. 1963. A new conifer genus Yatsenkoxylon
    sibiricum gen. et sp. nov. Dokl. Akad. Nauk USSR 148:
    163-165.

Shimakura, M. 1937. Studies on fossil woods from Japan and
    adjacent lands. Contribution II. The Cretaceous woods
    from Japan, Saghalien and Manchoukuo. Sci. Rep. Tohoku
    Imp. Umiv., 2nd Ser. 19: 1-73.

Shimakura, M. 1936. Studies on fossil woods from Japan and adjacent lands. Contribution I. Some Jurassic woods from Japan and Manchoukuo. Sci. Rep. Tohoku Imp. Univ., 2nd Ser. 18: 267-310.

Shininger, T.L. 1979. The control of vascular development. Ann. Rev. Pl. Physiol. 30: 313-337.

Shroder, J.F. and M. Schwarzbach. 1981. Comments and reply on "Axes of elongation of petrified stumps in growth position as possible indicators of paleosouth, Alaska Peninsula". Geology 10: 436-437.

Sitholey, R.V. 1940. Jurassic plants from Afghan-Turkistan. Mem. geol. Surv. India Palaeont. indica 29, Mem. No. 1.

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

_____ 1972. The kinetics of tracheid development in Tsuga canadensis Carr. and its relation to tree vigour. Ann. Bot. (London) 36: 179-187.

Slatyer, R.O. and P.J. Ferrar. 1977. Altitudinal variation in the photosynthetic characteristics of snow gum. Eucalyptus pauciflora Sieb. ex Spreng. II. Effects of growth temperature under controlled conditions. Austral. J. Pl. Physiol. 4: 289-299.

_____ and P.A. Morrow. 1977. Altitudinal variation in the photosynthetic characteristics of snow gum. Eucalyptus pauciflora Sieb. ex Spreng. I. Seasonal changes under field conditions in the Snowy Mountains area of South-eastern Australia. Austral. J. Bot. 25: 1-20.

Smirnoff, L. and W. Connelly. 1980. Axes of elongation of petrified stumps in growth position as possible indicators of paleosouth, Alaska Peninsula. Geology 8: 547-548.

Smith, A.G., A.M. Hurley, and J.C. Briden, 1981. Phanerozoic paleo-continental world maps, Cambs. Univ. Press, Cambridge.

Smith, C.J., R.W. Wellwood and G.K. Elliott. 1977. Effects of nitrogen fertiliser and current climate on wood properties of Corsican pine (Pinus nigra var. maritima (Ait.) Melv.). Forestry (Oxford) 50: 117-138.

Smith, D.M. 1955. A comparison of two methods for determining the specific gravity of small samples of second growth Douglas fir. U.S.D.A. Forest Serv. Dept. Publ. No. 2033.

Smolinski, M., M. Saniewski and J. Pieniazek. 1974. The suppression of tension wood formation in bent shoots of Aesculus hippocastanum L. by morphactin 3456. Bull. Acad. Polon. Sci. Ser. Sci. Biol. 22: 809-812.

Snow, R. 1935. Activation of cambial growth by pure hormones. New Phytol. 34: 347-360.

Söding, H. 1936. Über den Einfluss von Wuchsstof auf das Dickenwachstum der Bäume. Ber. Deutsch. Bot. Ges. 54: 291.

Spurr, S.H. 1979. Silviculture. Sci. Am. 240 (2): 62-75.

Squillace, A.E. and R.T. Bingham. 1958. Localized ecotypic variation in western white pine. Forest Sci. 4: 20-24.

Stopes. M.C. 1916. An early type of the Abietineae(?) from the Cretaceous of New Zealand. Ann. Bot. (London) 30: 111-125.

Timell, T.E. 1978. Ultrastructure of compression wood in Ginkgo biloba. Wood Sci. and Techn. 12: 89-103.

Tomlinson, P.B. and F.C. Craighead, Sr. 1972. Growth-ring studies on the native trees of sub-tropical Florida. Pages 39-51 in A.K.M. Ghouse and M. Yunus (eds.). K.A. Chowdhury commemoration volume. Tata McGraw Hill, New Delhi.

Torrey, J.G., D.E. Fosket and P.K. Hepler. 1971. Xylem formation: a paradigm of cytodifferentiation in higher plants. Amer. Sci. 59: 338-352.

Townsend, A.M., J.W. Hanover and B.V. Barnes. 1972. Altitudinal variation in photosynthesis, growth and monoterpene composition of western white pine (Pinus monticola Dougl.) seedlings. Silvae Genet. 21: 133-139.

Tranquillini. W. 1955. Die Bedeutung des Lichtes und der Temperatur fur die Kohlensäureassimilation von Pinus cembra L. Jungwuchs an einem hochalpinem Standort. Planta 46: 154-178.

_____ 1979. Physiological ecology of the alpine timberline. Springer-Verlag. Berlin, Heidelberg, NY.

_____ and K. Holzer. 1958. Über das Gefrieren und Auftauen von Coniferennedaln. Ber. Deutsch. Bot. Ges. 71: 143-156.

Trenard, Y. and P. Guéneau. 1975. Relation between longitudinal growth stresses and tension wood in Fagus sylvatica. Holzforschung 29: 217-223.

Tynan, E.J. 1959. Occurrence of Cordaïites michiganensis in Oklahoma. Okla. Geol. Notes 19: 43-46.

Unger, F. 1859. Der versteinerte Wald bei Cairo und einige andere Lager verkieselten Holzen in Ägypten. Sber. Akad. Wiss. Wien. 33: 209-233.

Vaartaja, O. 1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monogr. 29: 91-111.

_____ 1962. Ecotypic variation in photoperiodism of trees with special reference to Pinus resinosa and Thuja occidentalis. Canad. J. Bot. 40: 849-856.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw-Hill Book Co. London.

Voegeli, H. and O. Reinhart. 1956. Ergebnisse von Jahrringmessungen aus gleichaltrigen Föhrebestanden. Schweiz. Z. Forstwesen 107: 407-415.

Vowinckel, T., W.C. Oechel and W.G. Boll. 1975. The effect of climate on the photosynthesis of Picea mariana at the subarctic tree-line. I. Field measurements. Canad. J. Bot. 53: 604-620.

Wareing. P.F. 1951a. Growth studies in woody species. IV. the initiation of cambial activity in ring-porous species. Physiol. Pl. (Copenhagen) 4: 546-562.

_____ 1951b. Growth studies in woody species. III. Further photoperiodic effects in Pinus silvestris. Physiol. Pl. (Copenhagen) 4: 41:56.

_____ 1953. Growth studies in woody species. V. Photoperiodism in dormant buds of Fagus sylvatica L. Physiol. Pl. (Copenhagen) 6: 692-705.

_____ 1958. The physiology of cambial activity. J. Inst. Wood Sci. 1: 34-42.

_____, C.E.A. Hanney and J. Digby. 1964. The role of endogenous hormones in cambial activity and xylem differentiation. Pages 323-344 in M.H. Zimmermann (ed.). The formation of wood in forest trees. Academic Press. NY.

_____ and D.L. Roberts. 1956. Photoperiodic control of cambial activity in Robinia pseudacacia L. New Phytol. 55: 356-366.

Warren Wilson, J. 1964. Annual growth of Salix arctica in the high-arctic. Ann. Bot. (London) 28: 71-76.

_____ 1966. An analysis of plant growth and its control in arctic environments. Ann. Bot. (London) 30: 383-402.

Westing, A.H. 1965. Formation and function of compression wood in gymnosperms. Bot. Rev. 31: 381-480.

_____ 1968. Formation and function of compression wood in gymnopserms. Bot. Rev. 34: 51-78.

Whitmore, F.W. and R. Zahner. 1964. Indoleacetic acid synthesis by polyphenols in the extraction of Pinus phloem and cambial tissue. Science, NY. 145: 166-167.

_____ 1966. Development of the xylem ring in stems of young red pine trees. Forest Sci. 12: 198-210.

Wight, W. 1933. Radial growth of the xylem and starch reserves of Pinus sylvestris. New Phytol. 32: 77-96.

Williams, S. 1930. The geological collection from the South Central Sahara made by Mr. F. Rodd. III. Fossil wood. Q. Jl. geol. Soc. Lond. 86: 408-409.

Wilson, B.F., T.J. Wodzicki and R. Zahner. 1966. Differentiation of cambial derivatives: Proposed terminology. For. Science 12: 438-440.

Wilson, L.R. 1963. A new species of _Dadoxylon_ from the Seminole Formation (Pennsylvanian) of Oklahoma. Okla. Geol. Notes 23: 215-220.

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.

_____ 1968. On the question of occurrence of indole-3-acetic acid in _Pinus silvestris_. Amer. J. Bot. 55: 564-571.

_____ 1971. Mechanism of xylem differentiation in _Pinus silvestris_ L. J. Exp. Bot. 22: 670-687.

_____ and A.B. Wodzicki. 1973. Auxin stimulation of cambial activity in _Pinus sylvestris_. II. Dependence upon basipetal transport. Physiol. Pl. (Copenhagen) 29: 288-297.

Zahner, R. 1963. Internal moisture stress and wood formation in conifers. Forest Prod. Journ. 13: 240-247.

_____ 1968. Water deficits and growth of trees. Pages 191-254 in T.T. Kozlowski (ed.). Water deficits and plant growth. Academic Press, NY.

_____, J.E. Lotan and W.D. Baughman. 1964. Earlywood-latewood features of red pine grown under simulated drought and irrigation. Forest Sci. 10: 361-369.

_____ and W.W. Oliver. 1962. The influence of thinning and pruning on the date of summerwood initiation in red and jack pines. Forest Sci. 8: 51-63.

Zajaczkowski, S. 1973. Auxin stimulation of cambial activity in _Pinus sylvestris_. I. The differential cambial response. Physiol. Pl. (Copenhagen) 29: 281-287.

Zalessky, M. 1909. Communication preliminaire sur un nouveau _Dadoxylon_ provenant du Dévonien supérieur du bassin du Donetz. Bull. acad. Imp. sci. St. Pétersbourg, 26, 1175.

Zalessky, M. 1911. Étude sur l'anatomie du _Dadoxylon_ tchihatcheffi Goeppert. Mém. Comité géol. Russe. St. Pétersbourg 68: 18-29.

Zimmermann, W.A. 1936. Untersuchungen über die räumliche und
    zietliche Berteilung des Wuchsstoffen bei Bäumen. Z.
    Bot. 30: 209-252.

Zobel, B.J. 1964. Breeding for wood properties in forest
    trees. Unasylva 18: 89-103.

_____ and R.R. Rhodes. 1957. Specific gravity indices
    for use in breeding loblolly pine. Forest Sci. 3:
    281-285.

APPENDIX I

This Appendix consists of the Fossil Wood Record Sheets compiled during the course of the work and these are followed by an Index.

In the Record Sheets:
S.H. & B., 1981 refers to Smith, A.G., Hurley, A.M. & Briden, J.C. 1981.
    Phanerozoic palaeocontinental world maps.
    Cambridge University Press, Cambridge.

Information was obtained in three ways, indicated by (i), (ii) and (iii).

    (i)   From the text of a paper
    (ii)   From the figures in a paper
    (iii) From specimens

Each Fossil Wood Record Sheet comprises two pages. A & B.

In the Index the letters (a) to (f) stand for the following:
    (a)   Species
    (b)   Horizon
    (c)   Locality
    (d)   Evidence for in situ forest
    (e)   Palaeoposition
    (f)   Ring type (as defined in Part IV, 3c)

FOSSIL WOOD RECORD SHEET A

NO: 1   SPECIES: <u>Xenoxylon latiporosum</u> (Cramer) Gothan

LOCALITY   : Colville River, 4.8km S. of the junction
                   with the Awuna River, Alaska

EVIDENCE OF
IN SITU FOREST: Fragment in stratum

HORIZON   : Chandler Formation, Nanushuk Group, Lower
                   Cretaceous

PALAEOPOSITION: 80°N.

MAP REFERENCE : S.H.&B.,1981. Map 31 p.38

SPECIMEN
REFERENCE   : Arnold,   C.A.   1952.   Silicified   plant
                   remains from the Mesozoic & Tertiary of
                   Western North America II.   Some fossil
                   woods from Northern Alaska.   Pap. Mich.
                   Acad. Sci. Art. & Lett. 38, 9-20

SYNONYMY   : <u>Pinites latiporosus</u>,   Cramer   1868
                   <u>Xenoxylon latiporosum</u>, Gothan 1905

LOCATION OF
SPECIMEN   : No details given

NO. OF
SPECIMENS   : No details given

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET B

NO: 1   **SPECIES:** <u>Xenoxylon latiporosum</u> (Cramer) Gothan

DIAMETER   : 4.6cm (ii)

NO. OF RINGS : Not stated, 16 in photo of a portion only

**MEAN
SENSITIVITY** : Too few rings to give a useful result

LARGEST RING : 1mm in photo (1.25mm in text)

NO. OF CELLS : 50 (est.)(i) All cell sizes (i)
E/WOOD   : 48   **L/WOOD:** 2
LARGEST CELL : 50μm   **SMALLEST CELL:** 14μm

SMALLEST RING : 0.2mm (i) (ii)

NO. OF CELLS : 10 (est.)(i) All cell sizes (i)
E/WOOD   : 9   **L/WOOD:** 1
LARGEST CELL : 50μm   **SMALLEST CELL:** 12μm
                     (As only a part of a ring was figured, cell
                     numbers were estimated from the given cell
                     sizes) (i)

RING TYPE   : D

FALSE RINGS   : Some of the rings appear to be so narrow
                     that they could only reasonably be false
                     rings. They are much narrower than the
                     min. size in the text (0.2mm). However,
                     the author does not mention 'false rings'

DISTORTION   : None mentioned in text or evident in
                     photograph

NOTES   : Silicified wood. Only one or two cells in
                     the latewood of each ring

FOSSIL WOOD RECORD SHEET   A

NO: 2   SPECIES: Cedrus alaskensis Arnold

LOCALITY   :   At the junction of the Oolamnagavik River
                       and the Colville River, Alaska

EVIDENCE OF
IN SITU FOREST: Fragment in stratum

HORIZON   :   Nanushuk Group, Lower Cretaceous

PALAEOPOSITION: 80°N

MAP REFERENCE :   S.H.&B.,1981.   Map 31 p.38

SPECIMEN
REFERENCE   :   Arnold,   C.A.   1952.   Silicified   plant
                       remains   from   the   Mesozoic   &   Tertiary   of
                       Western   North   America   II.   Some   fossil
                       woods   from   Northern   Alaska.   Pap.   Mich.
                       Acad. Art. & Lett. 38, 9-20

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   No details given

NO. OF
SPECIMENS   :   No details given

SPECIMEN
SIZE   :   3 x 4cm in transverse section   (i)

FOSSIL WOOD RECORD SHEET B

NO: 2   SPECIES: <u>Cedrus alaskensis</u> Arnold

DIAMETER   : Photo shows ring boundaries almost
                  straight, therefore the diameter was likely
                  to have been very large

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : Too few rings to provide a reliable result

LARGEST RING   : 3.3mm   (ii)   (4mm in text)

NO. OF CELLS   : 45 (est.) (i)
                  (As only a part of a ring was figured, cell
                  numbers were estimated from the given cell
                  sizes) (i)
E/WOOD   : 40   **L/WOOD:** 5
LARGEST CELL   : 73μm(i)(ii) **SMALLEST CELL:** 14μm (ii)

SMALLEST RING   : 2.3mm   (ii)   (2mm in text)

NO. OF CELLS   : 31 (est.) (i)
                  (As only a part of a ring was figured, cell
                  numbers were estimated from the given cell
                  sizes) (i)
E/WOOD   : 27   **L/WOOD:** 4
LARGEST CELL   : 50μm(i)(ii) **SMALLEST CELL:** 12μm (ii)

RING TYPE   : D

FALSE RINGS   : None in photo or mentioned in text

DISTORTION   : None evident

NOTES   : Silicified wood. Found in association with
                  a 1m coal seam. As with Record No. 1, only
                  a very few cells in the latewood.

FOSSIL WOOD RECORD SHEET   A

NO: 3   SPECIES: <u>Protopiceoxylon exstinctum</u> Gothan

LOCALITY   : King Charles Land   (E. Spitzbergen)

EVIDENCE OF
IN SITU FOREST: Loose fragments

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 61°N

MAP REFERENCE : S.H.&B.,1981. Map 31 p.38

SPECIMEN
REFERENCE   : Gothan, W. 1907. Die fossilen Hölzer von
                     König Karls Land. Kungl. Svenska. Vetensk.
                     Akad. Handl. 42, 1-41

SYNONYMY   : <u>Protopiceoxylon exstinctum</u>   Gothan,   1907
                     <u>Protopiceoxylon extinctum</u>
                     Medlyn & Tidwell, 1979

LOCATION OF
SPECIMEN   : Collected   on   Nathorst's   North   Polar
                     Expedition, 1895.   Now   in   the   Swedish
                     Museum of Natural History

NO. OF
SPECIMENS   : 10 (incl. slides)

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 3   SPECIES: Protopiceoxylon exstinctum Gothan

DIAMETER   :   The photographs show the ring boundaries to be almost straight, therefore the diameters were probably large

NO. OF RINGS   :   11 on largest portion figured

MEAN
SENSITIVITY   :   Too few rings to analyse

LARGEST RING   :   4.4mm   (ii)

NO. OF CELLS   :   61   All cell sizes (ii)
E/WOOD   :   57   **L/WOOD:**   4 (est.)
LARGEST CELL   :   70μm   **SMALLEST CELL:** Totally black
                                                 in the photo

SMALLEST RING :   0.3mm   (ii)

NO. OF CELLS   :   7   All cell sizes (ii)
E/WOOD   :   5   **L/WOOD:**   2 (est.)
LARGEST CELL   :   60μm   **SMALLEST CELL:** Totally black
                                                 in the photo

RING TYPE   :   D

FALSE RINGS   :   One clearly indicated by the author

DISTORTION   :   A little in the widest ring

NOTES   :   Large variation in ring width.   Very little latewood.   Very sharp earlywood-latewood boundary (in the outer rings)

FOSSIL WOOD RECORD SHEET   A

NO: 4   SPECIES: <u>Protopiceoxylon exstinctum</u> Gothan

LOCALITY   : Green Harbour, Spitzbergen

EVIDENCE OF
IN SITU FOREST: Loose fragments

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 61°N

MAP REFERENCE : S.H.&B.,1981. Map 31 p.38

SPECIMEN
REFERENCE   : Gothan, W. 1910. Die fossilen Holzreste
                  von Spitzbergen. Kungl. Svenska. Vetensk.
                  Handl. 45, 1-56

SYNONYMY   : <u>Protopiceoxylon exstinctum</u> Gothan, 1907
                  <u>Protopiceoxylon extinctum</u>
                  Medlyn & Tidwell, 1979

LOCATION OF
SPECIMEN   : Swedish Museum of Natural History

NO. OF
SPECIMENS   : 4

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 4   SPECIES: Protopiceoxylon exstinctum Gothan

DIAMETER   : 20mm (ii)

NO. OF RINGS   : 22 (Photographed on very low power)

MEAN
SENSITIVITY   : Only the innermost rings were figured

LARGEST RING   : 1mm   (ii)   Magnification too   low   to
                    distinguish cells.

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   : 0.2mm (ii)

NO. OF CELLS   : 6   All cell sizes (ii)
E/WOOD   : 4   L/WOOD: 2
LARGEST CELL   : 40μm   SMALLEST CELL: 20μm (est.)

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None seen in the figures

NOTES   : The same species as described on King
                    Charles Land

FOSSIL WOOD RECORD SHEET   A

NO: 5   SPECIES: <u>Cedroxylon disjunctum</u> Bannan & Fry

LOCALITY   :   14km east of the western end of Strand
                       Fiord Peninsula on Axel Heiberg Island
                       (Canadian Arctic)

EVIDENCE OF
IN SITU FOREST: Loose fragment

HORIZON   :   Albian (Isachsen Formation), Lower
                       Cretaceous

PALAEOPOSITION: 75°N

MAP REFERENCE :   S.H.&B.,1981. Map 31 p.38

SPECIMEN
REFERENCE   :   Bannan, M.W. & Fry, W.L. 1957. Three
                       Cretaceous woods from the Canadian Arctic.
                       Can. J. Bot. 35, 327-337

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Geol. Survey of Canada plant type No. 3917

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   7.5cm in diam. (i)

FOSSIL WOOD RECORD SHEET   B

NO: 5   **SPECIES:** <u>Cedroxylon disjunctum</u> Bannan & Fry

DIAMETER   : 7.5cm (i)

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : 4mm (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 56μm   **SMALLEST CELL:** 8μm (est.) (ii)

SMALLEST RING : 1.5mm (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : B

FALSE RINGS   : None evident

DISTORTION   : None evident

NOTES   : Earlywood grades gradually into latewood

FOSSIL WOOD RECORD SHEET   A

NO: 6   SPECIES: <u>Piceoxylon christopheri</u> Bannan & Fry

LOCALITY   : In the south-eastern part of Amund Ringnes
                     Island (Canadian Arctic)

EVIDENCE OF
IN SITU FOREST: Loose fragment

HORIZON   : Albian   (Isachsen   Formation).   Lower
                     Cretaceous

PALAEOPOSITION: 75°N

MAP REFERENCE : S.H.&B.,1981.   Map 31 P.38

SPECIMEN
REFERENCE   : Bannan, M.W. & Fry, W.L. 1957.
                     (As for No 5)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Geol. Survey of Canada, plant type No. 3918

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 6cm (i)

FOSSIL WOOD RECORD SHEET   B

NO: 6   SPECIES: <u>Piceoxylon christopheri</u> Bannan & Fry

DIAMETER   : 6cm   (Pith 1.5mm) (i)

NO. OF RINGS : 4 (i) (The pith and the first four rings)

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : 6.5mm   (i)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 42μm   SMALLEST CELL:

SMALLEST RING : Not stated

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : B

FALSE RINGS   : None evident

DISTORTION   : None evident

NOTES   : Earlywood grades gradually into latewood

FOSSIL WOOD RECORD SHEET   A

NO: 7   SPECIES: <u>Piceoxylon thomsoni</u> Bannan & Fry

LOCALITY   : In the south-eastern part of Amund Ringnes
                     Island (Canadian Arctic)

EVIDENCE OF
IN SITU FOREST: Loose fragment

HORIZON   : Albian   (Isachsen   Formation),   Lower
                     Cretaceous

PALAEOPOSITION: 75°N

MAP REFERENCE : S.H.&B.,1981. Map 31 p.38

SPECIMEN
REFERENCE   : Bannan, M.W. & Fry, W.L. 1957.
                     (As for No 5)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Geol. Survey of Canada, plant type No. 3919

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 10cm in diam. (i)

FOSSIL WOOD RECORD SHEET   B

NO: 7   SPECIES: <u>Piceoxylon thomsoni</u> Bannan & Fry

DIAMETER   : 10cm (i)

NO. OF RINGS   : At least 70 (i) (These 70 rings in one
                   portion of the specimen total only 1.85mm)

MEAN
SENSITIVITY : Insufficient data

LARGEST RING   : 0.6mm (an inner one) (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 60μm(i)(ii) SMALLEST CELL: 10μm (est.)(ii)

SMALLEST RING   : 0.2mm (an outer one) (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : A

FALSE RINGS   : None

DISTORTION   : Very slight

NOTES   : The authors consider this specimen to fall
                   within the genus <u>Protopiceoxylon</u> (Gothan).
                   There is a very sharp transition between
                   earlywood and latewood. Only a few cells
                   of each sort. (cf. Bailey & Faull, 1934.
                   <u>Sequoia sempervirens</u>)

FOSSIL WOOD RECORD SHEET A

NO: 8   SPECIES: Protopiceoxylon dacotense (Knowlton)
                           Vogellehner

LOCALITY   : Black Hills, S. Dakota. 4.8km N.W. of
                     Sturgis, U.S.A.

EVIDENCE OF
IN SITU FOREST: Fragments only

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 48°N.

MAP REFERENCE : S.H.&B.,1981. Map 29/30 pp.36-37

SPECIMEN
REFERENCE   : Knowlton, F.G. 1900. Fossil wood from the
                     Jurassic of the Black Hills. U.S. Geol.
                     Surv. 20th Ann. Report 2, 419-422
                     (Description) Read, C.B. 1932. Pinoxylon
                     dakotense from the Cretaceous of the Black
                     Hills. Bot. Gaz. 93, 173-189

SYNONYMY   : Pinoxylon dakotense   Knowlton   1900
                     Protopiceoxylon dacotense (Knowlton)
                     Medlyn & Tidwell 1979

LOCATION OF
SPECIMEN   : 30871, U.S. National Museum

NO. OF
SPECIMENS   : 1 (and slides)

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 8   SPECIES: <u>Protopiceoxylon dacotense</u>   (Knowlton)
                            Vogellehner

DIAMETER   :   Not stated

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :

LARGEST RING   :   Only one ring figured: 1.25mm   (ii)

NO. OF CELLS   :   36 (ii)   All cell sizes (ii)
E/WOOD   :   15   L/WOOD: 21
LARGEST CELL   :   50μm –   SMALLEST CELL: 10μm

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   B

FALSE RINGS   :   There is a band of resin canals of
                      distinctly traumatic appearance which as it
                      is in the earlywood could well be a frost
                      effect, or an insect attack

DISTORTION   :   None evident

NOTES   :   Earlywood grades into a wide band of
                      latewood

FOSSIL WOOD RECORD SHEET   A

NO: 9   SPECIES: Protopiceoxylon wordii Walton

LOCALITY   : Near   Cape   Dufferin,   Stor   Fiord,
                      Spitzbergen. At an altitude of 500m on
                      west slope of the mountain south of Balt
                      Glacier

EVIDENCE OF
IN SITU FOREST: Fragments only

HORIZON   : Upper Jurassic

PALAEOPOSITION: 61°N

MAP REFERENCE : S.H.&B.,1981. Map 34 p.41

SPECIMEN
REFERENCE   : Walton, J. 1927.   On some fossil woods of
                     Mesozoic and Tertiary age from the Arctic
                     Zone. Ann. Bot. 61. 239-252

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : B.M. (N.H.) Slides V. 19059-62

NO. OF
SPECIMENS   : 'Several' mentioned in the paper (i)

SPECIMEN
SIZE   : As for diameter, no hand specimens

FOSSIL WOOD RECORD SHEET   B

NO: 9   SPECIES: <u>Protopiceoxylon wordii</u> Walton

DIAMETER   : Approx. 5cm, allowing for the specimen
                     having fractured in the process of slide
                     making (iii)

NO. OF RINGS   : 47 rings; innermost ones ignored when they
                     were measured (iii)

MEAN
SENSITIVITY   : 0.257

LARGEST RING   : 0.8mm (iii)

NO. OF CELLS   : 36   All cell sizes (iii)
E/WOOD   : 10   **L/WOOD:** 26
LARGEST CELL : 45µm   **SMALLEST CELL:** 13.5µm

SMALLEST RING : 0.15mm (iii)

NO. OF CELLS   : 7   All cell sizes (iii)
E/WOOD   : 4   **L/WOOD:** 3
LARGEST CELL : 27µm   **SMALLEST CELL:** 9µm

RING TYPE   : A

FALSE RINGS   : A ring of large resin canals in the 6th
                     year out from the pith, just after the
                     beginning of latewood; possibly due to
                     damage. Looks rather late in the season
                     for frost

DISTORTION   : Some, but not too severe as to affect
                     measurements

NOTES   : Much latewood in the rings throughout the
                     sequence. Occasional larger rings with
                     broad bands of latewood.

FOSSIL WOOD RECORD SHEET   A

NO: 10   **SPECIES:**   <u>Protocedroxylon araucarioides</u> Gothan

LOCALITY   :   Cape Dufferin, Stor Fiord, South of Agardh
                      Bay, Spitzbergen

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Jurassic

PALAEOPOSITION: 61°N

MAP REFERENCE :   S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   :   Walton, J. 1927. On some fossil woods of
                  Mesozoic and Tertiary age from the Arctic
                  Zone. Ann. Bot. 61, 239-252

SYNONYMY   :   <u>Protocedroxylon araucarioides</u> Gothan 1910.
                  <u>Protocedroxylon araucarioides</u> Vogellehner
                                                       1968

LOCATION OF
SPECIMEN   :   B.M. (N.H.) Slides V. 19063-4 (iii)

NO. OF
SPECIMENS   :   1 (i)

SPECIMEN
SIZE   :   5.5cm diameter. 3.3cm deep, R/L/S   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 10   SPECIES: Protocedroxylon araucarioides Gothan

DIAMETER   : 5.5cm   (iii)

NO. OF RINGS   : 75 in 23mm   (iii)

MEAN
SENSITIVITY   :

LARGEST RING   : 0.66mm   (iii)

NO. OF CELLS   : 20   All cell sizes (iii)
E/WOOD   : 18   L/WOOD: 2
LARGEST CELL   : 44μm   SMALLEST CELL: 11μm

SMALLEST RING : 0.12mm   (iii)

NO. OF CELLS   : 6   All cell sizes (iii)
E/WOOD   : 4   L/WOOD: 2
LARGEST CELL   : 44μm   SMALLEST CELL: 11μm

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : Only cracking   (iii)

NOTES   : Much latewood in the first few rings but
                   very little after that. Noted by Walton
                   and also Gothan

FOSSIL WOOD RECORD SHEET   A

NO: 11   SPECIES: <u>Planoxylon hectori</u> Stopes

LOCALITY   :   Western Side, Amuri Bluff, New Zealand

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Cretaceous
                         (D.C. Mildenhall 1980.   N.Z. Geol.Surv.)

PALAEOPOSITION: 67°S

MAP REFERENCE :   S.H.&B.,1981.   Map 24 p.31

SPECIMEN
REFERENCE   :   Stopes, M.C. 1916.   An early type of the
                         Abietineae(?) from the Cretaceous of New
                         Zealand. Ann. Bot. 30, 111-125

SYNONYMY   :   <u>Planoxylon hectori</u> Stopes 1916

LOCATION OF
SPECIMEN   :   B.M. (N.H.) V. 52823 and slides

NO. OF
SPECIMENS   :   One, cut into several pieces

SPECIMEN
SIZE   :   28 x 20 x 7cm thick.   More of one side of
                         the trunk preserved   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 11   SPECIES: <u>Planoxylon hectori</u> Stopes

DIAMETER   :   Originally at least 28cm, preservation of
                      wood structure does not extend fully to the
                      outside of the specimen.

NO. OF RINGS   :   108 (106 measured, starting the 3rd year).
                   Another run of 91 rings also measured on a
                   different portion of the specimen. As it
                   was impractical to tie the slides to the
                   rock specimen on which the ring
                   measurements were carried out, one large
                   and one small ring were chosen from a slide

MEAN
SENSITIVITY   :   106 rings: 0.290   91 rings: 0.326

LARGEST RING   :   1.1mm (iii) Large rings near the pith:
                   not well enough preserved to measure

NO. OF CELLS   :   36 (iii) All cell sizes (iii)
E/WOOD   :   9   L/WOOD: 27
LARGEST CELL   :   67.5μm   SMALLEST CELL: 11.25μm

SMALLEST RING :   0.25mm (iii)

NO. OF CELLS   :   7 (iii)   All cell sizes (iii)
E/WOOD   :   4   L/WOOD: 3
LARGEST CELL   :   58.5μm   SMALLEST CELL: 11.25μm

RING TYPE   :   A

FALSE RINGS   :   None seen

DISTORTION   :   Some, but not v. severe

NOTES   :   Large amounts of latewood in the rings,
                   especially the wider ones

FOSSIL WOOD RECORD SHEET   A

NO: 12   SPECIES: <u>Protopiceoxylon johnseni</u> (Schroeter)
                          Edwards

LOCALITY   :   King Charles Land   (E. Spitzbergen)

EVIDENCE OF
IN SITU FOREST: Loose fragment

HORIZON   :   Lower Cretaceous

PALAEOPOSITION: 61°N

MAP REFERENCE :   S.H.&B.,1981.   Map 31 P.38

SPECIMEN
REFERENCE   :   Edwards, W.N. 1925. On <u>Protopiceoxylon</u>
                      <u>johnseni</u> (Schroeter), a Mesozoic coniferous
                      wood. Ann. Bot. 39, 1-6

SYNONYMY   :

LOCATION OF
SPECIMEN   :   B.M. (N.H.) Slides V. 13139-41
                      (Possibly some of Schroeter's original
                      slides)

NO. OF
SPECIMENS   :   3 slides

SPECIMEN
SIZE   :   Largest dimension, 18mm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 12   SPECIES: <u>Protopiceoxylon johnseni</u> (Schroeter)
                            Edwards

DIAMETER   :   15mm   (iii)

NO. OF RINGS   :   32   (iii)   (30 measured)

MEAN
SENSITIVITY   :   0.315

LARGEST RING   :   0.7mm   (iii)

NO. OF CELLS   :   37   All cell sizes (iii)
E/WOOD   :   3   **L/WOOD:**   34
                      Transition latewood (Larson, 1969)
LARGEST CELL   :   45µm   **SMALLEST CELL:**   9.0µm

SMALLEST RING   :   Not well preserved therefore:-
                      A small ring: 0.23mm

NO. OF CELLS   :   17   All cell sizes (iii)
E/WOOD   :   4   **L/WOOD:**   13
                      Transition latewood (Larson, 1969)
LARGEST CELL   :   27µm   **SMALLEST CELL:**   6.75µm

RING TYPE   :   C

FALSE RINGS   :   None

DISTORTION   :   Most of the cells shrunken

NOTES   :   Some of the rings 'wedge out' on one side
                      of the specimen; it was probably a branch.
                      In measuring the ring widths, these rings
                      were measured where they were apparently of
                      normal width

FOSSIL WOOD RECORD SHEET   A

NO: 13   **SPECIES:**   <u>Dadoxylon kerguelenense</u> Seward
(See also No 17)

LOCALITY   :   Kerguelen Island

**EVIDENCE OF
IN SITU FOREST:**   Fragment

HORIZON   :   Early Tertiary

PALAEOPOSITION:

MAP REFERENCE :

**SPECIMEN
REFERENCE**   :   Edwards, W.N. 1921. Fossil coniferous wood
from Kerguelen Island. Ann. Bot. 35, 610-7

SYNONYMY   :

**LOCATION OF
SPECIMEN**   :   B.M. (N.H.) Slide V. 5867 (a) T/S

**NO. OF
SPECIMENS**   :   1 and slides V. 8388-90 made many years
earlier

**SPECIMEN
SIZE**   :

FOSSIL WOOD RECORD SHEET   B

NO: 13   **SPECIES:**   <u>Dadoxylon kerguelenense</u> Seward
(See also No 17)

DIAMETER   :   The very slight curvature of the rings
                          indicate that it was a large trunk

NO. OF RINGS :   47

**MEAN
SENSITIVITY**   :   0.256

LARGEST RING :   0.96mm   (iii)

NO. OF CELLS :   32   All cell sizes (iii)
E/WOOD   :   30   **L/WOOD:**   2
LARGEST CELL :   38.5μm   **SMALLEST CELL:**   15μm

SMALLEST RING :   0.27mm   (iii)

NO. OF CELLS :   8   All cell sizes (iii)
E/WOOD   :   7   **L/WOOD:**   1
LARGEST CELL :   33μm   **SMALLEST CELL:**   11μm

RING TYPE   :   E

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Only a few small tracheids at the end of
                          each season

FOSSIL WOOD RECORD SHEET A

NO: 14   SPECIES: Podocarpoxylon aparenchymatosum Gothan

LOCALITY   : Seymour Island, Antarctic Peninsula

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Tertiary

PALAEOPOSITION: 56°S

MAP REFERENCE : S.H.&B.,1981. Map 20 p.27

SPECIMEN
REFERENCE   : Gothan, W. 1908. Die fossilen Hölzer von
                       der Seymour und Snow Hill Insel.
                       Wissenschaftliche Ergebnisse der
                       schwedischen Südpolar-Expedition
                       3, Ch.8, 1-33

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated (i)

FOSSIL WOOD RECORD SHEET   B

NO: 14   SPECIES: Podocarpoxylon aparenchymatosum Gothan

DIAMETER   : Not given (i) Ring boundaries almost
                     straight so that a large specimen is
                     indicated

NO. OF RINGS   : Only 4 figured (i)

MEAN
SENSITIVITY   : Too few rings to calculate

LARGEST RING   : 1.8mm (i)

NO. OF CELLS   : 48 (i)
E/WOOD   :   L/WOOD:
                     No high power of T/S figured
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING : 1.2mm (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Only a few small tracheids at the end of
                  the season

FOSSIL WOOD RECORD SHEET   A

NO: 15   SPECIES: Dadoxylon pseudoparenchymatosum Gothan

LOCALITY   :   Seymour Island, Antarctic Peninsula

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Lower Tertiary

PALAEOPOSITION: 56°S

MAP REFERENCE :   S.H.&B.,1981.   Map 20 p.27

SPECIMEN
REFERENCE   :   As for No. 14

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   :

SPECIMEN
SIZE   :   Not stated   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 15   SPECIES: <u>Dadoxylon pseudoparenchymatosum</u> Gothan

DIAMETER   :   Not given (i). Ring boundaries almost
                      straight so that a large specimen is
                      indicated

NO. OF RINGS   :   Only 4 figured   (i)

MEAN
SENSITIVITY   :   Too few rings to calculate

LARGEST RING   :   1.7mm   (i)

NO. OF CELLS   :   Photo too poor in this region
E/WOOD   :   L/WOOD:
                   Details could not be seen
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :   1.1mm   (i)

NO. OF CELLS   :   38   (i)
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Just a few smaller tracheids at the end of
                   the season

FOSSIL WOOD RECORD SHEET   A

NO: 16   SPECIES: <u>Laurinoxylon uniseriatum</u> Gothan

LOCALITY   :   Snow Hill Island, Antarctic Peninsula

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Lower Tertiary

PALAEOPOSITION: 60°S

MAP REFERENCE :   S.H.&B.,1981.   Map 20 p.27

SPECIMEN
REFERENCE   :   (See No. 14)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 16   **SPECIES:** <u>Laurinoxylon uniseriatum</u> Gothan

DIAMETER   : Ring boundaries almost straight so that a
                        large specimen is indicated

NO. OF RINGS : Only 4 figured

**MEAN
SENSITIVITY**   : Not enough rings to calculate

LARGEST RING : 1.4mm (i)

NO. OF CELLS : Not clear in photo
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 0.14mm (i) **SMALLEST CELL:**
                        Vessel

SMALLEST RING : 1.3mm (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 0.14mm (i) **SMALLEST CELL:**
                        Vessel

RING TYPE   : B/C

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 17   SPECIES: Cupressinoxylon antarcticum Beust

LOCALITY   : Kerguelen Island

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Tertiary

PALAEOPOSITION:

MAP REFERENCE :

SPECIMEN
REFERENCE   : Slides not described by Edwards, 1921
                     (cf. No. 13) but very similar to his V.
                     13615a in Ann. Bot. 35, 1921

SYNONYMY   : Species described by Beust, 1884.
                     Beust, F. Untersuchung über fossile Hölzer
                     aus Grönland. Neue Denksch. d. allg.
                     Schweiz. Ges., Bd. XXIX

LOCATION OF
SPECIMEN   : B.M. (N.H.) Slide V. 20453a

NO. OF
SPECIMENS   : 1. 3 slides T/S, R/L/S, T/L/S

SPECIMEN
SIZE   : After slide-making, 9.5 x 3 x 1.75 cm

FOSSIL WOOD RECORD SHEET   B

NO: 17   SPECIES: Cupressinoxylon antarcticum Beust

DIAMETER   :   3cm

NO. OF RINGS   :   16

MEAN
SENSITIVITY   :

LARGEST RING   :   1.42mm   (iii)

NO. OF CELLS   :   47   All cell sizes   (iii)
E/WOOD   :   44   L/WOOD: 3
LARGEST CELL   :   42μm   SMALLEST CELL: 14μm

SMALLEST RING :   1.2mm   (iii)

NO. OF CELLS   :   30   All cell sizes   (iii)
E/WOOD   :   27   L/WOOD: 3
LARGEST CELL   :   35μm   SMALLEST CELL: 14μm

RING TYPE   :   E

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Growth ring boundaries rather indistinct, a
                             few small tracheids at the end of each
                             season

FOSSIL WOOD RECORD SHEET   A

NO: 18   SPECIES: <u>Nicolia aegyptiaca</u> Unger

LOCALITY   : 11.2km S.E. of Cairo, Egypt

EVIDENCE OF
IN SITU FOREST: Fragment, part of a fossil forest

HORIZON   : Upper Cretaceous, Lower Tertiary

PALAEOPOSITION: 5°N

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Unger, F. 1859. Der versteinerte Wald bei
                   Cairo und einige andere Lager verkieselten
                   Holzes in Ägypten. Sitzber. K. Abad. Wiss.
                   Wien. 33, 209-233

SYNONYMY   : Unger's species:-
                   in: Endl. Gen. Plant. Suppl. 2. p.102
                   in: Endl. Chlorid. prot. pag. LXXXIX, 533

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : Not known

SPECIMEN
SIZE   : Not known

FOSSIL WOOD RECORD SHEET   B

NO: 18   SPECIES: <u>Nicolia aegyptiaca</u> Unger

DIAMETER   : A large trunk, part of a fossil forest

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   :

LARGEST RING   : Dimensions not given for all the figures

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   : Very faint ring boundaries

FOSSIL WOOD RECORD SHEET   A

NO: 19   SPECIES: <u>Dadoxylon aegyptiacum</u> Unger

LOCALITY   :   11.2Km S.E. of Cairo, Egypt

EVIDENCE OF
IN SITU FOREST: Fragment, part of a fossil forest

HORIZON   :   Upper Cretaceous, Lower Tertiary

PALAEOPOSITION: 5°N

MAP REFERENCE :   S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   :   Unger, F. 1859.   Der versteinerte Wald bei
                    Cairo und eininge andere Lager verkieselten
                    Holzes in Ägypten.   Sitzber, K. Abad. Wiss.
                    Wien. 33, 209-233

SYNONYMY   :   Unger's species:-
                    in: Endl. Gen. Plant. Suppl. 2.   p.102
                    in: Endl. Chlorid. prot. pag. LXXXIX. 533

LOCATION OF
SPECIMEN   :   Not known

NO. OF
SPECIMENS   :   Not known

SPECIMEN
SIZE   :   Not known

FOSSIL WOOD RECORD SHEET   B

NO: 19   SPECIES: <u>Dadoxylon aegyptiacum</u> Unger

DIAMETER   :   A large trunk, part of a fossil forest

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :

LARGEST RING   :   Dimensions not given for all the figures

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :

DISTORTION   :

NOTES   :   Very faint ring boundaries

FOSSIL WOOD RECORD SHEET   A

NO: 20   **SPECIES:** <u>Dadoxylon rollei</u> Unger

LOCALITY   : 11.2km S.E. of Cairo, Egypt

EVIDENCE OF
IN SITU FOREST: Fragment, part of a fossil forest

HORIZON   : Upper Cretaceous, Lower Tertiary

PALAEOPOSITION: 5°N

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Unger, F. 1859. Der versteinerte Wald bei
Cairo und einige andere Lager verkieselten
Holzes in Ägypten. Sitzber. K. Akad. Wiss.
Wien. 33, 209-233

SYNONYMY   : Unger's species:-
in: Endl. Gen. Plant. Suppl. 2. p.102
in: Endl. Chlorid. prot. pag. LXXXIX, 533

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : Not known

SPECIMEN
SIZE   : Not known

FOSSIL WOOD RECORD SHEET   B

NO: 20   SPECIES: <u>Dadoxylon rollei</u> Unger

DIAMETER   : A large trunk, part of a fossil forest

NO. OF RINGS : None

MEAN
SENSITIVITY :

LARGEST RING : Dimensions not given for all the figures

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   :

NOTES   : Complete absence of rings

FOSSIL WOOD RECORD SHEET A

NO: 21   SPECIES: <u>Taxoxylon cretaceum</u> Unger

LOCALITY   : 11.2km S.E. of Cairo, Egypt

EVIDENCE OF
IN SITU FOREST: Fragment, part of a fossil forest

HORIZON   : Upper Cretaceous, Lower Tertiary

PALAEOPOSITION: 5°N

MAP REFERENCE : S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   : Unger, F. 1859. Der versteinerte Wald bei
                   Cairo und einige andere Lager verkieselten
                   Holzes in Ägypten. Sitzber. K. Akad. Wiss.
                   Wien. 33, 209-233

SYNONYMY   : Unger's species:-
                   in: Endl. Gen. Plant. Suppl. 2. p.102
                   in: Endl. Chlorid. prot. pag. LXXXIX, 533

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : Not known

SPECIMEN
SIZE   : Not known

FOSSIL WOOD RECORD SHEET   B

NO: 21   SPECIES: <u>Taxoxylon cretaceum</u> Unger

DIAMETER   : A large trunk, part of a fossil forest

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :

LARGEST RING : Dimensions not given for all the figures

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   : Just a few smaller cells at the ring
                  boundary

FOSSIL WOOD RECORD SHEET A

NO: 22   SPECIES: <u>Dadoxylon dantzii</u> Potonie´

LOCALITY   : Mbaragandu Valley, Tanzania

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Makonde Beds, Upper Cretaceous
                     (oberen Kreide)

PALAEOPOSITION: 28ºS

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Potonie´, H. 1902. Fossile Holzer aus der
                     oberen Kreide Deutsch-Ostafrikas, in:-
                     Die Reisen des Bergassessors Dr. Dantz in
                     den Jahren 1898-1900. Mitt. aus den
                     deutschen Schutzgebieten Bd. XV, 227-230

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : Not known

SPECIMEN
SIZE   : At least 6cm (i)

FOSSIL WOOD RECORD SHEET   B

NO: 22   SPECIES: <u>Dadoxylon dantzii</u> Potonie

DIAMETER   : At least 6cm   (i)

NO. OF RINGS : About 13 figured (ii)

MEAN
SENSITIVITY   :

LARGEST RING : About 0.5cm (ii)

NO. OF CELLS : No details given
E/WOOD   :   L/WOOD:
                 No magnification factor given
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None figured

DISTORTION   : None evident

NOTES   : Very slight growth ring boundaries

FOSSIL WOOD RECORD SHEET   A

NO: 23   SPECIES: <u>Protocedroxylon paronai</u> Negri

LOCALITY   : Rumia, near Iefren, (now Ya'Fran)
                      Tripolitania, Libya

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Middle Cretaceous

PALAEOPOSITION: 13°N

MAP REFERENCE : S.H.&B.,1981.   Map 26 p.33

SPECIMEN
REFERENCE   : Negri, G. 1914. Sopra alenni legni fossili
                      del Gebel Tripolitano.
                      Bull. Soc. Geol. Ital. 33, 321-344

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 23   SPECIES: <u>Protocedroxylon paronai</u> Negri

DIAMETER   : The straight ring boundaries indicate a
                     large trunk

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   :

LARGEST RING   : One ring quoted: 2.6mm (i)

NO. OF CELLS   : Not stated
E/WOOD   :   L/WOOD:
LARGEST CELL   : Av. 50µm   SMALLEST CELL:
                  (i) (ii)

SMALLEST RING : Not stated

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None stated

DISTORTION   : None seen (ii)

NOTES   : Ring boundary consisting of a few smaller
                     cells

FOSSIL WOOD RECORD SHEET   A

NO: 24   SPECIES: <u>Protocedroxylon paronai</u> Negri

LOCALITY   :   Scekscuik, near Iefren (now. Ya'Fran)
                    Tripolitania, Libya

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Middle Cretaceous

PALAEOPOSITION: 13°N

MAP REFERENCE :   S.H.&B.,1981.   Map 26 p.33

SPECIMEN
REFERENCE   :   Negri, G. 1914.   Sopra alenni legni fossili
                    del Gebel Tripolitano. Bull. Soc. Geol.
                    Ital. 33, 321-344

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Not known

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 24   SPECIES: Protocedroxylon paronai Negri

DIAMETER   : Not stated

NO. OF RINGS   : Rings absent

MEAN
SENSITIVITY   :

LARGEST RING   : Rings absent

NO. OF CELLS   : No details given for all cell sizes
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   : None seen (ii)

NOTES   : The same species as No. 23 but without
                   rings

FOSSIL WOOD RECORD SHEET   A

NO: 25   SPECIES: <u>Araucarioxylon madagascariense</u> Fliche

LOCALITY   :   Near Diego-Suarez, Malagasy (formerly
                      Madagascar)

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Cretaceous

PALAEOPOSITION: 31°S

MAP REFERENCE :

SPECIMEN
REFERENCE   :   Fliche, P. 1900. Note sur un bois fossile
                      de Madagascar. Bull. Soc. Geol. de France.
                      3°. Serie 28, 470-472

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Not known

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :

FOSSIL WOOD RECORD SHEET   B

NO: 25   SPECIES: <u>Araucarioxylon madagascariense</u> Fliche

DIAMETER   :   Only a brief descriptive note but a
                    definite statement that there were no
                    growth rings

NO. OF RINGS : None

MEAN
SENSITIVITY   :

LARGEST RING : No details

NO. OF CELLS : No details for all cell sizes
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING : .

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : 0

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 26   SPECIES: <u>Dadoxylon</u> sp.

LOCALITY   :   T'in Wana, 50km S.E. of Agades, Niger

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Lower Cretaceous

PALAEOPOSITION: 2°N

MAP REFERENCE :   S.H.&B.,1981.   Map 30 p.37

SPECIMEN
REFERENCE   :   Williams, S. 1930. The geological
                     collection from the South Central Sahara
                     made by Mr. F. Rodd. III. Fossil Wood.
                     Q.J.G.S. 86, 408-409

SYNONYMY   :

LOCATION OF
SPECIMEN   :   Not known

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   10 x 8.5 (radial) x 8cm (tangential)   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 26   SPECIES: <u>Dadoxylon</u> sp.

DIAMETER   : Ring boundary almost straight, indicating a
                       large trunk

NO. OF RINGS   : Only one ring boundary figured   (ii)

MEAN
SENSITIVITY   :

LARGEST RING   : Not applicable

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 41μm   SMALLEST CELL: 12μm
                   Data from figure (ii)

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None shown

DISTORTION   :

NOTES   : Just two or three smaller cells indicating
                    a ring boundary

FOSSIL WOOD RECORD SHEET   A

NO: 27   SPECIES: <u>Protopodocarpoxylon rochii</u> Boureau

LOCALITY   :   Lagon, 36km au Sud de Lere, sur la route de
                      Pala a Lere, Tchad Territory

EVIDENCE OF
IN SITU FOREST: Fragment of large trunk

HORIZON   :   Upper Jurassic, Lower Cretaceous

PALAEOPOSITION: 7°S

MAP REFERENCE :   S.H.&B.,1981.   Map 30 p.37

SPECIMEN
REFERENCE   :   Boureau, E. 1952.   Étude des flores
                      fossiles du Territoire du Tchad 1.
                      <u>ProtopodocarpoXylon rochii</u> N. sp., bois
                      fossile Mésozoïque. B. Mus. nat. Hist.
                      natur. 2° série 24, 223-232

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   4 x 8 x 11cm (i)

FOSSIL WOOD RECORD SHEET   B

NO: 27   **SPECIES:** <u>Protopodocarpoxylon rochii</u> Boureau

DIAMETER   : A portion of a substantial trunk

NO. OF RINGS : Slide 1. 11 rings   (i)
                   Slide 2.   9 rings   (i)

MEAN
SENSITIVITY   :

LARGEST RING : 4.4mm (i)

NO. OF CELLS : Figure only shows a part of a ring
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 81μm (i) **SMALLEST CELL:** 10μm (ii)

SMALLEST RING : 0.13mm (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : E

FALSE RINGS   :

DISTORTION   : None evident

NOTES   : Rings "nettement marques". "le bois final
                     peu developpe", only 1-4 flattened
                     tracheids

FOSSIL WOOD RECORD SHEET   A

NO: 28   SPECIES: <u>Dadoxylon</u> (cf. <u>australe</u> Arber)

LOCALITY   : Dannhauser, Natal

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Upper Ecca Formation, Natal Coal Measures,
                      Upper Permian

PALAEOPOSITION: 45°S

MAP REFERENCE :

SPECIMEN
REFERENCE   : Warren, E. 1912. On some specimens of
                      fossil woods in the Natal Museum. Ann.
                      Natal Museum 2, 345-380
                      Arber, E.A.N. 1910. A note on a fossil
                      wood from Intombi Camp, Ladysmith. Ann.
                      Natal Museum 2, 233 only
                      Arber, E.A.N. 1905. Catalogue of the
                      fossil plants of the Glossopteris flora in
                      the British Museum

SYNONYMY   :

LOCATION OF
SPECIMEN   : Natal Museum

NO. OF
SPECIMENS   : Many

SPECIMEN
SIZE   : No details given

FOSSIL WOOD RECORD SHEET   B

NO: 28   SPECIES: <u>Dadoxylon</u> (cf. <u>australe</u> Arber)

DIAMETER   : No details given

NO. OF RINGS   :

MEAN
SENSITIVITY   :

LARGEST RING   : 8mm (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 37μm   SMALLEST CELL: 28μm   (ii)

SMALLEST RING : 3mm (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : A

FALSE RINGS   :

DISTORTION   : Some crush zones (ii)

NOTES   : Well marked rings with 8-10 cells latewood.
                  Very sharp transition to latewood

FOSSIL WOOD RECORD SHEET   A

NO: 29   SPECIES: Protophyllocladoxylon maurianum Gazeau

LOCALITY   : Near M'Semrir, Morocco

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lias or Dogger, Lower Jurassic

PALAEOPOSITION: 24°N

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Gazeau, F. 1969. Sur quelques structures
                     des bois Mesozoiques du Maroc,
                     Protophyllocladoxylon maurianum Gazeau du
                     Jurassique du Haut Atlas. Notes et Mem.
                     Serv. Mines géol. du Maroc. Mem. 210,
                     108-117
                     Gazeau, F. & Koeniguer, J.C. 1967. Sur
                     quelques bois fossiles du Mesozoïque de
                     l'Afrique Nord-Equatoriale. C.R. 92°
                     Congr. Soc. Sav. Strasbourg.

SYNONYMY   :

LOCATION OF
SPECIMEN   : Fac. Sciences Paris No. 3556
                     (Boureau Coll.)

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : No details given

FOSSIL WOOD RECORD SHEET   B

NO: 29   SPECIES: <u>Protophyllocladoxylon maurianum</u> Gazeau

DIAMETER   : No details given

NO. OF RINGS   : No rings

MEAN
SENSITIVITY   :

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:
                   Cell size ranges from 40μm to 4μm, most
                   frequently 30μm   (i)

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   :

NOTES   : Growth rings absent

FOSSIL WOOD RECORD SHEET   A

NO: 30   SPECIES: <u>Protopodocarpoxylon teixeirae</u> Boureau

LOCALITY   : Au sud le Torres Vedras auprès du Mont du
                   Sorocco dans le hameau de Cadriceira.
                   Portugal. (Neocomian-au dessus du
                   Portlandian)

EVIDENCE OF
IN SITU FOREST: A large horizontal trunk

HORIZON   : Upper Jurassic

PALAEOPOSITION: 31°N

MAP REFERENCE : S.H.&B.,1981.   Map 30 p.37

SPECIMEN
REFERENCE   : Boureau, E. 1949. <u>Dadoxylon</u>
                   (<u>Araucarioxylon</u>) <u>teixeirae</u> N. sp. Bois
                   fossile du Jurassique supérieur portugais.
                   Com. Serv. géol. Portugal 29, 187-194

SYNONYMY   : Boureau, E. 1957. Sur le
                   <u>Protopodocarpoxylon teixeirae</u> Boureau.
                   Affinités Répartition géographique.
                   Signification stratigraphique. Com. Serv.
                   géol. Portugal 38, 423-430

LOCATION OF
SPECIMEN   : Museum National d'Histoire Naturelle de
                   Paris. Boureau 566

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 20m long, 1.3m diameter

FOSSIL WOOD RECORD SHEET   B

NO: 30   SPECIES: <u>Protopodocarpoxylon teixeirae</u> Boureau

DIAMETER   : 1.3m

NO. OF RINGS   : No rings

MEAN
SENSITIVITY   :

LARGEST RING   : Not applicable

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 60µm   SMALLEST CELL: 33µm

SMALLEST RING : Not applicable

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 31   SPECIES: <u>Protopodocarpoxylon teixeirae</u> Boureau

LOCALITY   : Dans un ravin en contrebas de la falaise
                    cretacee de Dir el Abiod, a une dizaine de
                    kilometres au nord d'Anonal et a environ
                    12km au sw d'ain Mellouk (Coordonnees
                    Lambert 719 x 243, feuille de Matarka).
                    Morocco

EVIDENCE OF
IN SITU FOREST: A large trunk

HORIZON   : Upper Jurassic or Lower Cretaceous

PALAEOPOSITION: 24°N.

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Boureau, E. 1951 Etude paleoxylologie de
                    l'Afrique du Nord (1): Presence de
                    <u>Dadoxylon (Araucarioxylon) teixeirae</u>
                    Boureau dans le Haut Atlas du Maroc. Notes
                    Serv. géol. Maroc 4, 123-133

SYNONYMY   : Boureau, E. 1957 Sur le
                    <u>Protopodocarpoxylon teixeirae</u> Boureau.
                    Affinités. Repartition geographique.
                    Signification stratigraphique. Com. Serv.
                    géol. Portugal 38, 423-430

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : Le tronc avait pres de deux metres de
                    longeur, mais etait debite en troncons de
                    differentes tailles et des menus fragments
                    qui jonchaient le sol

SPECIMEN
SIZE   : See above

FOSSIL WOOD RECORD SHEET   B

NO: 31   SPECIES: Protopodocarpoxylon teixeirae Boureau

DIAMETER   :   From the description it was clearly a large
                      trunk

NO. OF RINGS   :   Rings absent

MEAN
SENSITIVITY   :

LARGEST RING   :   Not applicable

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   70μm   SMALLEST CELL: 54μm

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   0

FALSE RINGS   :

DISTORTION   :

NOTES   :   No growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 32   SPECIES: Mesembrioxylon sp.

LOCALITY   :   S.W. of Barfak, Afghan-Turkistan

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Jurassic

PALAEOPOSITION: 22°N

MAP REFERENCE :   S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   :   Sitholey, R.V. 1940.   Jurassic plants from
                       Afghan-Turkistan. Mem. Geol. Surv.
                       Palaeontologica Indica 29, Mem. No. 1

SYNONYMY   :   Seward, A.C. 1919.   Fossil Plants. vol. 4.
                       Cambridge.
                       Sahni, B. 1931.   Revisions of Indian fossil
                       plants. II. Coniferales (b. petrifactions).
                       Palaeontologica Indica 11

LOCATION OF
SPECIMEN   :   K36/229 Geol. Surv. India.

NO. OF
SPECIMENS   :   26   (Not all well preserved)

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 32   SPECIES: <u>Mesembrioxylon</u> sp.

DIAMETER   : Not possible to interpret from figure

NO. OF RINGS   : Very indistinct in figure

MEAN
SENSITIVITY   :

LARGEST RING   : No information

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 46μm (ii)   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 33   SPECIES: Megaporoxylon zellei Kräusel

LOCALITY   :   Schlangenkopf bei Seeheim, (bezirk
                      Keetmanshoop) Reuning's Fossil Forest,
                      Amalia.   54km S.W. of Franzfontein,
                      Nambia, S.W. Africa

EVIDENCE OF
IN SITU FOREST: Fragment, 4ha of fossil trunks

HORIZON   :   Upper Dwyka Beds, Karroo Formation, Lower
                      Permian

PALAEOPOSITION: 42°S

MAP REFERENCE :   S.H.&B.,1981.   Map 57 p.70

SPECIMEN
REFERENCE   :   Kräusel, R. 1956.   Hölzer aus dem südlichen
                      Gebiet der Karru-Schichten Südwest-Afrikas.
                      Senckenbergiana Lethaea 37, 447-453

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Slides 7390/5-7 in the Senckenberg Museum,
                      Frankfurt a. M.

NO. OF
SPECIMENS   :   1 (in 5 pieces) in Windhoek Museum
                      4 in the Senckenberg, 7390/14

SPECIMEN
SIZE   :

FOSSIL WOOD RECORD SHEET   B

NO: 33   SPECIES: <u>Megaporoxylon zellei</u> Kräusel

DIAMETER   : One slice, 11 x 10 x 2cm (iii)   The
                   largest radius of the specimen is 11.2cm,
                   hence original diameter must have been at
                   least 22.4cm. The pith and inner 3(?)
                   rings are missing.   (iii)

NO. OF RINGS : 26 on the slide, not clear enough on the
                 specimen to justify counting   (iii)

MEAN
SENSITIVITY   : 0.268

LARGEST RING : 2.1mm   (iii)

NO. OF CELLS : 54   All cell sizes (iii)
E/WOOD   : 50   L/WOOD: 4
LARGEST CELL : 40µm   SMALLEST CELL: 19µm

SMALLEST RING : 0.35mm

NO. OF CELLS : 10   All cell sizes (iii)
E/WOOD   : 8   L/WOOD: 2
LARGEST CELL : 38µm   SMALLEST CELL: 19µm

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : Some crush zones

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 34   **SPECIES:**   Not well enough preserved to assign to
                             a genus, but quite possibly a member
                             of the Protopinaceae

LOCALITY   : Judge Daly Promontory, Ellesmere Island

EVIDENCE OF
IN SITU FOREST: Very large trunks, but not actual stumps

HORIZON   : Early Tertiary

PALAEOPOSITION: 76°N

MAP REFERENCE :   S.H.&B.,1981.   Map 19 p.26

SPECIMEN
REFERENCE   : Christie, R.L. 1964.   Geological
                     reconnaissance of north-eastern Ellesmere
                     Island, District of Franklin. Geol. Surv.
                     of Canada. Memoir 331, 1-77

SYNONYMY   : N/A

LOCATION OF
SPECIMEN   : Botany Department, Bedford College, London

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 10 x 2.5 x 4.5cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 34   SPECIES: Not well enough preserved to assign to
                         a genus, but quite possibly a member
                         of the Protopinaceae

DIAMETER   :   The original account mentions many large
                        trunks

NO. OF RINGS   :   11   (iii)

MEAN
SENSITIVITY   :

LARGEST RING   :   3mm   (iii)

NO. OF CELLS   :   63   The crushed zone in the smallest ring
                        precludes a count of cells
E/WOOD   :   33   **L/WOOD:**   30
LARGEST CELL   :   50μm   (iii) **SMALLEST CELL:**   12μm   (iii)

SMALLEST RING :   2.5mm   (iii)

NO. OF CELLS   :
E/WOOD   :   **L/WOOD:**
LARGEST CELL   :   **SMALLEST CELL:**

RING TYPE   :   A

FALSE RINGS   :   None seen   (iii)

DISTORTION   :   A distinct crushed zone in each ring

NOTES   :   There is a sharp transition to latewood
                   which is a broad zone in each ring

FOSSIL WOOD RECORD SHEET   A

NO: 35   SPECIES: <u>Kaokoxylon</u> sp. (?)

LOCALITY   : Reuning's Fossil Forest, S.W. Africa.

EVIDENCE OF
IN SITU FOREST: Fragment, 4ha of fossil trunks (See No. 33)

HORIZON   : Upper Dwyka beds, somewhat below the
                     Mesosaurus Horizon, Lower Permian

PALAEOPOSITION: 42°S

MAP REFERENCE : S.H.&B.,1981.   Map 57 p.70

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : No. 7383/1-5, Senckenberg Museum

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 8 x 7.5 x 8cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 35   SPECIES: Kaokoxylon sp. (?)

DIAMETER   : Only one ring described   (iii)

NO. OF RINGS : Rings very faint and not reliable enough to
                 count

MEAN
SENSITIVITY   :

LARGEST RING : A large ring: 4mm (iii)

NO. OF CELLS : 115   All cell sizes (iii)
E/WOOD   : 113   L/WOOD: 2
LARGEST CELL : 35.25µm   SMALLEST CELL: 30µm

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None

DISTORTION   : None

NOTES   : These rings appeared to be the large inner
                 rings of a tree

FOSSIL WOOD RECORD SHEET   A

NO: 36   **SPECIES:** <u>Abietopitys perforata</u> (Gothan) Kräusel

LOCALITY   : Reuning's Fossil Forest. (See No. 33)

**EVIDENCE OF
IN SITU FOREST:** Fragment, 4ha of fossil trunks

HORIZON   : Upper Dwyka, Lower Permian

PALAEOPOSITION: 42°S

MAP REFERENCE : S.H.&B.,1981. Map 57 p.70

**SPECIMEN
REFERENCE**   : Kräusel, R. 1956 (see No. 33)

SYNONYMY   : <u>Dadoxylon perforatum</u> Gothan

**LOCATION OF
SPECIMEN**   : 7394/1-4, Senckenberg Museum

**NO. OF
SPECIMENS**   : 1

**SPECIMEN
SIZE**   : 10.5 x 5.0 x 8.0cm   (iii)

FOSSIL WOOD RECORD SHEET B

NO: 36   **SPECIES:** <u>Abietopitys perforata</u> (Gothan) Kräusel

DIAMETER : 10cm, centre of branch or trunk, pith not preserved (iii)

NO. OF RINGS : The rings are not all well defined and are therefore unreliable for counting

MEAN
SENSITIVITY :

LARGEST RING : Only one ring described: 4.5mm

NO. OF CELLS : 255   All cell sizes (iii)
E/WOOD : 251   **L/WOOD:** 4
LARGEST CELL : 17µm   **SMALLEST CELL:** 12µm

SMALLEST RING :

NO. OF CELLS :
E/WOOD :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE : E

FALSE RINGS : None

DISTORTION : Some small crush zones

NOTES : Large first rings of the tree

FOSSIL WOOD RECORD SHEET   A

NO: 37   SPECIES: <u>Phyllocladoxylon capense</u> Walton

LOCALITY   : Ganikobis, Distr. Berseba, S.W. Africa

EVIDENCE OF
IN SITU FOREST: Considerable quantity of fossil wood

HORIZON   : Upper Dwyka, Karroo Formation, Lower
                   Permian

PALAEOPOSITION: 48°S

MAP REFERENCE : S.H.&B.,1981. Map 57 p.70

SPECIMEN
REFERENCE   : Kräusel, R. & Range, P. 1928. Beiträge zur
                   Kenntnis der Karruformation
                   Deutsch-Südwest-Afrikas.
                   Beitr. geol. Erforsch. dtsch. Sch. Geb. 20,
                   1-55

SYNONYMY   : <u>P. capense</u>. Walton, J. 1925.
                   On South African fossil woods.
                   Ann. Sth. African Museum 22, 1-26

LOCATION OF
SPECIMEN   : Kr. 20, Museum für Naturkunde,
                   Humboldt-Universität, Berlin

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 37   SPECIES: Phyllocladoxylon capense Walton

DIAMETER   : The growth ring boundaries are straight,
                   indicating a large stem

NO. OF RINGS : Only one complete ring figured

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : Only one ring figured: 1.04mm (ii)

NO. OF CELLS : 30   All cell sizes (ii)
E/WOOD   : 27   L/WOOD: 3
LARGEST CELL : 36μm   SMALLEST CELL: 15μm

SMALLEST RING : Only one ring figured

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None figured

DISTORTION   : None illustrated

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 38   SPECIES: <u>Taxopitys africana</u> Kräusel

LOCALITY   : Doroskrater, S.W. Africa

EVIDENCE OF
IN SITU FOREST: 4ha of logs in Reuning's Fossil Forest

HORIZON   : Upper Dwyka, Lower Permian

PALAEOPOSITION: 42°S

MAP REFERENCE : S.H.&B.,1981.   Map 57 p.70

SPECIMEN
REFERENCE   : Kräusel & Range, 1928   (See No. 37)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Kr. 50, Museum für Naturkunde,
                     Humboldt-Universität, Berlin.

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 5cm in diameter   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 38   SPECIES: <u>Taxopitys africana</u> Kräusel

DIAMETER   : 5cm (i)
                   Includes pith (1.5cm)

NO. OF RINGS :

MEAN
SENSITIVITY   :

LARGEST RING : No complete ring figured, only a faint ring
                 boundary (ii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 28μm (ii) SMALLEST CELL: 20μm (ii)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   : None shown

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 39   SPECIES: Dadoxylon agathioides N. sp.

LOCALITY   : Mandro, Rajmahal Hills, Bihar, India

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Rajmahal Stage, Middle Jurassic, Upper
                      Gondwana

PALAEOPOSITION: 40°S

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Kräusel, R. & Jain, K.P. 1964. New fossil
                      coniferous woods from the Rajmahal Hills,
                      Bihar, India. Palaeobotanist 12, 59-67

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 24288/255 B.S.I.P. Museum, Lucknow

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 7 x 3cm (i)

FOSSIL WOOD RECORD SHEET   B

NO: 39   .   SPECIES: <u>Dadoxylon agathioides</u> N. sp.

DIAMETER   :   No indication given.   Growth rings
                  indistinct in figure (ii)

NO. OF RINGS :   Not stated

MEAN
SENSITIVITY :   Too few rings

LARGEST RING :   Not stated

NO. OF CELLS :   Growth ring boundary too faint
E/WOOD   :   L/WOOD:
LARGEST CELL :   48µm (i)   SMALLEST CELL: 13µm (i)

SMALLEST RING :   Not stated

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :   None stated

DISTORTION   :   None stated

NOTES   :   Rings very faint

FOSSIL WOOD RECORD SHEET   A

NO: 40   **SPECIES:** Indet. Conifer Wood

LOCALITY   : Estcourt, Natal, S. Africa

**EVIDENCE OF
IN SITU FOREST:** Very large specimen

HORIZON   : Permian

PALAEOPOSITION: 36°S.

MAP REFERENCE : S.H.&B.,1981.   Map 53 p.66

**SPECIMEN
REFERENCE**   : Not described

SYNONYMY   :

**LOCATION OF
SPECIMEN**   : Senckenberg Museum IV 16/3

**NO. OF
SPECIMENS**   : 1

**SPECIMEN
SIZE**   : 20 x 18 x 17cm   (iii)

FOSSIL WOOD RECORD SHEET B

NO: 40   SPECIES: Indet. Conifer Wood

DIAMETER   : The largest radius is 20cm giving a
                   possible diameter of 40cm. The earlywood
                   and latewood appear to be represented as
                   light and dark bands in the wood, but on
                   checking with a microscope, these are seen
                   not to be related to growth rings (iii)

NO. OF RINGS   : Impossible to determine rings due to crush
                   zones

MEAN
SENSITIVITY   :

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 42.5µm(iii) SMALLEST CELL: 25µm(iii)

RING TYPE   : Impossible to determine

DISTORTION   : Considerable   (iii)

NOTES   : A large specimen, but unfortunately not
                   well preserved

FOSSIL WOOD RECORD SHEET A

NO: 41   SPECIES: Indet. (Possibly <u>Dadoxylon arberi</u>,
                         Rodin 1951)

LOCALITY   : Kräusel's handwritten note with the
                   specimen states "Reuning's alte Fundstelle
                   südl. Atsab." S.W. Africa

EVIDENCE OF
IN SITU FOREST: Large trunk, 4ha of fossil trunks

HORIZON   : Upper Dwyka Beds, Karroo Formation, Lower
                   Permian

PALAEOPOSITION: 42°S

MAP REFERENCE : S.H.&B.,1981. Map 57 p.70

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : Senckenberg Museum R2

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Very large, apparently having been a few
                   metres long. 15 x 13cm in cross-section

FOSSIL WOOD RECORD SHEET   B

NO: 41   **SPECIES:**   Indet. (Possibly <u>Dadoxylon arberi</u>,
                              Rodin 1951)

DIAMETER   :   15cm   (iii)   From slide

NO. OF RINGS :   41 (iii)

MEAN
SENSITIVITY   :   0.422

LARGEST RING :   A large ring: 2.6mm   (iii)

NO. OF CELLS :   74   All cell sizes (iii)
E/WOOD   :   71   **L/WOOD:** 3
LARGEST CELL :   35µm   **SMALLEST CELL:** 18µm

SMALLEST RING : 0.7mm

NO. OF CELLS :   23   All cell sizes (iii)
E/WOOD   :   21   **L/WOOD:** 2
LARGEST CELL :   31µm   **SMALLEST CELL:** 17µm

RING TYPE   :   D

FALSE RINGS   :   None

DISTORTION   :   Some slight crushing

NOTES   :   On outside of trunk a helical arrangement
                      of the ends of leaf traces (?)
                      (Maheshwari, 1972)

FOSSIL WOOD RECORD SHEET   A

NO: 42   SPECIES: Circoporoxylon amarjolense N. sp.

LOCALITY   : Amarjola, Amrapara, Dist., Pakaur, Rajmahal
                     Hills, Bihar, India

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Rajmahal Stage, Middle Jurassic, Upper
                     Gondwana

PALAEOPOSITION: 40°S.

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Kräusel & Jain, 1964 (See 39)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 31835/52 B.S.I.P. Museum, Lucknow

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 5 x 1.5cm   (i)

FOSSIL WOOD RECORD SHEET B

NO: 42   SPECIES: <u>Circoporoxylon amarjolense</u> N. sp.

DIAMETER   : Growth rings straight in direction,
                   indicating a large specimen   (ii)

NO. OF RINGS : Only two whole rings figured   (ii)

MEAN
SENSITIVITY   : Too few rings

LARGEST RING : 40 tracheids wide   (i)   Dimensions of
                 figure at variance with text causing
                 problems in measuring cell sizes in the
                 figure

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :30μm (i)   SMALLEST CELL:13μm (i)

SMALLEST RING : 10 tracheids wide   (i)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : C

FALSE RINGS   : None stated

DISTORTION   : None stated

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 43   SPECIES: Taxaceoxylon N. gen.
                          Taxaceoxylon cf. rajmahalense
                          (Bhardwaj) Krausel & Jain

LOCALITY   : Amarjola, Amrapara, Dist., Pakaur, Rajmahal
                    Hills, Bihar, India

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Rajmahal Stage, Middle Jurassic

PALAEOPOSITION: 40°S

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Kräusel & Jain 1964 (See Nos. 39, 42)

SYNONYMY   : Bhardwaj, D.C. 1952. On a new species of
                    Taxoxylon Unger from the Jurassic of the
                    Rajmahal Hills, Bihar, India. Lloydia 15
                    (4), 234-240

LOCATION OF
SPECIMEN   : 31834/52 B.S.I.P. Lucknow, India

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 6cm (long) x 2cm (broad) (i)

FOSSIL WOOD RECORD SHEET B

NO: 43   **SPECIES:** <u>Taxaceoxylon</u> N. gen.
<u>Taxaceoxylon</u> cf. <u>rajmahalense</u>
(Bhardwaj) Kräusel & Jain

DIAMETER   : Growth rings straight in direction and
                     therefore probably a large diameter   (ii)

NO. OF RINGS : Only two whole rings figured   (ii)

**MEAN
SENSITIVITY**   : Too few rings

LARGEST RING : 40 cells wide (i) Dimensions of figure at
                     variance with text causing problems in
                     measuring cell sizes in the figure

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 30μm (i)   **SMALLEST CELL:**   10μm (i)

SMALLEST RING : 20 cells wide   (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : C

FALSE RINGS   : None stated

DISTORTION   : None stated

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 44   SPECIES: Rhexoxylon tetrapteridoides Walton

LOCALITY   :   Matatiele. S. Africa   (See map in Walton,
                      1923)

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Stormberg Series, Late Triassic

PALAEOPOSITION: 57°S

MAP REFERENCE :   S.H.&B..1981.   Map 50 p.57

SPECIMEN
REFERENCE   :   Kräusel, R. 1956.   Lianen aus den
                      Karru-Schichten Süd-Afrikas.
                      Senckenbergiana Lethaea 37. 1-23

SYNONYMY   :   Walton, J. 1923.   On Rhexoxylon. Bancroft.
                      A Triassic genus of plants exhibiting a
                      liane-type of vascular organisation.
                      Phil. Trans. R. Soc. B212. 79-109

LOCATION OF
SPECIMEN   :   Slide 7258/2, Senckenberg Museum
                      (Spec. 124 in S.A. Museum, Capetown)

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   On slide: 7 x 6cm (T/S)   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 44   SPECIES: <u>Rhexoxylon tetrapteridoides</u> Walton

DIAMETER   : 7cm   (iii)

NO. OF RINGS : 22   (iii)   (Outer part of xylem bundle)

MEAN
SENSITIVITY : 0.416

LARGEST RING : 1.3mm   (iii)

NO. OF CELLS : 49   All cell sizes (iii)
E/WOOD   : 47   L/WOOD: 2
LARGEST CELL : 26μm   SMALLEST CELL: 13μm

SMALLEST RING : 0.33mm   (iii)

NO. OF CELLS : 13   All cell sizes (iii)
E/WOOD   : 11   L/WOOD: 2
LARGEST CELL : 25μm   SMALLEST CELL: 13μm

RING TYPE   : D

FALSE RINGS   : Only one

DISTORTION   : None

NOTES   : Very high mean sensitivity

FOSSIL WOOD RECORD SHEET   A

NO: 45   SPECIES: <u>Tordoxylon steynspruitense</u> gen. et sp.
                     nov.

LOCALITY   : Fourie Farm. Steynspruit. Orange Free
                     State. near Thaba 'Nchu. S. Africa

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Beaufort Beds. Karroo Formation.
                     Lower Triassic

PALAEOPOSITION: 46°S

MAP REFERENCE : S.H.&B..1981. Map 54 p.67

SPECIMEN
REFERENCE   : Kräusel. R. 1956 (See No. 44)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Specimen 7362. slides 7362/1-4. Senckenberg
                     Museum

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : On slide: 2.5 x 2.0cm (Specimen cut up to
                     make slides)

FOSSIL WOOD RECORD SHEET   B

NO: 45   SPECIES: <u>Tordoxylon steynspruitense</u> gen. et sp.
                         nov.

DIAMETER   :   Widest diameter 2.5cm   (iii)

NO. OF RINGS :   8 complete rings   (iii)

**MEAN
SENSITIVITY**   :   Insufficient data

LARGEST RING :   2.82mm   (iii)

NO. OF CELLS :   52   All cell sizes (iii)
E/WOOD   :   50   **L/WOOD:** 2
LARGEST CELL :   70.5µm   SMALLEST CELL: 16.5µm

SMALLEST RING :   0.82mm   (iii)

NO. OF CELLS :   19   All cell sizes (iii)
E/WOOD   :   17   **L/WOOD:** 2
LARGEST CELL :   56.4µm   SMALLEST CELL: 16.5µm

RING TYPE   :   E

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Stem with very asymmetric xylem

FOSSIL WOOD RECORD SHEET A

NO: 46   SPECIES: Indet.

LOCALITY   : Chemnitz. Hilbersdorf

EVIDENCE OF
IN SITU FOREST: Large specimen

HORIZON   : Rotliegendes. Lower Permian

PALAEOPOSITION: 5°N

MAP REFERENCE : S.H.&B..1981. Map 57 p.70

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : Senckenberg Museum (not registered)

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 21 x 19 x 3cm   (iii)
                     (c/section of trunk only, no slides)

FOSSIL WOOD RECORD SHEET   B

NO: 46   . SPECIES: Indet.

DIAMETER   :   Largest radius is 15.5cm. diam. - 31cm
                      (iii)

NO. OF RINGS :   Too faint to assess accurately

MEAN
SENSITIVITY   :

LARGEST RING :   Rings very difficult to distinguish but a
                  number appeared to be about 7mm wide
                  (iii)

NO. OF CELLS :   Cannot be estimated from specimen
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :   Not possible to establish

DISTORTION   :   Many crush zones   (iii)

NOTES   :   If the growth rings are annual. substantial
                  growth was made each year

FOSSIL WOOD RECORD SHEET   A

NO: 47   . SPECIES: <u>Anacardioxylon mollii</u> Kräusel

LOCALITY   : Boom Baru Palembang am Ajer Musi.
                     S. Sumatra. Indonesia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Middle Palembang Beds. Upper Miocene.
                     Tertiary of the foreland of Palembang

PALAEOPOSITION: 3°S

MAP REFERENCE :

SPECIMEN
REFERENCE   : Kräusel. R. 1922. Fossile Hölzer aus dem
                     Tertiär von Sud-Sumatra. Verh. geol.
                     mijnbouwk. Genootsch. Nederl. Kolon.. geol.
                     Ser. 5(ii). 231-287

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated (i)

FOSSIL WOOD RECORD SHEET   B

NO: 47   SPECIES: <u>Anacardioxylon mollii</u> Kräusel

DIAMETER   : Dicot. wood with faint rings   (ii)
                 Diffuse porous wood

NO. OF RINGS :

MEAN
SENSITIVITY   :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 48   SPECIES: Sapindoxylon janssonii Kräusel

LOCALITY   : Sungi Impus Melantjar, S. Sumatra.
                     Indonesia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Miocene. Tertiary of Barissangebirge
                     von Benkulen, Sumatra.

PALAEOPOSITION: 3°S

MAP REFERENCE :

SPECIMEN
REFERENCE   : Kräusel, R. 1922 (See No. 47)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated (i)

FOSSIL WOOD RECORD SHEET   B

NO: 48   SPECIES: <u>Sapindoxylon janssonii</u> Kräusel

DIAMETER   :   Dicot. wood without rings. Diffuse porous
                  wood (ii)

NO. OF RINGS :

MEAN
SENSITIVITY   :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   O

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 49   SPECIES: <u>Tarrietoxylon sumatrense</u> Kräusel

LOCALITY   : Muara Bungin am Sungi Pobungo. Indonesia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Middle Miocene. Tertiary of
                     Barissangebirges of Djambi and Benkulen.
                     Sumatra

PALAEOPOSITION: 3°S

MAP REFERENCE :

SPECIMEN
REFERENCE   : Kräusel. R. 1922 (See No 47)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   :

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated (i)

FOSSIL WOOD RECORD SHEET   B

NO: 49   SPECIES: <u>Tarrietoxylon sumatrense</u> Kräusel

DIAMETER   : Dicot. wood with very faint rings. Diffuse
                   porous wood (ii)

NO. OF RINGS :

MEAN
SENSITIVITY :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 50   SPECIES: <u>Eucalyptus</u> ?

LOCALITY   :   Numeralla, ca. 15km from Cooma, N.S.Wales,
                      Australia

EVIDENCE OF
IN SITU FOREST: Large fragment in river bed

HORIZON   :   Upper Cretaceous (?) 80MY

PALAEOPOSITION: 61°S

MAP REFERENCE :   S.H.&B.,1981.   Map 24 p.31

SPECIMEN
REFERENCE   :   Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   :   B 13144. Senckenberg Museum

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   25 x 19 x 9cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 50   SPECIES: Eucalyptus ?

DIAMETER   :   Diffuse porous dicot. wood from large
                      trunk. Although superficially, on the
                      outside of the specimen there appeared to
                      be rings, it was not possible to see
                      anything of them in the cellular detail of
                      the wood

NO. OF RINGS   :

MEAN
SENSITIVITY   :

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 51   SPECIES: Araucarites moellhausenianus Göpp

LOCALITY   : West side of Sierra Madre, New Mexico.
                     U.S.A.

EVIDENCE OF
IN SITU FOREST: Fragment, part of same formation as the
                 fossil forest of Arizona

HORIZON   : Triassic

PALAEOPOSITION: 13°N

MAP REFERENCE : S.H.&B.,1981. Map 49 p.56

SPECIMEN
REFERENCE   : Not described

SYNONYMY   : See Göppert for species

LOCATION OF
SPECIMEN   : Senckenberg Museum   (No reg. number)

NO. OF
SPECIMENS   : 1 & slide

SPECIMEN
SIZE   : 9 x 9 x 2cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 51   SPECIES: <u>Araucarites moellhausenianus</u> Gopp

DIAMETER   : From the curvature of the rings the
                     diameter appears to have been 26cm (iii)

NO. OF RINGS : 21 (iii)

MEAN
SENSITIVITY   : 0.489

LARGEST RING : 8.26mm (iii)

NO. OF CELLS : 252   All cell sizes (iii)
E/WOOD   : 249   L/WOOD: 3
LARGEST CELL : 35μm   SMALLEST CELL: 12μm

SMALLEST RING : 1.33mm (iii)

NO. OF CELLS : 44   All cell sizes (iii)
E/WOOD   : 41   L/WOOD: 3
LARGEST CELL : 30μm   SMALLEST CELL: 12μm

RING TYPE   : D

FALSE RINGS   :

DISTORTION   : None

NOTES   : Very high mean sensitivity

FOSSIL WOOD RECORD SHEET A

NO: 52   **SPECIES:**   <u>Dadoxylon santalense</u> N. sp.

LOCALITY   :   Mandro, Rajmahal Hills, Bihar, India

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Rajmahal Stage. Middle Jurassic

PALAEOPOSITION: 40°S

MAP REFERENCE : S.H.&B.,1981.   Map 38 p.45

SPECIMEN
REFERENCE   :   Sah, S.C.D. & Jain, K.P. 1964.   Some fossil
                      woods from the Jurassic of Rajmahal Hills,
                      Bihar, India.   Palaeobotanist 12. 169-180

SYNONYMY   : N.sp.

LOCATION OF
SPECIMEN   :   4506   B.S.I.P. Museum, Lucknow

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   9 x 11cm   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 52   SPECIES: <u>Dadoxylon santalense</u> N. sp.

DIAMETER   :   Not enough information to estimate.
                      Rings very indistinct (i)

NO. OF RINGS :   Rings very faint

MEAN
SENSITIVITY   :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   40μm (i)   SMALLEST CELL: 20μm (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :

DISTORTION   :   None mentioned or figured

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 53   SPECIES: <u>Dadoxylon amraparense</u> N. sp.

LOCALITY   : Amrapara, Rajmahal Hills, Bihar, India

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Rajmahal Stage, Middle Jurassic

PALAEOPOSITION: 40°S

MAP REFERENCE : S.H.&B.,1981. Map 38 p.45

SPECIMEN
REFERENCE   : Sah & Jain, 1964. (see No. 52)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 4511 B.S.I.P. Museum, Lucknow

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 13 x 20cm (i)

FOSSIL WOOD RECORD SHEET   B

NO: 53   SPECIES: <u>Dadoxylon amraparense</u> N. sp.

DIAMETER   :   Rings "distinct and regular". (i) Not
                      enough information to estimate diameter

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :

LARGEST RING :   70 tracheids wide. (i) Estimated on av.
                  cell size = 70 x 23μm = 1.61mm   (i)

NO. OF CELLS :   70
E/WOOD   :   Not enough info.   L/WOOD:
LARGEST CELL :   38μm (ii)   SMALLEST CELL: 8μm (i)

SMALLEST RING :   40 tracheids wide (i) Estimated on av.
                  cell size = 40 x 23μm = 0.92mm

NO. OF CELLS :   40 (i)
E/WOOD   :   Not enough info.   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   C

FALSE RINGS   :

DISTORTION   :   None stated or figured

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 54   SPECIES: Indet. conifer wood

LOCALITY   : Rio Grande do Sul, Brazil

EVIDENCE OF
IN SITU FOREST: Very large specimen

HORIZON   : Permian

PALAEOPOSITION: 30°S

MAP REFERENCE : S.H.&B.,1981. Map 57 p.70

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : Senckenberg Museum (not reg.)

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 45 x 45 x 3cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 54   SPECIES: Indet. conifer wood

DIAMETER   : 45cm - a complete c/section of the trunk.
                   The centre not preserved - some observable
                   rings start at 10cm from the centre (iii)

NO. OF RINGS   : Not all rings preserved, 21 rings from 10cm
                   from the centre to 13.5cm from the centre
                   (iii)

MEAN
SENSITIVITY   : 0.246

LARGEST RING   : Cellular detail could not be seen on the
                   specimen

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :

FALSE RINGS   :

DISTORTION   :

NOTES   : Preservation not good enough to classify
                   the rings

FOSSIL WOOD RECORD SHEET   A

NO: 55   SPECIES: Podocarpoxylon sp.

LOCALITY   :   Assistencia nr. Rio Claro, about 180km N.W.
                          of Sao Paulo, Brazil

EVIDENCE OF
IN SITU FOREST: Many large wood fragments

HORIZON   :   Irati formation.   Stratified limestone
                          interbedded with bituminous shales.
                          Permian: Artinskian

PALAEOPOSITION: 34°S

MAP REFERENCE :   S.H.&B..1981.   Map 57 p.70

SPECIMEN
REFERENCE   :   Leistikow. K.U. & Creber, G.T. (MS).
                          Botanisches Institut, Frankfurt.
                          BR 411 (The 'Black specimen')

SYNONYMY   :

LOCATION OF
SPECIMEN   :   As above, not described

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   27cm in diameter: part of large trunk
                          (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 55   SPECIES: <u>Podocarpoxylon</u> sp.

DIAMETER   : 34cm, pith off centre (the 102 rings were
                   in a radius of 17cm) (iii)

NO. OF RINGS : 102 (iii)

MEAN
SENSITIVITY   : 0.357

LARGEST RING : A large ring: 2.79mm (iii)
                 Largest ring 5.4mm; cellular details not
                 available   (iii)

NO. OF CELLS : 73   All cell sizes (iii)
E/WOOD   : 71   **L/WOOD:** 2
LARGEST CELL : 40μm   SMALLEST CELL: 10μm

SMALLEST RING : A small ring: 0.36mm (iii)

NO. OF CELLS : 10   All cell sizes (iii)
E/WOOD   : 9   **L/WOOD:** 1
LARGEST CELL : 40μm   SMALLEST CELL: 10μm

RING TYPE   : E

FALSE RINGS   : Some occur

DISTORTION   : None (iii)

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 56   SPECIES: Podocarpoxylon sp.

LOCALITY   :   Between Bagé and Acegua, 8km south of Bagé,
                        Brazil

EVIDENCE OF
IN SITU FOREST: Many large wood fragments

HORIZON   :   Equivalent to the Irati formation, the
                        White Band in South Africa with Mesosaurus.
                        Lower Permian

PALAEOPOSITION: 41°S.

MAP REFERENCE :   S.H.&B.,1981.   Map 57 p.70

SPECIMEN
REFERENCE   :   Leistikow, K.U. & Creber, G.T.   (MS)
                        Botanisches Institut, Frankfurt
                        BR 306   (The 'Yellow Specimen')

SYNONYMY   :

LOCATION OF
SPECIMEN   :   As above. not described

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   10   x 10cm in cross-section   (iii)

FOSSIL WOOD RECORD SHEET B

NO: 56   SPECIES: <u>Podocarpoxylon</u> sp.

DIAMETER   : Outer part of large trunk, estimated
                       diameter 20.2cm (iii)

NO. OF RINGS : 29 (iii)

MEAN
SENSITIVITY   : 0.231

LARGEST RING : 8.4mm.   Cellular details not available.
                    A large ring: 4mm   (iii)

NO. OF CELLS : 83 (iii) All cell sizes (iii)
E/WOOD   : 79   L/WOOD: 4
LARGEST CELL : 50µm   SMALLEST CELL: 10µm

SMALLEST RING : A small ring: 0.7mm (iii)

NO. OF CELLS : 16 (iii) All cell sizes (iii)
E/WOOD   : 14   L/WOOD: 2
LARGEST CELL : 50µm   SMALLEST CELL: 10µm

RING TYPE   : E

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 57   SPECIES: Protocedroxylon araucarioides Gothan

LOCALITY   :   Liaotung Peninsula, Manchuria, China

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Lower Cretaceous

PALAEOPOSITION: 35°N.

MAP REFERENCE :   S.H.&B.,1981.   Map 30 p.37

SPECIMEN
REFERENCE   :   Shimakura, M. 1937.   Studies on fossil
                     woods from Japan and adjacent lands.
                     Contribution II.   The Cretaceous woods from
                     Japan, Saghalien and Manchoukuo.   Science
                     reports from the Tohoku Imperial University
                     2nd Ser. 19, 1-73

SYNONYMY   :   Gothan, W. 1910.   Die fossilen Holzreste
                     von Spitzbergen.   Kgl. Svensk. Vetensk.
                     Akad. Handl. 15, 1-56

LOCATION OF
SPECIMEN   :   No. 58415, Institute of Geology and
                     Palaeontology, Tohoku Imperial University,
                     Sendai

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   4.5cm long;   5 x 6cm diameter   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 57   SPECIES: <u>Protocedroxylon araucarioides</u> Gothan

DIAMETER   : Ring boundaries almost straight, indicating
                    a large trunk or branch   (ii)

NO. OF RINGS   : Only one complete ring figured   (ii)

MEAN
SENSITIVITY   : Not enough rings

LARGEST RING   : Only one ring figured   (ii)
                  2.5mm   (ii)

NO. OF CELLS   : 53
E/WOOD   : 50   (ii)   L/WOOD: 3 (ii)
LARGEST CELL   : 50µm   SMALLEST CELL: 10µm

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : A/B

FALSE RINGS   : One possible 'false' ring

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 58   SPECIES: Dadoxylon cf. tankoense
                        (Stopes et Fujii)

LOCALITY   : Karahuto, South Sakhalin, Japan

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Senonian, Upper Cretaceous

PALAEOPOSITION: 56°N

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Shimakura, 1937 (See No. 57)

SYNONYMY   : Stopes, M.C. & Fujii, K. 1910. Studies on
                     the structure and affinities of Cretaceous
                     plants. Phil. Trans. R. Soc. B201, 1-90

LOCATION OF
SPECIMEN   : No. 58446   Inst. of Geol, and Pal. Tohoku
                     Univ., Sendai

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 15cm long; 2.5cm diam. (i)

FOSSIL WOOD RECORD SHEET   B

NO: 58   SPECIES: Dadoxylon cf. tankoense
                        (Stopes et Fujii)

DIAMETER   : Difficult to assess without clear ring
                    boundaries

NO. OF RINGS   : Ring boundaries very indistinct (i) (ii)

MEAN
SENSITIVITY   :

LARGEST RING   : Measurement not possible due to unclear
                  boundaries

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 80μm (ii) SMALLEST CELL: 60μm (ii)

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   :

NOTES   : Very large cells

FOSSIL WOOD RECORD SHEET   A

NO: 59   **SPECIES:**   <u>Phyllocladoxylon</u> aff. <u>gothani</u> (Stopes)

LOCALITY   :   Karahuto, South Sakhalin

**EVIDENCE OF
IN SITU FOREST:**   Fragment

HORIZON   :   Senonian, Upper Cretaceous

PALAEOPOSITION: 56°N

MAP REFERENCE :   S.H.&B.,1981.   Map 22 p.29

**SPECIMEN
REFERENCE**   :   Shimakura, 1937 (See No. 57)

SYNONYMY   :   cf. Stopes, M.C. 1915. Cat. Mes. Plants
                          Brit. Mus. The Cret. Flora. pp. 228-234

**LOCATION OF
SPECIMEN**   :   No. 58402, Dept. of Geol. and Pal. Tohoku
                         Imp. Univ. Sendai.

**NO. OF
SPECIMENS**   :   1

**SPECIMEN
SIZE**   :   5cm long: 2 x 3cm diameter   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 59   SPECIES: Phyllocladoxylon aff. gothani (Stopes)

DIAMETER   : Maximum 3cm. pith present

NO. OF RINGS   : Total not stated; one complete ring figured
                     (ii)

MEAN
SENSITIVITY   :

LARGEST RING   : 90 cells   (i)
                     Est. size = 3.7mm

NO. OF CELLS   : 90   (i)
E/WOOD   : 80   (est.)(i)   L/WOOD: 10   (est.)(i)
LARGEST CELL   : 45μm (ii)   SMALLEST CELL: 8μm (ii)

SMALLEST RING   : 2 cells (i)   Est. size = 0.05mm

NO. OF CELLS   : 2
E/WOOD   : 1   (i)   L/WOOD: 1   (i)
LARGEST CELL   : 45μm   (ii) SMALLEST CELL: 8μm(ii)

RING TYPE   : B

FALSE RINGS   : None stated

DISTORTION   : None

NOTES   : Ring widths vary from 2 to 90 cells wide
                     (i)

FOSSIL WOOD RECORD SHEET A

NO: 60   **SPECIES:** Planoxylon tylosissimum

LOCALITY   : Choshi, Chiba Prefecture. Japan

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 36°N

MAP REFERENCE : S.H.&B..1981.   Map 30 p.37

SPECIMEN
REFERENCE   : Nishida. M. 1937. On some petrified plants
                        from the Cretaceous of Choshi. Chiba
                        Prefecture VI. Botanical Magazine. Tokyo.
                        86. 189-202

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Nos. 71039 a. b. c and 71050. Lab. of
                        Phylogenetic Botany. Chiba University

NO. OF
SPECIMENS   : 5

SPECIMEN
SIZE   : 2 to 6cm long: 0.5 to 1.5cm and 1.2 to
                        2.0cm in short and long diameters   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 60   SPECIES: Planoxylon tylosissimum

DIAMETER   : Difficult to estimate without clear ring
                   boundaries

NO. OF RINGS : No ring boundaries   (i) (ii)

MEAN
SENSITIVITY   :

LARGEST RING : No ring boundaries   (i) (ii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 58μm (i)   SMALLEST CELL: 46μm   (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 61   SPECIES: <u>Protocedroxylon pseudo-araucarioides</u>

LOCALITY   :   Choshi. Chiba Prefecture. Japan

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Lower Cretaceous

PALAEOPOSITION: 36°N

MAP REFERENCE :   S.H.&B.,1981.   Map 30 p.37

SPECIMEN
REFERENCE   :   Nishida, M. 1973   (See No. 60)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   No. 71056 a. b. c.   Lab. of Phylogenetic
                       Botany. Chiba University

NO. OF
SPECIMENS   :   3

SPECIMEN
SIZE   :   4 to 7cm long; 0.5 to 1.2cm and 1.0 to
                       2.0cm in short and long diameters

FOSSIL WOOD RECORD SHEET   B

NO: 61   **SPECIES:** Protocedroxylon pseudo-araucarioides

DIAMETER   : Cannot be estimated without ring boundaries

NO. OF RINGS : No ring boundaries   (i) (ii)

MEAN
SENSITIVITY   :

LARGEST RING : No ring boundaries

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 40μm   (i)   **SMALLEST CELL:** 27μm   (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : O

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 62   SPECIES: <u>Taxaceoxylon japonomesozoicum</u>

LOCALITY   : Choshi, Chiba Prefecture, Japan

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 36°N

MAP REFERENCE : S.H.&B.,1981. Map 30 p.37

SPECIMEN
REFERENCE   : Nishida, M. 1973   (See No. 60)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : No. 70004. Lab. of Phylogenetic Botany,
                     Chiba University

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 3.0cm long; 0.8 and 1.5cm in short and long
                     diameters

FOSSIL WOOD RECORD SHEET   B

NO: 62   SPECIES: <u>Taxaceoxylon japonomesozoicum</u>

DIAMETER   : Difficult to estimate without ring
                  boundaries

NO. OF RINGS : No ring boundaries (i) (ii)

MEAN
SENSITIVITY   :

LARGEST RING : No ring boundaries

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 30µm (i)   SMALLEST CELL: 18µm (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : 0

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 63   SPECIES: Metasequoia milleri

LOCALITY   : 3km SSW of Allenby, British Columbia

EVIDENCE OF
IN SITU FOREST: Much other material (e.g. leafy shoots and
                 cones) indicating a forest locality

HORIZON   : Allenby Formation, Middle Eocene

PALAEOPOSITION: 62°N

MAP REFERENCE : S.H.&B..1981. Map 17 p.24

SPECIMEN
REFERENCE   : Basinger, J.F. 1981. The vegetative body
                     of Metasequoia milleri from the Middle
                     Eocene of southern British Columbia. Can.
                     J Bot. 59, 2379-410

SYNONYMY   : Rothwell, G.W. & Basinger, J.F. 1979.
                     Metasequoia milleri N. sp.. anatomically
                     preserved pollen cones from the Middle
                     Eocene (Allenby Formation) of British
                     Columbia.   Can. J. Bot. 57, 958-970

LOCATION OF
SPECIMEN   : Univ. of Alberta Palaeobotanical collection

NO. OF
SPECIMENS   : Many

SPECIMEN
SIZE   : One large specimen figured as 8cm in
                     diameter. no other dimensions given   (ii)

FOSSIL WOOD RECORD SHEET B

NO: 63   SPECIES: <u>Metasequoia milleri</u>

DIAMETER   : 8cm   (ii)

NO. OF RINGS : 5 figured in detail   (ii)

**MEAN
SENSITIVITY**   : Figure not clear enough to measure all of
the rings

LARGEST RING : **Figured:** 0.79mm (ii) **In text:** 1.3mm (i)

NO. OF CELLS : 17 (ii) All cell sizes (ii)
E/WOOD   : 11   **L/WOOD:** 6
LARGEST CELL : 66μm   **SMALLEST CELL:** 29μm

SMALLEST RING : **Figured:** 0.35mm (i)   **In text:** 0.3mm (i)

NO. OF CELLS : 9 (ii)   All cell sizes (ii)
E/WOOD   : 6   **L/WOOD:** 3
LARGEST CELL : 59μm   **SMALLEST CELL:** 29μm

RING TYPE   : D

FALSE RINGS   : None mentioned or figured

DISTORTION   : Some, but very slight   (ii)

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 64   SPECIES: Indet. Dicotyledonous Wood

LOCALITY   : Hare Island, W. Greenland

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Lower Tertiary

PALAEOPOSITION: 62°N

MAP REFERENCE : S.H.&B.,1981.   Map 19 p.26

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : No. S 4315, Palaeobotany Department,
                   Swedish Museum of Natural History,
                   Stockholm

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 14cm long; 7 x 7cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 64   SPECIES: Indet. Dicotyledonous Wood

DIAMETER   : At least 10cm   (iii)
                   Probably a small trunk as there is no
                   evidence of wider compression rings on one
                   side. which would indicate a branch

NO. OF RINGS : On slide: 7   (iii)

MEAN
SENSITIVITY   :

LARGEST RING : 5.39mm   (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:
                   Largest vessel 171µm in diameter   (iii)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : Some slight crushing   (iii)

NOTES   : A diffuse porous wood with ring boundaries
                 formed from a few smaller fibres. Vessels
                 in radial rows in some growth rings

FOSSIL WOOD RECORD SHEET A

NO: 65   SPECIES: Indet. Dicotyledonous Wood

LOCALITY   : Hare Island, W. Greenland

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Lower Tertiary

PALAEOPOSITION: 62°N

MAP REFERENCE : S.H.&B.,1981.   Map 19 p.26

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : No. S 2689, Palaeobotany Department.
                     Swedish Museum of Natural History,
                     Stockholm

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 12cm long; 8 x 4cm

FOSSIL WOOD RECORD SHEET   B

NO: 65   SPECIES: Indet. Dicotyledonous Wood

DIAMETER   : At least 16cm   (iii)

NO. OF RINGS : On slide: 4   (iii)

MEAN
SENSITIVITY   :

LARGEST RING : 5.27mm   (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:
                   Largest vessel 171μm in diameter   (iii)

SMALLEST RING : 2.4mm   (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : Some, but rings still very clear   (iii)

NOTES   : A diffuse porous wood with ring boundaries
                   formed from a few smaller fibres. Vessels
                   in radial rows in some growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 66   SPECIES: <u>Cedroxylon matsumurae</u>

LOCALITY   : Hokkaido, Japan

EVIDENCE OF
IN SITU FOREST: Part of a large trunk

HORIZON   : Upper Cretaceous

PALAEOPOSITION: 53°N

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Stopes, M.C. & Fujii, K. 1910. Studies on
                   the structure and affinities of Cretaceous
                   plants. Phil. Trans. Roy. Soc. 201, 1-90

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known definitely, but the authors
                   express the intention of donating them to
                   the B.M. (N.H.)   (i)

NO. OF
SPECIMENS   : 2 small pieces and a large trunk

SPECIMEN
SIZE   : Trunk 60cm in diameter

FOSSIL WOOD RECORD SHEET   B

NO: 66   SPECIES: Cedroxylon matsumurae

DIAMETER   : 60cm

NO. OF RINGS : 65   (i)   Only one ring figured

MEAN
SENSITIVITY   : Too few rings figured for actual
                   calculation but in text (ii). 2 rings, 80
                   cells and 11 cells wide described as
                   adjacent (4mm and 0.55mm - estimated).
                   This is an annual sensitivity of 1.51

LARGEST RING : Figured: 0.66mm   (i)

NO. OF CELLS : 20   All cell sizes (i)
E/WOOD   : 18   L/WOOD: 2
LARGEST CELL : 50μm   SMALLEST CELL: 10μm

SMALLEST RING : Two rings of equal size figured   (ii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None mentioned

DISTORTION   : Some (i) but none in figure

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 67   SPECIES: Taxodioxylon multiseriatum

LOCALITY   :   Rosedale. Drumheller. Alberta. Canada

EVIDENCE OF
IN SITU FOREST: Large stumps and horizontal trunks

HORIZON   :   Edmonton Formation, Upper Cretaceous

PALAEOPOSITION: 51°N

MAP REFERENCE :   S.H.&B.,1981.   Map 21 p.28

SPECIMEN
REFERENCE   :   Ramanujam, C.G.K. & Stewart, W.N. 1969.
                      Fossil woods of Taxodiaceae from the
                      Edmonton Formation (Upper Cretaceous) of
                      Alberta. Can. J. Bot. 47, 115-124

SYNONYMY   :   Ramanujam, C.G.K. & Stewart, W.N. 1969.
                      Nomenclatural changes for Taxiodioxylon
                      antiquum Ramanujam & Stewart and
                      T. antiquum Prakash. Can. J. Bot. 47.
                      1333-4

LOCATION OF
SPECIMEN   :   P.3, Dept. of Botany, Univ. of Alberta,
                      Edmonton

NO. OF
SPECIMENS   :   Many - unspecified by the authors

SPECIMEN
SIZE   :   Figured specimen - 32.5cm long;   13 x 5.5cm
                      in diameter   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 67   SPECIES: Taxodioxylon multiseriatum

DIAMETER   : Part of a large stump   (i)

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING   : Figured: 0.64mm   (ii)

NO. OF CELLS : 14   All cell sizes (ii)
E/WOOD   : 12   L./WOOD: 2
LARGEST CELL : 50μm   SMALLEST CELL: 20μm

SMALLEST RING : Figured: 0.14mm

NO. OF CELLS : 4   All cell sizes (ii)
E/WOOD   : 2   L/WOOD: 2
LARGEST CELL : 50μm   SMALLEST CELL: 20μm

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 68   SPECIES: <u>Taxodioxylon taxodii</u> Gothan

LOCALITY   : Rosedale, Drumheller, Alberta, Canada

EVIDENCE OF
IN SITU FOREST: Large stumps and horizontal trunks

HORIZON   : Edmonton Formation, Upper Cretaceous

PALAEOPOSITION: 51°N

MAP REFERENCE : S.H.&B.,1981.   Map 21 p.28

SPECIMEN
REFERENCE   : Ramanujam & Stewart, 1969 (See No. 67)

SYNONYMY   : Gothan, W. 1905. Zur Anatomie lebender und
                    fossiler Gymnospermen Hölzer. Abh. Preuss.
                    Geol. Landes. 44, 1-108

LOCATION OF
SPECIMEN   : P.54, Dept. of Botany, Univ. of Alberta,
                    Edmonton

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 10cm long; 7.5 x 3.5cm in diameter (i)

FOSSIL WOOD RECORD SHEET   B

NO: 68   SPECIES: <u>Taxodioxylon taxodii</u> Gothan

DIAMETER   : Straight ring boundaries indicate a large
                   trunk

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : One ring figured: 1.8mm   (ii)

NO. OF CELLS : 37   (ii)
E/WOOD   : 34   (ii)   L/WOOD: 3   (ii)
LARGEST CELL : 50µm   SMALLEST CELL: 10µm

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 69   SPECIES: <u>Taxodioxylon drumhellerense</u>

LOCALITY   :   Rosedale, Drumheller, Alberta, Canada

EVIDENCE OF
IN SITU FOREST: Part of a large flattened trunk

HORIZON   :   Edmonton Formation, Upper Cretaceous

PALAEOPOSITION: 51°N

MAP REFERENCE :   S.H.&B.,1981.   Map 21 p.28

SPECIMEN
REFERENCE   :   Ramanujam & Stewart, 1969   (See No. 67)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   P.43, Dept. of Botany, Univ. of Alberta,
                      Edmonton

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Hand specimen; 25cm long; 6.3 x 5cm in
                      diameter   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 69   SPECIES: Taxodioxylon drumhellerense

DIAMETER   : Part of large trunk

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : Figured: 1.2mm   (ii)

NO. OF CELLS : 32   All cell sizes (ii)
E/WOOD   : 29   L/WOOD: 3
LARGEST CELL : 40μm   SMALLEST CELL: 15μm

SMALLEST RING : Only one complete ring figured

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 70   SPECIES: Rhexoxylon piatnitzkyi Arch. & Brett

LOCALITY   :   La Rioja, Argentina

EVIDENCE OF
IN SITU FOREST: Many large trunks

HORIZON   :   Ischigualasto Formation, Upper Triassic

PALAEOPOSITION: 47°S

MAP REFERENCE :   S.H.&B.,1981.   Map 49 p.56

SPECIMEN
REFERENCE   :   Brett, D.W. 1968.   Studies on Triassic
                    fossil plants from Argentina III The trunk
                    of Rhexoxylon.   Palaeontology 11, 236-45

SYNONYMY   :   Archangelsky, S. & Brett, D.W. 1961.
                    Studies on Triassic fossil plants from
                    Argentina I Rhexoxylon from the
                    Ischigualasto formation.
                    Phil. Trans. Roy. Soc. B244, 1-19

LOCATION OF
SPECIMEN   :   Pb 3905, Peel section, Hunterian Museum,
                    Glasgow

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Cross-section 38.0 x 23.0cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 70   **SPECIES:** <u>Rhexoxylon piatnitzkyi</u> Arch. & Brett

DIAMETER   : Unless very eccentric, the radius of 27cm
indicates a possible diameter of 54cm
(iii)

NO. OF RINGS : Possibly 50, but not clearly marked off
(iii)

**MEAN
SENSITIVITY**   : Rings not sufficiently well defined to
warrant the measurement of a ring series

LARGEST RING : A large ring: 4.4mm   (iii)

NO. OF CELLS : 90   All cell sizes   (iii)
E/WOOD   : 88   **L/WOOD:** 2
LARGEST CELL : 50μm   **SMALLEST CELL:** 10μm

SMALLEST RING : A small ring: 0.5mm

NO. OF CELLS : 11   All cell sizes   (iii)
E/WOOD   : 10   **L/WOOD:** 1
LARGEST CELL : 50μm   **SMALLEST CELL:** 10μm

RING TYPE   : E

FALSE RINGS   : Very frequent

DISTORTION   : None seen

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 71   SPECIES: <u>Phyllocladoxylon heizyoense</u>

LOCALITY   : Pyong-Yang, North Korea

EVIDENCE OF
IN SITU FOREST: Large tree stumps

HORIZON   : Middle Daido Formation, Middle Jurassic

PALAEOPOSITION: 43°N

MAP REFERENCE : S.H.&B.,1981.   Map 38 p.45

SPECIMEN
REFERENCE   : Shimakura, M. 1936.   Studies on fossil
                   woods from Japan and adjacent lands.
                   Contribution I.   Some Jurassic woods from
                   Japan and Manchoukuo.
                   Sci. Rep. Tohoku Imp. Univ., 2nd Ser. 18,
                   267-310

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Nos. 6871-6879, Dept. of Geol. &
                   Palaeontology, Tohoku Imperial University,
                   Sendai

NO. OF
SPECIMENS   : 9

SPECIMEN
SIZE   : Av. 7cm long; 3cm diameter (i)

FOSSIL WOOD RECORD SHEET   B

NO: 71   SPECIES: <u>Phyllocladoxylon heizyoense</u>

DIAMETER   : Specimens collected as parts of large
                   trunks (ii)

NO. OF RINGS : Not stated

MEAN
SENSITIVITY : Insufficient data

LARGEST RING : 13mm (i)

NO. OF CELLS : 277 All cell sizes est. from text (i)
E/WOOD   : 273   L/WOOD: 4
LARGEST CELL : 47.5μm   SMALLEST CELL: 5μm

SMALLEST RING : 0.4mm (ii)

NO. OF CELLS : 12   All cell sizes (ii)
E/WOOD   : 10   L/WOOD: 2
LARGEST CELL : 40μm   SMALLEST CELL: 5μm

RING TYPE   : D

FALSE RINGS   : Some stated to occur (i)

DISTORTION   : Some evident in figure (ii)

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 72   SPECIES: <u>Dadoxylon (Araucarioxylon) japonicum</u>

LOCALITY   : Koti-ken, Southern Japan

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Torinosu Group, Upper Jurassic

PALAEOPOSITION: 36°N

MAP REFERENCE : S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   : Shimakura, M. 1936. (See No. 71)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : No. 53325, Dept. of Geol. & Palaeontology.
                     Tohoku Imp. University, Sendai

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 7cm long; 8 x 1.5cm diameter (i)

FOSSIL WOOD RECORD SHEET   B

NO: 72   SPECIES: <u>Dadoxylon (Araucarioxylon) japonicum</u>

DIAMETER   : Ring boundaries almost straight and hence
                     probably a large trunk or branch   (ii)

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING   : 3.0mm   (i)
                  Only one whole ring figured: 0.42mm   (ii)

NO. OF CELLS   : 12   All cell sizes   (ii)
E/WOOD   : 8   **L/WOOD:**   4
LARGEST CELL   : 50μm   **SMALLEST CELL:** 5μm

SMALLEST RING : Only one ring figured: 0.5mm   (i)

NO. OF CELLS   :
E/WOOD   :   **L/WOOD:**
LARGEST CELL   :   **SMALLEST CELL:**

RING TYPE   : D

FALSE RINGS   :

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 73   SPECIES: Dadoxylon (Araucarioxylon)
                        sidugawaense

LOCALITY   : Miyagi, Japan

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Kitakami Series. Lower Jurassic

PALAEOPOSITION: 55°N

MAP REFERENCE : S.H.&B.,1981. Map 42 p.49

SPECIMEN
REFERENCE   : Shimakura, M. 1936. (See No. 71)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : No. 44234, Dept. of Geol. & Palaeontology,
                   Tohoku Imp. University, Sendai

NO. OF
SPECIMENS   : Several (i)

SPECIMEN
SIZE   : Largest: 7cm long; 2 x 3cm diameter (i)

FOSSIL WOOD RECORD SHEET   B

NO: 73   SPECIES: <u>Dadoxylon (Araucarioxylon)</u>
                         <u>sidugawaense</u>

DIAMETER   :   Probably just a twig (i)

NO. OF RINGS :   Number not stated

MEAN
SENSITIVITY   :

LARGEST RING :   Ring details not very clear

NO. OF CELLS :
E/WOOD   :   L/WOOD: 4 to 14
                                                 (i)(ii)
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :

DISTORTION   :   Quite severe in places

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 74   SPECIES: Phyllocladoxylon cf. eboracense Holden

LOCALITY   :   Chulin, N. China (ex Manchuria)

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Middle Jurassic

PALAEOPOSITION: 50°N

MAP REFERENCE : S.H.&B.,1981.   Map 38 p.45

SPECIMEN
REFERENCE   :   Shimakura, M. 1936.   (See No. 71)

SYNONYMY   :   Holden, R.   Contributions to the anatomy of
                   Mesozoic conifers I.   Jurassic coniferous
                   wood from Yorkshire.   Ann. Bot. 27, 533-45

LOCATION OF
SPECIMEN   :   No. 30557,   Dept. of Geol. & Palaeontology,
                   Tohoku Imp. University. Sendai

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 74   SPECIES: <u>Phyllocladoxylon</u> cf. <u>eboracense</u> Holden

DIAMETER   :   Ring boundaries appear to be straight.
                      indicating a large trunk or branch

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   Insufficient data

LARGEST RING   :   Largest ring in text: 4.0mm   (i)
                   Only one entire ring figured: 1.3mm   (ii)

NO. OF CELLS   :   38   All cell sizes (ii)
E/WOOD   :   36   L/WOOD: 2
LARGEST CELL   :   40μm   SMALLEST CELL: 10μm

SMALLEST RING :   In text: 0.7mm   (i)
                  Only one ring figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :   None mentioned

DISTORTION   :   None evident

NOTES   :   Very faint ring boundaries

FOSSIL WOOD RECORD SHEET A

NO: 75   SPECIES: <u>Piceoxylon</u> sp. Gothan

LOCALITY   : Woburn, Bedfordshire

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Greensand, Lower Cretaceous

PALAEOPOSITION: 40°N

MAP REFERENCE : S.H.&B.,1981. Map 30 p.37

SPECIMEN
REFERENCE   : Not described

SYNONYMY   : Gothan, W. 1905. Zur anatomie lebender und
                     fossiler Gymnospermen-Hölzer.
                     König. Preuss. Geol. Landesanstalt u.
                     Bergakadamie, N.F. 44, 1-108

LOCATION OF
SPECIMEN   : Chelsea Dept. of Geology

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 17 x 12cm diameter; 1.5cm thick (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 75   SPECIES: <u>Piceoxylon</u> sp. Gothan

DIAMETER   : Diameter of whole trunk was probably about
                   30cm   (iii)

NO. OF RINGS   : 44   (iii)

MEAN
SENSITIVITY   : 0.180

LARGEST RING   : 4.85mm   (iii)

NO. OF CELLS   : Cellular details not well preserved
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING : 0.51mm   (iii)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : ?

FALSE RINGS   : Possibly one or two

DISTORTION   : Whole specimen crushed to elliptical shape
                   and each ring has a crush zone

NOTES   : Ring character very difficult to determine
                   because of poor preservation

FOSSIL WOOD RECORD SHEET   A

NO: 76   SPECIES: <u>Dammaroxylon africanum</u>

LOCALITY   : Mouth of the Umzamba River, East Pondo
                     Land, South Africa

EVIDENCE OF
IN SITU FOREST: Large logs, some bored by <u>Teredo</u>

HORIZON   . : Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE :   S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   : Schultze-Motel, J. 1966.
                  Gymnospermen-Hölzer aus den
                  oberkretazischen Umzamba-Schichten von
                  Ost-Pondoland (S-Afrika).
                  Senckenbergiana Lethaea 47, 279-337

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : SM.B 9622-9642, Albany Museum, Grahamstown

NO. OF
SPECIMENS   : 20

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET B

NO: 76   SPECIES: <u>Dammaroxylon africanum</u>

DIAMETER   : Not possible to estimate in view of the
                   lack of rings

NO. OF RINGS : None except some faint ones in 9641 & 9642

MEAN
SENSITIVITY   :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
                 No earlywood or latewood
LARGEST CELL : 54μm (i)(ii)SMALLEST CELL: 16μm (i)(ii)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : O/E

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Most specimens without rings, two with
                 faint rings

FOSSIL WOOD RECORD SHEET A

NO: 77   **SPECIES:** Podocarpoxylon angustiradiatum

LOCALITY   : Mouth of the Umzamba River, East Pondo
                         Land, South Africa

**EVIDENCE OF
IN SITU FOREST:** Large logs, some bored by Teredo

HORIZON   : Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

**SPECIMEN
REFERENCE**   : Schultze-Motel, J. 1966 (See No. 77)

SYNONYMY   : N. sp.

**LOCATION OF
SPECIMEN**   : SM.B. 9666, Albany Museum, Grahamstown

**NO. OF
SPECIMENS**   : 1

**SPECIMEN
SIZE**   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 77   **SPECIES:** Podocarpoxylon angustiradiatum

DIAMETER   : Not possible to estimate in view of the lack of rings

NO. OF RINGS : No rings

**MEAN
SENSITIVITY** :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
                 No earlywood or latewood
LARGEST CELL : 85μm (i)(ii) **SMALLEST CELL:** 50μm (i)(ii)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : O

FALSE RINGS :

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 78   SPECIES: <u>Podocarpoxylon umzambense</u>

LOCALITY   : Mouth of the Umzamba River, East Pondo Land, South Africa

EVIDENCE OF
IN SITU FOREST: Large logs, some bored by <u>Teredo</u>

HORIZON   : Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE : S.H.&B.,1981. Map 22 p.29

SPECIMEN
REFERENCE   : Schultze-Motel, J. 1966 (See No. 77)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : SM.B. 9667-9, Albany Museum, Grahamstown

NO. OF
SPECIMENS   : 3

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 78   SPECIES: Podocarpoxylon umzambense

DIAMETER   : Straight ring boundary indicates a large
                   diameter

NO. OF RINGS   : Only part of one ring figured

MEAN
SENSITIVITY   :

LARGEST RING   : Only part of one ring figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 30μm (i)(ii SMALLEST CELL: 20μm (i)(ii)

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 79   SPECIES: Indet. gymnosperm wood

LOCALITY   :   Mouth of the Umzamba River, East Pondo
                        Land, South Africa

EVIDENCE OF
IN SITU FOREST: Large logs, some bored by Teredo

HORIZON   :   Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE :   S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   :   Schultze-Motel, J. 1966 (See No. 77)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   SM.B. 9680, Albany Museum, Grahamstown

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 79   SPECIES: Indet. gymnosperm wood

DIAMETER   : Straight ring boundaries indicate a large
                   diameter

NO. OF RINGS : 27 in 3mm (i)
                 Only 3 figured (ii)

MEAN
SENSITIVITY :

LARGEST RING : Figured: 0.6mm (ii)

NO. OF CELLS : 19   All cell sizes (ii)
E/WOOD   : 16   **L/WOOD:** 3
LARGEST CELL : 35µm   **SMALLEST CELL:** 17µm

SMALLEST RING : Figured: 0.17mm (ii)

NO. OF CELLS : 8   All cell sizes (ii)
E/WOOD   : 6   **L/WOOD:** 2
LARGEST CELL : 25µm   **SMALLEST CELL:** 15µm

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 80   SPECIES: Xenoxylon hopeiense

LOCALITY   :   Hisa Chia Kou, Province of Hopeh. China

EVIDENCE OF
IN SITU FOREST: Part of a large trunk

HORIZON   :   Upper Jurassic

PALAEOPOSITION: 37°N

MAP REFERENCE :   S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   :   Chang, C.Y. 1929.   A new Xenoxylon from
                         North China.
                         Bull. geol. Soc. China 8, 243-251

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Not known

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Half of a trunk disc, 30cm in diameter,
                         7.5cm thick

FOSSIL WOOD RECORD SHEET   B

NO: 80   **SPECIES:** <u>Xenoxylon hopeiense</u>

DIAMETER   : 30cm

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :

LARGEST RING : 0.5cm   (i)
                    Only part of one ring figured

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 50μm   (i)   **SMALLEST CELL:**   13μm   (i)

SMALLEST RING : 0.1cm   (i)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : D

FALSE RINGS   :

DISTORTION   : None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 81   **SPECIES:** Indet. gymnosperm wood

LOCALITY   : Cerro Alto, Santa Cruz, S. Argentina

EVIDENCE OF
IN SITU FOREST: Petrified forest with in situ stumps

HORIZON   : Upper Jurassic

PALAEOPOSITION: 53°S

MAP REFERENCE : S.H.&B.,1981. Map 33 p.40

SPECIMEN
REFERENCE   . : Calder, M.G. 1953.
A coniferous petrified forest in Patagonia.
Bull. Brit. Mus. (N.H.) Geology 2, 99-138

SYNONYMY   : Not assigned to a species

LOCATION OF
SPECIMEN   : V. 30937 and slides, B.M.(N.H.)

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : A cylinder 3.5cm in diameter

FOSSIL WOOD RECORD SHEET   B

NO: 81   SPECIES: Indet. gymnosperm wood

DIAMETER   :   Although circular in cross-section, the
                    specimen is eccentric, the original stem
                    diameter was 4.4cm. It was the centre of a
                    branch or stem.   (iii)

NO. OF RINGS :   13   (iii)

MEAN
SENSITIVITY   :   0.533

LARGEST RING :   2.5mm   (iii)
                  Preservation not good enough to enable cell
                  measurements

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING : 0.3mm   (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :

DISTORTION   :   A little

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 82   SPECIES: Dadoxylon kaiparaense

LOCALITY   : Bull's Point, Kaipara Harbour, New Zealand

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Upper Cretaceous

PALAEOPOSITION: 62°S

MAP REFERENCE : S.H.&B.,1981. Map 21 p.28

SPECIMEN
REFERENCE   : Edwards, W.N. 1926.
                     Cretaceous plants from Kaipara, New
                     Zealand.
                     Trans. of the New Zealand Institute 56,
                     121-128

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 82   SPECIES: Dadoxylon kaiparaense

DIAMETER   :   Very little information given

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   A few small tracheids at the ring boundary
                    (i)

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 83   SPECIES: <u>Xenoxylon latiporosum</u> (Cramer) Gothan

LOCALITY   : Nong-Son, au S.O. de Tourane, in the
                       Province of Quang-Nam (Central Annam),
                       Vietnam

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Lias, Lower Jurassic

PALAEOPOSITION: 28°N

MAP REFERENCE : Map 42 p.49

SPECIMEN
REFERENCE   : Boureau, E. 1950. Contribution à l'étude
                       paléoxylogique de l'Indochine.
                       Bull. Serv. geol. Indochine 29, 1-13

SYNONYMY   : Cramer, C. 1868. Fossile Hölzer der
                       Arctischen Zone. Heer's Foss. Flor.
                       arct. 1, 167
                       Gothan, W. 1905. Zur Anatomie lebender und
                       fossiler Gymnospermen-Hölzer. Abh. K.
                       Preuss. geol. Landes. N.F., 44, 1.

LOCATION OF
SPECIMEN   : Service Géologique d'Indochine

NO. OF
SPECIMENS   : 2

SPECIMEN
SIZE   : 4 x 3 x 1cm; 8 x 6 x 3cm   (i)

FOSSIL WOOD RECORD SHEET B

NO: 83   **SPECIES:** <u>Xenoxylon latiporosum</u> (Cramer) Gothan

DIAMETER   : Straight ring boundary indicates a large
                        diameter   (ii)

NO. OF RINGS : Not stated. Ring boundaries marked by a
                    few smaller tracheids   (ii)

MEAN
SENSITIVITY :

LARGEST RING : Only a part of one ring figured   (ii)

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL : 38μm (i)   **SMALLEST CELL:** 3μm   (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : D

FALSE RINGS   :

DISTORTION   :

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 84   SPECIES: Terminalioxylon annamense

LOCALITY   : Plei Matroh in the valley of Song Ba, in
                   the province of Plei-Ku, Sud Annam, Vietnam

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Neogene, Middle Tertiary

PALAEOPOSITION: 15°N

MAP REFERENCE : S.H.&B.,1981.   Map 6 p.13

SPECIMEN
REFERENCE   : Boureau, E. 1950.   Contribution à l'étude
                   paleoxylologique de l'Indochine.
                   Bull. Serv. géol. Indochine 29, 5-11

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Service Géologique d'Indochine

NO. OF
SPECIMENS   :

SPECIMEN
SIZE   : 11 x 5 x 2cm   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 84   **SPECIES:** Terminalioxylon annamense

DIAMETER   : Not possible to estimate

NO. OF RINGS : Not stated

**MEAN
SENSITIVITY**   :

LARGEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : E

FALSE RINGS :

DISTORTION   : None

NOTES   : A diffuse porous dicotyledonous wood with
                     very faint ring boundaries

FOSSIL WOOD RECORD SHEET A

NO: 85   SPECIES: Sapindoxylon pleikuense

LOCALITY   : Plei Matroh in the valley of Song Ba, in
                     the province of Plei-Ku, Sud Annam, Vietnam

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Neogene, Middle Tertiary

PALAEOPOSITION: 15°N

MAP REFERENCE : Map 6 p.13

SPECIMEN
REFERENCE   : Boureau, E. 1950. Contribution à l'étude
                     paleoxylologique de l'Indochine.
                     Bull. Serv. geol. Indochine 29, 15-22

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Service Geologique d'Indochine

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 7 x 5 x 2cm   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 85   SPECIES: Sapindoxylon pleikuense

DIAMETER   : Not possible to estimate

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   :

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   : Slight

NOTES   : A diffuse porous dicotyledonous wood with
                  very faint ring boundaries

FOSSIL WOOD RECORD SHEET   A

NO: 86   **SPECIES:**   <u>Dipterocarpoxylon burmense</u>

LOCALITY   :   Gwedindin, Sagaing District, Burma

**EVIDENCE OF
IN SITU FOREST:**   A region with much fossil wood

HORIZON   :   Miocene

PALAEOPOSITION: 22°N

MAP REFERENCE :   Map 6 p.13

**SPECIMEN
REFERENCE**   :   Holden. R. 1916.   A fossil wood from Burma.
Rec. geol. Surv. India 47. 267-272

SYNONYMY   :   N. sp.

**LOCATION OF
SPECIMEN**   :   Not known

**NO. OF
SPECIMENS**   :   2

**SPECIMEN
SIZE**   :   Two blocks 25cm long   (i)

FOSSIL WOOD RECORD SHEET   B

NO: 86   SPECIES: Dipterocarpoxylon burmense

DIAMETER   : A large diameter is indicated by the
                   straight ring boundary   (ii)

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :

LARGEST RING : 0.9cm   (i)
                 Very faint ring boundaries

NO. OF CELLS : No details given
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING : 0.3cm   (i)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   : None

NOTES   : A diffuse porous dicotyledonous wood with
                 large isolated vessels   (i) (ii)

FOSSIL WOOD RECORD SHEET A

NO: 87   **SPECIES:** Circoporoxylon sp.

LOCALITY   : Fossil Bluff, Alexander Island, Antarctica

**EVIDENCE OF
IN SITU FOREST:** Fossil Forest

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 70°S

MAP REFERENCE : S.H.&B.,1981. Map 32 p.39

**SPECIMEN
REFERENCE**   : Jefferson, T.H. 1982. Fossil forests from
                        the Lower Cretaceous of Alexander Island,
                        Antarctica. Palaeontology 25, 681-708

SYNONYMY   : Kräusel, R. 1949.
                        Die fossilen Koniferen-Hölzer.
                        Palaeontographica B 89, 83-203

**LOCATION OF
SPECIMEN**   : KG 1704.10, British Antarctic Survey,
                        Cambridge

**NO. OF
SPECIMENS**   : 1   (Many others were collected)

**SPECIMEN
SIZE**   : 30 x 18cm in cross-section

FOSSIL WOOD RECORD SHEET   B

NO: 87   SPECIES: <u>Circoporoxylon</u> sp.

DIAMETER   : 30cm

NO. OF RINGS : 58

MEAN
SENSITIVITY   : 0.468

LARGEST RING : 0.9cm (i)

NO. OF CELLS : 227 (est.)
E/WOOD   : 225 (est.)   L/WOOD: 2 (est.)
LARGEST CELL : 50μm (iii) SMALLEST CELL: 10μm (iii)

SMALLEST RING : 0.75mm   (iii)

NO. OF CELLS : 15   All cell sizes (iii)
E/WOOD   : 13   L/WOOD: 2
LARGEST CELL : 50μm   SMALLEST CELL: 10μm

RING TYPE   : D

FALSE RINGS   : Some

DISTORTION   : Some   (iii)

NOTES   : A high mean sensitivity

FOSSIL WOOD RECORD SHEET A

NO: 88   SPECIES: Cupressinoxylon sp.

LOCALITY   : Chilko Lake, British Columbia, Canada

EVIDENCE OF
IN SITU FOREST: Very large trunks

HORIZON   : Lower Cretaceous

PALAEOPOSITION: 59°N

MAP REFERENCE : S.H.&B.,1981.   Map 29 p.36

SPECIMEN
REFERENCE   : Fry, W.L. 1958.   Petrified logs of
                      Cupressinoxylon from the West shore of
                      Chilko Lake, British Columbia.
                      Geol. Survey of Canada Bulletin 48, 11-14

SYNONYMY   : Not assigned to a species

LOCATION OF
SPECIMEN   : Geol. Survey of Canada

NO. OF
SPECIMENS   : Many, number not specified

SPECIMEN
SIZE   : Largest: 56.5cm in diameter   (i) (ii)

FOSSIL WOOD RECORD SHEET   B

NO: 88   **SPECIES:** <u>Cupressinoxylon</u> sp.

DIAMETER   : 56.5cm in diameter   (i) (ii)

NO. OF RINGS : Largest number counted: 86.
Widths not recorded

**MEAN
SENSITIVITY**   : Data not available

LARGEST RING : 75 cells (i) (est.: 5.6mm)

NO. OF CELLS : 75 (i)
E/WOOD   : 70   **L/WOOD:** 5
(Proportion estimated from figure) (ii)
LARGEST CELL : 83μm   **SMALLEST CELL:** 8μm (iii)
(Measurements taken from figure) (ii)

SMALLEST RING : 9 cells (i) (est.: 0.5mm)

NO. OF CELLS : 9   (i)
E/WOOD   : 6   **L/WOOD:** 3
(Proportion estimated from figure) (ii)
LARGEST CELL : 83μm   **SMALLEST CELL:** 8μm
(Measurements taken from figure) (ii)

RING TYPE   : D

FALSE RINGS   :

DISTORTION   : None mentioned

NOTES   : A few latewood cells at the end of each
season

FOSSIL WOOD RECORD SHEET   A

NO: 89   **SPECIES:** <u>Protocupressinoxylon purbeckensis</u>

LOCALITY   : Isle of Portland, Dorset

EVIDENCE OF
IN SITU FOREST: A fossil forest

HORIZON   : Great Dirt Bed, Upper Jurassic

PALAEOPOSITION: 36°N

MAP REFERENCE : S.H.&B.,1981. Map 34 p.41

SPECIMEN
REFERENCE   : Francis, J.E. 1983. The dominant conifer
of the Jurassic Purbeck Formation.
Palaeontology 26, 277-294

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : PB 24, J.E. Francis collection

NO. OF
SPECIMENS   : PB 24, 5 pieces; 20 other Purbeck specimens

SPECIMEN
SIZE   : Large stumps

FOSSIL WOOD RECORD SHEET   B

NO: 89   SPECIES: Protocupressinoxylon purbeckensis

DIAMETER   : PB 24: 9cm   (iii)

NO. OF RINGS   : PB 24: 54 rings; others range from 9-104
                   (iii)

MEAN
SENSITIVITY   : PB 24: 0.656; average for all specimens:
                   0.527

LARGEST RING   : 3.4mm   (iii)

NO. OF CELLS   : 77   All cell sizes (iii)
E/WOOD   : 75   L/WOOD: 2
LARGEST CELL   : 50µm   SMALLEST CELL: 5µm

SMALLEST RING : 0.5mm

NO. OF CELLS   : 13   All cell sizes (iii)
E/WOOD   : 11   L/WOOD: 2
LARGEST CELL   : 50µm   SMALLEST CELL: 4µm

RING TYPE   : D

FALSE RINGS   : Very frequent

DISTORTION   : Some collapse in places

NOTES   : A high mean sensitivity

FOSSIL WOOD RECORD SHEET   A

NO: 90   **SPECIES:**   5 Tracheidoxyl GR

LOCALITY   :   Helmsdale, East Sutherland

EVIDENCE OF
IN SITU FOREST: Considerable quantities of large specimens
                  of fossil wood

HORIZON   :   Kimmeridgian, Upper Jurassic

PALAEOPOSITION: 43°N

MAP REFERENCE :   S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   :   Creber, G.T. 1972. Gymnospermous wood from
                     the Kimmeridgian of East Sutherland and
                     from the Sandringham Sands of Norfolk.
                     Palaeontology 15, 655-661

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   K 5317, K 5295, and slides. Sedgwick
                     Museum, Cambridge

NO. OF
SPECIMENS   :   2

SPECIMEN
SIZE   :   K 5317, 15 x 10 x 10cm   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 90   SPECIES: 5 Tracheidoxyl GR

DIAMETER   :   Curvature of the rings indicates that this
                         was the central part of a trunk

NO. OF RINGS   :   Not recorded

MEAN
SENSITIVITY   :   No data available

LARGEST RING   :   9mm   (iii)

NO. OF CELLS   :   200   (est.)   All cell sizes   (iii)
E/WOOD   :   185   (est.)   L/WOOD: 15   (est.)
LARGEST CELL   :   50 μm   SMALLEST CELL: 10 μm

SMALLEST RING   :   Not recorded

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   A

FALSE RINGS   :   None

DISTORTION   :   Some crush zones in the rings   (iii)

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 91   **SPECIES:** <u>Metacedroxylon scoticum</u> Holden

LOCALITY   : Helmsdale, East Sutherland

**EVIDENCE OF
IN SITU FOREST:** Considerable quantities of large specimens
                   of fossil wood

HORIZON   : Kimmeridgian, Upper Jurassic

PALAEOPOSITION: 43°N

MAP REFERENCE : S.H.&B.,1981. Map 34 p.41

**SPECIMEN
REFERENCE**   : Holden, R. 1915.
                     A Jurassic wood from Scotland.
                     New Phytologist 14, 205-209

SYNONYMY   : N. sp.

**LOCATION OF
SPECIMEN**   : K 613 and slides, Sedgwick Museum,
                     Cambridge

**NO. OF
SPECIMENS**   : 1

**SPECIMEN
SIZE**   : 37.5 x 9.0cm in cross-section; 18cm long
                     (i)

FOSSIL WOOD RECORD SHEET   B

NO: 91   SPECIES: <u>Metacedroxylon scoticum</u> Holden

DIAMETER   :

NO. OF RINGS : 75 (i) (iii)

MEAN
SENSITIVITY   : 0.393

LARGEST RING : 11mm (i)

NO. OF CELLS : 323 (est. from a 9mm ring)
                 All cell sizes (iii)
E/WOOD   : 314   L/WOOD: 9
LARGEST CELL : 55μm   SMALLEST CELL: 7.5μm

SMALLEST RING : 2mm (i)

NO. OF CELLS : 59 (est. from a 9mm ring)
                 All cell sizes (iii)
E/WOOD   : 54   L/WOOD: 5
LARGEST CELL : 55μm   SMALLEST CELL: 7.5μm

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : Some but not very severe

NOTES   : At least one very large growth ring

FOSSIL WOOD RECORD SHEET A

NO: 92   SPECIES: Cedroxylon hornei

LOCALITY   : Helmsdale, East Sutherland

EVIDENCE OF
IN SITU FOREST: Considerable quantities of large specimens
                 of fossil wood

HORIZON   : Kimmeridgian, Upper Jurassic

PALAEOPOSITION: 43°N

MAP REFERENCE : S.H.& B.,1981   Map 34 p.41

SPECIMEN
REFERENCE   : Seward, A.C. Bancroft, N. 1913.
                     Jurassic plants from Cromarty and
                     Sutherland, Scotland.
                     Trans. R. Soc. Edinb. 48, 867-888

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : K 571 and slides, Sedgwick Museum,
                     Cambridge

NO. OF
SPECIMENS   : 1 and slides

SPECIMEN
SIZE   :

FOSSIL WOOD RECORD SHEET   B

NO: 92   SPECIES: <u>Cedroxylon hornei</u>

DIAMETER   :

NO. OF RINGS   :

MEAN
SENSITIVITY   :

LARGEST RING   :   4.24mm   (iii)
                    Very few rings on the slide, one larger one
                    chosen as an example

NO. OF CELLS   :   76   All cell sizes   (iii)
E/WOOD   :   62   L/WOOD: 14
LARGEST CELL   :   100μm   SMALLEST CELL: 20μm

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   B

FALSE RINGS   :

DISTORTION   :   None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 93   SPECIES: 4 Tracheidoxyl CH

LOCALITY   : West Dereham, Norfolk

EVIDENCE OF
IN SITU FOREST: An aggregation of a large number of small
                 specimens

HORIZON   : Sandringham Sands, Upper Jurassic

PALAEOPOSITION: 37°N

MAP REFERENCE : S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   : Creber, G.T. 1972 (See No. 90)

SYNONYMY   : Cedroxylon hornei, Seward & Bancroft 1913

LOCATION OF
SPECIMEN   : K 5276 and slides, Sedwick Museum,
                     Cambridge

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 3 x 3cm in cross-section; about 6cm long
                     (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 93   SPECIES: <u>4 Tracheidoxyl CH</u>

DIAMETER   :   About 3cm, from the curvature of the rings
                      and the presence of compression wood, the
                      specimen would appear to be part of a small
                      branch (iii)

NO. OF RINGS   :   At least 5 (iii)

MEAN
SENSITIVITY   :   Not sufficient rings

LARGEST RING   :   2.94mm (iii)
                   Only 5 rings on the slide, all of similar
                   width

NO. OF CELLS   :   155   All cell sizes (iii)
E/WOOD   :   151   **L/WOOD:**   4
LARGEST CELL   :   62μm   **SMALLEST CELL:**   25μm

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   **L/WOOD:**
LARGEST CELL   :   **SMALLEST CELL:**

RING TYPE   :   D

FALSE RINGS   :   Very frequent, as many as three in a ring

DISTORTION   :   None

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 94   SPECIES: 1 Tracheidoxyl MS

LOCALITY   : West Dereham, Norfolk

EVIDENCE OF
IN SITU FOREST: An aggregation of a large number of small
                 specimens

HORIZON   : Upper Jurassic

PALAEOPOSITION: 37°N

MAP REFERENCE : S.H.&B.,1981.   Map 34 p.41

SPECIMEN
REFERENCE   : Creber, G.T. 1972   (See No. 90)

SYNONYMY   : Metacedroxylon scoticum, Holden 1915

LOCATION OF
SPECIMEN   : K 5269 and slides, Sedgwick Museum,
                     Cambridge

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 1.25 x 1.25cm in cross-section; 5cm long
                     (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 94   **SPECIES:** 1 Tracheidoxyl MS

DIAMETER   : The specimen includes part of the pith and
                       about half of the cross-section of what
                       appears to be a branch.
                       Diameter about 2.5cm

NO. OF RINGS : 15

**MEAN
SENSITIVITY**   : 0.314

LARGEST RING : 1.64mm   (iii)

NO. OF CELLS : 65   All cell sizes (iii)
E/WOOD   : 58   **L/WOOD:** 7
LARGEST CELL : 40μm   **SMALLEST CELL:** 12μm

SMALLEST RING : 0.4mm   (iii)

NO. OF CELLS : 15   All cell sizes (iii)
E/WOOD   : 10   **L/WOOD:** 5
LARGEST CELL : 40μm   **SMALLEST CELL:** 12μm

RING TYPE   : B

FALSE RINGS   : None

DISTORTION   : None

NOTES   : A similar Mean Sensitivity to the East
                     Sutherland material

FOSSIL WOOD RECORD SHEET   A

NO: 95   SPECIES: Torreya antiqua

LOCALITY   : Near Fayetteville, North Carolina, U.S.A.

EVIDENCE OF
IN SITU FOREST: Large fragment

HORIZON   : Black Creek Formation, Upper Cretaceous

PALAEOPOSITION: 28°N

MAP REFERENCE : S.H.&B.,1981. Map 21 p.28

SPECIMEN
REFERENCE   : Boeshore, I. & Gray, W.D. 1936.
                       An Upper Cretaceous wood: Torreya antiqua
                       Amer. J. Bot. 23, 524-528

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 5 x 23cm in cross-section; 30cm long (i)

FOSSIL WOOD RECORD SHEET   B

NO: 95   SPECIES: Torreya antiqua

DIAMETER   : Straight ring boundaries indicate a large
                   specimen

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :

LARGEST RING : No ring widths given

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 56μm (i)   SMALLEST CELL: 18μm (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None stated

DISTORTION   : None

NOTES   : Very faint ring boundaries of 1 to 5
                   smaller tracheids

FOSSIL WOOD RECORD SHEET   A

NO: 96   SPECIES: Dadoxylon rhodeanum Goeppert

LOCALITY   :   Tai-Yuan-Fu, Pai-Tao-Tsun, Shansi, China

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Permian

PALAEOPOSITION: 60°N

MAP REFERENCE :   S.H.&B.,1981.   Map 54 p.67

SPECIMEN
REFERENCE   :   Gothan, W. & Sze, H.C. 1933.
                    Über fossil Hölzer aus China.
                    Mem. Nat. Res. Inst. Geol. Acad. Sinica 13,
                    87-103

SYNONYMY   :   Goeppert, H.R. 1850

LOCATION OF
SPECIMEN   :   No. 3562, Rijksmuseet Naturhistoriska,
                    Stockholm

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 96   **SPECIES:**   Dadoxylon rhodeanum Goeppert

DIAMETER   :   Not possible to estimate

NO. OF RINGS :   No rings

**MEAN
SENSITIVITY**   :

LARGEST RING :   No rings

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   90μm (ii)   **SMALLEST CELL:**   65μm (ii)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   :   0

FALSE RINGS   :

DISTORTION   :   None

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 97   SPECIES: <u>Protocupressinoxylon malayense</u>

LOCALITY   : Tandjong Riau, Soegi Island, Indonesia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Lower Mesozoic, probably Triassic

PALAEOPOSITION: 21°N

MAP REFERENCE : S.H.&B.,1981. Map 50 p.57

SPECIMEN
REFERENCE   : Roggeveen, P.M. 1932. Mesczoisches
                   Koniferenholz (<u>Protocupressinoxylon</u>
                   <u>malayense</u> N. sp.) von der Insel Soegi in
                   Riouw-Archipel, Niederländisch Ost-Indien.
                   Proceed. kon. Akad. Wetensch. Amsterdam 35,
                   580-4

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : Not known

NO. OF
SPECIMENS   : 20

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 97   SPECIES: Protocupressinoxylon malayense

DIAMETER   : Not possible to estimate

NO. OF RINGS   : No rings

MEAN
SENSITIVITY   :

LARGEST RING   : No rings

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 55μm (i)   SMALLEST CELL: 35μm (i)

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   : None stated

NOTES   :

FOSSIL WOOD RECORD SHEET   A

NO: 98   SPECIES: Hedcaryoxylon hortonioides

LOCALITY   :   Mouth of the Umzamba River, East Pondo
                       Land, South Africa

EVIDENCE OF
IN SITU FOREST: Many large trunks, some bored by Teredo

HORIZON   :   Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE :   S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   :   Mädel, E. 1960.   Monimiaceen-Hölzer aus den
                       oberkretazischen Umzamba-Schichten von
                       Ost-Pondoland (S-Africa).
                       Senckenbergiana Lethaea 41, 331-391

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   SM.B. 9082 and slides, Albany Museum,
                       Grahamstown

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 98   SPECIES: Hedcaryoxylon hortonioides

DIAMETER   : Portion of large trunk

NO. OF RINGS : No rings

MEAN
SENSITIVITY   :

LARGEST RING : A diffuse porous dicotyledonous wood

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : O

FALSE RINGS   :

DISTORTION   : None stated

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 99   **SPECIES:** Protoatherospermoxylon renniei

LOCALITY   : Mouth of the Umzamba River, East Pondo
Land, South Africa

EVIDENCE OF
IN SITU FOREST: Many large trunks, some bored by Teredo

HORIZON   : Upper Cretaceous, Umzamba Beds

PALAEOPOSITION: 48°S

MAP REFERENCE : S.H.&B.,1981.   Map 22 p.29

SPECIMEN
REFERENCE   : Mädel, E. 1960 (See No. 98)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : SM.B. 9022-9025 and slides, South African
Museum, Capetown

NO. OF
SPECIMENS   : 4

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 99   SPECIES: Protoatherospermoxylon renniei

DIAMETER   : Part of a large trunk

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   :

LARGEST RING   : A diffuse porous dicotyledonous wood with
                  faint rings

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   :

DISTORTION   : None stated

NOTES   :

FOSSIL WOOD RECORD SHEET A

NO: 100   **SPECIES:** Taxopitys arctica

LOCALITY   : Orulgansky Mountains, East Siberia, Russia

**EVIDENCE OF
IN SITU FOREST:** Fragment

HORIZON   : Upper Carboniferous

PALAEOPOSITION: 50°N

MAP REFERENCE : S.H.&B..1981. Map 57 p.70

**SPECIMEN
REFERENCE**   : Shilkina. I.A. 1960. Cordaitalean wood –
                      Taxopitys arctica sp. nov. from the Upper
                      Carboniferus of Eastern Siberia. (in
                      Russia). Palaeont, Zhurnal 3, 123-126

SYNONYMY   : N. sp.

**LOCATION OF
SPECIMEN**   : 674/1 Komarov Institute. Leningrad

**NO. OF
SPECIMENS**   : 1

**SPECIMEN
SIZE**   : 6 x 4 x 1.5cm

FOSSIL WOOD RECORD SHEET   B

NO: 100   SPECIES: <u>Taxopitys arctica</u>

DIAMETER   :   The straight ring boundary indicates a
                      large specimen

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   Not enough data to calculate

LARGEST RING   :   5mm (i)
                   Only one ring boundary figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   51.5μm (ii) SMALLEST CELL: 10.3μm (ii)

SMALLEST RING :   3mm   (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   B

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Very distinct growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 101   **SPECIES:** Taxopitys karagandensis

LOCALITY   : Karaganda Basin. Kazakhtan. Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Lower Permian

PALAEOPOSITION: 33°N

MAP REFERENCE : S.H.&B.,1981. Map 57 p.70

SPECIMEN
REFERENCE   : Lepekhina, V.G. 1963. New woods of
                      Cordaites from the Upper Palaeozoic of
                      Kazakhstan. Palaeont. Zhurnal 4, 103-109

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 1/8421 Central Geological Museum. Leningrad

NO. OF
SPECIMENS   : 5

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 101   SPECIES: <u>Taxopitys karagandensis</u>

DIAMETER   :   No ring boundary figured and hence tree
                      diameter impossible to estimate

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : No data

LARGEST RING   : 5mm (i)
                  Only part of one ring figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 27.5µm   SMALLEST CELL: Not figured

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None

DISTORTION   : None stated

NOTES   : Just a few smaller tracheids at the end of
                  each season

FOSSIL WOOD RECORD SHEET A

NO: 102   SPECIES: <u>Callixylon kazakhstanum</u>

LOCALITY   : 10km N.W. of Vladimirovka. Kazakhstan.
                     Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Upper Devonian

PALAEOPOSITION: 21°N

MAP REFERENCE : S.H.&B..1981. Map 66 p.79

SPECIMEN
REFERENCE   : Lepekhina. V.G. 1963. (See No. 101)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 6/8421 Central Geological Museum. Leningrad

NO. OF
SPECIMENS   : 14

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 102   SPECIES: <u>Callixylon kazakhstanum</u>

DIAMETER   : Without ring boundaries in the figure it is
                   impossible to estimate diameter

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : No data

LARGEST RING   : Only part of one ring figured. no ring
                   boundaries included

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 50μm   (ii) SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : E

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Very faint growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 103   SPECIES: Yatsenkoxylon sibiricum

LOCALITY   :   Koryak Range. Koryak National District.
                      Eastern Siberia. Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Santonian / Campanian. Upper Cretaceous

PALAEOPOSITION: 72°N

MAP REFERENCE :   S.H.&B..1981.   Map 22 p.29

SPECIMEN
REFERENCE   :   Shilkina. I.A. 1963.   A new conifer genus
                      Yatsenkoxylon sibiricum gen. et sp. nov.
                      Dokl. Akad. Nauk USSR 148. 163-165.
                      (in Russian)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   605 Palaeobotany Laboratory, Botanical
                      Institute, Leningrad

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   20cm diameter: 15cm long

FOSSIL WOOD RECORD SHEET   B

NO: 103   SPECIES: Yatsenkoxylon sibiricum

DIAMETER   :   The author estimates the diameter of the
                      original tree to have been about 50cm

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   No data

LARGEST RING   :   3mm   (i)
                   Only parts of two rings figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   134µm (ii) SMALLEST CELL: 38µm (ii)

SMALLEST RING :   1mm   (i)

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   B

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Clearly defined growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 104   SPECIES: Ginkgo asiae-mediae

LOCALITY   :   S.W. Kyzylkum. Uzbekhistan. Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Lower upper Cretaceous, Cenomanian /
                      Turonian

PALAEOPOSITION: 32°N

MAP REFERENCE :   S.H.&B..1981.   Map 26 p.33

SPECIMEN
REFERENCE   :   Khudayberdyev. R. 1962. Ginkgo wood from
                      the upper Cretaceous of south-west
                      Kyzylkum.   Dokl. Akad. Nauk USSR 145.
                      422-424. (in Russian)

SYNONYMY   :   Originally published as Ginkgoxylon. the
                      name was changed to Ginkgo in: Sikstel,
                      T.A.. Kuzichkina. U.M.. Savitskaya. L.I..
                      Khudayberdyev. R. and Shevetsova. E.M.
                      1971.   The evolution of Ginkgo in Central
                      Asia.   Palaeobotanika Uzbekhistana II. (in
                      Russian)

LOCATION OF
SPECIMEN   :   Komarov Botanical Institute. Leningrad

NO. OF
SPECIMENS   :   4

SPECIMEN
SIZE   :   Cross-section 5 x 8cm

FOSSIL WOOD RECORD SHEET   B

NO: 104   SPECIES: Ginkgo asiae-mediae

DIAMETER   :   In the absence of a figured growth ring
                    boundary, no estimate of diameter is
                    possible

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   No data

LARGEST RING   :   Only part of one ring figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   45µm (ii) SMALLEST CELL: 13.6µm (ii)

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   E

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Very faintly developed growth rings

FOSSIL WOOD RECORD SHEET A

NO: 105   SPECIES: <u>Araucariopitys dibneri</u>

LOCALITY   : Franz Joseph Land

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   : Upper Triassic

PALAEOPOSITION: 60°N

MAP REFERENCE : S.H.&B..1981.   Map 50 p. 57

SPECIMEN
REFERENCE   : Shilkina. I.A. 1967.   The fossil woods of
                    Franz Joseph Land.   Palaeobotanika 6.
                    32-50. (in Russian)

SYNONYMY   : N. sp.

LOCATION OF
SPECIMEN   : 655 Palaeobotany Laboratory. Komarov
                    Institute. Leningrad

NO. OF
SPECIMENS   : 4

SPECIMEN
SIZE   : Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 105   SPECIES: <u>Araucariopitys dibneri</u>

DIAMETER   :   A large specimen is indicated by the
straight ring boundary

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   :   No data

LARGEST RING : 5mm (i)
Only part of a ring figured

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 45μm   SMALLEST CELL: 9μm

SMALLEST RING : 2mm (i)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   B

FALSE RINGS : None

DISTORTION   :   None

NOTES   :   Very clearly marked growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 106   SPECIES: <u>Phyllocladoxylon eboracense</u>
                          (Holden) Kräusel

LOCALITY   :   Muyana. Nr. Kuvasay. South Fergana. Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Bajocian. Middle Jurassic

PALAEOPOSITION: 32°N

MAP REFERENCE :   S.H.&B..1981.   Map 38 p.45

SPECIMEN
REFERENCE   :   Nematulaevy. S. & Khudajberdyev. R. 1968.
                      Jurassic woods from Muyana (South Fergana).
                      Palaeobotanika Uzbekhistana 1. 88-94.
                      (in Russian)

SYNONYMY   :   Holden. R. (1913).   Contributions to the
                      anatomy of Mesozoic conifers.   No.1.
                      Jurassic coniferous wood from Yorkshire.
                      Ann. Bot. 27. 533-545

LOCATION OF
SPECIMEN   :   Komarov Institute. Leningrad

NO. OF
SPECIMENS   :   7

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 106   SPECIES: <u>Phyllocladoxylon eboracense</u>
                      (Holden) Kräusel

DIAMETER   : A straight ring boundary indicates a large
                   diameter

NO. OF RINGS   : Not stated

MEAN
SENSITIVITY   : No data

LARGEST RING   : Only part of one ring figured

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   : 45μm (i)   SMALLEST CELL: 15μm (i)

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   : D

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Weakly developed growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 107   SPECIES: <u>Phyllocladoxylon heizyoense</u> Shimakura

LOCALITY   :   Muyana. Nr. Kuvasay, South Fergana. Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Bajocian. Middle Jurassic

PALAEOPOSITION: 32°N

MAP REFERENCE :   S.H.&B..1981.   Map 38 p.45

SPECIMEN
REFERENCE   :   Nematulaevy. S. & Khudajberdyev. R. 1968.
                              (See No. 106)

SYNONYMY   :   Shimakura, M. 1936.   Studies on fossil ,
                              woods from Japan and adjacent lands,
                              Contribution 1.   Some Jurassic woods from
                              Japan and Manchoukuo, Sci. Rep. Tohoku Imp.
                              Univ. 2nd Ser. 18, 267-311

LOCATION OF
SPECIMEN   :   Komarov Institute, Leningrad

NO. OF
SPECIMENS   :   23

SPECIMEN
SIZE   . :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 107   SPECIES: <u>Phyllocladoxylon heizyoense</u> Shimakura

DIAMETER   :   Straight ring boundaries indicate a large
                    diameter

NO. OF RINGS :   2 (ii)
                  Only two figured

MEAN
SENSITIVITY   :   No data

LARGEST RING :   0.28mm (ii)
                  One of 2 rings figured

NO. OF CELLS :   13
E/WOOD   :   8   L/WOOD: 3
LARGEST CELL :   32μm (i) SMALLEST CELL: 9μm (i)

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :   None

DISTORTION   :   None

NOTES   :   Weakly developed growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 108   SPECIES: Pseudolaricixylon firmoides

LOCALITY   :   Smolino. Nr. Chelyabinsk, Russia

EVIDENCE OF
IN SITU FOREST: Fragments

HORIZON   :   Upper Oligocene / Lower Miocene

PALAEOPOSITION: 55°N

MAP REFERENCE :   S.H.&B..1981.   Map 10 p.17

SPECIMEN
REFERENCE   :   Khudajberdyev. R. 1958.   Fossil wood from
                      the vicinity of Smolino.   Botanical Journal
                      43, 704-710. (in Russian)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Komarov Institute. Leningrad

NO. OF
SPECIMENS   :   3

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 108   SPECIES: Pseudolaricixylon firmoides

DIAMETER   : Not possible to determine as no ring
                  boundary figured

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   : No data

LARGEST RING : Only part of one ring figured

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL : 74μm (ii) SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   : B

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Clearly marked growth rings

FOSSIL WOOD RECORD SHEET   A

NO: 109   SPECIES: Podocarpoxylon uralense

LOCALITY   :   Smolino, Nr. Chelyabinsk, Russia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Oligocene / Lower Miocene

PALAEOPOSITION: 55°N

MAP REFERENCE :   S.H.&B.,1981.   Map 10 p. 17

SPECIMEN
REFERENCE   :   Khudajberdyev. R. 1958.   (See No. 108)

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Komarov Institute. Leningrad

NO. OF
SPECIMENS   :   Not stated

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 109   **SPECIES:** <u>Podocarpoxylon uralense</u>

DIAMETER   : Large diameter indicated by the straight
                        ring boundary

NO. OF RINGS : Not stated

**MEAN
SENSITIVITY**   : Insufficient data

LARGEST RING : 0.375mm (ii)
                     Only one whole ring figured

NO. OF CELLS : 25   All cell sizes (ii)
E/WOOD   : 10   **L/WOOD:** 15
LARGEST CELL : 43μm   **SMALLEST CELL:** 11μm

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   **L/WOOD:**
LARGEST CELL :   **SMALLEST CELL:**

RING TYPE   : C

FALSE RINGS   : None

DISTORTION   : None

NOTES   : Well marked rings with steady decrease in
                        size of cells across the ring

FOSSIL WOOD RECORD SHEET   A

NO: 110   SPECIES: Dadoxylon eugeniae Zalessky

LOCALITY   :   Berezniki. Nr. Perm, Russia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Permian

PALAEOPOSITION: 38°N

MAP REFERENCE :   S.H.&B.,1981.   Map 53 p.66

SPECIMEN
REFERENCE   :   Sheshukov. N.G. & Lepechina, V.G. 1964.
                         Fossil wood from the salt deposits of
                         Berezniki.   Transactions of the All-Union
                         Geol. Inst. Leningrad 95. 70-74

SYNONYMY   :

LOCATION OF
SPECIMEN   :   Central Geological Museum, Leningrad

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   , :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 110   SPECIES: <u>Dadoxylon eugeniae</u> Zalessky

DIAMETER   :   Difficult to assess with such faint ring
                      boundaries

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :   Insufficient data

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :   Not stated

DISTORTION   :   None

NOTES   :   Very faint ring boundaries

FOSSIL WOOD RECORD SHEET   A

NO: 111   **SPECIES:**   Septomedullopitys sibirica

LOCALITY   :   Gramoteina, Kuznetsk Basin, Russia

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Permian

PALAEOPOSITION: 29°N

MAP REFERENCE   :   S.H.&B.,1981.   Map 53 p.66

SPECIMEN
REFERENCE   :   Lepekhina, V.G. 1972.   Woods of Palaeozoic
                          pycnoxylic gymnosperms with special
                          reference to North Eurasia representatives.
                          Palaeontographica B 138, 44-106

SYNONYMY   :   N. sp.

LOCATION OF
SPECIMEN   :   Central Geological Museum, Leningrad

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 111   SPECIES: <u>Septomedullopitys sibirica</u>

DIAMETER   :   Insufficient evidence to assess the
                     diameter

NO. OF RINGS   :   Not stated

MEAN
SENSITIVITY   :

LARGEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING   :

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :   D

FALSE RINGS   :

DISTORTION   :

NOTES   :   Just a few smaller tracheids at the end of
                     each season

FOSSIL WOOD RECORD SHEET   A

NO: 112   SPECIES: Indet. Wood

LOCALITY   : Lackman Crags, James Ross Island,
                     Antarctica

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Upper Cretaceous

PALAEOPOSITION: 64°S

MAP REFERENCE : S.H.&B.,1981.   Map 24 p.31

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : D 424.1 British Antarctic Survey

NO. OF
SPECIMENS   : 1

SPECIMEN
SIZE   : 15cm long, 4 x 5cm cross-section (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 112   SPECIES: Indet. Wood

DIAMETER   : 5cm (iii)

NO. OF RINGS : 8   (iii)

MEAN
SENSITIVITY   : Ring width data not sufficiently accurate

LARGEST RING : 7mm   (iii)
                    Preservation not good enough to show sizes
                    of cells

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING : 1mm   (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :

FALSE RINGS   : No evidence

DISTORTION   : Very slightly elliptical in cross-section

NOTES   : A partially carbonised branch (or centre of
                    a trunk) with definite rings but the type
                    cannot be determined

FOSSIL WOOD RECORD SHEET   A

NO: 113   SPECIES: Indet. wood

LOCALITY   :   Lackman Crags, James Ross Island,
                        Antarctica

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   :   Upper Cretaceous

PALAEOPOSITION: 64°S

MAP REFERENCE :   S.H.&B.,1981.   Map 24 p.31

SPECIMEN
REFERENCE   :   Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   :   8731 British Antarctic Survey

NO. OF
SPECIMENS   :   1

SPECIMEN
SIZE   :   5cm long; 7 x 7cm in cross-section   (iii)

FOSSIL WOOD RECORD SHEET   B

NO: 113   SPECIES: Indet. wood

DIAMETER   : 22cm deduced from the curvature of the
                    rings

NO. OF RINGS : 15 (iii)
                 First few rings missing

MEAN
SENSITIVITY   : Ring width data not sufficiently accurate

LARGEST RING   : 6mm (iii)
                  Preservation not good enough to show sizes
                  of cells

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING : 3mm (iii)

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :

FALSE RINGS   : No evidence

DISTORTION   : Not possible to determine

NOTES   : Definite rings but type cannot be
                  distinguished

FOSSIL WOOD RECORD SHEET A

NO: 114   SPECIES: Indet. wood

LOCALITY   : Dagger Peak, The Naze, James Ross Island,
                     Antarctica

EVIDENCE OF
IN SITU FOREST: Fragment

HORIZON   : Upper Cretaceous

PALAEOPOSITION: 64°S

MAP REFERENCE : S.H.&B.,1981.   Map 24 p.31

SPECIMEN
REFERENCE   : Not described

SYNONYMY   :

LOCATION OF
SPECIMEN   : D 87 British Antarctic Survey

NO. OF
SPECIMENS   : 2

SPECIMEN
SIZE   : (a) 15cm long;   5cm x 5cm in cross-section
                     (b) 11.5cm long; 5cm x 5cm in cross-section

FOSSIL WOOD RECORD SHEET   B

NO: 114   SPECIES: Indet. wood

DIAMETER   :   5cm

NO. OF RINGS   :   20

**MEAN
SENSITIVITY**   :   Ring width data not sufficiently accurate

LARGEST RING   :   1.1mm
                         Preservation not good enough to show sizes
                         of cells

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

SMALLEST RING :   0.6mm

NO. OF CELLS   :
E/WOOD   :   L/WOOD:
LARGEST CELL   :   SMALLEST CELL:

RING TYPE   :

FALSE RINGS   :   No evidence

DISTORTION   :   Not possible to determine

NOTES   :   Definite rings but type cannot be
                         distinguished

FOSSIL WOOD RECORD SHEET   A

NO: 115   SPECIES: Indet. Cheirolepidiaceous wood

LOCALITY   :   Curio Bay, South Island, New Zealand

EVIDENCE OF
IN SITU FOREST: Fossil forest with in situ stumps

HORIZON   :   Temaikan Stage, Middle Jurassic

PALAEOPOSITION: 78°S

MAP REFERENCE :   S.H.&B.,1981.   Map 40 p.47

SPECIMEN
REFERENCE   :   Pole, M. 1982.   The geology of Slope Point
                      to Curio Bay.   Unpublished MS. Geology
                      Department, Otago University.

SYNONYMY   :   -

LOCATION OF
SPECIMEN   :   Geology Department, Otago University

NO. OF
SPECIMENS   :   Not stated

SPECIMEN
SIZE   :   Max. recorded = 12cm in diameter.   (iii)
                                              (With ring
                      details)

FOSSIL WOOD RECORD SHEET   B

NO: 115   SPECIES: Indet. Cheirolepidiaceous wood

DIAMETER   :   Range from a few centimetres to more than
                     21cm; the larger ones without ring details.
                     (iii)

NO. OF RINGS :   Max. recorded = 100   (iii)

MEAN
SENSITIVITY   :   No data

AVERAGE RING :   1.1mm
                  No cellular details available

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

SMALLEST RING :

NO. OF CELLS :
E/WOOD   :   L/WOOD:
LARGEST CELL :   SMALLEST CELL:

RING TYPE   :   -

FALSE RINGS   :   None recorded

DISTORTION   :   None recorded

NOTES   :   An in situ fossil forest at a very high
                  latitude

FOSSIL WOOD RECORD SHEET   A

NO: 116   SPECIES: <u>Araucarioxylon japonicum</u> Shimakura

LOCALITY   :   South east of Ban Kut Bot, Changwat
                        Kalasin, Thailand

EVIDENCE OF
IN SITU FOREST: Fragments associated with coal

HORIZON   :   Lower Jurassic, Phu Kadung Formation

PALAEOPOSITION: 27°N

MAP REFERENCE :   S.H.&B.,1981.   Map 42 p.49

SPECIMEN
REFERENCE   :   Asama, K. 1982.   Contributions to the
                        geology and palaeontology of south-east
                        Asia, CCXXII: <u>Araucarioxylon</u> from Khorat,
                        Thailand.   Geol. Pal. Southeast Asia 23:
                        57-64

SYNONYMY   :   Shimakura, M. 1936.   Studies of fossil
                        woods from Japan and adjacent lands.
                        Contribution I.   Sci. Rep. Tohoku Imp.
                        University, Ser. 2 (Geol.) 18, 267-310

LOCATION OF
SPECIMEN   :   NSMT-PP7537, PP7538. PP7539. PP7540
                        National Science Museum, Tokyo.

NO. OF
SPECIMENS   :   4

SPECIMEN
SIZE   :   Not stated

FOSSIL WOOD RECORD SHEET   B

NO: 116   **SPECIES:** <u>Araucarioxylon japonicum</u> Shimakura

DIAMETER   : From the ring curvature the author
                     estimates the diameters of the trees to
                     have been 30-50cm.   (i)

NO. OF RINGS : Not stated

MEAN
SENSITIVITY   : Insufficient data

LARGEST RING : 8.5mm (i)
                    No cellular details available

NO. OF CELLS : 199 (i)
E/WOOD   : 196 (ii)   **L/WOOD:** 3 (ii)
LARGEST CELL : 80µm (ii) **SMALLEST CELL:** 20µm (ii)

SMALLEST RING : 1.0mm (i)

NO. OF CELLS : 11 (i)
E/WOOD   : 9 (ii)   **L/WOOD:** 2 (ii)
LARGEST CELL : 80µm (ii) **SMALLEST CELL:** 20µm (ii)

RING TYPE   : D

FALSE RINGS   : Very frequent

DISTORTION   : Some very slight crushing

NOTES   :

APPENDIX I

INDEX

In the Index the letters (a) to (f) stand for the following:

    (a) Species

    (b) Horizon

    (c) Locality

    (d) Evidence for _in situ_ forest

    (e) Palaeoposition

    (f) Ring type (as defined in Part IV)

INDEX

NO 1 (a) Xenoxylon latiporosum (Cramer) Gothan (b) Lower Cretaceous

(c) Colville River, 4.8km S. of the junction with the (d) Fragment in stratum
Awuna River, Alaska

(e) 80ºN (f) D

NO 2 (a) Cedrus alaskensis Arnold (b) Lower Cretaceous

(c) At the junction of the Oolamnagavik River and the (d) Fragment in stratum
Colville River, Alaska

(e) 80ºN (f) D

NO 3 (a) Protopiceoxylon exstinctum Gothan (b) Lower Cretaceous

(c) King Charles Land (E. Spitzbergen) (d) Loose fragments

(e) 61ºN (f) D

NO 4 (a) Protopiceoxylon exstinctum Gothan (b) Lower Cretaceous

(c) Green Harbour. Spitzbergen (d) Loose fragments

(e) 61ºN (f) D

NO 5 (a) Cedroxylon disjunctum Bannan & Fry (b) Lower Cretaceous

(c) 14km east of the western end of Strand Fiord (d) Loose fragment
Peninsula on Axel Heiberg Island (Canadian Arctic)

(e) 75ºN (f) B

NO 6 (a) Piceoxylon christopheri Bannan & Fry (b) Lower Cretaceous

(c) In the south-eastern part of Amund Ringnes Island (d) Loose fragment
(Canadian Arctic)

(e) 75ºN (f) B

INDEX

INDEX

NO 13 (a) Dadoxylon kerguelenense Seward   (b) Early Tertiary

(c) Kerguelen Island   (d) Fragment   (e)   (f) E

NO 14 (a) Podocarpoxylon aparenchymatosum Gothan   (b) Lower Tertiary

(c) Seymour Island, Antarctic Peninsula   (d) Fragment   (e) 56°S (f) D

NO 15 (a) Dadoxylon pseudoparenchymatosum Gothan   (b) Lower Tertiary

(c) Seymour Island, Antarctic Peninsula   (d) Fragment   (e) 56°S (f) D

NO 16 (a) Laurinoxylon uniseriatum Gothan   (b) Lower Tertiary

(c) Snow Hill Island, Antarctic Peninsula   (d) Fragment   (e) 60°S (f) B/C

NO 17 (a) Cupressinoxylon antarcticum Beust   (b) Lower Tertiary

(c) Kerguelen Island   (d) Fragment   (e)   (f) E

NO 18 (a) Nicolia aegyptiaca Unger   (b) Upper Cretaceous. Lower Tertiary

(c) 11.2km S.E. of Cairo, Egypt   (d) Fragment, part of a fossil forest   (e) 5°N (f) E

INDEX

NO 19 (a) <u>Dadoxylon aegyptiacum</u> Unger (b) Upper Cretaceous. Lower Tertiary

(c) 11.2km S.E. of Cairo, Egypt (d) Fragment.
part of a fossil forest (e) 5°N (f) E

NO 20 (a) <u>Dadoxylon rollei</u> Unger (b) Upper Cretaceous, Lower Tertiary

(c) 11.2km S.E. of Cairo, Egypt (d) Fragment.
part of a fossil forest (e) 5°N (f) O

NO 21 (a) <u>Taxoxylon cretaceum</u> Unger (b) Upper Cretaceous, Lower Tertiary

(c) 11.2km S.E. of Cairo, Egypt (d) Fragment,
part of a fossil forest (e) 5°N (f) E

NO 22 (a) <u>Dadoxylon dantzii</u> Potonie (b) Upper Cretaceous

(c) Mbaragandu Valley, Tanzania (d) Fragments (e) 28°S (f) E

NO 23 (a) <u>Protocedroxylon paronai</u> Negri (b) Middle Cretaceous

(c) Rumia, near Iefren, (now Ya'Fran), Tripolitania,
Libya (d) Fragment (e) 13°N (f) E

NO 24 (a) <u>Protocedroxylon paronai</u> Negri (b) Middle Cretaceous

(c) Scekscuik, near Iefren, (now Ya'Fran),
Tripolitania, Libya (d) Fragment (e) 13°N (f) O

INDEX

INDEX

449

INDEX

451

INDEX

NO 49 (a) Tarrietoxylon sumatrense Kräusel (b) Middle Miocene (c) Muara Bungin am Sungi Pobungo. Indonesia (d) Fragment (e) 3°S (f) E

NO 50 (a) Eucalyptus ? (b) Upper Cretaceous (c) Numeralla, ca. 15km from Cooma. N.S. Wales. Australia (d) Large fragment in river bed (e) 61°S (f) -

NO 51 (a) Araucarites moellhausenianus Gopp (b) Triassic (c) West side of Sierra Madre. New Mexico. U.S.A. (d) Fragment, part of same formation as the fossil forest of Arizona (e) 13°N (f) D

NO 52 (a) Dadoxylon santalense N. sp. (b) Middle Jurassic (c) Mandro. Rajmahal Hills. Bihar. India (d) Fragment (e) 40°S (f) E

NO 53 (a) Dadoxylon amraparense N. sp. (b) Middle Jurassic (c) Amrapara. Rajmahal Hills, Bihar. India (d) Fragment (e) 40°S (f) C

NO 54 (a) Indet. conifer wood (b) Permian (c) Rio Grande do Sul, Brazil (d) Very large specimen (e) 30°S (f) -

INDEX

INDEX

NO 61 (a) Protocedroxylon pseudo-araucarioides (b) Lower Cretaceous

(c) Choshi, Chiba Prefecture, Japan (d) Fragments (e) 36°N (f) O

NO 62 (a) Taxaceoxylon japonomesozoicum (b) Lower Cretaceous

(c) Choshi, Chiba Prefecture, Japan (d) Fragment (e) 36°N (f) O

NO 63 (a) Metasequoia milleri (b) Middle Eocene

(c) 3km S.S.W of Allenby, British Columbia (d) Much other material indicating a forest locality (e) 62°N (f) D

NO 64 (a) Indet. Dicotyledonous Wood (b) Lower Tertiary

(c) Hare Island, W. Greenland (d) Fragments (e) 62°N (f) D

NO 65 (a) Indet. Dicotyledonous Wood (b) Lower Tertiary

(c) Hare Island, W. Greenland (d) Fragments (e) 62°N (f) D

NO 66 (a) Cedroxylon matsumurae (b) Upper Cretaceous

(c) Hokkaido, Japan (d) Part of a large trunk (e) 53°N (f) D

INDEX

INDEX

455

INDEX

INDEX

INDEX

INDEX

INDEX

NO 103 (a) Yatsenkoxylon sibiricum
(b) Upper Cretaceous
(c) Koryak Range, Koryak National District, Eastern Siberia, Russia
(d) Fragments
(e) 72°N (f) B

NO 104 (a) Ginkgo asiae-mediae
(b) Lower upper Cretaceous
(c) S.W. Kyzylkum, Uzbekhistan, Russia
(d) Fragments
(e) 32°N (f) E

NO 105 (a) Araucariopitys dibneri
(b) Upper Triassic
(c) Franz Joseph Land
(d) Fragments
(e) 60°N (f) B

NO 106 (a) Phyllocladoxylon eboracense (Holden) Krausel
(b) Middle Jurassic
(c) Muyana, Nr. Kuvasay, South Fergana, Russia
(d) Fragments
(e) 32°N (f) D

NO 107 (a) Phyllocladoxylon heizyoense Shimakura
(b) Middle Jurassic
(c) Muyana, Nr. Kuvasay, South Fergana, Russia
(d) Fragments
(e) 32°N (f) D

NO 108 (a) Pseudolaricixylon firmoides
(b) Lower Miocene
(c) Smolino, Nr. Chelyabinsk, Russia
(d) Fragments
(e) 55°N (f) B

461

APPENDIX II

CLIMATIC INDICATIONS FROM GROWTH RINGS IN
FOSSIL WOODS

G.T. CREBER and W.G. CHALONER

Botany Department, Bedford College,
London NW1 4NS

1. INTRODUCTION

The wood in fossil trees represents a unique 'data store' of the climatic conditions under which it was formed (Chaloner and Creber, 1973; Creber, 1977). Fossil wood has an abundant world-wide distribution from the Upper Devonian to the present day. This is partly due to the fact that it is a relatively resistant material which readily becomes fossilised in a number of ways: petrifaction (siliceous, pyritic or calcareous); charcoalification (by partial combustion) or incorporation in peat or lignite. The world-wide distribution is also a reflection of the original widespread occurrence of the trees which makes them very suitable as indicators of climate on a global scale. Compared with other biological evidence of past climates, trees are specifically the product of the climate on land. As illustrated in Figure 1, the study of fossil wood and particularly of the presence or absence of 'growth rings' gives a direct measure of continental (as against marine) biological productivity, and the intensity of seasonality.

2. THE FORMATION OF GROWTH RINGS

The trunk, branches and larger roots of a tree consist largely of wood formed as a result of the active division of a layer of cells called the vascular cambium. As the products of this layer expand, the cambium is displaced in an outward direction. In many trees, particularly those growing in temperate latitudes, but also including some in equatorial regions, cambial activity is not constant throughout the year. The discontinuity, particularly the cessation of cell division in the unfavourable season, leads to the appearance of rings in a cross-section of the wood. In the wood of coniferous trees there is a striking difference between the small thick-walled cells termed

Figure 1. Possible deductions from fossil wood. A. The existence of <u>in situ</u> stumps establishes that climatic conditions permitted the growth of substantial trees.
B. The spacing and diameters of the stumps enables forest density and basal area to be estimated. C. The presence or absence of rings indicates seasonality of climate, or lack of it. D. Ring width is an indication of productivity and the amount of variance provides a measure of seasonal range in the environment.
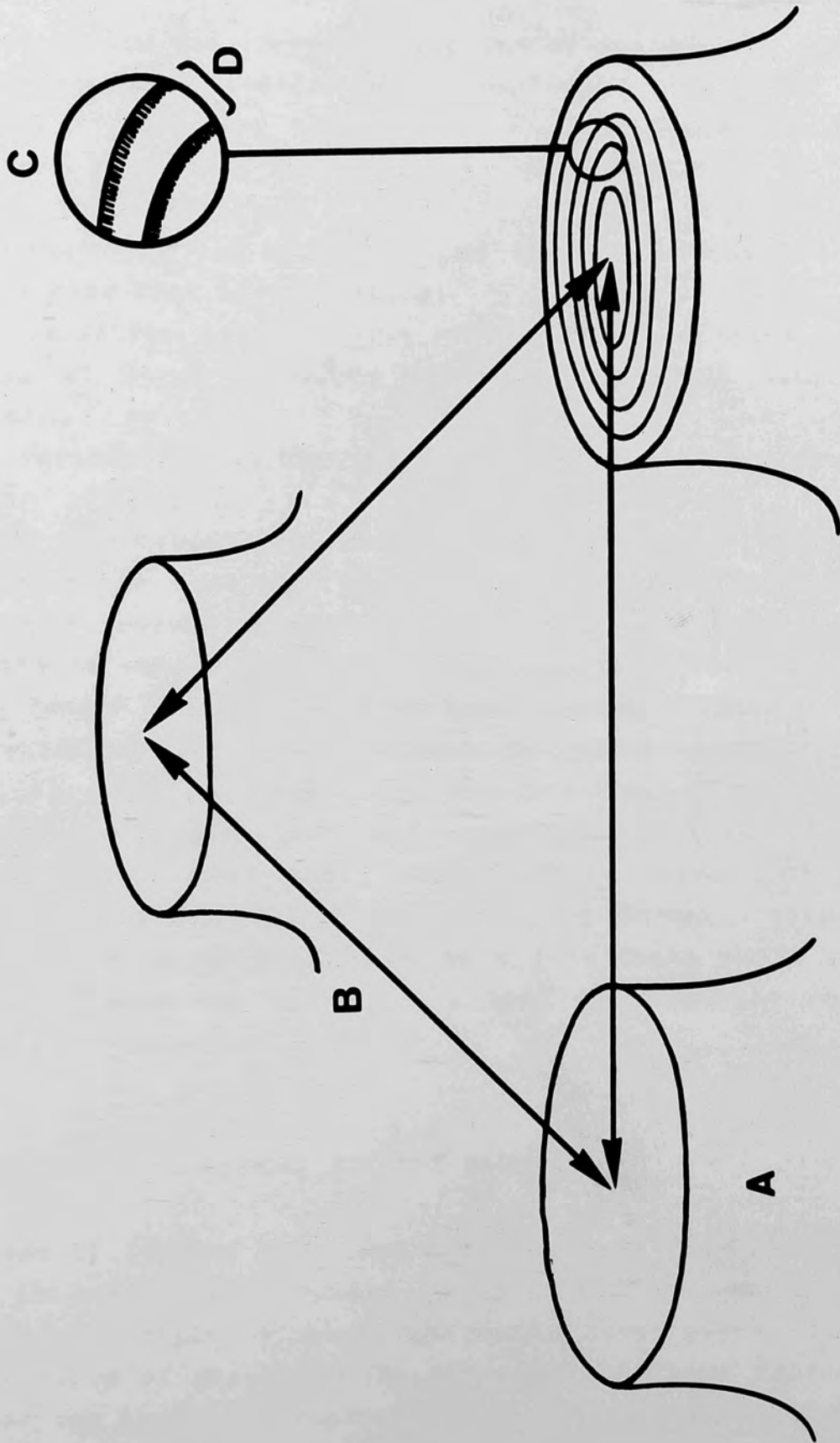
C D

B

A

latewood, which are formed at the end of the growing season and the larger thin-walled cells, earlywood, formed at the beginning of the next season (Figure 6a). There are four parameters that arise from this mode of growth:

1. The width of the ring;
2. The width of the earlywood and the proportion of the whole ring that it represents;
3. The variation in cell size across the ring (i.e. the ratio of large earlywood cells to the small latewood ones).
4. The variability of the ring widths, from one year to the next.

The magnitudes of these parameters have climatic significance in that they are strongly influenced by length of growing season, ambient temperatures, rainfall and the stability or otherwise of the climatic pattern from year to year. Zahner (1963) describes some specimen examples of rings which may form under various environmental conditions (Table 1). 'False rings' may form when water supply is seriously limiting so that cell expansion is prevented and thus a band of very small cells results which mimics a normal end-of-season boundary. A ring of damaged cells in the earlywood is an indication of a late frost and a tree may also produce at this time a band of traumatic resin canals, if it is a conifer.

3. ENVIRONMENTAL CONTROL OF WOOD FORMATION

The range of factors which may affect growth increments of trees includes water supply to the roots, atmospheric humidity, daylength, mineral nutrients, temperature, light and the force of gravity. The operation of these factors, some varying through a seasonal pattern, interacting on one another and on the genetically controlled growth potential of any individual tree, produces a situation of some complexity (Fritts, 1976; Creber, 1977: Kramer and

Table 1. Some examples of data from tree rings formed under various environmental water conditions.
(Data from Zahner, 1963.)

WATER SUPPLY DURING THE GROWING SEASON	RING WIDTH	PERCENTAGE OF LATEWOOD	
		UPPER BOLE	LOWER BOLE
Average throughout the season	Average	15%	35%
Higher than average throughout the season	Wide	5%	10%
Average early in the season, drought in the later part	Narrow	15%	10%
Brief drought in early part of season, higher than average later	Wider than average with 'false ring' in upper bole only	10% (including 'false ring')	55%
Longer drought in early part of season, higher than average later	Slightly wider than average with very pronounced 'false ring' in earlywood throughout the tree	20% (including 'false ring')	35% (including 'false ring')

Kozlowski, 1979). The activity of the vascular cambium in laying down the current year's growth increment, is controlled primarily by growth substances (plant hormones in the broad sense) being produced in the young leaves and shoots at the crown of the tree (Larson, 1964). The decisive role that the seasonal character of the environment plays in cambial activity is therefore indirect so far as the wood of the tree trunk is concerned. The direct effect of the climate acts on the crown of the tree, controlling both the production of carbohydrate as raw material, and the formation of growth hormones, which in turn govern the thickness and character of the secondary wood laid down (Denne, 1976).

The situation is further complicated by the fact that the actual time of onset of new elongation growth in the spring, the consequent triggering of cambial activity, and the later transition from earlywood production to latewood formation are not controlled primarily either by the ambient temperature and water availability or by the rate of photosynthesis. In evolutionary terms, it has evidently proved disadvantageous to use the sporadic occurrence of warm weather or high light intensity in the spring as a triggering mechanism for the onset of renewed rapid growth of young shoots and the development of the year's production of leaves. Instead, the mechanism for initiating the irreversible onset of the expansion of new leaves involves the process called photoperiodism, which is the response by the plant to changing daylength. Provided that dormancy has been broken by chilling, shoots will develop in response to the lengthening days. Photoperiodism is also the process which generally initiates the flowering process in angiosperms. Salisbury (1981) uses the phrases 'back-up' and 'fail-safe' to describe this mechanism. The beginning of earlywood formation in conifers, and the subsequent change to latewood production, appears to be largely controlled by daylength rather than the more or less

seasonally linked, but unpredictable, light intensity, temperature and water-availability cycles. The initiation of a growth ring shown by a typical temperate tree trunk (whether gymnosperm or angiosperm) has been to some extent, therefore, programmed for induction by an increase in daylength, while the amount of both earlywood and latewood is controlled by the environment to which the crown of the tree is exposed.

The precision of this photoperiodic adaptation is shown by the fact that some species with wide latitudinal range may have races with different photoperiods, matching the spring-time daylengths appropriate to their latitudes (Vaartaja, 1962; Wareing and Phillips, 1970). In examining the record of fossil woods it may reasonably be supposed that at any time in the past, a given species of tree would have been adapted to its environment not merely in a climatic sense but also in terms of photoperiod. The establishment of forest in a new location by migration, or actual climatic change affecting a species within its existing range would both presumably have been slow enough for the species to have had time to adapt to the new situation. If it did not, it would have been ousted by competition. The presence of a sequence of growth rings in a fossil, as in living wood, must be construed as normally reflecting climatic periodicity to which the tree is not merely responding, but to which it was adapted in terms of a photoperiodic response, if one was involved.

Despite the complexity of these controlling factors, it is still a valid observation that the formation of uninterrupted secondary wood is generally to be correlated with a uniform, seasonless climate. Wood entirely lacking growth rings is generally confined to those areas in the tropics, especially the tropical rain forest, in which the climate is relatively seasonless. The converse is not, of course, true; within the tropics, some trees show a periodic leaf shedding and leaf flushing pattern with resulting

growth rings in the wood. Tomlinson and Craighead (1972) examined the woods of the trees of sub-tropical Florida south of latitude 26°N. Eighty-seven species were observed and although they were growing closely together in the same environment, 51 species produced obvious growth rings whilst 36 were without rings in their wood. Nevertheless, it is significant that even in tropical latitudes where daylength may vary only between 11½ and 12½ hours throughout the year, this seemingly inconspicuous difference forms the basis of a seasonal control of leaf flushing (Njoku, 1963, 1964; Longman and Jeník, 1974).

4. FOSSIL WOOD THROUGH GEOLOGICAL TIME

4a. The Devonian

In a relatively short time, considered geologically, after gaining a foothold on the land, plants became capable of producing stems more than 1m in diameter (Chaloner and Sheerin, 1979). The wood known as Callixylon, represents the trunk or major branch of a large progymnosperm, Archaeopteris. It has been described from Indiana (Elkins and Wieland, 1914; Arnold, 1931), New York State (Hylander, 1922, Arnold, 1930; Beck, 1953) and the Donetz Basin (Zalessky, 1909, 1911). The first two occurrences had palaeolatitudes of 19°S and 17°S respectively, whilst the latter was at 3°N. The American specimens from the margins of the Devonian tropics usually have very weakly defined growth rings whilst those from the Russian locality close to the palaeoequator are completely devoid of rings. The ring boundaries in the American specimens are marked by the presence of only two or three smaller diameter tracheids. There is not the sharp distinction between the latewood of one year and the earlywood of the next as is seen in the ring boundaries of temperate woods (Figure 6a). Elkins and Wieland (1914) point out, too, that the rings are rather

variable in width, with quite large rings adjacent to much smaller rings. The indication is that there was only a temporary hiatus in the process of cell expansion before normal growth was resumed. This type of growth ring and the absence of rings in the Donetz Basin in Russia are consistent with growth within the Devonian tropics which the palaeomagnetic evidence indicates as the location of these sites.

Matten and Banks (1967) describe some secondary wood of the genus Sphenoxylon from the Upper Devonian of New York with extremely weakly developed ring boundaries. Another locality which has yielded Devonian wood is Spitzbergen; Høeg (1942) figures a fragment of secondary wood of gymnospermous type of Upper or Middle Devonian age, showing no trace of growth zones within the limits of a rather small specimen (8 mm x 8 mm). This means either that there were growth rings in excess of 8 mm (a measure of a high level of forest productivity), (see p.4.93) or that growth was of uninterrupted character, with the implication of more or less seasonless conditions. Hoeg's specimen was at a palaeolatitude of 20°N which was just within the Devonian tropical belt. The distribution of fossil plants generally in the Devonian gives little indication of any clear latitudinal change in vegetation type (Edwards, 1973). The growth characteristics of Devonian wood from high palaeolatitudes would therefore be of great interest, since so far as we are aware there is no record of any wood from the Devonian from outside the tropics of that period.

4b. The Carboniferous

A great diversity of large stems without rings are known from growth sites ranging from Kansas eastwards across the Mid-West of the United States, and from Western Europe through to the Donetz Basin in Russia. Furthermore, this lack of growth rings is a feature not only of gymnosperm

woods but also of the lycopods, articulates and seed-ferns. Arnold (1947) figures a piece of secondary wood (Dadoxylon romingerianum) from the Middle Pennsylvanian of Coshocton, Ohio (palaeolatitude 11°S) in which there were no growth rings in a radial distance of 3.5 cm. Specimens of similar size from tree stumps of the genus Pitus (Pitys of many authors) in situ on the English-Scottish border (Long, 1979) are also entirely without rings (Figure 6f). Such continuous growth is entirely consistent with the tropical distribution of the Euramerian coal-swamp flora of the Carboniferous period as indicated by the palaeomagnetic evidence.

Although examples of Carboniferous woods with growth rings are hard to find, that is not to say there are none at all. The following species of Callixylon with faint growth rings have been recorded from the Northern hemisphere Lower Carboniferous. C. whiteanum was described by Arnold (1934) from the Woodford Chert of Oklahoma (palaeolatitude 18°S) of Lower Mississippian age. Also, from this period, Hoskins and Cross (1951) re-described C. brownii from the upper part of the New Albany Shale of Kentucky (palaeolatitude 17°S). Another Lower Carboniferous genus, Eristophyton, occurs in the Cementstone Group of the Calciferous Sandstone Series of Southern Scotland (palaeolatitude 2°S). E. beinartium was described by Absalom (1931) from the Tweed Valley and E. waltoni by Lacey (1953) from Dunbartonshire. The former had about 40, quite pronounced, growth rings of 4 mm average width but in the latter species they were rather faint. Rings were also exhibited by Cordaites recentium (Goldring, 1921) and Dadoxylon (Cordaites) sp. (Jensen, 1982) from the Pennsylvanian of Oklahoma. Jensen invokes the effect of the Ouachita-Marathon orogeny as a possible explanation for the occurrence of rings in her specimen. She suggests that the orogenic activity created regional changes in elevation; presumably these might have accentuated a seasonal precipitation pattern. In the nearby state of Kansas,

Arnold (1947) showed that specimens of Cordaites recentium and C. materiarum have rings varying from 3 to 8 mm in width. Also from Kansas, is a wood specimen from the Upper Pennsylvanian (Baxter and Hartman, 1954) of Cordaitalean affinities which showed faintly developed rings. It is a feature, too, of this period that the same area may yield some specimens with rings and some without. Oklahoma has also been the source of Cordaites michiganense (Tynan, 1959) and Dadoxylon adaense (Wilson, 1963) which, in contrast to those mentioned earlier, were lacking in rings.

The existence of these few occurrences of Carboniferous rings vitiates Antevs' (1925) suggestion that perhaps trees of the Palaeozoic had not yet the capability of true ring formation. He put forward the view that the scarcity of rings in the Palaeozoic could not unequivocally be taken as evidence of a seasonless climate if the trees had been unable to show seasonal wood formation. The cases cited above would seem to indicate that the trees could make rings if there was sufficient fluctuation in the environmental control. In the context of the Carboniferous coal swamps, fluctuations in the water supply would seem to be the most likely cause.

4c. The Permian

As in the Upper Carboniferous. the majority of European Permian fossil woods are lacking in growth rings (Frentzen, 1931). Lemoigne and Tyroff (1967) and Schweitzer (1968) have reported exceptions but, in general, the situation for the European Permian remains much as it was summarised by Gothan (1911) who said that for this period growth rings were "lacking or at best only doubtfully developed". In North America, Holden (1913) described a Tylodendron stem from Prince Edward Island (palaeolatitude 3°S in the Permo-Carboniferous) which was lacking in rings. Again, this seems entirely consistent with the tropical situation

of the Euramerian province during this period.

However, the woods from Gondwanaland are significantly different and they emphasise the fact that away from the tropical belt, in the higher latitudes, rings were produced by the trees (Figure 6e). A typical example of a Gondwanan wood is Dadoxylon bakeri from the Permo-Carboniferous of the Falkland Islands (palaeolatitude about 55°S). This wood has well marked growth rings with a distinct band of latewood in each (Seward and Walton, 1923). D. indicum and D. bengalense are two examples from Bengal, India (Holden, 1917). Their growth site palaeolatitude of about 62°S in the Permo-Carboniferous places them within the glaciated area of India (Frakes, 1979). Presumably they grew immediately after the great Stephanian-Sakmarian glaciation of Gondwanaland. A further example from Bengal, of Upper Permian age, is Palaeospiroxylon heterocellularis (Prasad and Chandra, 1980); by this time Bengal had moved to 39°S. All of these Bengalese specimens had growth rings.

Maheshwari (1972) has reviewed the published accounts of Permian antarctic fossil wood which occurs at a number of sites in the Trans-antarctic Mountains bordering the coastline of the Ross Sea, ranging from the Horlick Mountains to Southern Victoria Land. As there is abundant evidence of glaciation of the whole of this region in Early Permian times (Frakes, 1979), the wood must be of later age. The palaeolatitude of these sites was within the palaeo-Antarctic Circle. All of the wood specimens have clearly marked growth rings from 5 to 8 mm in width or more.

These occurrences of fossil woods in high palaeolatitudes are of significance in several respects. Firstly, the existence of large pieces of wood up to 8 m long and 60 cm in diameter (Doumani and Long, 1962), more or less in situ in Antarctica indicates that sizeable trees were capable of growing there, at latitudes in which trees cannot grow under our present global climatic regime (Figure 3). Secondly, the presence of growth rings indicates a

strongly seasonal climate, as would be expected. The third and most noteworthy feature of these high latitude woods is the actual size of the growth increments mentioned above. Present day gymnosperm trees will only develop comparable growth increments of the order of 1 cm per year, under very favourable middle latitude conditions (see p.493). The occurrence of these Permian woods from within the Permian Antarctic Circle raises fundamental problems involving tree physiology and the nature of palaeoclimates.

4d.   The Mesozoic

It is from within the Mesozoic and Early Tertiary that the greatest latitudinal spread of tree growth is seen. In the Lower Cretaceous it appears that substantial trees (up to at least 50 cm in diameter) were able to flourish well inside the palaeo-Arctic and Antarctic Circles. Figure 2 shows some of the published records of Mesozoic woods plotted on a palaeoreconstruction map. The map symbols indicate the presence or absence of growth rings and if they are present, the ring thickness. There is evidently a general occurrence of growth-ring-free woods in Cretaceous mid-latitudes, with growth rings predominantly restricted to higher latitudes. However, as in the Permian, there are relatively broad growth rings, indicating high rates of growth, in the high latitudes of both hemispheres (e.g. Brainard's Forest, Ellesmere Island, palaeolatitude 75° North (Figure 6b) and Jefferson's Forest, Alexander Island, 70° South (Figure 6d): both in situ examples). The data plotted in Figure 2 appear in Table 2. The problems raised by these trees growing in high palaeolatitudes will be considered in Section 5.
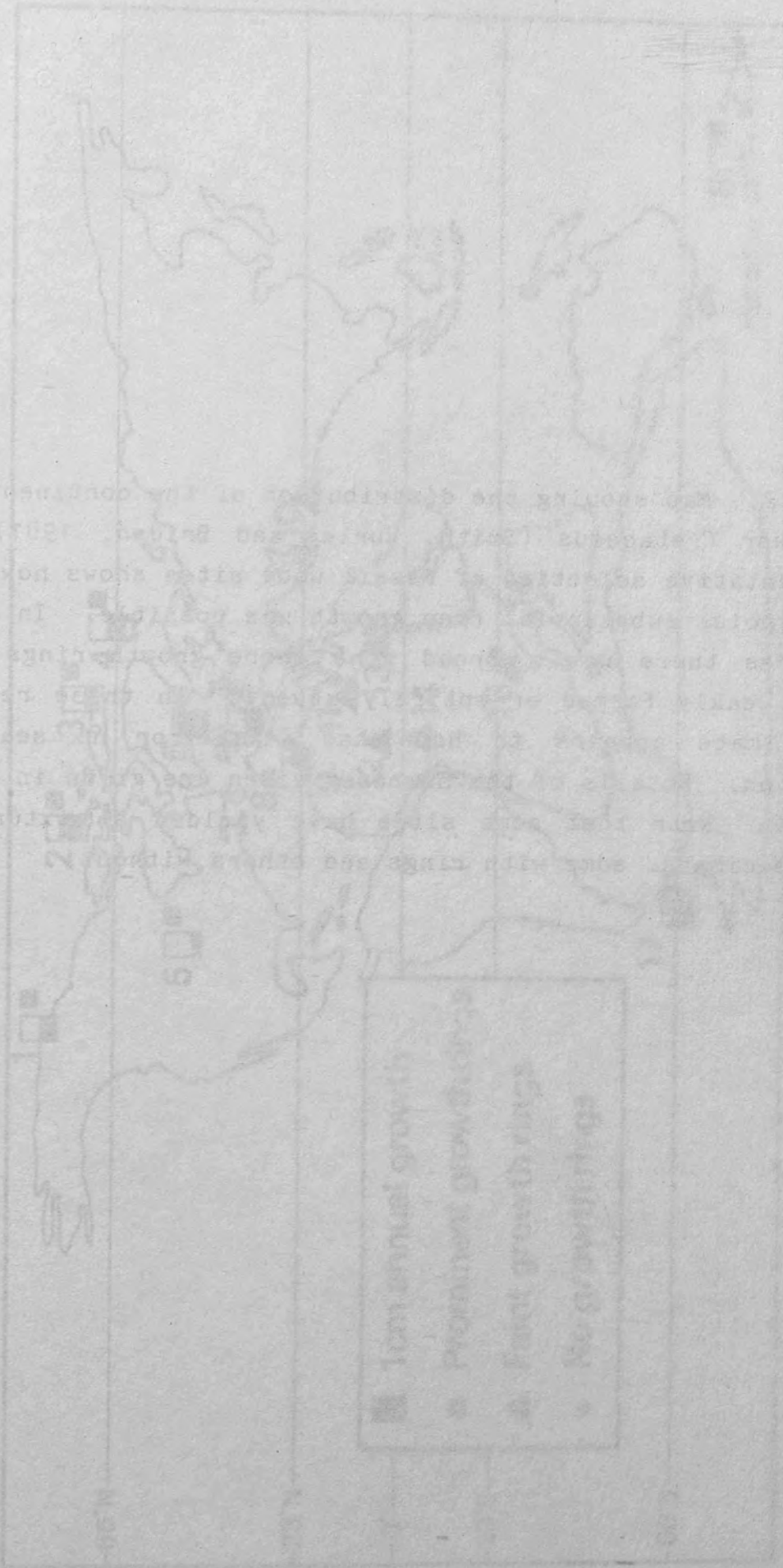
Figure 2. Map showing the distribution of the continents in the Lower Cretaceous (Smith. Hurley and Briden. 1981). A representative selection of fossil wood sites shows how near to the poles substantial tree growth was possible. In lower latitudes there was a broad zone where growth rings were either weakly formed or entirely absent. In these regions the climate appears to have had little or no seasonal variation. Details of the numbered sites are given in Table 2. Note that some sites have yielded a mixture of wood specimens, some with rings and others without.
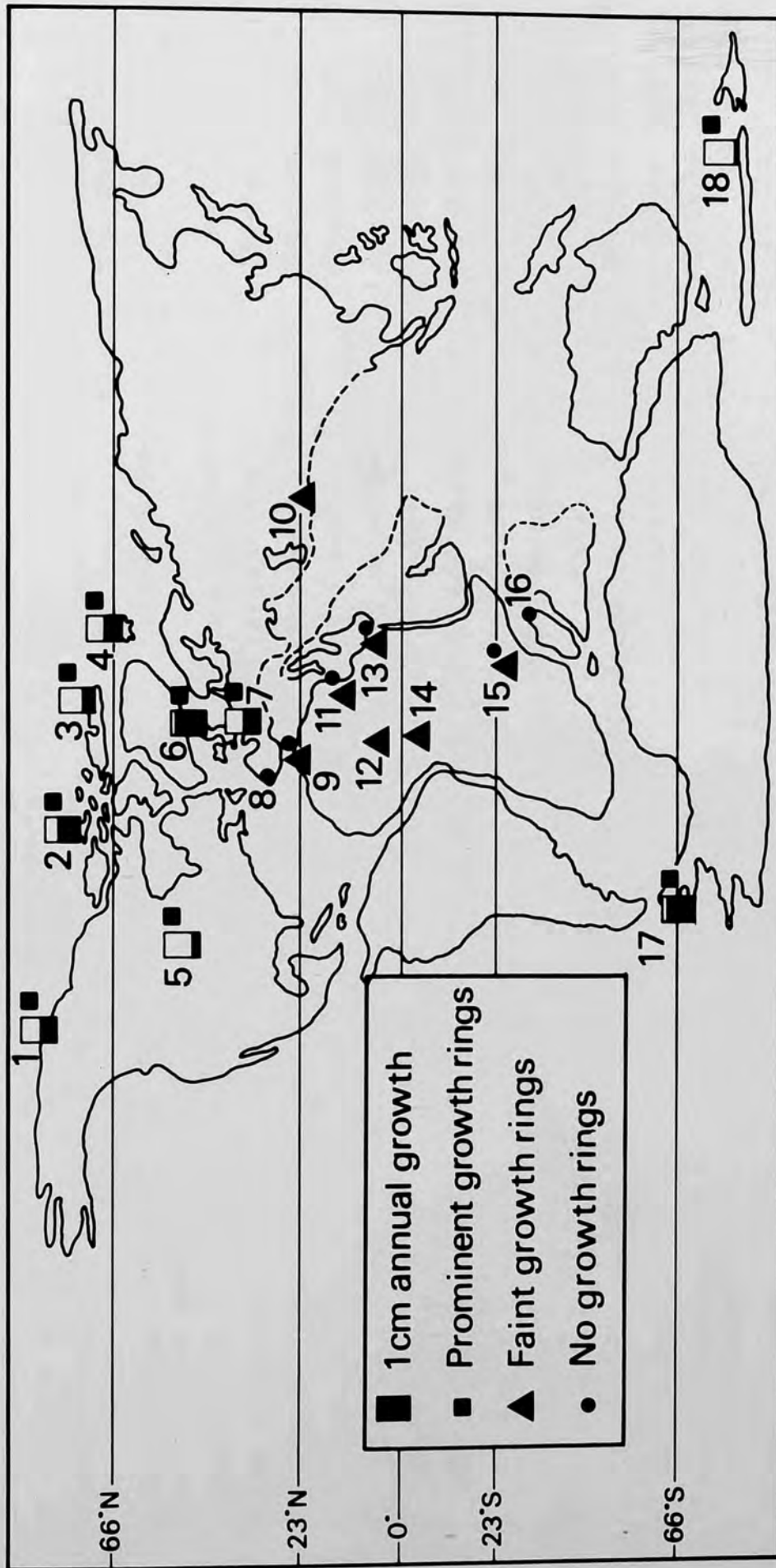
Table 2. Upper Jurassic, Cretaceous and Early Tertiary fossil woods plotted on Figure 2.

LOCALITY	SITE ON MAP	PALAEOLATITUDE	RING DETAILS	REFERENCE
Northern Alaska	1	80°N	Largest:4mm	Arnold, 1952
Amund Ringnes Island	2	75°N	Largest:6.5mm	Bannan and Fry, 1957
Ellesmere Island	3	74°N	Largest:3mm	Christie, 1964
				Bradley, 1982 (pers. comm.)
Spitzbergen, King Charles Land	4	61°N	Largest:4.4mm	Gothan, 1907
Dakota, U.S.A.	5	48°N	Largest:1.25mm	Read, 1932
East Sutherland	6	43°N	Largest:9mm	Creber, 1972
Dorset	7	36°N	Largest:3.7mm	Francis, 1983
Portugal	8	31°N	Absent	Boureau, 1949
Morocco	9	24°N	Faint or absent	Boureau, 1951
Afghanistan	10	22°N	Faint	Sitholey, 1940
Tripolitania	11	13°N	Faint or absent	Negri, 1914
Niger	12	2°N	Faint	Williams, 1930
Cairo	13	5°N	Faint or absent	Unger, 1859
Tchad	14	7°S	Faint	Boureau, 1952
Tanzania	15	28°S	Faint or absent	Potonié, 1902
Madagascar	16	31°S	Absent	Fliche, 1900
Alexander Island, Antarctica	17	70°S	Largest:9mm	Jefferson, 1982 (and pers. comm.)
New Zealand, South Island	18	67°S	Largest:1mm	Stopes, 1916

4e.   The Tertiary

By the beginning of the Tertiary the angiosperms had already become the dominant form of plant life on land, and must have ousted gymnosperms as forest dominants from many habitats particularly in low and middle latitudes (Hughes, 1976; Doyle, 1977).

The nature of angiosperm secondary wood is significantly different from that of gymnosperms. In particular, the great majority of dicotyledonous trees form vessels in the wood instead of the simpler closed elements called tracheids which characterise gymnosperm wood. This, coupled with the development of a diversity of other types of wood elements (fibre-tracheids, fibres, axial parenchyma) produces a complexity of growth ring expression in dicotyledonous trees unmatched in gymnosperms. Thus direct comparison between dicotyledonous wood growth features and those of the antecedent gymnosperms becomes more complicated. We have not attempted any overall survey of angiosperm wood growth, partly for this reason, but also since our understanding of plant palaeogeography through the Tertiary is in any case much fuller.

Because of the evidently close relationship of Tertiary dominants to extant groups, our basis for Tertiary climatic reconstruction from plant fossils has a different order of validity than that for earlier periods. It is clear from abundant early Tertiary records of angiosperm leaf floras in high latitudes that the broad temperate belts of the Cretaceous, extending almost to the poles, prevailed into at least the early Tertiary (Wolfe, 1978). We are not aware of any evidence from growth ring data in conflict with this.

5. THE PROBLEM OF FORESTS AT HIGH PALAEOLATITUDES

The evidence of in situ fossil forests in regions where there is now a climatic regime such as that seen within the Arctic and Antarctic Circles raises a major palaeobiological challenge. Coniferous forest does not extend at the present day more than a few degrees north of the Arctic Circle (Figure 3). It is very hard to visualise large forest trees growing in an environment in which darkness prevails for several months of the year and with the extremely low temperatures experienced at present in those latitudes. As Frakes (1979) remarks, in discussing the high palaeolatitude Cretaceous coals of New Zealand and Alaska, "the main problem which arises from these distributions has to do with availability of sunlight for plant growth. It has been stated by many workers that the limitation on the existence of plants at high latitudes is the sunlight factor."

Two very different kinds of explanation may be invoked to account for tree growth within the palaeo-Arctic and Antarctic Circles. One involves movement of the earth's axis relative to the position of the sun to produce a daylength/latitude relationship (and hence a climatic zonation) drastically different from that of the present day. The other assumes fixity of the earth's axis (or only the relatively minor Milankovitch wobble) but a change of climatic zonation and mean temperature distribution without any change in daylength pattern. These two possible mechanisms will now be explored in turn.

5a. Climatic change associated with changing inclination of the earth's axis
(A more extended treatment of this subject is given in PART II).

Among the planets of the solar system, while our own and most others generally have axes of rotation nearly
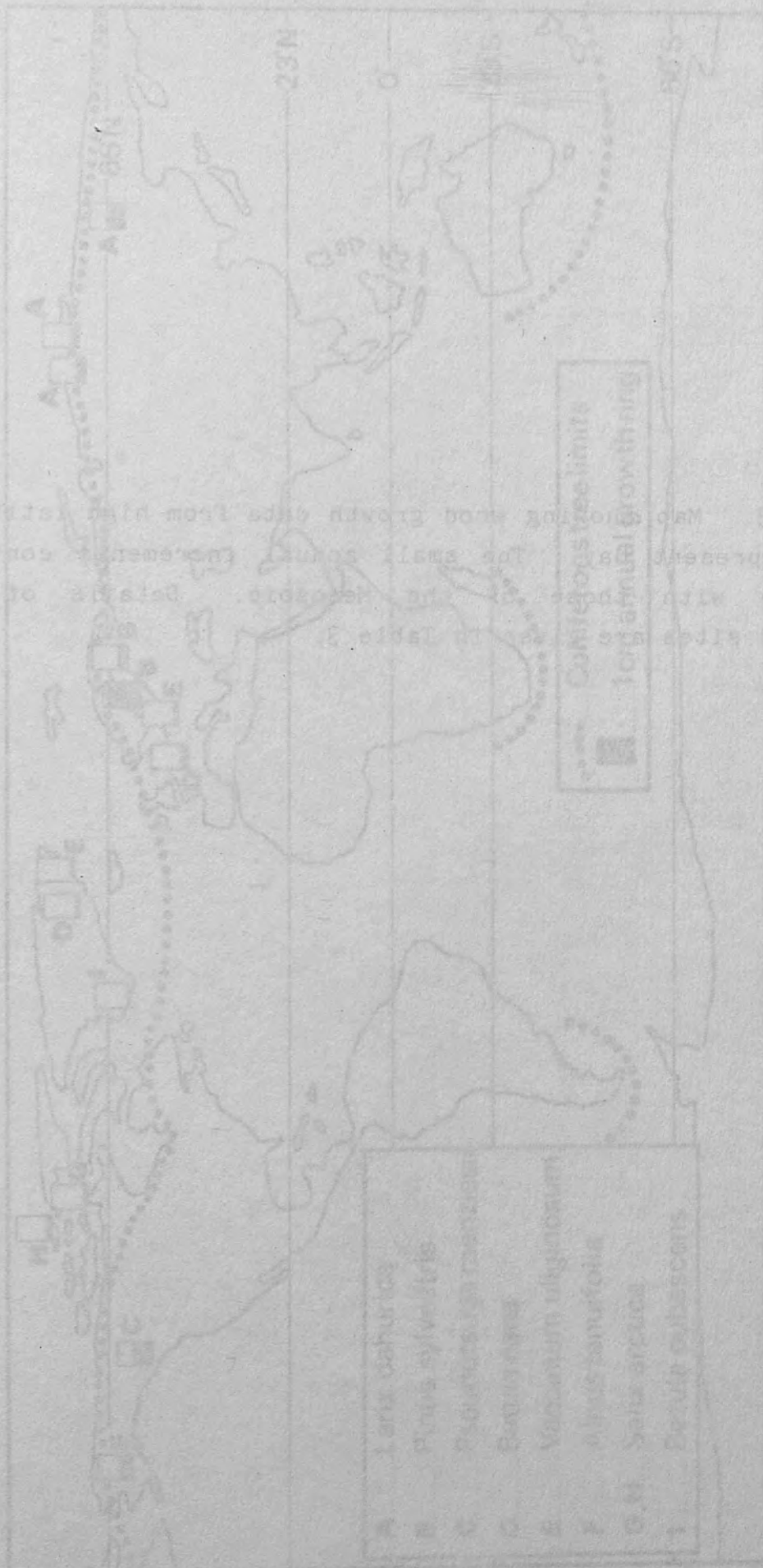
Figure 3   Map denoting areal growth data from high latitudes at the present day.

Figure 3. Map showing wood growth data from high latitudes at the present day. The small annual increments contrast strongly with those of the Mesozoic. Details of the lettered sites are given in Table 3.

23'N

0'

23'S

66'S

66'N

A   Larix dahurica
B   Pinus sylvestris
C   Pseudotsuga menziesii
D   Betula nana
E   Vaccinium uliginosum
F   Alnus tenuifolia
G,H Salix arctica
I   Betula pubescens

.... Coniferous tree limits
■   1cm annual growth ring
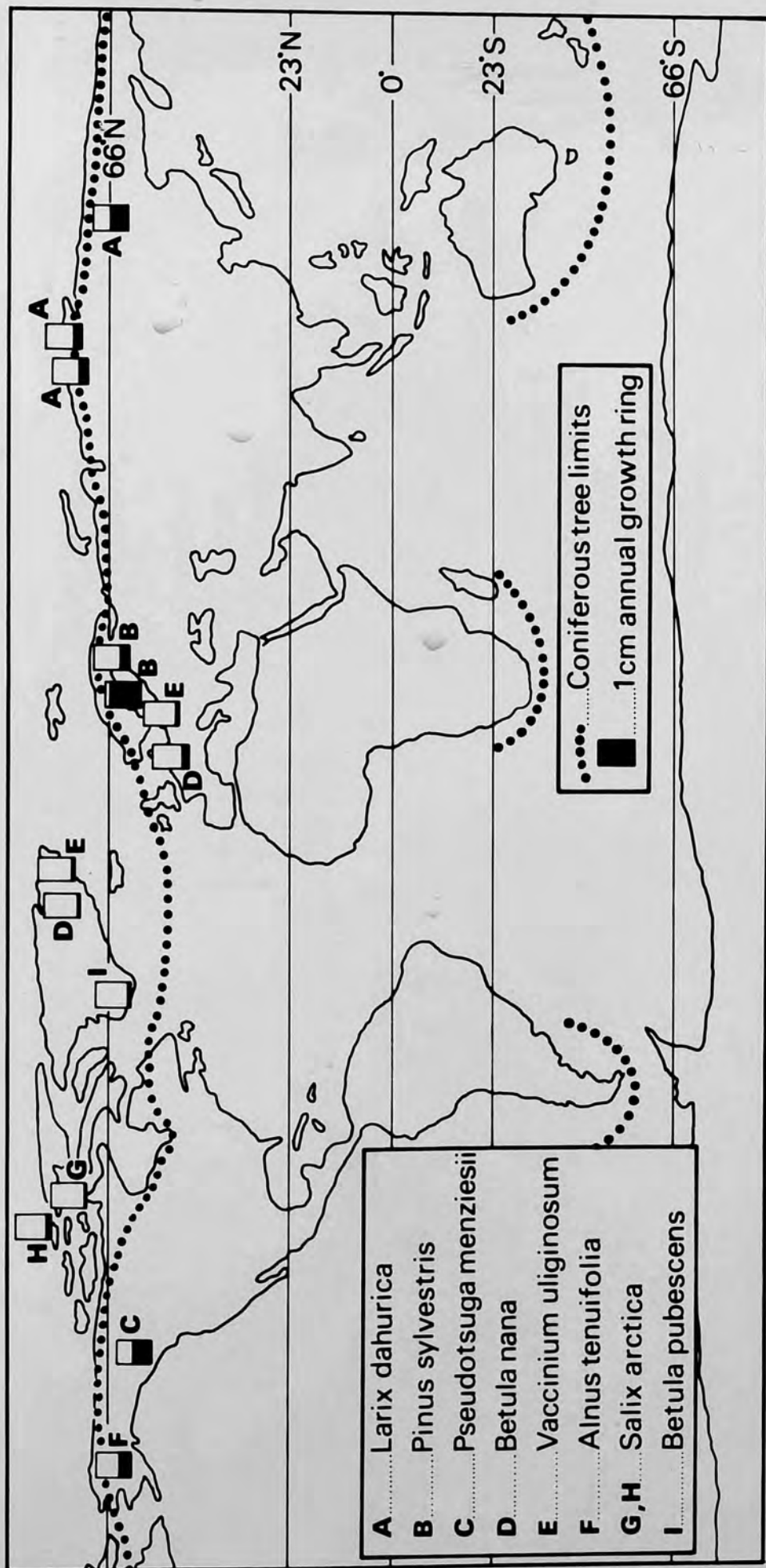
Table 3. Recent ring width data from high latitudes plotted on Figure 3.

SPECIES	MAP SITE	WIDEST RING (mm)	LOCALITY	LATITUDE (°N)
Larix dahurica	A	2.0	River Novaja	72
"	A	1.9	River Boganida	71
"	A	5.0	Between Amginsk and the River Aldan	60
Pinus sylvestris	B	2.1	Leningrad	60
"	B	9.0	Estonia	59
Pseudotsuga menziesii	C	5.0	British Columbia	55
		AVERAGE RING WIDTH		
Betula nana	D	0.14	Kaiser Franz Joseph's Fjord, East Greenland	73
"	D	1.6	Wurzburg, Germany	48
Vaccinium uliginosum	E	0.032	Kaiser Franz Joseph's Fjord, East Greenland	73
"	E	0.7	Erlanger, Germany	49
Alnus tenuifolia	F	2.7	Glacier Bay, Alaska	59
Salix arctica	G	0.07	Cornwallis Island	75
"	H	0.2	Axel Heiberg Island	79
Betula pubescens	I	0.5	S.W. Greenland	61

The above data were obtained from: Middendorf, 1867 (A&B); British Columbia Forest Service, 1947 (C); Kraus, 1874 (D&E); Cooper, 1931 (F); Warren Wilson, 1964 (G); Beschel and Webb, 1963 (H); Elkington and Jones, 1974 (I).

perpendicular to the plane of the solar system, it may be noted that Uranus has its axis lying more or less in the plane of its orbit around the sun. If a hypothesis of common origin of the planets is accepted, the example of Uranus raises the possibility that change in axial orientation could have occurred during the history of the solar system.

The consequences of axial change for earth history are enormous. An axis with zero obliquity, perpendicular to the ecliptic (the plane of rotation of the planets), would give strong latitudinal climatic zonation but no seasonality of climate. If the axis were to be in the plane of the ecliptic, like Uranus', an intensely seasonal climate would result, globally, with a bizarre annual alternation of polar and equatorial weather conditions in each year. This possibility has been seriously advanced by Williams (1972, 1973, 1975) who postulates a cyclic rotation of the plane of the ecliptic with respect to the sun. With this challenging hypothesis he attempts to explain a number of anomalous climatic phenomena through geological time. However, it must be pointed out that it raises as many problems (eg. the tidal consequences of this process) as it seems to solve.

If there has been major change in the inclination of the axis through geological time, this could certainly have produced higher temperatures (and higher angles of incident sunlight) in temperate and polar regions than offered by the present configuration. Any value for the inclination greater than that at the present would also give heightened seasonality of climate at all latitudes. Few authors (see eg. Chaloner, 1981) seem disposed to explore the consequences of such a situation as proposed by Williams (1972, 1973, 1975). None the less, increase in obliquity is a phenomenon which could probably increase biological productivity at high latitudes, although the extent of this increase would be influenced by considerations explored further below. Wolfe (1978) has advanced a much less

drastic order, of change of obliquity as an explanation for climatic phenomena. particularly in high palaeolatitudes. The palaeoarctic floras of the Early Tertiary contain many elements which at the present day are restricted to much lower latitudes. and Wolfe (1978) explains their Tertiary distribution in terms of <u>reduced</u> obliquity and hence diminished alternation of polar summer and winter. Each day throughout the year would thus have more or less the same period of sunlight. and an equable climate might be expected.

In view of the enormous climatic consequences that would ensue from major axial movement. it is appropriate to review here briefly the possible causal mechanisms. Because the moon raises tides in the oceans. it has the effect of slowing down the rate of rotation of the earth. Since angular momentum must be conserved. the moon moves outwards from the earth into a larger orbit thus taking up the angular momentum lost by the earth (Darwin. 1879. 1880: MacDonald. 1964). However. the earth's angular momentum is resolvable into two components. one perpendicular to the ecliptic and the other in the ecliptic plane; it is largely the former which is progressively transferred to the moon and hence the ratio of the two components is altered. This leads to a gradual increase in the earth's obliquity (O'Keefe, pers. comm. 1980). Daylength. and the earth-moon distance are thus linked to obliquity change. Stephenson (1978) has shown that from the evidence of Babylonian and Chinese observations of eclipses starting from about 1375 BC. the length of the day is declining by about 1.78 ms cy^{-1}. This retardation of the earth's rotation leads to a rate of recession of the moon of about 4 cm y^{-1}. This has been verified for the last 13 years since the first astronauts placed on the moon a laser beam reflector. enabling the very accurate measurement of the earth-moon distance (Stephenson and Morrison. 1982).

If this rate is extrapolated back into past geological

time bearing in mind that it is not a linear process. the
moon would have approached very close to the earth at about
1.5 by (Krohn and Sündermann. 1982).   At this point. the
'Gersternkorn event). catastrophic results would have ensued
on both the earth and the moon.   That these have not taken
place is clear from geological evidence of many kinds.

The possibility has to be considered. therefore. that
the present tidal friction in the oceans is at a high value
which has not obtained throughout geological time. making
such extrapolation invalid.   There is evidence for this from
the work of Krohn and Sündermann (1982) who have carried out
numerical   modelling   of   palaeotidal   effects   using   the
distribution   of   the   oceans   in   a   number   of   geological
periods.   Their results indicate in the Upper Permian and
Upper Cretaceous much reduced values as compared with that
of   the   present   day.   It   has   also   been   shown   by   Brosche
(1981)   that   different   values   of   tidal   friction   arise   in
models   in   which   the   widening   of   the   Atlantic   Ocean   is
simulated in steps of a few degrees of longitude at a time.
Brosche   concludes   that   for   realistic   calculations   of   the
history of the earth-moon system many closely spaced oceanic
tidal model would be required; the present day value for
tidal friction may not be a representative average for even
the   last   10   my.   It   is   interesting   that   one   of   Darwin's
conclusions was that the obliquity may well not have changed
by more than 1^O in about 500 my. which is also supported by
one of MacDonald's models in which he has a 'Gersternkorn
event'   prior   to   about   3.5   by.   This   small   amount   of
obliquity   change   is   certainly   not   enough   to   provide   what
Wolfe seeks and in any event it would be largely masked by
the   Milankovitch   wobble   in   which   the   obliquity   varies   from
22.5^O to 24°.   The   latter   variation   is   thought   to   be   the
mechanism   involved   in   the   Pleistocene   glaciation   cycles.
Changes   in   the   earth-moon   system   alone   therefore   seem
inadequate   as   a   basis   for   any   major   changes   in   the   high
latitude daylight regime. although the case for larger scale
rotation   of   the   plane   of   the   ecliptic   about   the   sun   as

advocated by Williams. cannot be ruled out on the considerations reviewed above.

5b. Climatic change associated with higher mean global temperatures

(A more extended treatment of the estimation of tree productivity is given in PART III)

The problems raised by postulating major changes in the inclination of the earth's axis of rotation force us to reconsider whether perhaps tree growth might have been possible within the Arctic and Antarctic Circles under a polar light regime similar to that of the present day. but with higher mean annual temperatures. It is generally agreed that in the Mesozoic. at least. equable climates prevailed into higher latitudes than at present. Writing of the Mesozoic Era as a whole Frakes (1979) suggests that it "presents excellent evidence for warm dry climates far beyond the present tropics" and shows "a degree of equability seldom seen elsewhere in the geological record." For the Jurassic in particular he states that "there are no proven glacial deposits" and for the Cretaceous "climates analogous to those of modern polar regimes are totally undocumented" and "temperate climates stretched almost to the (palaeo-)poles". Various phenomena. associated with plate movement. topography and ocean currents (Frakes. 1979· Lloyd. 1982) have been invoked to explain the Mesozoic equability of climate. A mild CO_2 greenhouse effect might also have been involved (Revelle. 1982).

Furthermore such an increase in the concentration of the atmospheric carbon dioxide would also have the effect of enhancing photosynthetic activity; this might be part of the explanation for the wide rings produced by some of the Mesozoic high latitude trees. That it was certainly warmer in the seas off Antarctica even by the Paleocene has been shown by Kennett (1977) who produced palaeotemperature

evidence for a surface sea water temperature of about 19°C. In considering the Mesozoic climate it seems appropriate at this point to re-examine the potential for photosynthetic productivity offered by the polar light regime if the ambient temperatures were higher within polar latitudes. Contemporary work based on stem increments of woody plants, at first suggests that some limitation operates on wood production at high latitudes at the present day.

Warren Wilson (1964), who has made an extensive study of plant growth in the arctic, showed that the annual radial growth of Salix arctica was only 0.07 mm on Cornwallis Island (75°N) whereas in southern Alaska (60°N). Cooper (1931) found that for Alnus tenuifolia it was 2.73 mm. Further evidence of low productivity in high latitudes is provided by Elkington and Jones (1974) who showed that Betula pubescens s. lat. in South-west Greenland (61°N) had only 25% of the annual productivity of Betula in England (Ovington and Madgwick, 1959). Other examples of arctic tree growth are shown in Figure 3 and Table 3. All these data bear out the general evidence from forest zonation with altitude in the tropics that, under the same daylength pattern as lowland vegetation, temperature is a very important regulating factor. The actual flux of light energy within the Arctic Circle does not of itself seem to be a limiting factor.

In his analysis of arctic plant growth Warren Wilson (1966) points out that in June the solar radiation input on Cornwallis Island (where the mean summer arctic temperature is only 4°C) is barely less than that for Washington D.C. in the same month (Table 4). It seems therefore that the ambient temperature is the limiting factor for plant growth rather than the light energy. In his view the temperature limits those metabolic processes involved in the transport and use of photosynthate very much more than it does photosynthesis itself. Thus assimilates accumulate and their concentration in the leaves rises to a level which

depresses assimilation to a rate which roughly balances their rate of use. Russell (1940) and Warren Wilson (1966) have shown that the sugar concentration in the leaves of

Table 4. Solar radiation in high latitudes; daily rate in
June.

LOCATION	LATITUDE (^{O}N)	MEAN JUNE TEMPERATURE (^{O}C)	SOLAR RADIATION RATE (MJ M^{-2} DAY $^{-1}$)
Abisko, Sweden	68	6.3	19.7
Umiat, Alaska	69	8.5	17.2
Resolute, Cornwallis Island	75	4·0	27.8
Greenharbour, Spitzbergen	78	2.4	22.9
Sveanor, Spitzbergen	80	2.1	24.4
Lower latitude site for comparison.			
Washington, D.C.	39	23.7	31.5

It should be noted that the receipt of solar radiation per
day at all latitudes above the Arctic Circle is enhanced by
the fact that there is sunlight throughout 24 hours.

such arctic plants as <u>Ranunculus glacialis</u>, <u>Oxyria digyna</u> and <u>Salix herbacea</u> is twice to four times the concentration of comparable leaves of plants of warmer climates.

Limitations to tree growth at high latitudes have much in common with those at the alpine timberline. Oswald (1969) found that the annual timber increment of <u>Picea abies</u> in the Central Massif, France, at about 1200 m elevation was nine times that at the timberline at 1650 m. This reduction is attributed to the low temperatures in the early and late parts of the growing season. In effect, temperatures in high latitudes at the present day have reduced to zero the growing season for trees.

For trees to grow in high latitudes they need in addition to a suitable ambient temperature, adequate light and the ability to intercept it at low angles without excessive mutual shading of adjoining trees. The light season must also be of sufficient length. As regards quantity of light energy, Warren Wilson (1966) has indicated its adequacy in the arctic environment. At two sites well within the Antarctic Circle (La Grange, 1963 (82°S); Farman and Hamilton, 1978 (75.5°S)) the annual radiation energy flux has been shown to be greater than that for East Anglia (Ovington, 1961).

Here again, there would appear to be no growth-limiting shortage of light, near the South Pole. However, for its adequate interception, the trees would need to be spaced sufficiently far apart and to have appropriate crown shapes. The most detailed description of a fossil forest in high latitudes is that of Jefferson (1982) on Alexander Island (palaeolatitude 70°S). In one continuous geological exposure there were 31 gymnosperm tree stumps in an area of 550 m^2; a density of 1 tree per 17 m^2. In forestry terms, these are rather widely spaced at 563 trees ha^{-1}, since comparable trees in forest plantations are capable of growing at a density of 900 trees ha^{-1}. In order to estimate the area of crown that may be presented to the

incoming radiation, the formula of Jahnke and Lawrence (1965) is used to calculate areas of interception of conically shaped trees of a range of dimensions and a range of angles of solar elevation. The authors point out that for interception of solar radiation at low angles of elevation, a cone-shaped tree whose crown height is much greater than the basal radius has the best characteristics (Figure 4). It is perhaps significant that the conifers, the trees which so successfully form forest at high latitudes, generally show this growth habit.

Conical crowns of height 17 m and basal radius 1.6 m could have been borne by Jefferson's trees without the lower branches being in contact. Such crowns have light-intercepting areas at low solar angles of about 25 m^2. Obviously some allowance for shading must be made but it has to be pointed out that in midsummer at latitude 70°S the sun travels through 360° and reaches an angle of 43.5° above the horizon at midday. For two months in the summer it only just touches the horizon at midnight and still reaches an elevation of 40° at midday. With a directly illuminated effective surface area of 25 m^2 the tree could intercept over 80,000 MJ of direct radiation during the illuminated part of the year. With a total conical surface area of 86 m^2 the tree would be well placed to receive diffuse radiation which, as Monteith (1973) points out, may be up to 25% of incoming radiation even on a cloudless day.

The annual increment of wood produced by a tree represents, in terms of energy only a small part of the total annual amount of light energy incident upon it (Figure 5). Ovington (1961) estimates that a coniferous forest utilises about 1% of the incident sunlight and Kozlowski (1962) considers that the resulting photosynthetic product is divided between trunk wood and all other uses in the ratio 40%:60%. Jefferson (1982) stated that average ring width for his antarctic fossil trees was 2.5 mm which for one tree would represent about 7.8 kg of wood with an energy
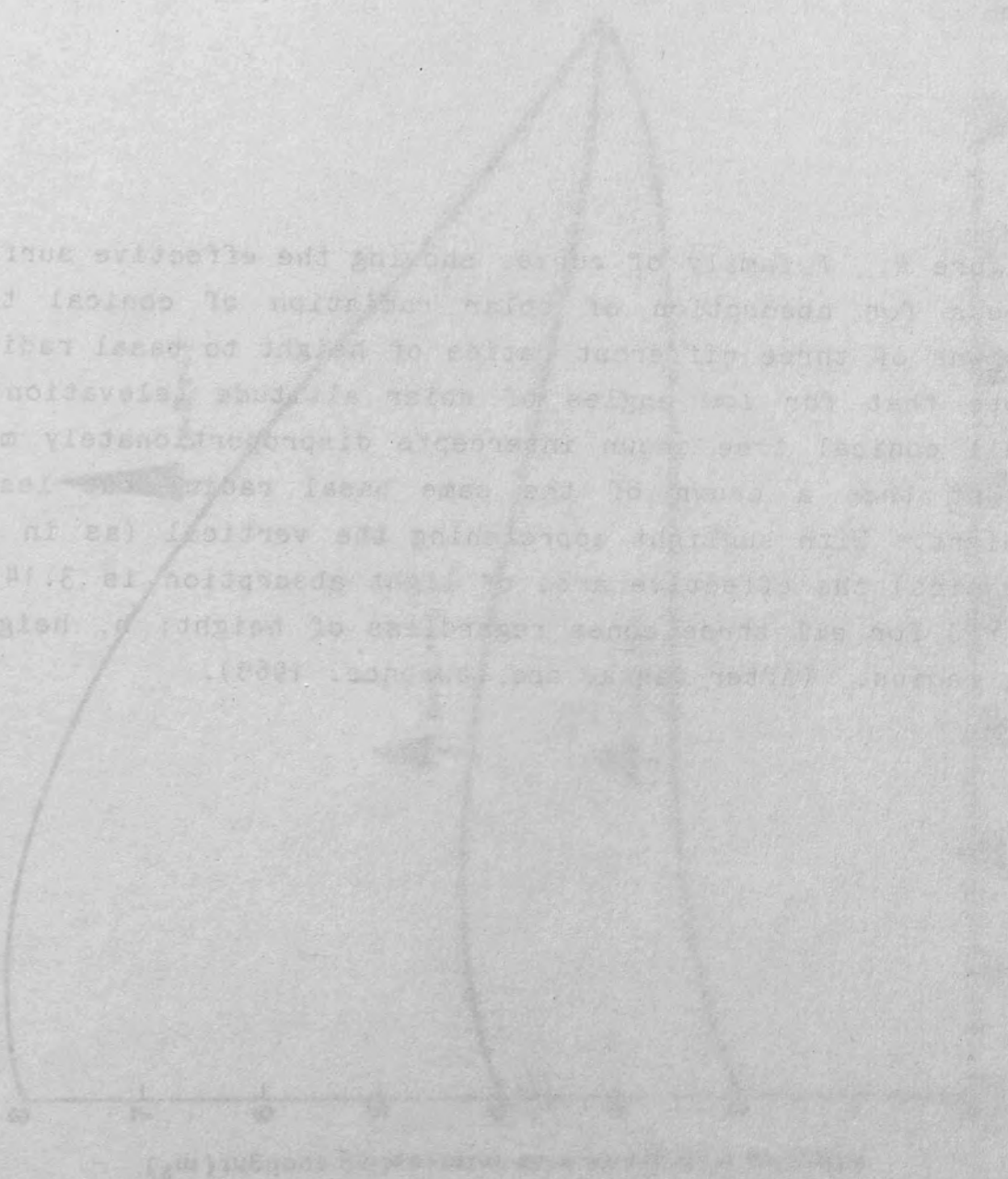
Figure 4.   A family of curves showing the effective surface
areas for absorption of solar radiation of conical tree
crowns of three different ratios of height to basal radius.
Note that for low angles of solar altitude (elevation) a
tall conical tree crown intercepts disproportionately more
light than a crown of the same basal radius but lesser
height.   With sunlight approaching the vertical (as in the
tropics) the effective area of light absorption is 3.14 m^2
(r^2) for all three cones regardless of height; h, height;
r, radius.   (After Jahnke and Lawrence, 1965).

Effective tree crown area intercepting sunlight (m²)

Solar altitude (elevation of sun above horizon)

h=8, r=1

h=4, r=1

h=2, r=1
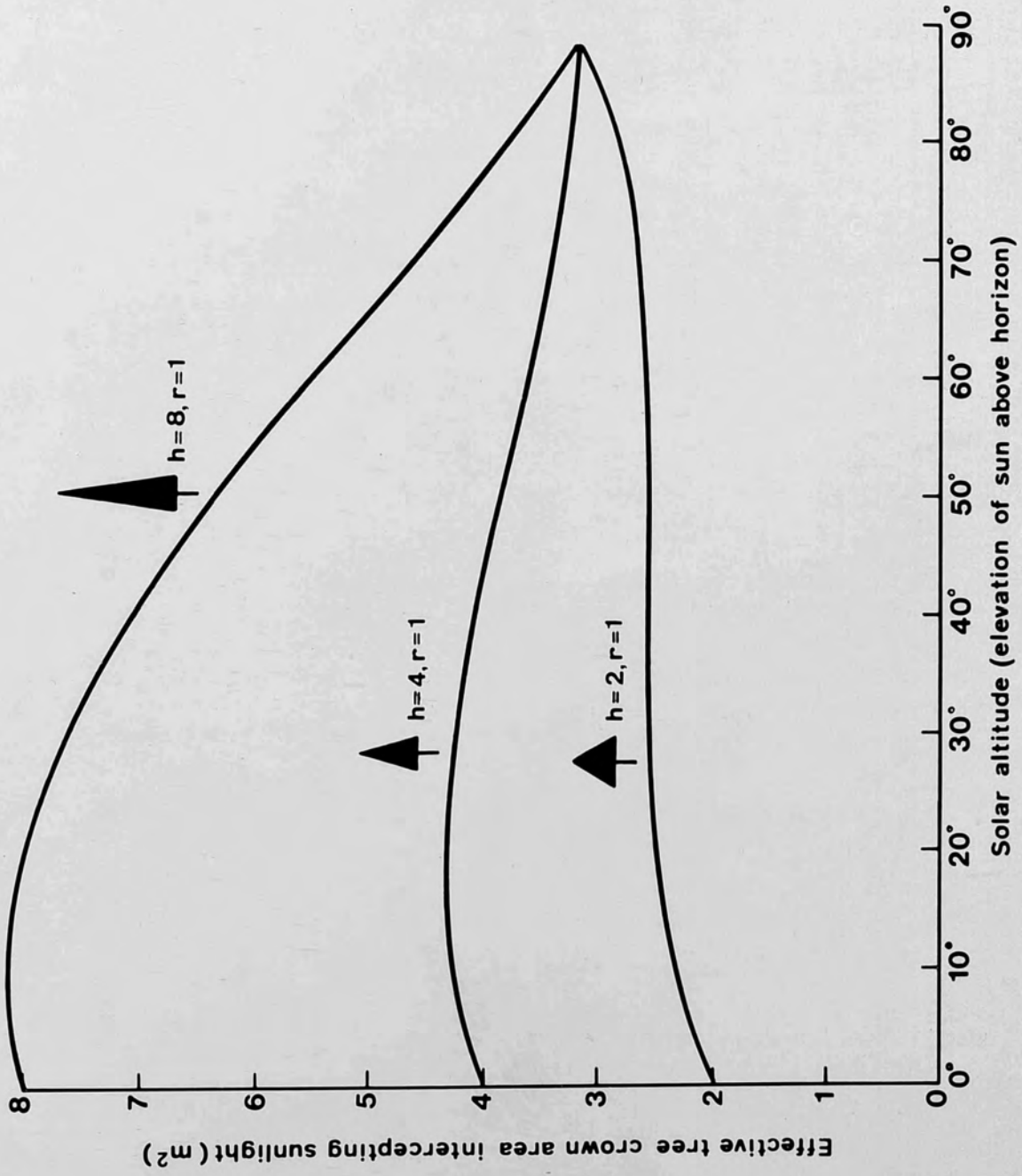
Figure 5. The fate of solar radiation upon a tree. Only about 1% of the total solar input is utilised and this is apportioned approximately in the ratio 40%:60% between trunk wood and all other uses.

Total solar input

1%

60%

Leaves, branches, roots and respiration

40%

Increment of trunk wood
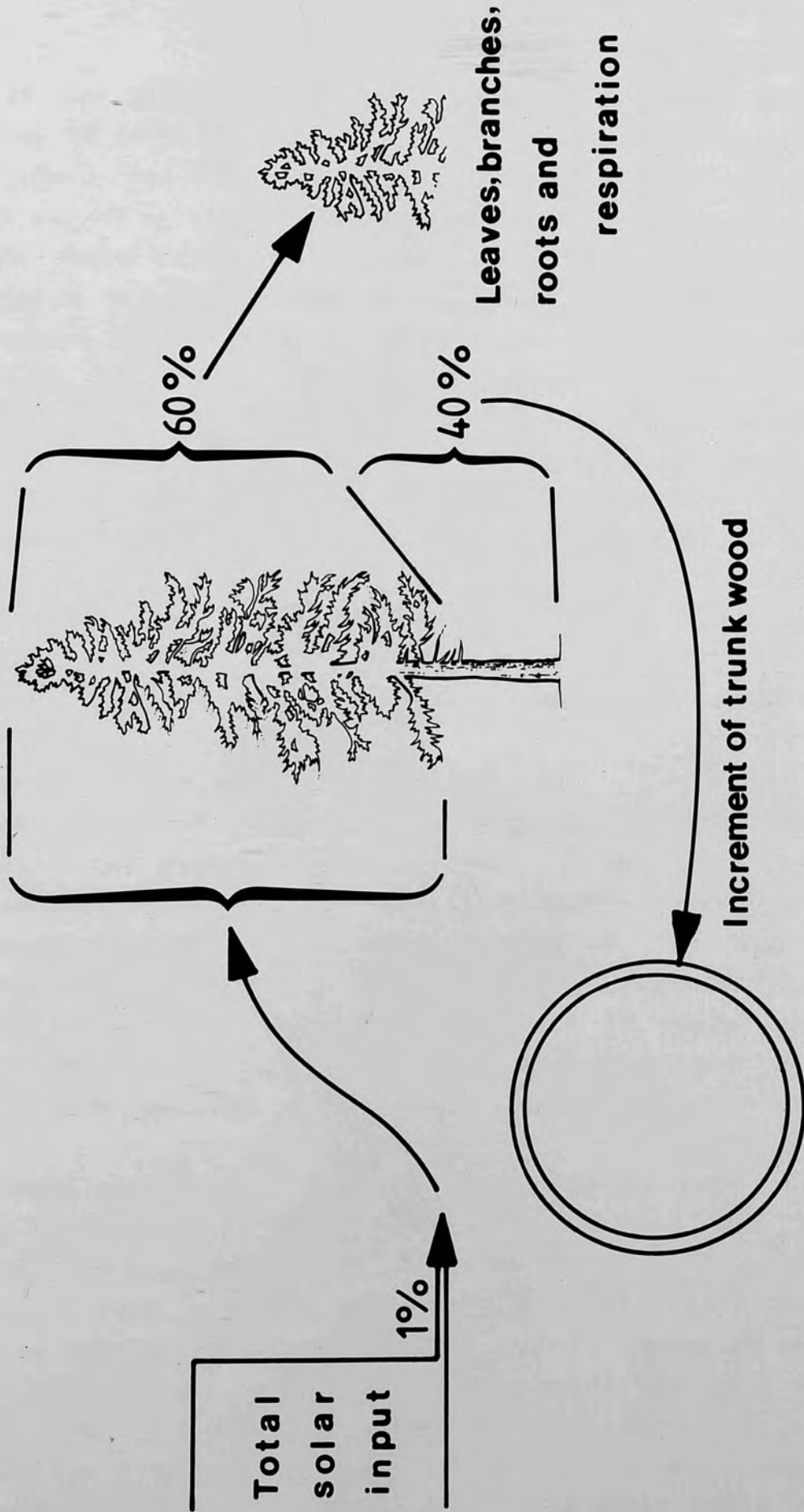
content of about 164 MJ. With a possible incident light energy flux of 80.000 MJ for the year, the 164 MJ required for wood production only represents 0.2% of the total rather than 0.4% according to Ovington and Kozlowski above.

There would seem to be plenty of allowance here for losses due to cloud and some mutual shading of the trees. With a production of 7.8 kg of wood on trees spaced one per 17 m^2 this represents an annual timber increment of 0.46 kg m^2 of forest. A temperate coniferous forest at the present day may be producing over 1 kg m^2. so that a productivity of 0.46 kg m^2 would appear quite possible in the antarctic light regime. if the ambient temperature was adequate.

Two other aspects of tree growth at high latitudes need to be examined:

1. The very long hours of daylight during the growing season;

2. The length of the growing season.

As regards the hours of daylight, Vaartaja (1962) has demonstrated the existence of photoperiodic ecotypes in a wide variety of modern tree species which only produce their best growth in their natural habitats in the higher latitudes. Attempts to grow them in shorter photoperiodic conditions result only in stunted growth. It would seem likely therefore that in Cretaceous times, the very high latitude forest species would have had such photoperiodic ecotypes.

Although necessarily the growing season in very high latitudes is relatively short, there is evidence that it could certainly have been adequate in the past. Ford et al. (1978) showed that in Sitka spruce, xylem mother cells were produced by the cambial initial in a file of cells at the rate of 4 per day when the light energy input was 22.5 MJ m^{-2} day^{-1}. At very high latitudes the light input is of this order for 3 months at least. Thus 360 cells of. say. 40μm radial diameter could be formed with a total width of

14.40 mm; this rate of production is clearly adequate to form even the largest ring widths normally encountered in forest trees in the most favourable environments.

Even though relatively long periods are available to temperate trees for their seasonal growth, many do not use them to the full. Kramer (1943) showed that Pinus resinosa only requires 140 days and Abies balsamea and Pinus strobus complete their seasonal growth in 120 days. In very high latitudes the illuminated part of the year could well have been adequate as a growing season. This is emphasised by Gosz et al. (1978) who show that an entire, temperate. deciduous forest ecosystem is in fact supported on only that quantity of light energy that falls on the trees in the few months that they are in leaf. Whereas 5267 MJ m^{-2} are received in a year. the trees are only in a position to absorb 2016 MJ m^{-2} during the summer. This quantity is substantially less than that received within the Arctic and Antarctic Circles during a polar summer.

Figure 6. Transverse sections of extant and fossil woods. The latest formed wood is uppermost in each photograph. The scale bars represent 1 mm.

a) Thuja plicata (Western red cedar) grown in Western North America. The distinct band of latewood in each ring is characteristic of modern temperate conifer wood.

b) Lower Tertiary coniferous wood from Brainard's Forest, Ellesmere Island (Figure 2, No.3). Parts of three rings appear in the photograph.

c) Lower Cretaceous coniferous wood from Jefferson's Forest, Alexander Island, Antarctic Peninsula (Figure 2, No.17). Wide rings with very little latewood.

d) Protocupressinoxylon purbeckensis from the Upper Jurassic of Dorset (Figure 2, No.7). Very little latewood in each ring.

e) Podocarpoxylon sp. from the Permian of Southern Brazil (palaeolatitude $34°S$). Ring boundaries marked only by a few smaller cells.

f) Pitus primaeva from the Lower Carboniferous at Spadeadam on the Scottish Border. There are no growth rings. The vertical features are very broad wood rays. narrower examples of which may be seen in 'd' above.
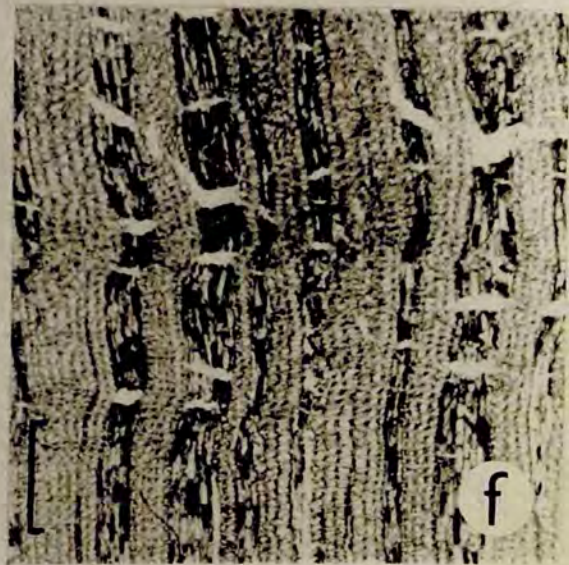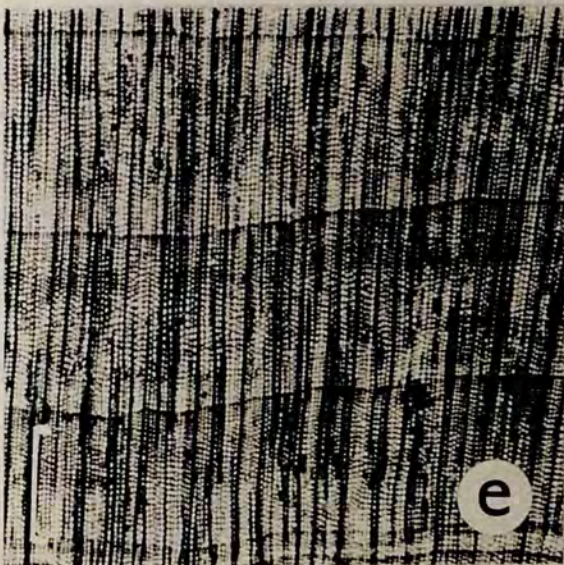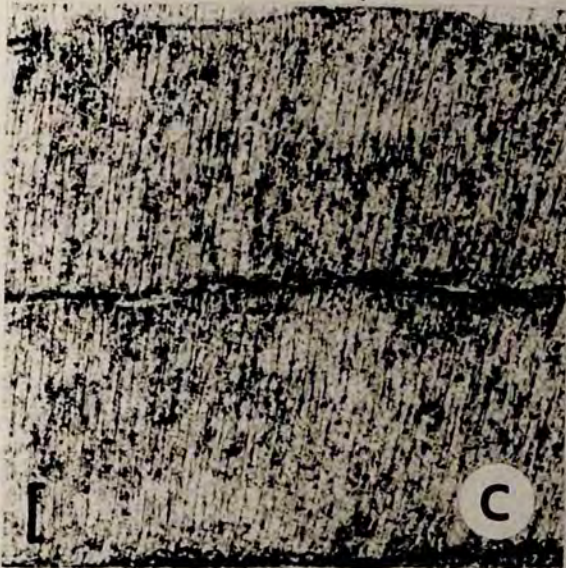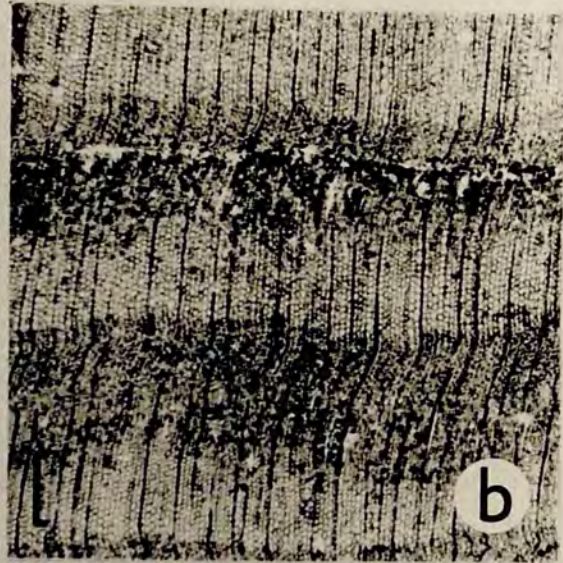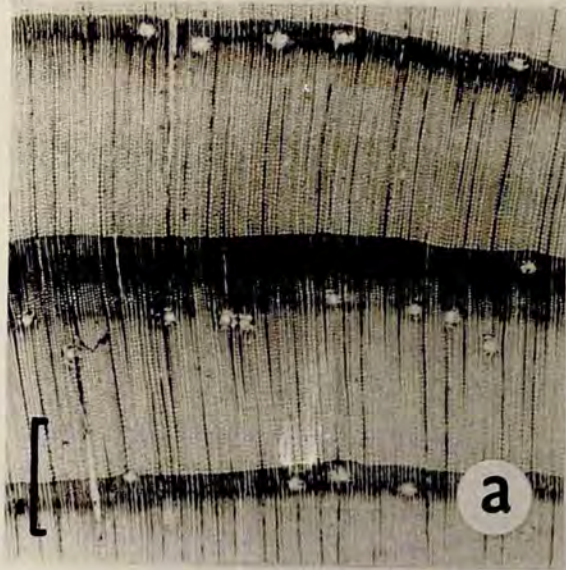
6. CONCLUSION

Through the Upper Palaeozoic, fossil wood with subdued
growth rings, or with growth rings entirely lacking,
characterise the contemporaneous tropical latitudes as
deduced from palaeomagnetic evidence. In this, growth ring
studies provide useful confirmation of the palaeolatitudes
of continents as far back as the Devonian. Furthermore, the
fossil wood constitutes irrefutable evidence that in the
Late Palaeozoic and in the Mesozoic, trees were able to
flourish much nearer to the poles than they can at present.
We are forced to conclude that a suitable climate must have
prevailed in high latitudes for substantial forest growth.

Levels of light-energy flux at high latitudes at the
present day are evidently adequate for a much higher
productivity than actually takes place. Evidently, the
ambient temperature inside the Arctic and Antarctic Circles
at the present time is the factor limiting tree growth just
as it determines the tree line altitudinally in low
latitudes. If the present angle of inclination of the
earth's axis to the plane of the ecliptic has changed little
over the last 400 my, then higher ambient temperatures in
high latitudes would have sufficed to make forest growth
possible. Available data on solar energy flux do not
indicate that limitation of the 'sunlight factor' would have
prevented high latitude tree growth, as has been suggested.

This paper is part of a study still in progress. As
more records of growth-ring data are accrued, it is hoped
that the evidence of tree growth patterns on a global scale
will become clearer and will contribute further in testing
the palaeolatitude values derived from palaeomagnetic
studies.

REFERENCES

Absalom, R.G. (1931). Calamopitys (Eristophyton) beinertiana
    (Goeppert) containing annual rings.
    NWest. Nat., 6, 70-74.
Antevs, E. (1925). The climatologic significance of annual
    rings in fossil woods.
    Amer. J. Sci. 5th Ser., 9, 296-302
Arnold, C.A. (1930). The genus Callixylon from the Upper
    Devonian of central and western New York.
    Pap. Mich. Acad. Sci., 11, 1-50
Arnold C.A. (1931). On Callixylon newberrryi (Dawkins)
    Elkins et Wieland.
    Mich. Univ. Mus. Palaeont. Contr., 3, 207-232.
Arnold C.A. (1934). Callixylon whiteanum sp. nov., from the
    Woodford Chert of Oklahoma. Bot.Gaz., 96, 180-185.
Arnold, C.A. (1947). An introduction to paleobotany,
    McGraw-Hill Book Co., New York.
Arnold, C.A. (1952). Silicified plant remains from the
    Mesozoic and Tertiary of Western North America II.
    Some fossil woods from Northern Alaska.
    Pap. Mich. Acad. Sci., 38, 9-20
Bannan, M.W. and Fry, W.L. (1957). Three Cretaceous woods
    from the Canadian Arctic. Can. J. Bot., 35, 327-337.
Baxter, R.W. and Hartman, E.L. (1954). The coal-age flora
    of Kansas - V. A fossil coniferophyte wood.
    Phytomorphology, 4, 316-325.
Beck, C.B. (1953). A new root species of Callixylon.
    Amer. J. Bot., 40, 226-233.
Beschel, R.E. and Webb, D. (1963). Growth ring studies on
    Arctic willows, in Axel Heiberg Island, Preliminary
    Report 1961-2 (Ed. F. Muller), pp. 189-198, McGill
    University, Montreal.
Boureau, E. (1949). Dadoxylon (Araucarioxylon) teixeirae n.
    sp. Bois fossile du Jurassique superieur portugais.
    Comuncoes Servs. geol. Port., 29, 187-194.

Boureau, E. (1951). Étude paleoxylologie de l'Afrique du
    Nord (1): Présence de Dadoxylon (Araucarioxylon)
    teixeirae Boureau dans le Haut Atlas de Maroc.
    Notes Mém. Serv. Mines Carte géol. Maroc. 4, 123-133.

Boureau, E. (1952). Étude des fossiles du Territoire du
    Tchad: 1. Protopodocarpoxylon rochii n.sp. Bois fossile
    mésozoïque.
    Bull. Mus. Hist. nat., Paris, 2° Série, 24, 223-232.

British Columbia Forest Service (1947). Yield Data.
    B.C. For. Service.

Brosche, P. (1981). Oceanic tides and the rotation of the
    earth. European Regional Meeting in Astromony,
    Dubrovnik.

Chaloner, W.G. (1981). Problems in seeking causality in the
    past distribution of plants.
    Abstracts, 13th Int. Bot. Congr. Sydney, Australia.

Chaloner, W.G. and Creber, G.T. (1973). Growth rings in
    fossil woods as evidence of past climates, in
    Implications of Continental Drift to the Earth Sciences
    (Eds. D.H. Tarling and S.K. Runcorn), pp. 425-437,
    Academic Press, London.

Chaloner, W.G. and Sheerin, A. (1979). Devonian macrofloras.
    Special Papers in Palaeontology No. 23, 145-161.

Christie, R.L. (1964). Geological reconnaissance of
    northeastern Ellesmere Island, District of Franklin.
    Bull. geol. Surv. Can., Memoir 331, 1-77.

Cooper, W.S. (1931). A third expedition to Glacier Bay,
    Alaska. Ecology, 12, 61-95.

Creber, G.T. (1972). Gymnospermous wood from the
    Kimmeridgian of East Sutherland and from the Sandringham
    sands of Norfolk. Palaeontology, 15, 655-661.

Creber, G.T. (1977). Tree rings: a natural data-storage
    system. Biol. Rev., 52, 349-383.

Darwin, G.H. (1879). On the precession of a viscous spheroid
    and on the remote history of the earth.
    Phil. Trans. R. Soc., 170, 447-530.

Darwin, G.H. (1880). On the secular change in the elements of the orbit of a satellite revolving about a tidally distorted planet. Phil. Trans. R. Soc., 171, 713-891.

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

Doumani, G.A. and Long, W.E. (1962). The ancient life of the antarctic. Scient. Am., 207(3). 168-184.

Doyle, J.A. (1977). Patterns of evolution in early angiosperms, in Patterns of Evolution (ed. A. Hallam). pp.501-546, Elsevier, Amsterdam.

Edwards, D. (1973). Devonian floras, in Atlas of Palaeobiogeography (Ed. A. Hallam). pp.105-115, Elsevier, Amsterdam.

Elkington, T.T. and Jones, B.M.G. (1974). Biomass and primary productivity of Birch (Betula pubescens s. lat.) in south-west Greenland. J. Ecol., 62, 821-830.

Elkins, M.G. and Wieland, G.R. (1914). Cordaitean wood from the Indiana black shale. Am. J.Sci.. 38, 65-78.

Farman, J.C. and Hamilton, R.A. (1978). Measurements of radiation at the Argentine Islands and Halley Bay. 1963-72. Brit. Antarct. Surv. Scient. Rept., No. 99.

Fliche, P. (1900). Note sur un bois fossile de Madagascar. Bull. Soc. géol. Fr., 3° Série, 28, 470-472.

Ford, E.D., Robards, A.W. and Piney, M.D. (1978). Influence of environmental factors on cell production and differentiation in the early wood of Picea sitchensis. Ann. Bot., 42, 683-692.

Frakes, L.A. (1979). Climates throughout geologic time. Elsevier, Amsterdam.

Francis. J.E. (1983). The dominant conifer of the Jurassic Purbeck Formation, England. Palaeontology. 26. 277-294.

Frentzen, K. (1931). Die palaeogeographische Bedeutung des Auftretens von Zuwachszonen (Jahresringen) bei Hölzern der Sammelgattung Dadoxylon Endl. aus dem Carbon und dem Rotliegenden des Oberrheingebietes. Zentbl. Miner. Geol. Palaont. Jr., 1931B, 617-624.

Fritts, H.C. (1976). Trees rings and climate,
    Academic Press, New York.

Goldring, W. (1921). Annual rings of growth in Carboniferous
    wood. Bot. Gaz.. 72, 326-330.

Gosz, J.R., Holmes, R.T., Likens, G.E. and Bormann, F.H.
    (1978). The flow of energy in a forest ecosystem.
    Scient. Am., 238(3), 92-102.

Gothan, W. (1907). Die fossilen Holzer von Konig Karls Land.
    K. svenska Vetensk-Akad. Handl., 42, 1-41.

Gothan, W. (1911). Die Jahresringlosigkeit der paläozoischen
    Bäume und die Bedeutung dieser Erscheinung für die
    Beurteilung des Klimas dieser Perioden.
    Naturw. Wschr., N.F., 10, 1-13.

Høeg, O.A. (1942). The Downtonian and Devonian Flora of
    Spitsbergen. Norges Sva-
    lb. Ishavs-Undersok., 83, 1-128.

Holden, R. (1913). Some fossil plants from Eastern Canada.
    Ann. Bot., 27, 243-255.

Holden, R. (1917). On the anatomy of two palaeozoic stems
    from India. Ann. Bot., 31, 315-326.

Hoskins, J.T. and Cross, A.T. (1951). The structure and
    classification of four plants from the New Albany shale.
    Amer. Midl. Nat., 46, 684-716.

Hughes, N.F. (1976). The palaeobiology of angiosperm
    origins, Cambridge University Press, Cambridge.

Hylander, C.J. (1922). A Mid-Devonian Callixylon.
    Am. J. Sci., 4, 315-321.

Jahnke, L.S. and Lawrence, D.B. (1965). Influence of
    photosynthetic crown structure on potential productivity
    of vegetation, based primarily on mathematical models,
    Ecology, 46, 319-326.

Jefferson, T.H. (1982). Fossil forests from the Lower
    Cretaceous of Alexander Island, Antarctica.
    Palaeontology, 25, 681-708.

Jensen, K.N. (1982). Growth rings in Pennsylvanian fossil
    wood found in Oklahoma. Okla. Geol. Notes. 42, 7-10.

Kennett, J.P. (1977). Cenozoic evolution of antarctic
    glaciation, the circum-antarctic ocean, and their impact
    on global paleoceanography. J. geophys. Res., 82,
    3843-3860.

Kozlowski, T.T. (1962). Photosynthesis, climate and tree
    growth, in Tree growth (Ed. T.T. Kozlowski), pp.149-164,
    Ronald Press, New York.

Kramer, P.J. (1943). Amount and duration of growth of
    various species of tree seedlings.
    Plant Physiol., 18, 239-251.

Kramer, P.J. and Kozlowski, T.T. (1979). Physiology of woody
    plants, Academic Press, New York.

Kraus, G. (1874). Einige Bemerkungen über Alter
    Wachstumverhältnisse ostgrönlandischer Holzgewächse, in
    Die Zweite deutsche Nordpolarfahrt in den Jahrem 1869
    und 1870, 2, 1, Leipzig.

Krohn, J. and Sundermann, J. (1982). Paleotides before the
    Permian, in Tidal Friction and the earth's rotation II
    (Eds. P. Brosche and J. Sundermann). pp.190-209.
    Springer-Verlag, Berlin.

Lacey, W.S. (1953). Scottish Lower Carboniferous plants:
    Eristophyton waltoni sp. nov. and Endoxylon zonatum
    (Kidston) Scott from Dunbartonshire.
    Ann. Bot., 17, 579-596.

La Grange, J.J. (1963). Trans-Antarctic Expedition 1955-58
    Scientific Report No. 13. Meteorology 1. Shackleton,
    Southice and the journey across Antarctica.
    Trans-Antarctic Expedition Comittee.

Larson, P.R. (1964). Some indirect effects on wood formation,
    in The Formation of wood in forest trees (Ed. M.H.
    Zimmermann), pp.345-365, Academic Press, New York.

Lemoigne, Y. and Tyroff, H. (1967). Caractères anatomiques
    d'un fragment de bois appartenant a l'èspèce Walchia
    (Lebachia) piniformis du Permien d'Allemagne.
    C. r. hebd. Séanc. Acad. Sci., Paris, 265, 595-597.

Lloyd, C.R. (1982). The mid-Cretaceous earth:
    palaeogeography; ocean circulation and temperature;
    atmospheric temperature. J. Geol., 90, 393-413.

Long, A.G. (1979). Observations on the Lower Carboniferous
    genus Pitus Witham. Trans. R. Soc. Edin., 70, 111-127.

Longman, K.A. and Jeník, J. (1974). Tropical forest and its
    enviromnent, Longman Group, London.

MacDonald, G.J.F. (1964). Tidal friction. Rev. Geophys., 2,
    467-541.

Maheshwari, H.K. (1972). Permian wood from Antarctica and
    revision of some Lower Gondwana wood taxa.
    Palaeontographica B, 138, 1-43.

Matten, L.C. and Banks, H.P. (1967). Relationship between
    the Devonian progymnosperm genera Sphenoxylon and
    Tetraxylopteris. Bull. Torrey Bot. Club, 94, 321-323.

Middendorf, A.T.ⱱ. (1867). Die Gewächse Sibiriens, in Reise
    in den äussersten Norden und Osten Sibiriens, 4, 1,
    St. Petersburg.

Monteith, J.L. (1973). Principles of environmental physics,
    Edward Arnold, London.

Negri, G. (1914). Sopra alenni legni fossili del Gebel
    Tripolitano. Bull. Soc. Geol. Ital., 33, 321-344.

Njoku, E. (1963). Seasonal periodicity in the growth and
    development of some forest trees in Nigeria. I.
    Observations on mature trees. J. Ecol., 51, 617-624.

Njoku, E. (1964). Seasonal periodicity in the growth and
    development of some forest trees in Nigeria. II.
    Observations on seedlings. J. Ecol., 52, 19-26.

O'Keefe, J.A. (1980). NASA: Goddard Space Flight Center,
    Greenbelt, Maryland 20771, U.S.A.

Oswald, H. (1969). Conditions forestières et potentialité de
    l'épicéa en haute ardèche.
    Ann. Sci. Forest., 26, 183-224.

Ovington, J.D. (1961). Some aspects of energy flow in
    plantations of Pinus sylvestris L.
    Ann. Bot., N.S., 25, 12-20.

Ovington, J.D. and Madgwick, H.A.I. (1959). The growth and composition of natural stands of birch. 1. Dry-matter production. Pl. Soil, 10, 271-283.

Potonie, H. (1902). Fossile Hölzer aus der oberen Kreide Deutsch-Ostafrikas, in Die Reisen der Bergassessors Dr. Dantz in Deutsch-Ostafrika in den Jahren 1898-1900, Mitt. aus den deutschen Schutzgebieten, Bd. 15 Heft 4, 227-230.

Prasad, M.N.V. and Chandra, S. (1980). Palaeospiroxylon - a new gymnospermous wood from Raniganj coalfield, India. Palaeobotanist, 26, 230-236.

Read, C.B. (1932). Pinoxylon dakotense from the Cretaceous of the Black Hills. Bot. Gaz., 93, 173-189.

Revelle, R. (1982). Carbon dioxide and world climate. Scient. Am., 247(2), 33-41.

Russell, R.S. (1940). Physiological and ecological studies on an arctic vegetation. III. Observations on carbon assimilation, carbohydrate storage and stomatal movement in relation to the growth of plants on Jan Mayen Island. J. Ecol., 28, 289-309.

Salisbury, F.B. (1981). Responses to photoperiod, in Physiological Plant Ecology I. (Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler), pp.135-167, Springer-Verlag, Berlin.

Schweitzer, H. -J. (1968). Die Flora des oberen perms in Mitteleuropa. Naturw. Rdsch., Braunschw., 21, 93-102.

Seward, A.C. and Walton, J. (1923). On fossil plants from the Falkland Islands. Q. Jl. geol. Soc. Lond., 79, 313-333.

Sitholey, R.V. (1940). Jurassic plants from Afghan-Turkistan. Mem. geol. Surv. India Palaeont. indica, 29, Mem. No. 1.

Smith, A.G., Hurley, A.M. and Briden, J.C. (1981). Phanerozoic paleocontinental world maps, Cambs. Univ. Press, Cambridge.

Stephenson, F.R. (1978). Pre-telescopic astronomical
    observations, in Tidal friction and the Earth's rotation
    (Eds. P. Brosche and J. Sündermann), pp.5-21,
    Springer-Verlag, Berlin.

Stephenson, F.R. and Morrison, L.V. (1982). History of the
    earth's rotation since 700 B.C., in Tidal Friction and
    the Earth's Rotation II (Eds. P. Brosche and J.
    Sundermann), pp.29-50, Springer-Verlag, Berlin.

Stopes, M.C. (1916). An early type of the Abietineae (?)
    from the Cretaceous of New Zealand.
    Ann. Bot., 30, 111-125.

Tomlinson, P.B. and Craighead, F.C. Sr. (1972). Growth-ring
    studies on the native trees of sub-tropical Florida, in
    Research trends in plant anatomy (Eds. A.K.M. Ghouse and
    M. Yunus), K.A. Chowdhury commemoration volume,
    pp.39-51, Tata McGraw Hill, New Delhi.

Tynan, E.J. (1959). Occurrence of Cordaites michiganensis in
    Oklahoma. Okla. Geol. Notes, 19, 43-46.

Unger, F. (1859). Der versteinerte Wald bei Cairo und einige
    andere Lager verkieselten Holzen in Ägypten.
    Sber. Akad. Wiss. Wien., 33, 209-233.

Vaartaja, O.)1962). Ecotypic variation in photoperiodism of
    trees with special reference to Pinus resinosa and Thuja
    occidentalis. Can. J. Bot., 40, 849-856.

Wareing, P.F. and Phillips, I.D.J. (1970). The control of
    growth and differentiation in plants, Pergamon Press.
    Oxford.

Warren Wilson, J. (1964). Annual growth of Salix arctica in
    the high-arctic. Ann. Bot., N.S., 28, 71-76.

Warren Wilson, J. (1966). An analysis of plant growth and
    its control in arctic environments.
    Ann. Bot., N.S., 30, 383-402.

Williams, G.E. (1972). Geological evidence relating to the
    origin and secular rotation of the solar system.
    Mod. Geol., 3, 165-181.

Williams, G.E. (1973). Geotectonic cycles, lunar
    evolution, and the dynamics of the earth-moon system.
    Mod. Geol., 4, 159-183.

Williams, G.E. (1975). Late Precambrian glacial climate and
    the Earth's obliquity. Geol. Mag., 112, 441-465.

Williams, S. (1930). The geological collection from the
    South Central Sahara made by Mr. F. Rodd. III. Fossil
    wood. Q. Jl. geol. Soc. Lond., 86, 408-409.

Wilson, L.R. (1963). A new species of Dadoxylon from the
    Seminole Formation (Pennsylvanian) of Oklahoma.
    Okla. Geol. Notes, 23, 215-220.

Wolfe, J.A. (1978). A palaeobotanical interpretation of
    Tertiary climates in the Northern Hemisphere.
    Am. Scient., 66, 694-703.

Zahner, R. (1963). Internal moisture stress and wood
    formation in conifers. Forest Prod. J., 13, 240-247.

Zalessky, M. (1909). Communication preliminaire sur un
    nouveau Dadoxylon provenant du Dévonien supérieur du
    bassin du Donetz.
    Bull. acad. Imp. sci. St. Pétersbourg, 26, 1175.

Zalessky, M. (1911). Étude sur L'anatomie du Dadoxylon
    tchihatcheffi Goeppert.
    Mém. Comité géol. Russe, St. Pétersbourg, 68, 18-29.

APPENDIX III

Four published papers (in pocket)

1.   Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham Sands of Norfolk.
G.T. Creber. 1972. Palaeontology 15, 655-661.

2.   Growth rings in fossil woods as evidnece of past climates.
W.G. Chaloner and G.T. Creber. 1973. In 'Implications of continental drift to the earth sciences' (Eds. D.H. Tarling and S.K. Runcorn) pp. 425-437. Academic Press, London,

3.   The effects of gravity and the earth's rotation on the growth of wood.
G.T. Creber. 1975. In 'Growth rhythms and history of the earth's rotation' (Eds. G.D. Rosenberg and S.K. Runcorn) pp. 75-87. Wiley, London.

4.   Tree rings: A natural data-storage system.
G.T. Creber. 1977. Biological Reviews 52, 349-383.

349

TREE RINGS: A NATURAL DATA-STORAGE SYSTEM

By G. T. CREBER

Botany Department, Birkbeck College, London WC1E 7HX

CONTENTS

I. INTRODUCTION

The trunk, branches and larger roots of a tree contain a high proportion of wood; this is the secondary xylem tissue formed by the activity of a layer of cells called the vascular cambium. Active cell division in this layer produces cells which expand and displace the cambium in an outward direction. In many trees, particularly those growing in temperate latitudes but also including some in equatorial regions, cambial activity is not constant throughout the year. This discontinuity causes the phenomenon of growth rings (Plate 1, fig. 1; Text-fig. 1). The growth rings are cylinders or, more correctly, long, slightly tapered cones of wood which appear as rings when they are cut transversely. Because of the regular alternation of summer and winter conditions the growth rings of trees in temperate latitudes, with certain exceptions, accurately reflect the annual cycle. The wood of trees grown in equatorial regions may show no periodicity or there may be growth rings which are related to events such as flowering or leaf replacement. Such rings are therefore not necessarily annual in nature.

In the wood of trees in temperate regions the growth rings are normally well-defined increments whose boundaries are delimited by abrupt changes in cell size which
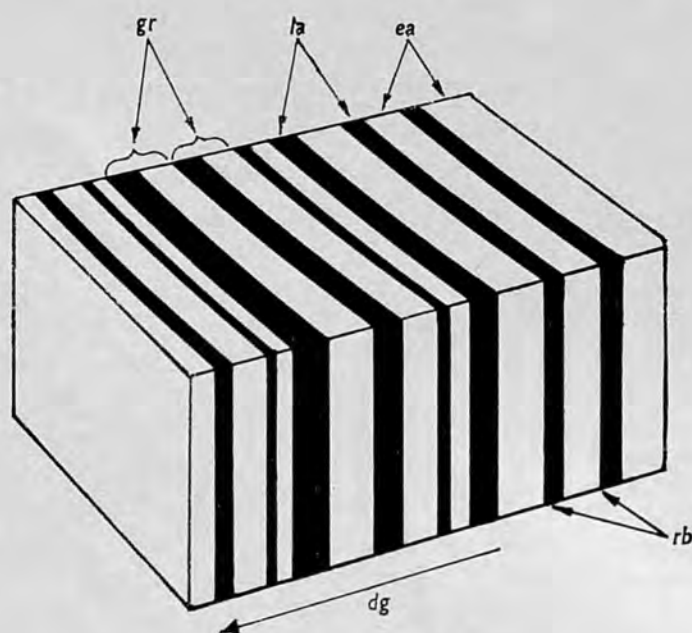
Text-fig. 1. A representation of the growth rings in a piece of wood. The rings may be as much as 10 mm wide but more commonly they are within the range 2–3 mm. Similarly, nearly half of each ring may be latewood but it may be as little as one-tenth or be almost totally absent. Other anatomical features, such as the rays, which are not significant in dendrochronological or dendroclimatological studies have been omitted. *dg*. direction of growth; *ea*, zones of early-wood; *gr*, growth rings (tree rings); *la*, zones of latewood: *rb*, ring boundaries.

mark the seasonal breaks in growth. In the wood of coniferous trees there is a striking difference between the small, thick-walled cells termed latewood, which are formed at the end of the growing period and the larger thin-walled cells, earlywood, formed at the onset of the next period (Plate 1, fig. 2; Text-fig. 1). The terms earlywood and latewood were recommended by the International Association of Wood Anatomists (1933) for use in place of springwood and summerwood; the latter terms imply a precise time of formation for each category which may not be the case in practice. Nevertheless the use of springwood and summerwood has not entirely ceased and indeed the terms lightwood and densewood may also be encountered in the literature of the timber industry. The reference here is to the quality of the wood produced rather than to the time of its formation. In dicotyledonous trees the growth rings are not always so clearly delimited as they tend to be in conifers; this is due to the fact that dicotyledonous wood is much more complex in structure and the ring boundary may be marked by only a few radially flattened elements formed at the end of the growing period. The great variety of types of growth ring in coniferous and dicotyledonous trees has been emphasized by Zimmermann & Brown (1971), Kozlowski (1971) and by Glock, Studhalter & Agerter (1960).

The study of growth rings in trees has been pursued by research workers in many scientific disciplines. An appreciation of the development of these studies may be gained from the works of Douglass (1919, 1928, 1936), Glock (1937, 1941, 1955), Studhalter (1955), Studhalter, Glock & Agerter (1963) and Agerter & Glock (1965), the last of

which takes the form of an annotated bibliography of over 2600 papers on tree growth published between 1950 and 1962. Most of the studies on tree rings have been carried out in the United States of America but Eckstein (1972) gives a summary of European research. The most recent major work in the field is that of Fritts (1976).

One application of growth-ring studies is the dating of wood samples, either in situ as forest trees or in human habitations. This, known as dendrochronology, is widely used in archaeology. Another use is in the assessment of climatic influences and is known as dendroclimatology. This may be pursued in two ways: (1) By correlating the growth-ring measurements of trees with the contemporary meteorological data and then extrapolating back, it is possible to reconstruct the probable climatic patterns of the past from the growth-ring data. This is extrapolatory dendroclimatology. (2) By examination of the growth rings alone deductions can be made about the climate in which the tree grew. This is interpretative dendroclimatology. In practice the extrapolatory workers study the climate of the Quaternary (i.e. the Pleistocene and Recent periods) whereas the interpretative may be working on any period of the geological time-scale in which fossil wood is found. These two aspects of tree-ring studies, chronology and climatology, although distinct in purpose are in fact closely linked. Statistical procedures that are used in chronology must be carried out before climatic inferences may be drawn. Extrapolatory work has enabled the reconstruction of the climatic patterns of the past several hundred years and current research is attempting to reach further back towards the end of the Ice Age. This knowledge of past climate is also being used to make tentative predictions about future climatic variations.

II. DENDROCHRONOLOGY

The most obvious use of growth rings is that by which the age of a tree grown in temperate latitudes can be found by counting the rings visible on a felled trunk. This has been practised since the time of the ancient Greeks and possibly earlier (Studhalter, 1955). Each ring in a trunk may be dated by counting the rings back from one of known date. Since some trees may be extremely long-lived, extensive chronologies are obtainable. For example, the oldest Great Basin bristlecone pine (*Pinus longaeva* Bailey) of the White Mountains of California on record is about 4600 years old (Morey, 1973). Although such chronologies from individual trees are very valuable they can be greatly enhanced by cross-dating (cross-identification).

(i) *Cross-dating*

The germ of the idea for this technique is attributed to some 18th Century naturalists, each of whom, counting back the rings in felled trunks, reached the one for 1709 in which they all noticed severe frost effects. These observations were widely separated: in France (Du Hamel & De Buffon, 1737); in Germany (Burgsdorf, 1783); and in Sweden (Linnaeus, 1745, 1751). Historical records contain references to the severe winter of 1709. This linkage of the chronologies of individual trees is considered to be the beginning of cross-dating (Studhalter, 1955). It depends on the recognition of idiosyncrasies in the ring sequences of individual trees which are caused by a variety of

environmental effects which may be climatic (Fritts, 1966) or biotic (Fletcher, 1974). The widths of the rings vary from year to year (Plate 1, fig. 1) in a random fashion such that sequences are never repeated with exactly the same patterns.

(ii) *Chronology construction*

Thus, once the special pattern or 'signature' (Douglass, 1936, plate 9) for a particular sequence of years has been recognized, it is sought in other trees growing on local or distant sites. If it is located near the centre of a trunk it may possibly be found in the outer rings of another, older, tree or felled trunk. The pursuit of a sequence in this way (Text-fig. 2) enables a chronology to be built up; for example one has been constructed from bristlecone pine trunks which now extends back over 8000 years (Ferguson, 1968; LaMarche, 1975). Chronologies of this kind have proved useful in a number of ways; in the United States of America, archaeological sites have been dated from the ring sequences in the ponderosa pine logs (*Pinus ponderosa* Laws.) used in log cabins (Peterson, 1935; Douglass, 1941; McGregor, 1942). Other archaeological references are given by Zeuner (1958) and Dimbleby (1967). An interesting use is illustrated by Fletcher, Tapper & Walker (1974) who are using an oak (*Quercus robur* L. and *Q. sessiliflora* Salisb.) chronology for Northern Europe to date the oak boards used by mediaeval artists for their paintings. The same chronology has been used to date mediaeval timber-framed buildings (Neiss, 1968) and also a boat which sank in Bremen harbour soon after it was launched in 1380 (Fliedner & Pohl-Weber, 1964; Bauch, 1969). Barefoot (1975) has dated oak timbers in HMS *Victory* and matched them with oaks growing in the vicinity of Winchester. In Ireland bog oaks are being used to extend the chronology back through the Quaternary period by Smith *et al.* (1972). A pine chronology (species not stated) has been used to determine intervals at which the wooden pavements of Novgorod were replaced (Kolchin, 1962). Further Russian work may be found in: "Papers presented at the 1st (Vilnius, 1968) and 2nd (Kaunas, 1972) All-Union Conferences on Dendrochronology and Dendroclimatology". J. R. Fletcher of the Oxford University Research Laboratory for Archaeology and the History of Art, has translations and abstracts of these papers.

An outstanding contribution to the accuracy of archaeological dates has been made by dendrochronology in correcting those derived by the ^{14}C method of dating organic remains (Renfrew, 1971). From its inception in 1949 this method had been relied upon throughout the world to date sites accurately. Now, archaeological theories have been revised as a result of the calibration of the ^{14}C time-scale by the tree-ring method. The latter necessitated the removal of small samples of wood from the growth rings of the tree trunks used to construct long chronologies (Ferguson, Huber & Suess, 1966. Ferguson, 1970). These rings were known to have been formed at certain dates along the chronology but the dates obtained from them by the ^{14}C method were different; A portion of a growth ring formed in 2500 BC gave a date of 2000 BC by the ^{14}C method. The error increases to about 800 years at 5000 BC. The graph of the relation between the two sequences of dates is not a straight line (Renfrew, 1971; Watkins, 1975). Instead there is a continuous series of oscillations throughout the whole period, thought to be due to variations in the $^{14}C/^{12}C$ ratio in atmospheric carbon dioxide
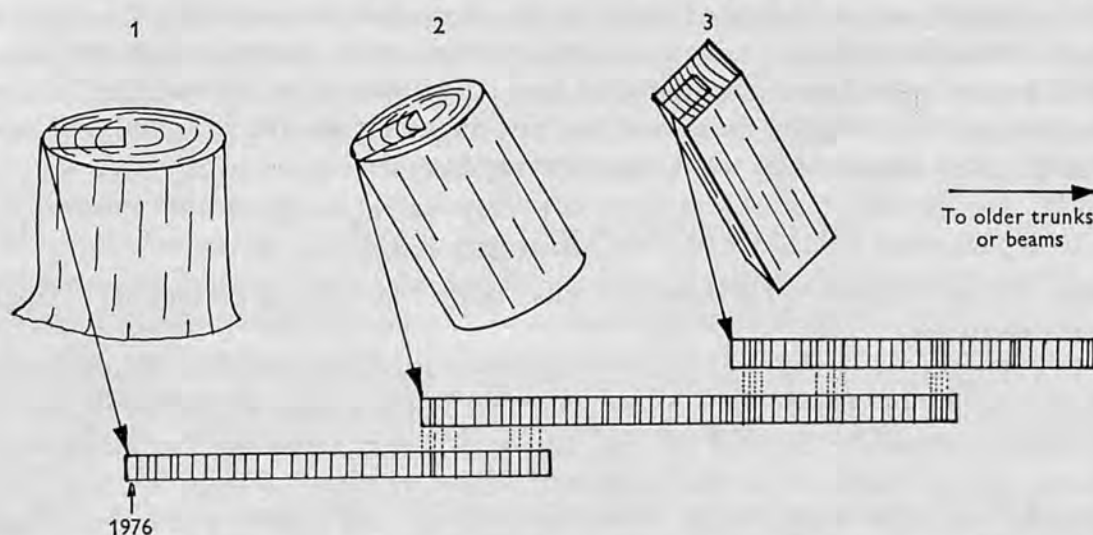
Text-fig. 2. A diagram illustrating the process by which a chronology is constructed. The trunk (2) felled in 1955 overlaps the stump (1) sufficiently for cross-dating to be achieved. Similarly the cross-dated overlap with the trunk (2) shows the oldest ring in the beam (3) to have been formed in 1925.

influenced by fluctuating cosmic radiation. The dendrochronological calibration of ^{14}C dates is now fully accepted in archaeology; it was at first based on only one tree-ring sequence, that of Ferguson (1970), but in 1973 LaMarche & Harlan published an independent one that differed from Ferguson's by only two years. In the same year Ralph, Michael & Han produced a comprehensive calibration which incorporated virtually all of the long tree-ring sequences made by the principal laboratories for the period from 5383 BC until 1849 AD.

Ecological studies have benefited, too, from dendrochronology; Spencer (1964) was able to estimate the size of a population of porcupines in the Mesa Verde National Park (Colorado, U.S.A.) and to study fluctuations in this population over the period 1690–1960. The growth-ring patterns of the trees damaged by the porcupines were sufficiently anomalous to indicate the years in which the animals had fed upon them. The trees were pinyon pine (*Pinus edulis* Engelm.) and ponderosa pine; they were cross-dated to a master dendrochronological key, based on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), that had been developed for the Park Area by Schulman (1946, 1947).

(iii) *Mean sensitivity*

There is a considerable variation between species and between sites as to the amount by which successive growth rings differ in width. In order to classify individual trees in this respect Douglass (1928) used the terms 'complacent' and 'sensitive'. The first term describes a sequence of ring widths in which there is little or no variation over a period of years whilst the converse of that situation is described as 'sensitive'. For successful cross-dating it is necessary to have somewhat sensitive sequences because there must be distinctive patterns in the ring sequences which can be recognized in different trees. Only then can long chronologies be constructed. Although

ring sequences can be roughly judged by eye as sensitive or complacent, Douglass (1928) devised a coefficient which enables sequences to be accurately assessed. This coefficient he called 'mean sensitivity'; Glock (1955) was of the opinion that "it was the most revealing of all of the devices that give an insight into the vicissitudes of tree history". It is calculated by using the following formula:-

$$\text{Mean sensitivity} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|, \qquad (1)$$

where x is the ring width, t is the year number of the ring and n is the number of rings in the sequence.

The ring widths in the sequence are treated as consecutive pairs and the difference (neglecting the sign) between each pair is divided by the average width. An average is then taken of the sum of all of the calculations. An extra advantage that arises from the use of this coefficient is that unwanted trends are removed from the data. For example, the rings formed early in the life of a tree are usually wider than those formed later (Plate 1, fig. 1); such an effect which has no special significance is thus eliminated.

Schulman (1956) and Fürst (1963) used the formula in a modified form:

$$\text{Mean sensitivity} = \frac{1}{n-1} \frac{\sum\limits_{t=1}^{t=n-1} \left| x_{t+1} - x_t \right|}{\frac{1}{n} \sum\limits_{t=1}^{n} x_t}. \qquad (2)$$

In this modification, each calculation is performed by dividing the difference between a consecutive pair of ring widths by the average ring width of the whole sequence; not, as in formula 1, where each difference is divided by the average of that pair only. They claimed that formula 2 produced a coefficient very close to that of Douglass and also that it was easier to calculate. With the advent of the high-capacity computer the latter advantage cannot now be claimed. It is noticeable, too, that Fürst had to discard the data from the first 50 rings in each of his trees, having lost the advantage of formula 1 which removes unwanted trends such as those in the earlier rings of a tree. He also multiplied his mean sensitivity coefficients by 100 and expressed them as percentages; other workers seem not to have followed this practice.

Most mean sensitivities fall within the range 0 to 0·6; by convention those below 0·3 are termed complacent whilst those above are sensitive. A figure of 0·3 would indicate that a tree's water supply was somewhat limited and variable from year to year; 0·6 would result from a water supply extremely restricted in average quantity and very variable in the amount of replenishment each year. Trees in mountainous areas, growing on thin soils often produce figures of this order. In spite of the sophisticated statistical techniques now available the coefficient is still widely used. Dendrochronologists would use it as a criterion of the usefulness, or otherwise, of the data from a tree or group of trees. For successful cross-dating there must be a reasonably high figure (about 0·3) for necessary diagnostic patterns to arise. In this connexion the problems that a dendrochronologist may encounter are made clear by Douglass (1928). Of *Sequoia sempervirens* Endl. he says: "The coast redwood has been a disappointment,

because after most careful tests it has failed entirely to show cross-identification." Similarly the Englemann Spruce (*Picea englemanni* Parry) of high altitudes "is even less valuable in this respect, its rings have little variation and do not cross-identify with neighbouring pines and Douglas-firs". In contrast to this, he says, "The western yellow pine (ponderosa pine) is perhaps the best tree for these studies, on account of its precision and length of record (over 500 years) and its wide distribution." That such remarks cannot be taken as generalizations that will apply universally is illustrated by Schulman (1956); he found in various localities in the semi-arid South Western U.S.A. that ponderosa pine had an average coefficient of only 0·24, whereas the figure for Douglas-fir was 0·53. As regards the genus *Sequoia* he was in agreement with Douglass in that he found the figure for *Sequoia gigantea* (Lindl.) Decne. to be 0·17. Clearly preliminary work has to be done on the trees of an area before deciding which to use.

This coefficient is also used by the extrapolatory and interpretative climatologists. The former would require sensitive tree-ring sequences partly for the construction of chronologies but also to provide data that vary with variable climatic conditions. The interpretative climatologist uses the coefficient as an indication of (*a*) the genotypic potential of a species to respond to environmental differences in successive years; (*b*) the growth of the tree in a site where this potential was realized; (*c*) a sensitive response resulting from the genotypic potential coupled with the effect of a suitable site. Whereas the dendrochronologist requires a reasonably high mean sensitivity as a *sine qua non* for the construction of long chronologies, the interpretative dendroclimatologist can make deductions from complacent as well as sensitive sequences. As stated above, *Sequoia sempervirens* is a disappointment to the dendrochronologist because of the complacency of its ring sequences but to the dendroclimatologist this very feature indicates that the trees grew in a moist climate at low altitudes. That it was not possible to find any member of this species with a sensitive ring sequence also indicates that the climate and altitude are prerequisites for its survival.

III. DENDROCLIMATOLOGY

(i) *Extrapolatory*

(a) Environmental effects on tree growth

Early attempts to establish correlations between ring-width measurements and the rainfall and temperature records for the localities in which the trees grew were rather unsuccessful. Indeed, work outside dendrochronology produced ample data to show this lack of correlation. These data were collected by the use of instruments known as dendrometers. Studhalter, Glock & Agerter (1963) and Kozlowski (1971) trace the history of these devices through the past 150 years. Although they take various forms, dendrometers all provide a means of measuring the girth of a tree and the more recent ones are termed dendrographs because they have attachments which enable a continuous series of readings to be automatically recorded. The first dendrograph was described by MacDougal (1918) and using such a device he took annual measurements of the girth of a specimen of *Pinus radiata* D. Don (Monterey pine) growing at Carmel

in California. He also obtained the official rainfall figures for the sixteen years in which he took the dendrograph readings (MacDougal, 1936). From his data it is possible to calculate the correlation coefficient between increase in trunk diameter and rainfall; this has the low figure of $+0.32$.

Attempts were then made to use periods of time other than the conventional January–December calendar year and these proved to be rather more successful. In Northern Arizona, Glock (1938) found that the rainfall of January, February and April gave the best agreement with tree growth. Lyon (1943) found that the best correlations of Eastern white pine (*Pinus strobus* L.) and Eastern hemlock (*Tsuga canadensis* (L.) Carr.) ring sequences in trees within a 80 km radius of Boston (Mass.) were for the periods May–July and May–August. Salisbury & Jane (1940) found excellent graphic correlation between spring and summer rainfall and the ring sequences in hazel (*Corylus avellana* L.) growing on the chalk cliffs in Dorset. Other work has been devoted to correlating tree-ring data with hydrological data for streamflow either in the locality of tree growth or in some part of the catchment area of the region.

In this connexion the work of Cooperrider & Sykes (1938) on the Salt River watershed above Roosevelt Dam in Arizona may be mentioned. They compared rainfall figures with streamflow in local rivers. A very complex relationship was revealed which, when compared with tree-ring data, showed more parallel trends than opposite ones for the period studied (1902–36). It would appear that the streamflow for any interval of time does not entirely depend on the amount of rainfall during that interval. Evidence for one of the possible causes of this effect comes from the work of Henry (1931). He pointed out that although 1930 was what might be termed an 'average' year for rainfall in Arkansas with 96% normal, the amount of rain in individual months was as follows:

January	223% normal
May	200% normal
June	22% normal
July	19% normal

Obviously data such as these are of prime importance in attempting to assess annual rainfall from tree-ring data. If the rain in a 'wet' year did not fall at a time when it could influence tree growth, then it will not be recorded in the corresponding tree ring. A given amount of precipitation early in the growing season when the soil moisture may be at field capacity will have little effect on cambial growth, whereas half that amount later in the season when the soil is dry will have a marked effect.

Schulman (1951–2) studied the correlation between surface run-off and ring sequences. Two Douglas-firs growing in the Mesa Verde were selected and ring data from them for a period of 70 years were compared with the records for the same period for the run-off in the Rio Grande 100 miles away. A correlation coefficient of $+0.72$ was obtained. In a similar study near Pecos, New Mexico, the same coefficient resulted in a comparison of tree-ring data with run-off figures for the Pecos River 12 miles away. Glock & Agerter (1962) provide some very useful examples of ring-width patterns that are associated with rainfall regimes in West Texas and California.

More recently, Stockton (1971) has used tree-ring data to extrapolate stream-flow records back in time beyond the range of the existing hydrological data. Using these techniques Stockton & Fritts (1971) have extended back to 1810 the water level record for Lake Athabasca in Canada. This was achieved by using ring sequences from white spruce (*Picea glauca* (Moench) Voss) growing alongside waterways associated with the lake. In another study of this kind, LaMarche & Fritts (1971) correlated ring-width sequences from specimens of the Swiss stone pine (*Pinus cembra* L.) growing at high altitudes in the Alps with records of glacial advance and retreat. The linear relationship that emerged enabled the tree-ring chronologies to be used in reconstructing past glacial activity.

The last work indicates that the ambient temperature may be important for seasonal growth, especially in regions where soil moisture is normally adequate. Hustich (1941) showed clearly the effect of temperature in Northern Finland. He found that radial growth was strongly correlated ($r = +0.86$) with the mean temperature of the warmest month of the year. Ording (1941) in Norway and Schove (1950) in Scotland have found similar correlations with summer temperatures. In an interesting study based on oak, beech, fir and spruce (species not stated) grown in East and West Germany, Fürst (1963) showed that the ring sequences become more sensitive as trees are sampled in a progressively eastward direction, the direction in which the climate also changes from oceanic to continental with increasing annual temperature range and a fall in the average annual rainfall from 1350 mm to 700 mm. He was also able to show that the increasingly oceanic climate in this part of Europe in the last 150 years is revealed by a decrease in the average fluctuation of the annual ring curves in comparison with the period before 1800 AD. These findings are well supported by historical accounts of the climatic conditions of the period.

Individual environmental factors may exert their influence on growth at different times during the growing season. The ambient temperature was shown by Fritts (1956) to control cambial growth of *Fagus silvatica* L. (European beech) early in the growing season. Later, however, as soil moisture approached the wilting coefficient, water deficits exerted a strong controlling influence on the growth of *Quercus alba* L. (white oak), *Acer saccharum* Marsh and *Fagus grandifolia* Ehrh. (American beech) (Fritts, 1959 *a, b*). Kozlowski, Winget & Torrie (1962) also showed that ambient temperature was an environmental factor that varied during the year in its influence on cambial growth in *Quercus ellipsoidalis* E. J. Hill (Northern pine oak) grown on sandy soil in Wisconsin. The influence of temperature declined in late summer as soil moisture became depleted and growth was much more dependent on water supplies.

Fritts (1962 *a*) demonstrated the lag effects of environmental factors. He showed that the conditions of the previous year might be equally or even more effective than those of the current year on ring-width variation in the American beech. Ring width was inversely related to the severity of drought during the August of the previous year and more directly related to the May–July temperatures of that year rather than those of the current one. The lag effect of temperature on cambial growth in Finland is most pronounced near the timber line where a narrow ring is formed in the year following (one with lower than average temperatures (Mikola, 1962). Zahner & Stage (1966

devised a method of measuring water deficit in trees. During the course of their work they also took readings of ambient temperatures throughout the growing period (May–September). They studied the influence of these factors during both the current and previous years on the growth of *Pinus monticola* Dougl. (Western white pine) in Northern Idaho. Water deficits during the June of both the current and previous years tended to inhibit growth. Higher than average temperatures in the previous year favoured growth in the next year; higher temperatures in the current year impeded growth early in the season but had little effect later.

Rainfall and temperature are the most potent influences on wood production. Humidity and wind speed are usually only secondary for the following reason. In dry, windy conditions trees lose water rapidly by transpiration but if rainfall has provided reserves in the soil, the growth of the trees continues unimpeded. Schulman & Bryson (1965) found that narrow rings were formed in those years when rainfall was low and evaporation high during July. They concluded that there was a strong dependence on water availability in the soil. These factors may operate on a local basis causing differences in ring widths between trees growing on soils with differing capacities for retaining water. Humidity may occasionally be an important factor, as in the case of the distribution of *Sequoia sempervirens* (see p. 355). In this part of California persistent summer mists reduce transpiration and the soil reserves are never exhausted.

Growth rings may also give evidence of biotic effects such as insect attack. Fletcher (1974) describes the defoliation of oaks by caterpillars of the moth *Tortrix viridana* L. which were very numerous in the period 1917–24. Weakened trees were rendered more susceptible to fungal disease. The group of narrow rings for this period is a distinct feature of wood from oaks in Western Europe. Koerber & Wickman (1970) describe the use of ring-width data in estimating the severity of insect attacks. Some insect defoliators of evergreen conifers such as *Choristoneura fumiferana* Clemens, the spruce budworm, may destroy the current-year foliage whilst leaving all of the older leaves. The ring produced that year near the trunk base is unaffected but that of the following year is much reduced (Williams, 1967). Stark & Cook (1957) found a lag of two years between an attack by *Recurvaria milleri* Busck, the lodgepole needle miner, on *Pinus contorta* Dougl. (lodgepole pine) and the occurrence of narrow rings in the wood. The porcupine damage described above (see p. 353) is another example of a biotic effect recorded in tree rings. (See Addendum).

Scars on trees are often used to reconstruct the past frequency of forest fires. Man-made effects such as pollution are likely to be increasingly studied in the future. Fritts (1976) cites some examples, in one of which it would appear that industrial fumes suppressed tree growth and resulted in smaller ring widths after the onset of industrial activity. Further work is necessary to substantiate a correlation between atmospheric pollution and tree growth. It is interesting to note that one of the earliest correlations attempted in tree-ring studies, that of Douglass with the sunspot cycle, now seems to have been largely unfounded. LaMarche & Fritts (1972) were unable to establish that any significant relationship existed between tree-ring data and the sunspot cycle and they concluded that any further search for empirical relations between the two is likely to prove disappointing.

A new stimulus to environmental studies came with the advent of a technique based on the fractionation of isotopes. The latter process is temperature-dependent and the discovery that isotope ratios vary between rings and even different parts of rings has enabled the retrieval of past temperature data. Wood is made up of cellulose ($\sim$ 50%) lignin ($\sim$ 30%) and other compounds such as hemicelluloses (15%), resins and alcohols. Libby & Pandolfi (1974) measured the $^{13}C/^{12}C$ and the $^{18}O/^{16}O$ ratios in the cellulose of the wood of an oak (species not stated) grown in Germany and calibrated them against official temperature records which exist from 1755 in the region of growth. In more recent work, in New Zealand, on the wood of *Pinus radiata* Wilson & Grinsted (1977a) have measured the $^{13}C/^{12}C$ ratio in both the cellulose and lignin. They found a similarity in the variation in this ratio in both substances. This was taken as evidence that the temperature-dependent steps in the pathways leading to both substances are early in the sequence, probably in the leaves. Thus the monitored temperature is that of the crown of the tree rather than the trunk. Wilson & Grinsted (1975) also studied the deuterium/hydrogen ratio in the cellulose of the wood of *Pinus aristata* Engelm. (Rocky Mountain bristlecone pine) and showed that the seasonal variation in temperature was evident here too. Wilson & Grinsted (1977b) have produced a comprehensive account of all of their studies in isotope fractionation.

(b) Principles

Excellent summaries of the principles of extrapolatory dendroclimatology have been presented by Fritts (1971, 1976). The first principle is termed the law of limiting factors. The activity of the vascular cambium in giving rise to secondary xylem to form a growth ring cannot proceed more rapidly than is permitted by the most limiting factor. The rate and duration of cell division and enlargement may be limited by water stress during the growing season, by low temperatures or by the conditions of the previous season. The second principle is that of site selection which emphasizes the necessity of selecting the best sites when a particular aspect of a past climate is being studied. For example, when drought is the basis of the study, it is important to use data from trees that are in the driest sites for each particular species. In temperature studies, the best trees in very high latitudes are within 100 m of the upper climatic tree line because it is only in the vicinity of this line that the temperature is sufficiently limiting to override other growth-controlling factors. The third principle is that of sensitivity and measurement of high and low frequency variability. Mean sensitivity is a relative measure of first differences; it is influenced largely by the short-term changes (or high-frequency variations) in climate. Longer-term (or low-frequency variations) in a tree-ring sequence can be measured by correlating the sequence with itself with the individual indices out of step by 1 to n steps. That is, one obtains the correlation coefficient between x_y and x_{y+n}, where y is the year of the ring measurement and n is a factor by which the individual years are out of step. This technique is known as autocorrelation. Thus if a high positive correlation is obtained when, say, $n = 19$ then a 20-year cycle is demonstrated.

Standard deviation, in contrast to mean sensitivity and the above autocorrelation technique, measures variability in all frequency ranges. Standard deviation is increased

more than is mean sensitivity whenever long-term variations occur in the ring sequences, e.g. if early growth increments are all much larger than those produced later in the life of the tree. Dendrochronologists prefer to use mean sensitivity rather than standard deviation because they are concerned more with the high-frequency variation that reflects minor climatic oscillations. Trees of high mean sensitivity have very variable ring sequences which cross-date satisfactorily and facilitate the construction of long chronologies. There is the further advantage that such trees show a very high 'signal' to 'noise' ratio in their ring sequences. Dendroclimatologists use standard deviation which indicates long-term major variations in climate.

The fourth principle is cross-dating which has already been described. The fifth is termed the principle of replication. To the dendrochronologist this is a vital element in the cross-dating process. It is equally important to the dendroclimatologist for somewhat different reasons. If climate has been a rather less potent factor than others in influencing a ring sequence and the climatic 'signal' in the sequence is weak it becomes necessary to replicate the data by analysing a large sample of trees all showing the same 'run' of years in their ring sequences and accurately cross-dated. In so doing the non-climatic noise is reduced in the averaging process and the mean growth for each year approaches the climatic chronology for the site.

Fritts (1971, 1976) uses the concept of the 'climatic window' to express what a tree does when, by means of its various physiological processes, it passes and converts the climatic and environmental effects into a certain ring width. The tree is acting as a kind of filter and the purpose of dendroclimatology is to identify the various responses to the climatic effects. The rings in trees growing on less arid sites are less dependent upon the moisture falling during the growing season and they are also less related to climatic variability than the rings in trees on the arid sites. Thus trees on diverse sites may be limited by different sets of climatic factors and thus exhibit different climatic windows. With the aid of the statistical techniques described in the next section, it has been found possible to reveal differences in the climatic windows of the same species on contrasting sites and geographical locations. There is also evidence that the same environmental factor may influence individual trees in different ways so that they exhibit a variety of responses to that factor. If the climatic windows and response functions for two groups of trees on contrasting sites or for different species on the same site can be adequately defined and if these responses differ by only one factor, it may be possible to use the differences between the respective ring-width chronologies to estimate variations in that factor (Fritts, Blasing, Hayden & Kutzbach, 1971).

(c) Statistical techniques

Analysis of ring-width data should proceed in 4 basic phases:

(1) The raw data are converted into ring-width indices by standardization. This is done by fitting a regression curve to the ring-width series and dividing the actual ring widths by the yearly values of the fitted curve. This transforms ring-width values into indices which have a mean of 1·00 and a variance that is independent of tree age, position within the trunk and the mean growth of the tree. Since the mean index is the

same for all radii, indices have an added advantage over raw ring-width data since they all receive equal weight when used in calculations, regardless of their origin in fast- or slow-growing parts of the tree. If a cross-dated set of trees is available, the indices of all of the rings formed in the same year are averaged to obtain a mean ring-width index for that year. Each year in the sequence can then be treated in this way.

(2) The standard statistical characteristics of the indices of each series should be obtained. That is to say, the mean, standard deviation and mean sensitivity should be calculated and some autocorrelation carried out. In cases where two or more radii of the trunks were measured, the standard error, standard deviation and variance for each year of the sequence should be obtained.

(3) The definition of the climatic window and response function should be carried out by calibrating the ring-width series with existing meteorological or hydrological data. A multiple regression analysis may be employed to predict yearly growth indices as a function of the meteorological variables (Hustich, 1948; Fritts, 1962a, b; Serre, Lück & Pons, 1964; Schulman & Bryson, 1965; Julian & Fritts, 1968). A more efficient technique involving the extraction of eigenvectors from monthly precipitation values has also proved to be very successful (Fritts *et al.*, 1971).

(4) Further analysis may be undertaken after the tree-ring data have been evaluated and the climatic relationships assessed. Groups of the chronologies over a wide geographical area which have a similar climatic response may be selected. Each annual growth index may be normalized by subtracting the mean and then dividing by the standard deviation for a given period. These normalized values may be averaged for pentads or decades, plotted on maps and contoured to show anomalous variations in past growth. If the chronologies have been calibrated with climate, it is then possible to infer which climatic variations have occurred by observing the areas of high and low tree-growth.

Using the above techniques, Fritts (1965, 1969, 1972) and LaMarche (1974) have produced climatic maps for North America showing the variations that have taken place during the last few hundred years. A similar study is now in progress at the Climatic Research Unit of the University of East Anglia (B. M. Gray & P. M. Kelly, personal communication, 1976). Using tree-ring and other data the Unit plans to produce climatic maps for the British Isles for the period 1500–1800 AD. It is also planned to extend this mapping back to 1000 AD after the first period has been completed. In view of the climatic extremes currently being experienced in the British Isles there is considerable interest in this work.

(ii) *Interpretative*

Much less work has been done on this aspect of dendroclimatology. I have embarked on a study designed to make use of the considerable quantities of fossil wood both in museums and available for collection in the field. The aims of such a study, as stated in 1973 (Chaloner & Creber), are to obtain a broad picture of past climates by analysis of all the features of fossil wood specimens. These will be examined for: (*a*) presence or absence of growth rings as an indication of palaeolatitude; (*b*) absolute width of the rings as an indication of the growing conditions; (*c*) asymmetry of rings indicating

362 G. T. CREBER

effects of gravity; (d) 'false' rings as indicators of frost or attacks of defoliating organisms; (e) the earlywood–latewood ratio in the rings as an indication of summer rainfall.

It is also hoped that the statistical techniques of the extrapolatory workers will be used to deduce climatic effects on an empirical basis without the benefit of contemporary meteorological data. The absence of the latter will entail a different approach from that of the extrapolatory dendroclimatologists. The genetical potential of the trees will be unknown and the original positions of the wood samples in the tree (i.e. trunk, branch or root) are likely to be somewhat uncertain. The geological time-scale is vast and hence cross-dating will be virtually impossible. The year-by-year sequence of ring widths cannot therefore be used for chronological work but will be used entirely for interpretative deductions.

(a) The earlywood–latewood ratio

In addition to the ring-width data the earlywood–latewood ratio within each ring is also a possible indicator of environmental conditions. This ratio is of some considerable interest in forestry and in the wood pulp and paper industries as it is linked with wood quality. There is a substantial literature in the journals of these industries on the subject of wood quality and the factors in the forest environment that influence its development. Naturally, although both the forester and the dendroclimatologist are interested in the earlywood–latewood ratio they have entirely different viewpoints on the subject. The forester wants to grow trees in such a way that they produce a considerable quantity of latewood whereas the dendroclimatologist can assess from the quantity of latewood produced the climatic conditions in which the trees grew.

In such a study there are many problems, not the least of which is the present lack of agreement among workers in this field as to the definition of latewood. The classical definition is that of Mork (1928) which states: "All tracheids in which the common wall between two cell cavities (lumina) multiplied by two is equal to or larger than the width of the lumen, are considered as summerwood (latewood); those in which the value is less than the width of a lumen are considered as springwood (earlywood)" (Text-fig. 3). The definition was originally devised for Norway spruce (*Picea abies* (L.) Karst.) and is unsatisfactory as it only gives acceptable results with a few gymnosperm species and it is quite unworkable with angiosperms. Elliott & Brook (1967) review other definitions and give the results obtained when they were used to determine the earlywood–latewood boundaries in the rings of a number of tree species. It was found that the positions of the boundaries varied with the definition used.

Greater success has attended the use of scanning microphotometers in determining the earlywood–latewood boundaries in wood samples. In these devices a beam of light is passed through a thin transverse section of the wood which is traversed across the beam by a motorized mechanical stage. Schanderl (1939) showed by using one these machines that the amount of light passing through the cell lumina was proportional to their areas and could therefore be used as a measure of cell size. The microphotometer built by Green & Worrall (1963) at the Pulp and Paper Institute of Canada enabled them to record automatically a number of wood features such as: growth ring widths, cell wall area and lumen area (and hence the ratio between them),

(a)   (b)

10 μm
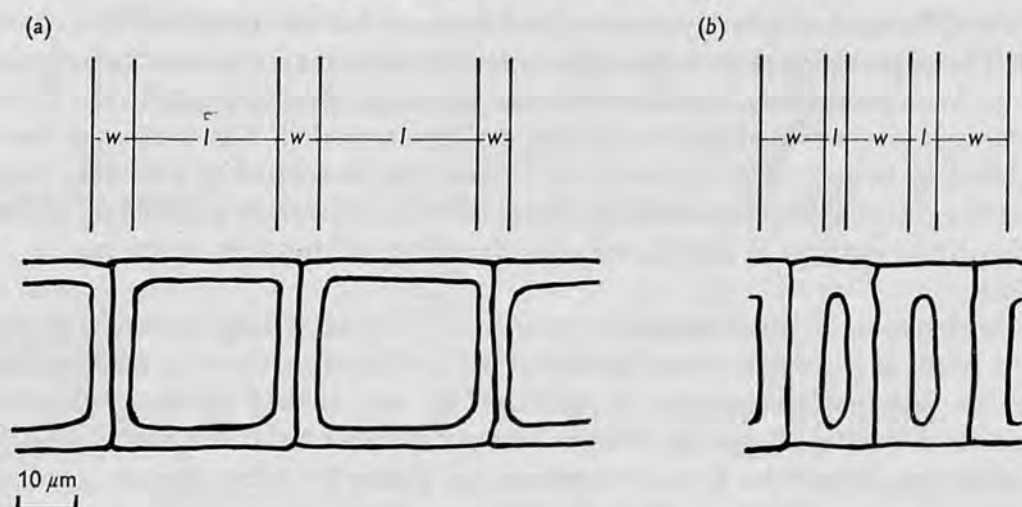
Text-fig. 3. (*a*) Tracheids from the earlywood of *Pinus sylvestris* cut in transverse section to show the relative proportions of lumen and wall. (*b*) Tracheids from the latewood of the same species showing a reversal of the lumen and wall proportions with respect to those of the earlywood. *l*, lumen; *w*, wall.

for a series of growth rings, for individual growth rings and for parts of rings. The occurrence of reaction wood (see p. 370) and interruptions in growth within rings ('false' and 'frost' rings) were also recorded. An improved version of the machine (Green, 1965) enabled the data to be recorded on paper tape suitable for direct input to a computer.

Green & Worrall adopted the midpoint of the transmission range as the earlywood–latewood boundary. That is to say the average of the highest and lowest amount of light passed by the largest and smallest cells, respectively, in the growth ring. Elliott & Brook (1967), contemporaneously with Green & Worrall, also developed a microphotometer at the Forestry Department of the University of Bangor and used Green & Worrall's criterion for determining the earlywood-latewood boundaries in wood samples. They were so satisfied with the results that they went as far as to say that: "There seems to be no serious objection to the universal applicability of this technique." However, in spite of their enthusiasm this criterion for establishing the earlywood–latewood boundary has not been adopted as widely as they anticipated. It represents a definite improvement on Mork's definition, particularly when used on the wood of gymnosperms, but in the case of angiosperms it does not indicate quantitatively the properties of the wood in the two zones of the ring. Doley (1974) suggested that ratios based on cell diameter and wall thickness or the relative amounts of fibres and other cell types should be used.

A further development of the microphotometer technique is one in which pencil-like sticks of wood, square in cross-section of side 5 mm × 5 mm, are shaped from cores drilled radially out of tree trunks with an increment borer. The latter is commonly used whenever wood samples are required from living trees since very little damage results from its use. Alternatively the sticks may be cut from sawn timber. When prepared they are then laid on X-ray film and irradiated to produce an X-ray negative. In this

way the different densities of earlywood and latewood become translated into shades of grey. The negative is run on a microphotometer in the same way as a section of wood is run on such a machine (some authors use the term 'densitometer'): the different intensities of light passed by the negative are thus recorded. The technique was first described by Polge (1966). An improved version was developed by Rudman, McKinnell & Higgs (1969) which showed significant differences between phenotypic variations in *Eucalyptus regnans* F. Muell and also the effects of nutrient deficiency in *Pinus radiata*.

Determination of wood density in growth rings by subjecting the wood to a collimated beam of β-particles was first described by Cameron, Berry & Phillips (1959). Since no intermediate negative is produced by this method the microphotometer operation is omitted altogether. Phillips (1960) determined variations in wood density by projecting β-particles from a strontium 90 source by measuring the number of particles absorbed. Phillips, Adams & Hearmon (1962) improved the β-ray method and obtained a continuous chart record of density variations within growth rings. Harris & Polge (1967) and Polge (1969) compared the X-ray and β-ray techniques for measuring wood density. They concluded that the X-ray technique had superior resolving power and could be used to measure wood density in narrower growth rings than could the β-ray apparatus. The X-ray apparatus had the further advantage that it was much more rapid; only 2 min were required to obtain a set of readings from a 100 mm stick of wood. Fletcher & Hughes (1970), working in Oxford, describe the use of the X-ray technique for both density determination and dendrochronology.

The distinction between earlywood and latewood is not merely of academic interest. For timber to be of acceptable quality there has to be sufficient latewood in each ring to raise the relative density to a high value. Wood of low relative density, and hence with little latewood, proves to be structurally unsound if used in buildings or other load-supporting structures. Wilson (1965) showed that the relative density of the woods of five species of coniferous (gymnosperm) trees ranged from 0·2 for earlywood to 0·7 for latewood. This is a considerable variation and Doley (1974) has suggested that this kind of differentiation might be used as a criterion to establish the earlywood–latewood boundary in the growth rings. It would have the added advantage that it could be quickly determined whereas his other suggestions would require many time-consuming measurements. This saving of time could be an important factor in industry. It is possible to disintegrate pieces of wood entirely into their component cells by maceration. Jones, Campbell & Nelson (1966) have shown that after maceration it is possible to separate the lighter, thin-walled cells of the earlywood from the heavier, thick-walled cells of the latewood by centrifugation. This process is very rapid and simple, and this should make it very acceptable to the papermaking industry. The earlywood–latewood boundary could then be based on the differences between the groups of cells separated by the centrifuge. The dendroclimatologist would have a different interest in this process; he would see the effects of climate in controlling the development of the various features of the cells. He would hope to be able to read back from the cell characters the climatic factors that produced them.

Table 1. *Positive correlations recorded by various authors between increased proportion of latewood in the growth rings and environmental and other effects*

Species	Correlated effects	Authors
Pseudotsuga menziesii (Douglas-fir)	Trees grown near to a river	Barrow (1951)
Picea excelsa Link (Norway spruce) and *Pinus silvestris* L. (Scots pine) *Picea* sp. (spruce) *Pseudotsuga menziesii* *Fagus silvatica* (European beech)	Slower rate of growth	Burger (1941) Hale (1924) Harris (1958) Burger (1940)
Picea sitchensis (Bong.) Carr. (Sitka spruce) *Pseudotsuga menziesii* *P. menziesii* *Pinus palustris* Mill. (longleaf pine) and *P. taeda* (loblolly pine)	Increasing age of tree	Bryan & Pearson (1955) Göhre (1955) Harris (1958) Lodewick (1933)
Fagus silvatica	Increasing suppression of the tree in the community	Burger (1940)
Quercus borealis Michx. (red oak)	Lower than average temperatures during the growing season	Bauer (1954)
Picea sitchensis *Pinus sylvestris*	Decreasing latitude of growth site	Bryan & Pearson (1955)
Abies alba Mill. (European silver fir) *Pinus sylvestris* *Dacrydium cupressinum* Sol. (red pine) *Fagus silvatica*	Increasing distance from the crown of the tree	Bielczyk (1956) Cooper (1960) Burger (1940)
Pinus sylvestris	Growth on cold sites which delay the start of the growing season	Schwappach (1892)

(b) Factors favouring the development of latewood

In forestry, the production of substantial quantities of latewood in growth rings is a characteristic much sought after in trees. Species and variants of species that have been shown to possess this characteristic are grown on specially chosen sites where the conditions tend to enhance the production of latewood. A most useful reference source for literature on timber quality is a monograph of the Technical Association of the Pulp and Paper Industry (frequently cited as 'TAPPI') edited by Larson (1962). In this work nearly 900 papers ranging in date from the middle of the last century up to 1962 are abstracted. Table 1 contains some of the correlations recorded by various authors, between an increased proportion of latewood in the growth rings and environmental or positional effects. There is evident difficulty in establishing a single clear cause for the production of large amounts of latewood in the growth rings. In fact it was the opinion of Göhre (1958) that, "The results of the author's investigations on various tree species

were not in agreement with the values recorded by other workers. Statistical comparisons of relative densities between individual trees from the same locality showed such a wide dispersion of values that the differences between trees of different localities or regions of growth were of no importance."

Nevertheless, in spite of this rather pessimistic view, there seems to be enough evidence accumulated more recently that the tree's water supply affects the timing of latewood initiation for the earlywood–latewood boundary to have climatological significance. Kraus & Spurr (1961) found that there was very close agreement between the dates of the onset of soil-water shortage in the summers of 1954 and 1955 in Michigan and the timing of the earlywood–latewood transition in the wood formed in those years. Kennedy (1961) found that variation in latewood percentages in Douglas-firs was related to the amounts of precipitation; the largest amounts of latewood being found in those trees which had the longest periods later in the growing season with abundant rainfall. These findings were reinforced by Smith & Wilsie (1961) who also recorded larger amounts of latewood in the growth rings of *Pinus taeda* L. (loblolly pine) in those years in which the soil moisture content remained at a higher level throughout the growing season. In a specifically climatological study, Cleaveland (1975) has shown that the latewood component of each growth ring in *Pinus echinata* Mill. (shortleaf pine) is more sensitive to climatic variation than is earlywood or total ring width. Fritts (1962a) showed in a study on the growth of *Quercus alba* in Illinois that the amount of latewood formed was dependent upon the availability of soil moisture during June and July. It must be remembered that the earlywood–latewood ratio cannot be discussed entirely separately from other ring characteristics. Burger (1940, 1941), Hale (1924) and Harris (1958) all found that there was a connexion between the rate of growth of trees and the earlywood–latewood ratio. That is to say, when the ring widths are narrow as in a slow-growing tree there is a higher proportion of latewood in each ring. In any deduction, therefore, that is made from the earlywood–latewood ratio due regard must be paid to all of the possible factors that may influence the ratio.

(c) Ring widths in some Recent and fossil woods

As a preliminary to the work on fossil wood, a few specimens of Recent woods were studied. They were chosen from a number of widely dispersed sites in order to show the differences in ring sequences that arise in different climatic situations. Both continental and oceanic sites are represented. The results obtained are given in Table 2. The mean sensitivity and the average percentage variation of each wood were calculated. The average percentage variation is a statistic which has not hitherto been used in tree-ring studies. It is calculated by taking the difference between a consecutive pair of ring widths and expressing the difference as a percentage of the larger of the pair. Each consecutive pair of ring widths is dealt with in this way all through the sequence. An average is then taken of all of the annual percentage variations. The final statistic is found to have a strong positive correlation with the mean sensitivity. For each wood specimen, a graph of the cumulative sum of the ring widths was plotted in order to see how, in effect, the radius of the tree increased from year to year. This shows whether

Table 2. *Data obtained from some Recent and fossil woods*

Species	Source and locality	Average percentage variability	Mean sensitivity	No. of rings
RECENT	Wood Museum, Royal Botanic Gardens, Kew			
Pinus roxburghii	Punjab	24·90	0·310	66
Larix decidua	Argyll, Scotland	17·65	0·207	109
Pseudotsuga menziesii 95–1907	Missoula, Montana	20·75	0·265	160
Juniperus pachyphloea	Arizona	33·40	0·452	152
Taxus baccata	Author's collection, south-west Scotland	26·18	0·324	56
Pseudotsuga menziesii MV 23	Figured by Douglass (1936, plate 6) Arizona	24·10	0·296	59
Pinus ponderosa, BE 133	Arizona	11·50	0·128	59
FOSSIL	Sedgwick Museum Cambridge			
Cedroxylon sp. K 5322	Upper Jurassic, East Sutherland	26·84	0·339	77
Metacedroxylon scoticum, K 613		29·99	0·393	76
Cedroxylon sp., K 5318		24·03	0·29	18
Cedroxylon sp., K 5317		39·34	0·578	13
Cedroxylon sp., K 5307		15·55	0·176	17
Pityoxylon sp., K 5311		15·39	0·176	15
Cedroxylon sp., G 4	Author's collection Upper Jurassic, East Sutherland	34·26	0·453	18
Cedroxylon sp., V 58746	British Museum (Natural History) Middle Jurassic, Mull	21·59	0·255	64

the tree grew steadily throughout the whole sequence of years or whether there were changes of gradient in the graph due to, say, the effect of shading as nearby trees increased in size. In order to make further use of the initial calculations which are used to find the mean sensitivity, the individual annual sensitivities of some of the specimens have been arranged into histograms (Text-fig. 4). This, again, seems not to have been done hitherto and it serves to show that although two woods may have the same, or nearly the same, mean sensitivity, they may have different patterns of annual sensitivities.

The data from the two Scottish wood specimens show rather contrasting situations. *Larix decidua* Mill. from Argyll has a constant gradient in its cumulative graph of radial growth and its low mean sensitivity of 0·207 indicates that it grew under very equable conditions. Its histogram pattern (Text-fig. 4a), too, shows all of the annual sensitivities grouped in the lower end of the scale. This is clearly a tree that grew with a constant supply of all of the necessary requirements for growth. It might possibly have grown in open parkland such that it was not shaded by any nearby trees. The rather
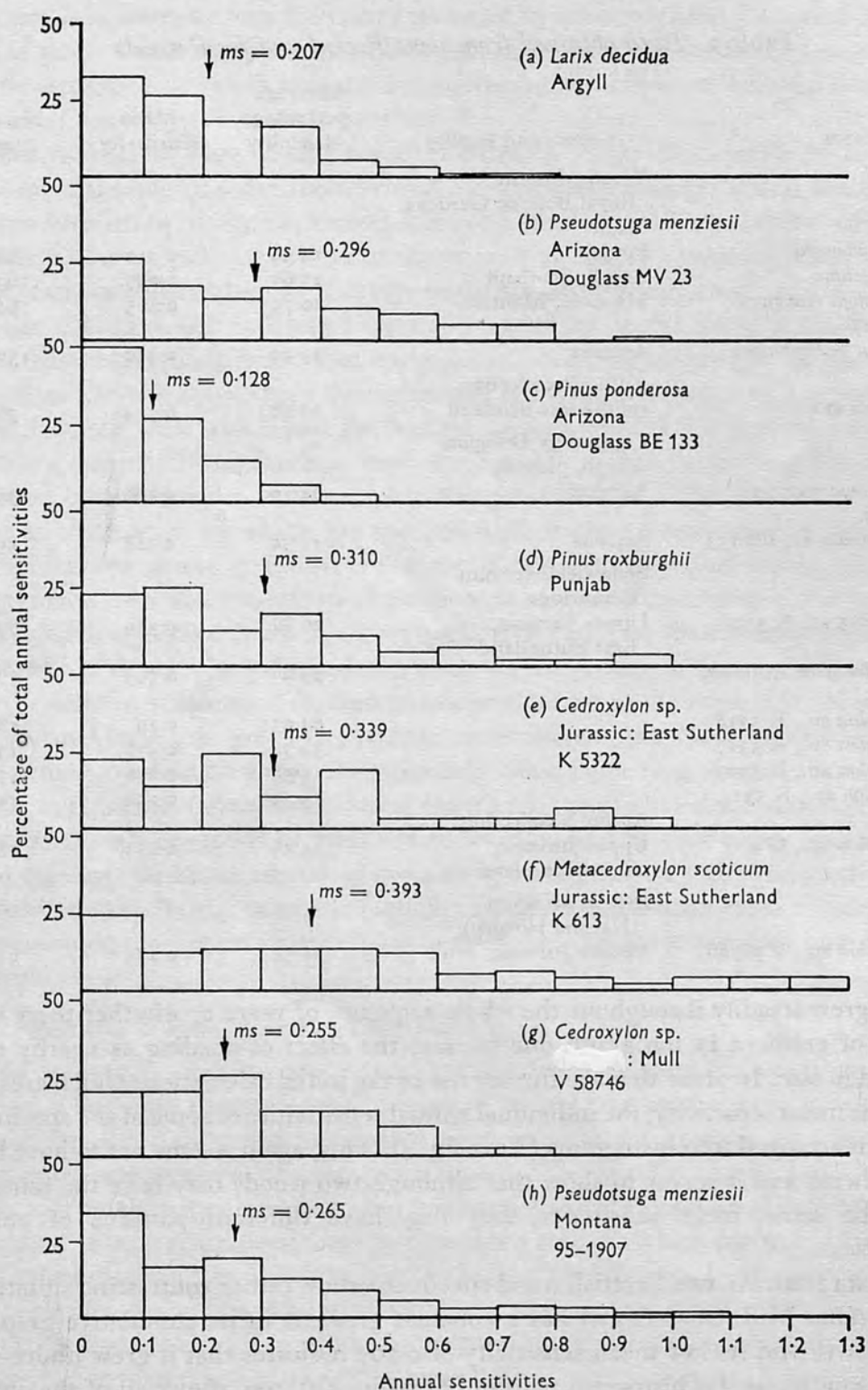
Text-fig. 4. A series of histograms comparing the variability of the ring-width sequences of Recent and fossil woods. The extreme left-hand column (0–0·1) represents all of the consecutive pairs of years in which there was a minimum variation in ring width; the columns to the right of this represent increasing variations in ring widths between consecutive pairs of years up to the maximum recorded. *ms*, mean sensitivity.

ERRATUM
Pp. 368–370

Specimen V58746 from Mull was later shown to be
a homoxylic angiosperm wood with very small vessels.
It is therefore not Jurassic, as stated, but very
likely to be from the Tertiary interbasaltic beds.
Thus its growth ring characteristics, which are
different from the Jurassic specimens, tend to
confirm its geological separation from them.

:r stress on the tree.
geographical region,
ss with a mean sen-
:hanges of gradient;
:r 23 years. As there
:h material and thus
nfluenced the rate of
:h grown in a region
and insufficient for

figured by Douglass
respectively. On the
:xample has a mean
' 0·300 which is the
patterns are vastly
whilst MV 23 shows
yan tree, *Pinus rox-*
a mean sensitivity of
...lar to that of MV 23

and one may infer that this tree may have grown on rather thin soil in a mountainous region with little reserve moisture in years when rainfall was below the optimum for the tree to produce a large ring. Further statistical details regarding this tree are given in the next section. The specimen of *Juniperus pachyphloea* Torr. has a high mean sensitivity; clearly this is a tree that grew under conditions that were highly variable, rainfall being the most likely factor. However, in spite of these variations from year to year the graph of the cumulative sum of its ring widths shows the same gradient throughout the 152 years of growth. Apparently the short-term variations in climate oscillated about a constant mean.

The fossil specimens examined so far are from the Kimmeridgian (Upper Jurassic) collected in the vicinity of Helmsdale, East Sutherland (Holden, 1915; Creber, 1972) There is an additional specimen from the Oxfordian (Middle Jurassic) collected in Ardanalish Bay on the Island of Mull. They are all calcareous petrifactions; the East Sutherland specimens are from a conglomerate that accumulated at the base of a submarine fault-scarp. It would appear that both animal and plant material was swept down from the upthrow side of the fault by tidal waves energized by earthquakes along the fault. Much less is known about the specimen from Mull; it is the first specimen of Jurassic wood to be found at this locality and efforts are being made to collect more, for reasons that will be made clear below. The specimen of *Cedroxylon* sp., K 5322, (Text-fig. 4e) from Helmsdale has a relatively high mean sensitivity of 0·339 and the specimen of *Metacedroxylon scoticum* Holden, K 613 (Text-fig. 4f) has an even higher figure at 0·393. There are five more specimens from the same locality; two of them, K 5317 and G 4, have high mean sensitivities. K 5318 at 0·29 is just below the sensitive threshold whilst K 5307 and K 5311 have fairly low mean sensitivities. It is interesting to see that although the last two specimens are of different

humid climate of Argyll, also, would not have imposed any water stress on the tree. The specimen of *Taxus baccata* L., although grown in the same geographical region, has quite different coefficients. It is definitely in the sensitive class with a mean sensitivity of 0·324. Its cumulative graph of radial growth has two changes of gradient; one, an increase after 12 years and another, a distinct decrease after 23 years. As there is reaction wood (see p. 370) present it seems likely that it is branch material and thus changes in the pattern of shading from other branches might have influenced the rate of growth. The high mean sensitivity would indicate that, although grown in a region of high average annual rainfall, the soil water capacity was low and insufficient for periods of drought.

Specimens MV 23 (Text-fig. 4*b*) and BE 133 (Text-fig. 4*c*) were figured by Douglass (1936, plate 6) as examples of a sensitive and a complacent tree respectively. On the whole this is borne out by the statistics although the sensitive example has a mean sensitivity of 0·296 which is marginally just below the figure of 0·300 which is the accepted minimum figure for a sensitive tree. Their histogram patterns are vastly different. In BE 133, 50% of its annual sensitivities are below 0·1 whilst MV 23 shows a broad range of sensitivities extending up to 1·0. The Himalayan tree, *Pinus roxburghii* Sarg. (chir pine) (Text-fig. 4*d*) is of interest in that it has a mean sensitivity of 0·31 which places it in the sensitive class. Its histogram is very similar to that of MV 23 and one may infer that this tree may have grown on rather thin soil in a mountainous region with little reserve moisture in years when rainfall was below the optimum for the tree to produce a large ring. Further statistical details regarding this tree are given in the next section. The specimen of *Juniperus pachyphloea* Torr. has a high mean sensitivity; clearly this is a tree that grew under conditions that were highly variable, rainfall being the most likely factor. However, in spite of these variations from year to year the graph of the cumulative sum of its ring widths shows the same gradient throughout the 152 years of growth. Apparently the short-term variations in climate oscillated about a constant mean.

The fossil specimens examined so far are from the Kimmeridgian (Upper Jurassic) collected in the vicinity of Helmsdale, East Sutherland (Holden, 1915; Creber, 1972) There is an additional specimen from the Oxfordian (Middle Jurassic) collected in Ardanalish Bay on the Island of Mull. They are all calcareous petrifactions; the East Sutherland specimens are from a conglomerate that accumulated at the base of a submarine fault-scarp. It would appear that both animal and plant material was swept down from the upthrow side of the fault by tidal waves energized by earthquakes along the fault. Much less is known about the specimen from Mull; it is the first specimen of Jurassic wood to be found at this locality and efforts are being made to collect more, for reasons that will be made clear below. The specimen of *Cedroxylon* sp., K 5322, (Text-fig. 4*e*) from Helmsdale has a relatively high mean sensitivity of 0·339 and the specimen of *Metacedroxylon scoticum* Holden, K 613 (Text-fig. 4*f*) has an even higher figure at 0·393. There are five more specimens from the same locality; two of them, K 5317 and G 4, have high mean sensitivities. K 5318 at 0·29 is just below the sensitive threshold whilst K5307 and K5311 have fairly low mean sensitivities. It is interesting to see that although the last two specimens are of different

species, their mean sensitivities are identical. These five specimens are small; the maximum number of years represented in any one specimen is only 18. The data from the large specimens were therefore analysed to see whether on fracture they might yield some smaller fragments with mean sensitivities of the smaller specimens. All of the possible pieces of 15 consecutive years each that could be derived were calculated and found to range from 0·542 to 0·245 for the specimen of *Cedroxylon* sp. K 5322 and from 0·460 to 0·258 for the specimen of *Metacedroxylon scoticum*. The process was repeated for the possible 10-year fragments and these ranged from 0·588 to 0·192 for K 5322 and from 0·656 to 0·204 for *Metacedroxylon scoticum*. It would seem quite reasonable therefore to suppose that the five smaller specimens are compatible with the larger ones. The high mean sensitivities that occur at this site (Helmsdale) and the large spread in the histograms (Text-fig. 4*e, f*) indicate that it was a region where there were marked variations in growing conditions from year to year.

The significance of the histogram technique becomes evident in a comparison of the Middle Jurassic *Cedroxylon* sp., V 58746, from Mull (Text-fig. 4*g*) with the Douglas-fir from Missoula, Montana (Text-fig. 4*h*). Their mean sensitivities are very close, being 0·255 and 0·265 respectively. However, their histogram patterns show marked differences; the wood from Montana has some very high sensitivities (e.g. 0·9, 1·0 and 1·1) whereas in the Jurassic specimen there are none higher than 0·7. This indicates that at the Montana site there were a number of occasions when an extreme climatic event such as a severe summer drought took place. Whilst the Jurassic wood could not be regarded as very complacent with a mean sensitivity of 0·255, the histogram pattern is such that the annual sensitivities are bunched towards the lower end of the scale. It would appear that although the climate was somewhat variable, no really extreme events took place during the 64 years recorded in the rings. Whereas all of the East Sutherland specimens appear as a coherent group, the wood from Mull is of a different character and it would be very desirable to have more specimens from this locality. It must be emphasized that conclusions can only be drawn when sufficient material is available and the data from them becomes significant. It might be pointed out at this stage that an additional benefit may accrue from a climatological study of fossil wood in that the evidence may also be used on a stratigraphical basis. That is to say, two assemblages of fossil wood found in localities quite close together are unlikely to have arisen at the same geological time if it can be shown that their ring data are very different.

(d) Circuit uniformity

A statistical analysis by Chalmers (personal communication, 1975) of the data from the wood specimen of *Pinus roxburghii* (Table 2; Text-fig. 4*d*) showed that it had some anomalous features. The trunk was somewhat eccentric, the pith being offset from the geometrical centre. This effect may result from the growth of a tree upon a slope; asymmetric growth of reaction wood maintains the tree in a vertical position with respect to gravity (Creber, 1975). Indeed, Kennedy & Farrar (1965) used this effect to 'label' growth rings in seedling trees by tilting them for two days and then returning them to the vertical position. When at a later date the wood was examined in trans-

verse section an arc of greatly lignified tracheids (with unusually thick walls) could be seen in the growth ring extending for about half of the stem circumference. Such asymmetric growth produces differences in ring widths when measured along different radii of the trunk. Chalmers found that the correlation, one with another, of eight radial ring-width sequences produced positive coefficients ranging from 0·61 to 0·91. This wide range of coefficients highlights a problem to which dendrochronologists have already devoted some attention.

Glock (1937), under the heading 'Circuit Uniformity', examined the uniform behaviour of a growth ring in its course around a trunk at a given level. He examined two aspects of the problem: (1) The variation in the thickness of a ring around the trunk and (2) the relationship between adjacent rings in a circuit of the trunk. He found that in general almost all rings vary in width around a trunk. However, most importantly, he also found that although there may be variation in thickness around the circuit, each ring at any given point bears the same relationship to its immediate neighbours at that point as it does at any other point. This is borne out by the ring sequences along the 8 radii of the specimen of *Pinus roxburghii* for although they have a wide range of correlation coefficients, their mean sensitivities show much less variation. Further analysis of Glock's data shows positive correlation coefficients ranging from 0·87 to 0·94 between six radial growth-ring sequences. For the dendrochronologist it is clearly very important to establish that there is a high degree of similarity between the variability (i.e. mean sensitivity) of ring sequences measured along different radii. For the palaeoclimatologist it is of even greater importance as fossil wood often occurs in fragments in which the whole circuit is not represented. To overcome a situation illustrated by the somewhat anomalous specimen of *Pinus roxburgii* it is clearly desirable to obtain plenty of material when working on fossil wood.

(e) Woods from equatorial regions

All of the woods discussed above have strongly marked rings. There are, however, many examples of woods, both fossil and Recent, that do not exhibit growth rings when cut in transverse section. This is usually the case with wood of trees grown within the humid part of equatorial regions. However, in detailed studies made of the trees in such regions it is noticeable that some actually produce growth rings. Alvim (1964) cites the following figures:

Amazon rain forest tree species	35% with clear growth rings
	22% with poorly defined rings
	43% with no rings
Indian rain forest	25% with growth rings
	75% without growth rings

In a more recent study, Tomlinson & Craighead (1972) examined the woods of the trees of sub-tropical Florida south of latitude 26° North. Eighty-seven species were observed and although they were growing closely together in the same environment, 51 species produced obvious growth rings whilst 36 were without rings in their wood.

Such was the complexity of the situation that Tomlinson & Craighead could only say: "When one becomes aware of the variety and variability of growth expression of the native trees of South Florida, one despairs of finding simple correlations between extension growth, climate, phenology and the development of growth rings, if the latter are formed. One is forced to the conclusion that the ability to develop growth rings is primarily determined by the genetic make-up of the individual species and only in a limited number of species is there a correlation with climate such that one distinct ring per year is produced." No support could be found for previously discovered correlations such as that of Hallé & Martin (1968) for *Hevea brasiliensis* (Kunth) Müll.-Arg. (the rubber tree) in which the formation of growth rings was shown to be coincidental with periods of extension growth. In fact Tomlinson & Craighead's observations tend to suggest that the radial growth and flushing (bursting of buds) may not be directly related. For example they found that *Swietenia heterophylla* King (a mahogany) underwent several periods of flushing throughout the year with individual trees out of phase with their neighbours and single branches out of phase with others on the same tree. As a complete contrast to this foliar activity the species has a consistent tendency to produce one growth ring per year. Some of their observations are at variance with those of others who have studied equatorial species. For instance, Amobi (1972) showed that in *Monodora tenuifolia* Benth. (African nutmeg) many growth rings were formed in one year in phase with multiple bud flushes.

Amobi (1973, 1974) also described a staining technique which demonstrates periodicity in a wood that appears to be quite homogeneous when unstained sections are examined under the microscope. It would be interesting to know whether some of the woods of tropical regions which appear to be without rings, would be so if Amobi's technique were to be used on them. By experiments and anatomical investigations, Coster (1927–8) showed that in Javanese trees there was a general connexion between bud-flushing and cambial activity. That the stimulus for cambial activity lay in the expanding buds was demonstrated by removing the buds and showing that there was then no cambial activity. Similarly, cambium which was isolated from twigs by ring-barking the stem, remained dormant. As a possible stimulus, photosynthesis was eliminated by showing that cambial activity was stimulated by bud-flushing in plants which were kept in the dark. Coster proposed that a hormone might be responsible for stimulating the cambium when such substances had only recently been discovered. In fact his work in this field, carried out 50 years ago, remains a landmark to this day. He also showed that the ring boundaries in the woods of tropical trees are not always typical bands of latewood but may consist of parenchyma or fibres. At the present day the hormonal explanation is the most widely accepted hypothesis for the mechanism of cambial stimulation (Wareing, Hanney & Digby, 1964; Larson, 1964).

Thus in equatorial trees one may envisage a whole spectrum of wood types ranging from those that appear to have completely homogeneous wood, passing through those that have some kind of periodicity effects and terminating with those that have as sharply defined rings as any temperate tree. Part of the explanation for this situation probably lies in the fact that there is also a spectrum of foliar behaviour among equatorial trees. Longman & Jeník (1974) divide such trees into four types: A,

Deciduous type with periodic growth. In this type leaf-fall occurs well before bud-flushing and thus the whole tree is leafless for a distinct period of the year. Leaf-fall and bud-flushing appear not to be linked together. B, Leaf-exchanging type with periodic growth. Here bud-flushing takes place whilst the old leaves are still falling. C, Evergreen-type with periodic growth. In this case the tree is truly evergreen with the old leaves falling for a distinct period after bud-flushing. As in Type A there seems little connexion between leaf-fall and bud-flushing. D, Evergreen type with continuous growth. In these trees there is continual production and loss of leaves. There is no bud-flushing as such but the rates of leaf production and abscission (leaf-fall) may each vary considerably according to changes in the environment or to competitive effects. Thus the number of leaves present on the tree may fluctuate between wide limits. It is not surprising, therefore, that with this range of types of foliar behaviour there is also a wide range of wood types with, in each case, the cambium receiving a different pattern of stimulation during each year.

Apart from the foliar behaviour of tropical trees there is also a periodicity exhibited in the production of flowers and fruit. There is as much diversity in the timing of flowering as there is in bud-flushing. Richards (1952, 1973), Alvim (1964) and Longman & Jeník (1974) give accounts of the flowering regimes of tropical trees. Although there has long existed an undercurrent of thought that the flowering process is subject to an endogenous rhythm, the modern view, e.g. that of Richards (1973), is that it is determined by a subtle interplay of climatic factors. The latter require very careful measurement to show the variations that occur in the apparently unchanging tropical climate. Njoku (1963, 1964) showed that in Nigeria a number of tropical tree species may show a photoperiodic response even though the annual variation in daylight may only be between $11\frac{1}{2}$ h and $12\frac{1}{2}$ h per day. If such small environmental variations as these can be perceived by trees then there is a distinct possibility that others may be as well. As Longman & Jeník say in the conclusion to their book, there is clearly a need for much more research on tropical trees.

IV. ENDOGENOUS RHYTHMS

Whilst most rhythms in growth-ring formation are determined by external influences, it is widely accepted that some are internally determined or endogenous. Before the great proliferation of studies on plant hormones took place, Priestley & Scott (1936) noted that earlywood and latewood might form at different times in widely separated places in the wood of the same tree; they came to the conclusion that the type of wood that was formed at a given place and time depended on "the internal conditions of the tree". Today the phenomenon that they recorded would be given an hormonal explanation. There is now considerable evidence (Zimmermann & Brown, 1971) that cambial activity is stimulated by endogenous auxin (IAA, indoleacetic acid) arising in the apical regions of growing shoots. Cambial division begins beneath the expanding buds and a wave of division spreads down the trunk (Priestley, Scott & Malins, 1933). Hejnowicz & Tomaszewski (1969) showed that in decapitated *Pinus sylvestris* shoots the formation of xylem is arrested until

bud-flushing takes place. They found that there was no shortage of stored food which might limit xylem formation but a deficiency of IAA was clearly indicated. This was established in further experiments in which they applied IAA to decapitated shoots and found that some new xylem was formed for a short distance below the point of application. The fact that the amount of cambial division thus stimulated did not approach that occurring in normal intact shoots suggested that some other factor, in addition to IAA, was involved.

Wareing, Hanney & Digby (1964) described experiments in which both IAA and gibberellic acid (GA) were applied to disbudded twigs. On later examination it was found that a wide zone of new xylem had formed in them. It was established that these two substances (IAA and GA) operated synergically; GA applied on its own stimulated cambial division but the resulting cells did not differentiate into xylem tissue. Conversely, the application of IAA caused only a small stimulation of cambial division but the cells so produced differentiated fully into xylem. Such endogenous hormones are apparently also involved in the earlywood–latewood ratio. Balatinecz & Kennedy (1967) established this by applying IAA to young *Larix decidua* trees that were producing latewood; after the application the trees reverted to the formation of earlywood. In later work (1968) they found, as with cambial stimulation, that more than one endogenous growth regulator seems to be involved. Besides IAA they also isolated 5-hydroxy-IAA together with a phenolic growth inhibitor. During earlywood formation there were higher concentrations of the indolic substances in the phloem and cambial zones whereas their concentrations fell and the amount of phenolic substance increased during latewood formation. These studies indicate that cambial activity is regulated by the relative concentrations of different growth regulators rather than by IAA alone. This concept of the function of IAA is supported by Kefford & Goldacre (1961) who considered it as a predisposing agent rather than a determining one in plant growth. Recent work by Denne (1976) also strongly supports the hormone theory; she showed that substrate availability had little or no effect on wood growth in *Picea sitchensis* seedlings. Thus the small size of latewood cells is not due to lack of photosynthate but is contolled by growth regulators.

The existence of an endogenous rhythm is also suggested by the behaviour of a specimen of *Pinus radiata* described by Mirov (1967) and cited by Chaloner & Creber (1973). Grown in Hawaii (ca. 20° North) it did not produce the obvious growth rings that are seen when in its normal environment. Instead, there were indistinct fluctuations in tracheid diameter which might well have reflected a residual rhythm of the type known to operate in many organisms. What seems to occur in the normal environment is that the endogenous rhythm becomes 'locked' on to the seasonal periodicity so that the effects of the latter become impressed as it were, on the wood in the form of growth rings. In the tropical environment a very complex situation arises in which there is interplay between endogenous rhythms and small variations in climate.

A rather different form of periodicity was discovered by analysis of a series of measurements made along radial files of cells in completed growth rings in gymnosperm wood (Creber, 1975). Although there is, in general, a decline in the radial diameters of the cells from the earlywood to the latewood, there is not a continuous

diminution in cell size. Instead there is a distinct periodicity imposed upon the slope That the periodicity is purely internal, can be shown by superimposing the measurements of one row of tracheids upon those of its neighbours. Each row of tracheids behaves independently of the rows nearby; Fourier analysis of the periodicity has shown that there is no similarity of periodicities between the adjacent files of cells. The differences between the files of cells are such that those in one file may be passing through a phase of increasing cell size whilst those of an adjacent file may be decreasing. Thus although all cells at the same distance from the cambium may be receiving the same hormonal stimulus, other forces are coming into play which are modifying the hormonal effect. There is as yet no satisfactory explanation for this phenomenon which has been observed in a wide range of gymnosperm genera, both fossil and Recent. M. W. Bannan (personal communication, 1975) has suggested that it may be related to the behaviour of a number of the xylem mother cells which are formed by the cambium. These may themselves undergo further division to form small groups of cells; expansion of a few of these at the expense of others might then give rise to the observed cycles of cell size. Bannan (1964) showed that the number of these dividing mother cells was related to the width of the growth ring. In the work completed so far it does appear that the number of cycles across a given ring approaches Bannan's figure for the expected number of xylem mother cells. Further material is currently under examination in order to check these preliminary findings.

Ford & Robards (1976) described short-term variations in tracheid development in the earlywood of *Picea sitchensis*. They found positive correlations between the rhythms of parallel files of cells. These are at variance with my findings and an explanation is sought. Their observations are of cells in the post wall-thickening stage in the earlywood of a currently forming ring whilst mine are based on mature cells; the process of maturation may cause changes in cell sizes that mask the original similarities between the files.

V. SUMMARY

1. The wood of trees grown in temperate regions shows a periodicity in the form of rings which, with certain known exceptions, accurately reflects the annual cycle of the seasons. The wood thus has a built-in dating system.

2. Tree rings are not always the same width in successive years; the widths show a positive correlation with variations in environmental factors.

3. Trees in a given geographical area influenced by the same environmental conditions show similar patterns in their ring sequences and may thus be cross-dated.

4. Ring sequences from cross-dated trees may be used to construct long, accurate chronologies. This practice, the science of dendrochronology, is now so reliable that it is widely used in archaeology and has also served to calibrate the ^{14}C dating method.

5. The extent of the variation in a ring sequence may be expressed in the form of a coefficient known as the mean sensitivity.

6. The climatic effects recorded in the growth rings are those which operate at certain crucial periods, such as the growing season. The effects are primarily those of rainfall and temperature; humidity is usually only secondary.

7. Damage by insects or fire may be dated by examination of ring sequences.

8. As tree-ring sequences correlate positively with contemporaneous meteorological data, they may be used in the reconstruction of past climates. This is the basis of extrapolatory dendroclimatology.

9. New isotope techniques have been developed which indicate the possibility of deducing the ambient temperature of the tree's environment whilst its wood was being formed.

10. Interpretative dendroclimatology aims to deduce from the features of a sample, or preferably from a number of samples of wood, the nature of the climate which influenced their development.

11. The wood of most growth rings is divisible into two zones, earlywood and latewood. The former consists of larger, thin-walled cells while in the latter the cells are smaller and thick-walled.

12. Beams of light, X-rays and β-rays have been used in various instruments to determine the earlywood–latewood ratio.

13. The earlywood–latewood ratio is dependent upon genetic as well as climatic factors. Of the latter, summer rainfall is the most potent in producing latewood.

14. The ring-width data from a number of Recent and fossil wood specimens have been analysed to show that certain deductions may be made about the climate in which they were formed.

15. A histogram technique has been devised to show differences between wood specimens with otherwise similar coefficients.

16. Evidence has been produced in support of earlier work to the effect that ring-width sequences from different radii of a tree trunk have fundamentally similar features, thus demonstrating 'circuit uniformity'.

17. The interpretation of the features of tropical woods is more complex. The mode of development of such a wood is the resultant of the interplay of genetical factors, endogenous rhythms and slight variations in environmental conditions.

18. There is evidence that endogenous rhythms are also involved in the development of woods in temperate as well as tropical regions.

VII. REFERENCES

AGERTER, S. R. & GLOCK, W. S. (1965). *An annotated bibliography of tree growth and growth rings 1950–1962*. University of Arizona Press, Tucson, Arizona.

ALVIM, P. DE T. (1964). Tree growth periodicity in tropical climates. In *The Formation of Wood in Forest Trees* (ed. M. H. Zimmermann), pp. 479–95. Academic Press, New York and London.

AMOBI, C. C. (1972). Multiple bud growth and multiple wood formation in the seedlings of *Monodora tenuifolia* Benth. *Annals of Botany* **36**, 199–205.

AMOBI, C. C. (1973). Periodicity of wood formation in some trees of lowland rainforest in Nigeria. *Annals of Botany* **37**, 211–18.

AMOBI, C. C. (1974). Periodicity of wood formation in twigs of some tropical trees in Nigeria. *Annals of Botany* **38**, 931–6.

BALATINECZ, J. J. & KENNEDY, R. W. (1967). Mechanism of earlywood–latewood differentiation. *Technical Association of the Pulp and Paper Industry* (TAPPI), 4th Biology Conference Report, 36–55.

BALATINECZ, J. J. & KENNEDY, R. W. (1968). Mechanism of earlywood–latewood differentiation in *Larix decidua*. *Technical Association of the Pulp and Paper Industry* (TAPPI) **51**, 414–22.

BANNAN, M. W. (1964). Tracheid size and anticlinal divisions in the cambium of *Pseudotsuga*. *Canadian Journal of Botany* **42**, 603–31.

BAREFOOT, A. C. (1975). A Winchester dendrochronology for 1635–1972 A.D. Its validity and possible extension. *Journal of the Institute of Wood Science* **7**, 25–32.

BARROW, G. P. (1951). Loss of weight of three Douglas-fir poles. *Quarterly Journal of Forestry* **45**, 235–6.

BAUCH, J. (1969). Die Bauzeit der Bremer Kogge. *Bremer Hanse-Kogge Monograph* No. 8, 123–6.

BAUER, F. (1954). Wertholzanteil und Furnierfähigkeit der Roteiche. *Holz-Zentralblatt* **80**, 23–5.

BIELCZYK, S. (1956). Investigations of the physical and mechanical properties of the wood of *Abies alba* and *Pinus sylvestris* originating from a forest community resembling a natural community. *Prace Instytutu Drewna* **3**, 86–106.

BRYAN, J. & PEARSON, F. G. O. (1955). The quality of Sitka spruce grown in Great Britain. *Empire Forestry Review* **34**, 144–59.

BURGER, H. (1940). Holz, Blattmenge und Zuwachs, IV. Ein 80-jahriger Buchenbestand. *Mittel Schweizerische Centralanstalt Forstlich Versuchsweise* **21**, 307–84.

BURGER, H. (1941). Holz, Blattmenge und Zuwachs. V. Fichten und Föhren verschiedener Herkunft auf verschiedenen Kulturorten. *Mittel Schweizerische Centralanstalt Forstlich Versuchsweise* **22**, 10–62.

BURGSDORF, F. A. L. VON (1783). *Versuch einer vollständigen Geschichte vorzüglicher Holzarten in systematischen Abhandlungen zur Erweiterung der Naturkunde und Forsthaushaltungs-Wissenschaft*, vol. 1. Joachim Pauli, Berlin.

CAMERON, J. F., BERRY, P. F. & PHILLIPS, E. W. J. (1959). The determination of wood density using beta rays. *Holzforschung* **13**, 78–84.

CHALMERS, C. P. (1975). Personal communication. Statistics Department, Birkbeck College, London WC1E 7HX.

CHALONER, W. G. & CREBER, G. T. (1973). Growth rings in fossil woods as evidence of past climates. In *Implications of Continental Drift to the Earth Sciences* (ed. D. H. Tarling and S. K. Runcorn), pp. 425–37. Academic Press, New York and London.

CLEAVELAND, M. K. (1975). *Relationships of shortleaf pine (Pinus echinata Mill.) in the South Carolina Piedmont*. M.S. thesis, Clemson University. Clemson, South Carolina.

COOPER, G. A. (1960). Specific gravity of red pine as related to stem and crown-formed wood. *Iowa State College Journal of Science* **34**, 693–707.

COOPERRIDER, C. K. & SYKES, G. G. (1938). The relationship of streamflow to precipitation on the Salt River Watershed above Roosevelt Dam. *University of Arizona College of Agriculture and Agricultural Experimental Station Technical Bulletin* No. **76**, 1–69.

COSTER, C. (1927–8). Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. *Annales du Jardin Botanique de Buitenzorg* **37**, 49–160; **38**, 1–114.

CREBER, G. T. (1972). Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham Sands of Norfolk. *Palaeontology* **15**, 655–61.

CREBER, G. T. (1975). The effects of gravity and the earth's rotation on the growth of wood. In *Growth Rhythms and History of the Earth's Rotation* (ed. G. D. Rosenberg and S. K. Runcorn), pp. 75–87. John Wiley, New York and London.

DENNE, M. P. (1976). Effects of environmental change on wood production and wood structure in *Picea sitchensis* seedlings. *Annals of Botany* **40**, 1017–28.

DIMBLEBY, G. (1967). *Plants and Archaeology*. John Baker, London and New York.

DOLEY, D. (1974). Alternatives to the assessment of earlywood and latewood in dicotyledonous trees: a study of structural variation in growth rings of apple (*Malus pumila* Mill.). *New Phytologist* **73**, 157–71.

DOUGLASS, A. E. (1919). *Climatic cycles and tree growth*. Carnegie Institution of Washington Publication No. 289, vol. I. Carnegie Institution, Washington.

DOUGLASS, A. E. (1928). *Climatic cycles and tree growth*. Carnegie Institution of Washington Publication No. 289, vol. II. Carnegie Institution, Washington.

DOUGLASS, A. E. (1936). *Climatic cycles and tree growth*. Carnegie Institution of Washington Publication No. 289, vol. III. Carnegie Institution, Washington.

DOUGLASS, A. E. (1941). Age of Forestdale Ruin. *Tree-ring Bulletin* **8**, 7–8.

DU HAMEL & DE BUFFON (1737). Observations des différents effets que produisent sur les végétaux, les grandes gelées d'hiver et les petites gelées du printemps. *Mémoires de l'Académie Royale de la Science* **1737**, 273–98.

ECKSTEIN, D. (1972). Tree-ring research in Europe. *Tree-Ring Bulletin* **32**, 1–18.

ELLIOTT, G. K. & BROOK, S. E. G. (1967). Microphotometric technique for growth-ring analysis. *Journal of the Institute of Wood Science* **3**, 24–43.

FERGUSON, C. W. (1968). Bristlecone pine: science and esthetics. *Science* **159**, 839–46.

FERGUSON, C. W. (1970). Dendrochronology of bristlecone pine, *Pinus aristata*. Establishment of a 7484-year chronology in the White Mountains of east-central California, U.S.A. In *Radiocarbon Variations and Absolute Chronology* (ed. I. U. Olsson), pp. 237–59. John Wiley, New York and London.

FERGUSON, C. W., HUBER, B. & SUESS, H. E. (1966). Determination of the age of Swiss lake dwellings as an example of dendrochronologically-calibrated radiocarbon dating. *Zeitschrift für Naturforschung* **21a**, 1173–7.

FLETCHER, J. M. (1974). Annual rings in modern and medieval times. In *The British Oak* (ed. M. G. Morris and F. H. Perring), pp. 80–97. Classey, Faringdon, Berkshire.

FLETCHER, J. M. & HUGHES, J. F. (1970). Uses of X-rays for density determinations and dendrochronology. *Bulletin of the Faculty of Forestry of the University of British Columbia* **7**, 41–54.

FLETCHER, J. M., TAPPER, M. C. & WALKER, F. S. (1974). Dendrochronology – a reference curve for slow grown oaks A.D. 1230–1546. *Archaeometry* **16**, 31–40.

FLIEDNER, S. & POHL-WEBER, R. (1964). *Der Bremer Kogge*. Focke-Museum Broschüre 35. Bremen, Focke-Museum.

FORD, E. D. & ROBARDS, A. W. (1976). Short term variation in tracheid development in the early wood of *Picea sitchensis*. In *Wood Structure in Biological and Technical Research* (ed. A. J. Bolton, D. M. Catlin and P. Baas), University Press, Leiden (in the press).

FRITTS, H. C. (1956). Radial growth of beech and soil moisture in a central Ohio forest during the growing season of 1952. *Ohio Journal of Science* **56**, 17–28.

FRITTS, H. C. (1959a). The relation of radial growth to maximum and minimum temperatures in three tree species. *Ecology* **40**, 261–5.

FRITTS, H. C. (1959b). The growth-environmental relationships of mature forest trees. *Yearbook of the American Philosophical Society* 1959, 269–70.

FRITTS, H. C. (1962a). The relation of growth-ring widths in American beech and white oak to variations in climate. *Tree-Ring Bulletin* **25**, 2–10.

FRITTS, H. C. (1962b). An approach to dendroclimatology: screening by multiple regression techniques. *Journal of Geophysical Research* **67**, 1413–20.

FRITTS, H. C. (1965). Tree-ring evidence for climatic changes in western North America. *Monthly Weather Review* **93**, 421–43.

FRITTS, H. C. (1966). Growth rings of trees: their correlation with climate. *Science* **154**, 973–9.

FRITTS, H. C. (1969). Tree-ring analysis: a tool for water resources research. *Transactions of the American Geophysical Union* **50**, 22–9.

FRITTS H. C. (1971). Dendroclimatology and dendroecology. *Quaternary Research* **1**, 419–49.

FRITTS, H. C. (1972). Tree rings and climate. *Scientific American* **226**, 92–100.

FRITTS, H. C. (1976). *Tree Rings and Climate*. Academic Press, New York and London.

FRITTS, H. C., BLASING, T. J., HAYDEN, B. P. & KUTZBACH, J. E. (1971). Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. *Journal of Applied Meteorology* **10**, 845–64.

FÜRST, O. (1963). Vergleichende Untersuchungen über räumliche und zeitliche Unterscheide interannueller Jahrringbreitenschwankungen und ihre klimatologische Auswertung. *Flora* **153**, 469–508.

GLOCK, W. S. (1937). *Principles and Methods of Tree-ring Analysis*. Carnegie Institution of Washington Publication No. 486. Carnegie Institution, Washington.

GLOCK, W. S. (1938). In A. E. Douglass' annual report on Historical Climatology for 1937/38. p. 235. *Carnegie Institution of Washington Yearbook* No. 37. Carnegie Institution, Washington.

GLOCK, W. S. (1941). Growth rings and climate. *Botanical Review* **7**, 649–713.

GLOCK, W. S. (1955). Tree Growth II. Growth rings and climate. *Botanical Review* **21**, 73–188.

GLOCK, W. S. & AGERTER, S. R. (1962). Rainfall and tree growth. In *Tree Growth* (ed. T. T. Kozlowski). pp. 23–56. Ronald Press, New York.

GLOCK, W. S., STUDHALTER, R. A. & AGERTER, S. R. (1960). *Classification and multiplicity of growth layers in the branches of trees at the extreme lower forest border*. Smithsonian Miscellaneous Collection No. 140, Publication No. 4421. Smithsonian Institution, Washington.

GÖHRE, K. (1955). Die Rohwichte des Douglasienholzes, ihre Verteilung in Stamm und Abhangigheit vom Abstand vom Mark, Jahrringbreite und Spätholzanteil. *Archiv für Forstwesen* **4**, 639–61.

GÖHRE, K. (1958). Über die Verteilung der Rohweite in Stamm und ihre Beeinflussung durch Wuchs-gebiet und Standort. *Holz als Roh- und Werkstoff* **16**, 77–90.

GRAY, B. M. & KELLY, P. M. (1976). Personal communication. Climatic Research Unit, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ.

GREEN, H. V. (1965). *Wood characteristics IV: The study of wood characteristics by means of a photometric technique.* Pulp and Paper Research Institute of Canada Technical Report No. 419, 1–17.

GREEN, H. V. & WORRALL, J. (1963). *Wood quality studies Part 1. Scanning microphotometer for auto-matically measuring and recording certain wood characteristics.* Pulp and Paper Research Institute of Canada Technical Report No. 331, 1–37.

HALE, J. D. (1924). Effect of rate of growth on density and fibre characteristics of pulpwood. *Pulp and Paper Magazine of Canada* **22**, 273–4.

HALLÉ, F. & MARTIN, R. (1968). Étude de la croissance rhythmique chez l'Hévéa. (*Hevea brasiliensis* (Kunth) Müll.-Arg. Euphorbiaceés-Crotonoideés). *Adansonia* **8**, 470–503.

HARRIS, J. M. (1958). *The physical and mechanical properties of New Zealand grown Douglas-fir. Part 1. The physical properties of New Zealand grown Douglas-fir.* New Zealand Forest Service, Forest Research Institute, Technical Paper No. 24, 7–39.

HARRIS, J. M. & POLGE, H. (1967). A comparison of X-ray and beta ray techniques for measuring wood density. *Journal of the Institute of Wood Science* **4**, 34–42.

HEJNOWICZ, A. & TOMASZEWSKI, M. (1969). Growth regulators and wood formation in *Pinus sylvestris*. *Physiologia Plantarum* **22**, 984–92.

HENRY, A. J. (1931). The calendar year as a time unit in drought statistics. *Monthly Weather Review* **59**, 150–4.

HOLDEN, R. (1915). A Jurassic wood from Scotland. *New Phytologist* **14**, 205–9.

HUSTICH, I. (1941). Något om periodec och växlingar i Lapplands växtoch djurväld senaste årtionden. *Memoranda Sällskap pro Fauna et Flora Fennica* **17**, 200–9.

HUSTICH, I. (1948). The Scotch pine and its dependence on climate in the last decades. *Acta Botanica Fennica* **42**, 1–75.

INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS (1933). The terms earlywood and latewood. *Tropical Woods* **36**, 3.

JONES, E. D., CAMPBELL, R. T. & NELSON, G. G. (1966). Springwood–summerwood separation of southern pine pulp to improve paper qualities. *Technical Association of the Pulp and Paper Industry* (TAPPI) **49**, 410–4.

JULIAN, P. R. & FRITTS, H. C. (1968). *On the possibility of quantitatively extending climatic records by means of dendroclimatological analysis.* Proceedings of the First Statistical Meteorological Conference, pp. 76–82. American Meteorological Society, Hartford, Connecticut.

KEFFORD, N. P. & GOLDACRE, P. L. (1961). The changing concept of auxin. *American Journal of Botany* **48**, 643–50.

KENNEDY, R. W. (1961). Variation and periodicity of summerwood in some secondary growth Douglas-fir. *Technical Association of the Pulp and Paper Industry* (TAPPI) **44**, 161–6.

KENNEDY, R. W. & FARRAR, J. L. (1965). Tracheid development in tilted seedlings. In *Cellular Ultra-structure of Woody Plants* (ed. W. A. Coté Jr.), pp. 419–53. Syracuse University Press, Syracuse, New York.

KOERBER, T. W. & WICKMAN, B. E. (1970). Use of tree-ring measurements to evaluate impact of insect defoliation. In *Tree-Ring Analysis with Special Reference to Northwest America* (ed. J. H. G. Smith and J. Worrall), pp. 101–6. University of British Columbia Faculty of Forestry Bulletin No. 7.

КОЛЧИН. Б. А. (KOLCHIN, B. A.) (1962). Дендрохронология Новгорода (Novgorod dendrochro-nology). *Советская археология* (*Soviet Archaeology*) (1962), 113–39.

KOZLOWSKI, T. T. (1971). *Growth and Development of Trees*, vol. II. Academic Press, New York and London.

KOZLOWSKI, T. T., WINGET, C. H. & TORRIE, J. H. (1962). Daily radial growth of oak in relation to maximum temperature. *Botanical Gazette* (University of Chicago) **124**, 9–17.

KRAUS, J. F. & SPURR, S. H. (1961). Relationship of soil moisture to the springwood–summerwood transition in southern Michigan red pine. *Journal of Forestry* **59**, 510–11.

LaMARCHE, V. C. JR. (1974). Paleoclimatic inferences from long tree-ring records. *Science* **183**, 1043–8.

LaMARCHE, V. C. JR. (1975). Climatic clues from tree rings *New Scientist* **66** (943), 8–11.

LaMARCHE, V. C. JR. & FRITTS, H. C. (1971). Tree rings, glacial advance and climate in the Alps. *Zeitschrift für Gletscherkunde und Glazialgeologie* **7**, 125–31.

LaMARCHE, V. C. JR. & FRITTS, H. C. (1972). Tree rings and sunspot numbers. *Tree-Ring Bulletin* **32**, 19–33.

LaMARCHE, V. C. JR. & HARLAN, T. P. (1973). Accuracy of tree-ring dating of bristlecone pine for calibration of the radiocarbon time scale. *Journal of Geophysical Research* **78**, 8849–58.

LARSON, P. R. (1962). *The Influence of Environment and Genetics on Pulpwood Quality*, An Annotated Bibliography (ed. P. R. Larson). Technical Association of the Pulp and Paper Industry (TAPPI), Monograph No. 24.

LARSON, P. R. (1964). Some indirect effects of environment on wood formation. In *The Formation of Wood in Forest Trees* (ed. M. H. Zimmermann), pp. 345–65. Academic Press, New York and London.

LIBBY, L. M. & PANDOLFI, L. T. (1974). Calibration of two isotope thermometers $^{13}C/^{12}C$ and $^{18}O/^{16}O$, in a European oak using official weather records. In *Proceedings of the International Conference on Mapping the Atmospheric and Oceanic Circulations and other Climatic Parameters at the time of the Last Glacial Maximum about 17000 years ago*. (ed. H. H. Lamb), pp. 21–6. University of East Anglia, Norwich.

LINNAEUS, C. (1745). *Öländska och Gothländska Resa*. Gottfried Kieswetter, Stockholm, Uppsala.

LINNAEUS, C. (1751). *Skanska Resa*. Lars Salvii, Stockholm.

LODEWICK, J. E. (1933). Some summerwood percentage relationships in the southern pines. *Journal of Agricultural Research* **46**, 543–56.

LONGMAN, K. A. & JENÍK, J. (1974). *Tropical Forest and its Environment*. Longman Group, London.

LYON, C. J. (1943). Water supply and the growth rates of conifers around Boston. *Ecology* **24**, 329–44.

MacDOUGAL, D. T. (1918). The dendrograph; a new instrument for recording growth and other variations in the dimensions of trees, pp. 59–60. *Carnegie Institution of Washington Yearbook* No. 17. Carnegie Institution of Washington, Washington.

MacDOUGAL, D. T. (1936). *Studies in tree growth by the dendrographic method*. Carnegie Institution of Washington Publication No. 462. Carnegie Institution, Washington.

McGREGOR, J. C. (1942). Dates from Wupatki Pueblo. *Tree-Ring Bulletin* **8**, 18–21.

MIKOLA, P. (1962). Temperature and tree growth near the northern timber line. In *Tree Growth* (ed. T. T. KOZLOWSKI), pp. 265–87. Ronald Press, New York.

MIROV, N. T. (1967). *The Genus Pinus*. Ronald Press, New York.

MOREY, P. R. (1973). *How Trees Grow*. Edward Arnold, London.

MORK, E. (1928). Der Qualität des Fichtenholzes unter besonderer Rucksichtnahme auf Schief- und Papierholz. *Papierfabrikant* **26**, 741–7.

NEISS, W. (1968). Dendrochronology for the building history of the castle and church at Büdingen. *Kunstchronik* **21**, 183–7.

NJOKU, E. (1963). Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. *Journal of Ecology* **51**, 617–24.

NJOKU, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. *Journal of Ecology* **52**, 19–26.

ORDING, A. (1941). Årringanalyser på gran og furu. *Meddelelser fra det Norske Skogsforsøksvesen* **7**, 105–354.

PETERSON, A. (1935). Specimens from the Pueblo area collected by the First Beam Expedition 1923. *Tree-Ring Bulletin* **3**, 23–4.

PHILLIPS, E. W. J. (1960). The beta ray method of determining the density of wood and the proportion of summer wood. *Journal of the Institute of Wood Science*, No. 5, 16–28.

PHILLIPS, E. W. J., ADAMS, E. H. & HEARMON, R. F. S. (1962). The measurements of density variation within the growth rings in thin sections of wood using beta particles. *Journal of the Institute of Wood Science* No. 10, 11–28.

POLGE, H. (1966). Établissement des courbes de variation de la densité du bois par exploration de radiographies d'échantillons prélevés à la tarière sur des arbres vivants. *Annales des Sciences Forestières* **23**, 1–206.

POLGE, H. (1969). Further considerations about the X-ray and beta ray methods for determining wood density. *Journal of the Institute of Wood Science* **4**, 39–44.

PRIESTLEY, J. H. & SCOTT, L. I. (1936). A note upon summer wood production in the tree. *Proceedings of the Leeds Philosophical and Literary Society*, Science Section **3**, 235–48.

PRIESTLEY, J. H., SCOTT, L. I. & MALINS, M. E. (1933). A new method of studying cambial activity. *Proceedings of the Leeds Philosophical and Literary Society*, Science Section, **2**, 365–75.

RALPH, E. K., MICHAEL, H. N. & HAN, M. C. (1973). Radiocarbon dates and reality. *Museum Applied Science Centre for Archaeology* (MASCA) *Newsletter* **9**, 1–20. Philadelphia, University Museum.

RENFREW, C. (1971). Carbon 14 and the prehistory of Europe. *Scientific American* **225** (4), 63–72.

RICHARDS, P. W. (1952). *The Tropical Rain Forest*. University Press, Cambridge.

RICHARDS, P. W. (1973). The tropical rain forest. *Scientific American* **229**(6), 58–67.

RUDMAN, P., McKINNELL, F. & HIGGS, M. (1969). Quantitative determination of wood density by X-ray densitometry. *Journal of the Institute of Wood Science* **4**, 37–43.

SALISBURY, E. J. & JANE, F. W. (1940). Charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times. *Journal of Ecology* **28**, 310–25.

SCHANDERL, H. (1939). Versuchs- und Forschungsanstalt für Wein, Obst- und Gartenbau Geisenheim am Rhein Wissenschaftlicher Jahresbericht für 1937. *Landwirtschaftlicher Jahrbucher* 87, 356–63.

SCHOVE, C. J. (1950). Tree rings and summer temperature. *Scottish Geographical Magazine* 66, 37–42.

SCHULMAN, E. (1946). Dendrochronology at Mesa Verde National Park. *Tree-Ring Bulletin* 12, 18–24.

SCHULMAN, E. (1947). An 800-year Douglas-fir at Mesa Verde. *Tree-Ring Bulletin* 14, 1–8.

SCHULMAN, E. (1951–1952). Definitive dendrochronologies: a progress report. *Tree-Ring Bulletin* 18, 10–18.

SCHULMAN, E. (1956). *Dendroclimatic Changes in Semi-arid America*. University of Arizona Press, Tucson, Arizona.

SCHULMAN, M. D. & BRYSON, R. A. (1965). A statistical study of dendroclimatic relationships in south central Wisconsin. *Journal of Applied Meteorology* 4, 107–11.

SCHWAPPACH, A. (1892). Beitrage zur Kenntniss der Qualität des Kiefernholzes. *Zeitschrift für Forst- und Jagdwesen* 24, 71–88.

SERRE, F., LÜCK, H. P. & PONS, A. (1964). Premières recherches sur les relations entre les variations des anneaux ligneux chez *Pinus halepensis* Mill. et les variations annuelles du climat. *Oecologia Plantarum* 1, 117–35.

SMITH, A. G., BAILLIE, M. G. L., HILLAM, J., PILCHER, J. R. & PEARSON, G. W. (1972). Dendrochronological work in progress in Belfast: the prospects for an Irish post-glacial tree-ring sequence. In *Proceedings of the 8th International Conference on Radiocarbon Dating* (ed. T. A. Rafter and T. Grant-Taylor), 1, pp. A92–6. Wellington, New Zealand.

SMITH, D. M. & WILSIE, M. C. (1961). Some anatomical responses of loblolly pine to soil-water deficiencies. *Technical Association of the Pulp and Paper Industry* (TAPPI) 44, 179–85.

SPENCER, D. A. (1964). Porcupine population fluctuations in past centuries revealed by dendrochronology. *Journal of Applied Ecology* 1, 127–49.

STARK, R. W. & COOK, J. A. (1957). The effects of defoliation by the lodgepole needle miner. *Forest Science* 3, 376–95.

STOCKTON, C. W. (1971). *The feasibility of augmenting hydrologic records using tree-ring data*. Ph.D. dissertation. University of Arizona, Tucson, Arizona.

STOCKTON, C. W. & FRITTS, H. C. (1971). *An empirical reconstruction of water levels for Lake Athabasca (1810–1867) by analysis of tree rings*. Report, Laboratory of Tree-ring Research, University of Arizona, Tucson, Arizona.

STUDHALTER, R. A. (1955). Tree Growth I. Some historical chapters. *Botanical Review* 21, 1–72.

STUDHALTER, R. A., GLOCK, W. S. & AGERTER, S. R. (1963). Tree growth – some historical chapters in the study of diameter growth. *Botanical Review* 29, 245–365.

TOMLINSON, P. B. & CRAIGHEAD, F. C. Sr. (1972). Growth-ring studies on the native trees of sub-tropical Florida. In *Research Trends in Plant Anatomy – K. A.* Chowdhury commemoration volume (ed. A. K. M. Ghouse & M. Yunus), pp. 39–51. Tata McGraw Hill, New Delhi.

WAREING, P. F., HANNEY, C. E. A. & DIGBY, J. (1964). The role of endogenous hormones in cambial activity and xylem differentiation. In *The Formation of Wood in Forest Trees* (ed. M. H. Zimmermann), pp. 323–44. Academic Press, New York and London.

WATKINS, T. (1975). Introduction. In *Radiocarbon: Calibration and Prehistory* (ed. T. Watkins), pp. 1–4. University Press, Edinburgh.

WILLIAMS, C. B. JR. (1967). Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir and Engelmann spruce. *Forest Science* 13, 274–85.

WILSON, A. T. & GRINSTED, M. J. (1975). Palaeotemperatures from tree rings and the D/H ratio of cellulose as a biochemical thermometer. *Nature, London* 257, 387–8.

WILSON, A. T. & GRINSTED, M. J. (1977a). $^{12}C/^{13}C$ in cellulose and lignin as palaeothermometers. *Nature, London* 265, 133–5.

WILSON, A. T. & GRINSTED, M. J. (1977b). The possibilities of deriving past climate information from stable isotope studies on tree rings. In *Proceedings of the International Conference on Stable Isotopes 1976* (in the press). Institute of Nuclear Sciences. Lower Hutt, New Zealand.

WILSON, J. W. (1965). *Organisation within the coniferous growth ring*. Pulp and Paper Research Institute of Canada, Woodlands Paper No. 7.

ZAHNER, R. & STAGE, A. R. (1966). A procedure for calculating daily moisture stress and its utility in regressions of tree growth on weather. *Ecology* 47, 64–74.

ZEUNER, F. E. (1958). *Dating the Past*. Methuen, London.

ZIMMERMANN, M. H. & BROWN, C. L. (1971). *Trees: Structure and Function*. Springer-Verlag, Berlin.

VIII. ADDENDUM

In a recent paper, Libby & Pandolfi (1977) analyse further the $^{18}O/^{16}O$ and D/H ratios that they measured in an 1800 year tree-ring sequence in a specimen of Japanese cedar (*Cryptomeria japonica* D. Don) grown in southern Japan. Fourier analysis of the data, originally published in 1976 by Libby *et al.*, has revealed 10 climatic cycles with a range of periods from 50 to 280 years. It is of considerable interest that these periods match very closely those found in the $^{18}O/^{16}O$ ratio in Greenland ice by Johnsen, Dansgaard, Clausen & Langway (1971) in an 800 year span. Johnsen *et al.* found that the periodicity of the $^{18}O/^{16}O$ ratio in the ice was in opposite phase to the $^{14}C/^{12}C$ ratio in the bristlecone pines of southern California (Suess, 1970). Similarly Libby & Pandolfi (1977) also found that there was an opposite phase relationship between the $^{18}O/^{16}O$ periodicity in the Japanese cedar and the $^{14}C/^{12}C$ periodicity in the bristlecone pines. With these observations, involving as they do, Greenland, southern Japan and southern California, climatic variation is seen as a global phenomenon. This is further emphasized by the fact that three of the climatic periodicities, 78, 179 and 285 years, are in agreement with those in tidal stresses calculated for the sun–earth–moon system by Roosen, Harrington, Giles & Browning (1976).

In a new book, Fleming (1976) gives a comprehensive account of the tree-ring dating of archaeological objects. Further details are given of oak chronologies for different parts of Europe and their use in dating buildings and paintings. Students of Rembrandt and Rubens in particular have received much assistance from such work; a ring sequence established for the oak panels used by Rembrandt has enabled the authentication of works previously not assignable to this artist with confidence. Fleming also examines critically the correlation of the tree-ring and ^{14}C dating systems.

Tree rings have been used in a rather wider range of studies than is indicated above. They have been used by various workers in reconstructing the history of events such as floods, landslides, fault movements (earthquakes) and avalanches. Heath (1960) has studied the succession of landslides in Lassen Volcanic National Park (California) caused by eruptions of steam. Each successive zone of virgin soil exposed became colonized by conifers which were dated by their ring sequences. Sigafoos & Hendricks (1961) reconstructed the advances and recessions of the Nisqually Glacier in Washington State. They, and Heath, faced the dating problem caused by the interval between the exposure of new soil and the establishment of the first trees. In a later study (1969) they described a variety of sites at which they followed the process of colonization. They concluded that 10 years should be allowed at high altitudes (above 2000 m) and 5 years at lower. Potter (1969) dated avalanches in Wyoming by observing three effects: (1) scars on trunks and branches; (2) production of reaction wood resulting from the tilting of trees; (3) increases in ring widths due to the removal of overshadowing trees. Similar methods were used by Sigafoos (1964) to date floods on the Potomac River near Washington D.C., by Helley & LaMarche (1973) on northern Californian streams and by Page (1970)

in studying earth movements along the Fairweather Fault zone in S.E. Alaska. Here he was able to show that trees which had benefited from the removal of neighbours actually returned to earlywood formation in the latter part of the 1958 growing season. The earthquake, which took place on 10 July in that year, also resulted in changes in the water table and produced effects which were detectable in the ring sequences formed after the event. LaMarche & Wallace (1972) have studied in a similar way earth movements along the San Andreas fault, south of San Francisco in California. Work of this type has been carried out largely in the U.S.A.; an example from elsewhere is that of Druce (1966) who dated volcanic eruptions on Mount Egmont in New Zealand.

REFERENCES

DRUCE, A. P. (1966). Tree-ring dating of recent volcanic ash and lapilli, Mt. Egmont. *New Zealand Journal of Botany* 4, 1–41.

FLEMING, S. (1976). *Dating in Archaeology*. Dent: London.

HEATH, J. P. (1960). Repeated avalanches at Chaos Jumbles, Lassen Volcanic National Park. *American Journal of Science* 258, 744–51.

HELLEY, E. J. & LaMARCHE, V. C. JR. (1973). Historic flood information for Northern California streams from geological and botanical evidence. *United States Geological Survey Professional Paper* No. 485E, 1–16.

JOHNSEN, S. J., DANSGAARD, W., CLAUSEN, H. B. & LANGWAY, H. J. (1971). Climatic oscillations 1200–2000 A.D. *Nature, London* 227, 482–3.

LaMARCHE, V. C. JR. & WALLACE, R. E. (1972). Evaluation of effects on trees of past movements on the San Andreas fault, northern California. *Bulletin of the Geological Society of America* 83, 2665–76.

LIBBY, L. M. & PANDOLFI, L. J. (1977). Climate periods in tree, ice and tides. *Nature, London* 266, 415–17.

LIBBY, L. M., PANDOLFI, L. J., PAYTON, P. H., MARSHALL, J. III, BECKER, B. & GIERTZ-SIENBIENLIST, V. (1976). Isotopic tree thermometers. *Nature, London* 261, 284–8.

PAGE, R. (1970). Dating effects of faulting from tree rings: effects of the 1958 rupture of the Fairweather fault on tree growth. *Bulletin of the Geological Society of America* 81, 3085–94.

POTTER, N. JR. (1969). Tree-ring dating of snow avalanche tracks and the geomorphic activity of avalanches, Northern Absaroka Mountains, Wyoming. United States Contributions to Quaternary Research. *Geological Society of America Special Paper* No. 123, 141–65.

ROOSEN, R. G., HARRINGTON, R. S., GILES, J. & BROWNING, I. (1976). Earth tides, volcanos and climatic change. *Nature, London* 261, 680–2.

SIGAFOOS, R. S. (1964). Botanical evidence of floods and flood-plain deposition. *United States Geological Survey Professional Paper* No. 485A, 1–35.

SIGAFOOS, R. S. & HENDRICKS, E. L. (1961). Botanical evidence of the modern history of the Nisqually glacier, Washington. *United States Geological Survey Professional Paper* No. 387A, 1–20.

SIGAFOOS, R. S. & HENDRICKS, E. L. (1969). The time interval between stabilization of alpine glacial deposits and establishment of tree seedlings. *United States Geological Survey Professional Paper* No. 650B, 89–93.

SUESS, H. E. (1970). Bristlecone pine calibration of the radiocarbon timescale 5200 B.C. to the present. In *Radiocarbon Variations and Absolute Chronology* (ed. I. U. Olsson), pp. 303–12. John Wiley: New York and London.

EXPLANATION OF PLATE 1

Fig. 1. *Pseudotsuga menziesii*. (Specimen No. 95–1907, Wood Museum, Royal Botanic Gardens, Kew). A portion of a transverse section of the trunk close to the centre. The data obtained from the ring widths of this specimen, from Missoula, Montana, appear in Table 2 and Text-fig. 4h. In each ring there is a light zone (earlywood) and a dark zone (latewood) (Text-fig. 1); ×2.

Fig. 2. *Cedroxylon hornei* Seward and Bancroft. (Specimen No. K 571, Sedgwick Museum, Cambridge). A ring boundary (Text-fig. 1) in a piece of fossil wood from the Kimmeridgian of East Sutherland. The small thick-walled cells to the right are latewood whilst those to the left are earlywood. The orientation is as in Fig. 1 above and in Text-fig. 1; ×200 approx.

Plate 1
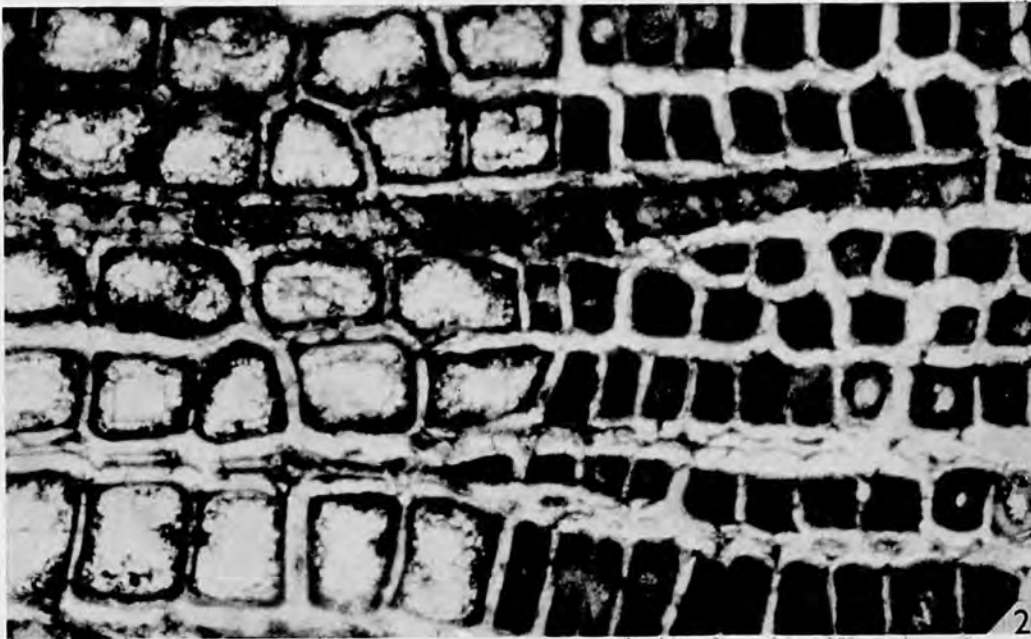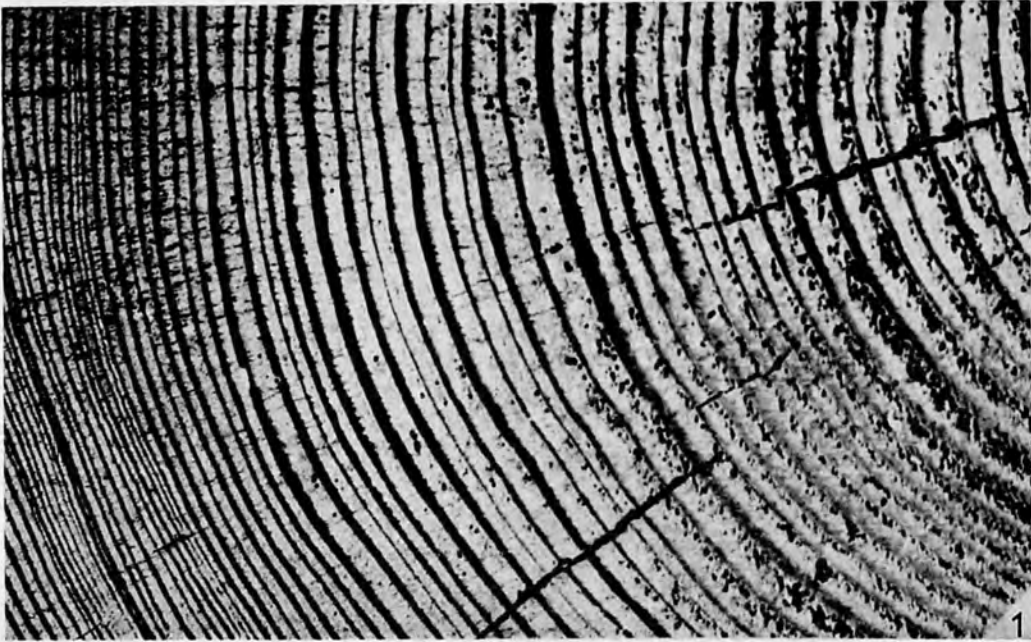
G. T. CREBER

Growth Rhythms
and
The History
of
The Earth's Rotation

Edited by

G. D. Rosenberg
and
S. K. Runcorn

Department of Geophysics, School of Physics,
University of Newcastle upon Tyne

A Wiley–Interscience Publication

JOHN WILEY & SONS
London · New York · Sydney · Toronto
1975

THE EFFECTS OF GRAVITY AND THE EARTH'S ROTATION ON THE GROWTH OF WOOD

G. T. CREBER

Department of Botany, Birkbeck College, London, UK

Abstract

The trunk and branches of a tree consist largely of wood; this is secondary xylem tissue formed by the activity of a single layer of cells called the vascular cambium. Active cell division of this layer produces cells which expand and displace the cambium outwards. The extent to which the newly formed cells expand is influenced by a number of factors both internal and external, e.g. seasonal changes in temperate latitudes cause the well-known phenomenon of growth rings. In the humid tropics the absence of such rings results from the constancy of the environment.

Wood is abundant in the fossil record, the earliest being found in the Devonian (ca. 360×10^6 years). Its characteristics are a reflection of the environment in which it grew; many specimens from the Carboniferous are devoid of growth rings but are found in rocks now in temperate latitudes, providing evidence of continental movement or changes in the Earth's axis of rotation.

Wood that is formed under the effects of a transverse or oblique gravitational stimulus is known as *reaction wood*. This is of normal occurrence in lateral branches which grow more or less at right-angles to the line of action of the force of gravity; it occurs also in trunks which have become displaced from the vertical. The *reaction wood* of angiosperm (flowering plant) trees, known as *tension wood*, forms along the upper sides of trunks and branches while in gymnosperms (e.g. conifers) it is called *compression wood* and forms on the lower sides of trunks and branches. The formation of *reaction wood* results from changes in the distribution of hormone (auxin) in the affected parts.

Wood is the secondary xylem tissue formed by the activity of a layer of cells known as the vascular cambium. Division of these cells in a tangential plane leads to the production internally of xylem initials. Some or all of these may divide again before finally differentiating into mature xylem cells.

In gymnosperms (e.g. conifers such as *Pinus*) the xylem is a homogeneous tissue composed largely of tracheids (Figure 1). These are elongate cells which may attain 2–3 mm in length and are very regularly arranged in rows which follow closely the cambial cell from which they were originally derived (Figure 2). The extent to which the xylem initials enlarge depends, in temperate latitudes, upon the time of year. In early summer the tracheids achieve a greater radial diameter and have thinner cell walls than those differentiated later in the growing season. A marked boundary is seen (Figure 2) between the last-formed cells of one season and the first of the next. The growth increment between two such boundaries is known as a growth ring.

These basic features which are exhibited by wood result from the effects of a
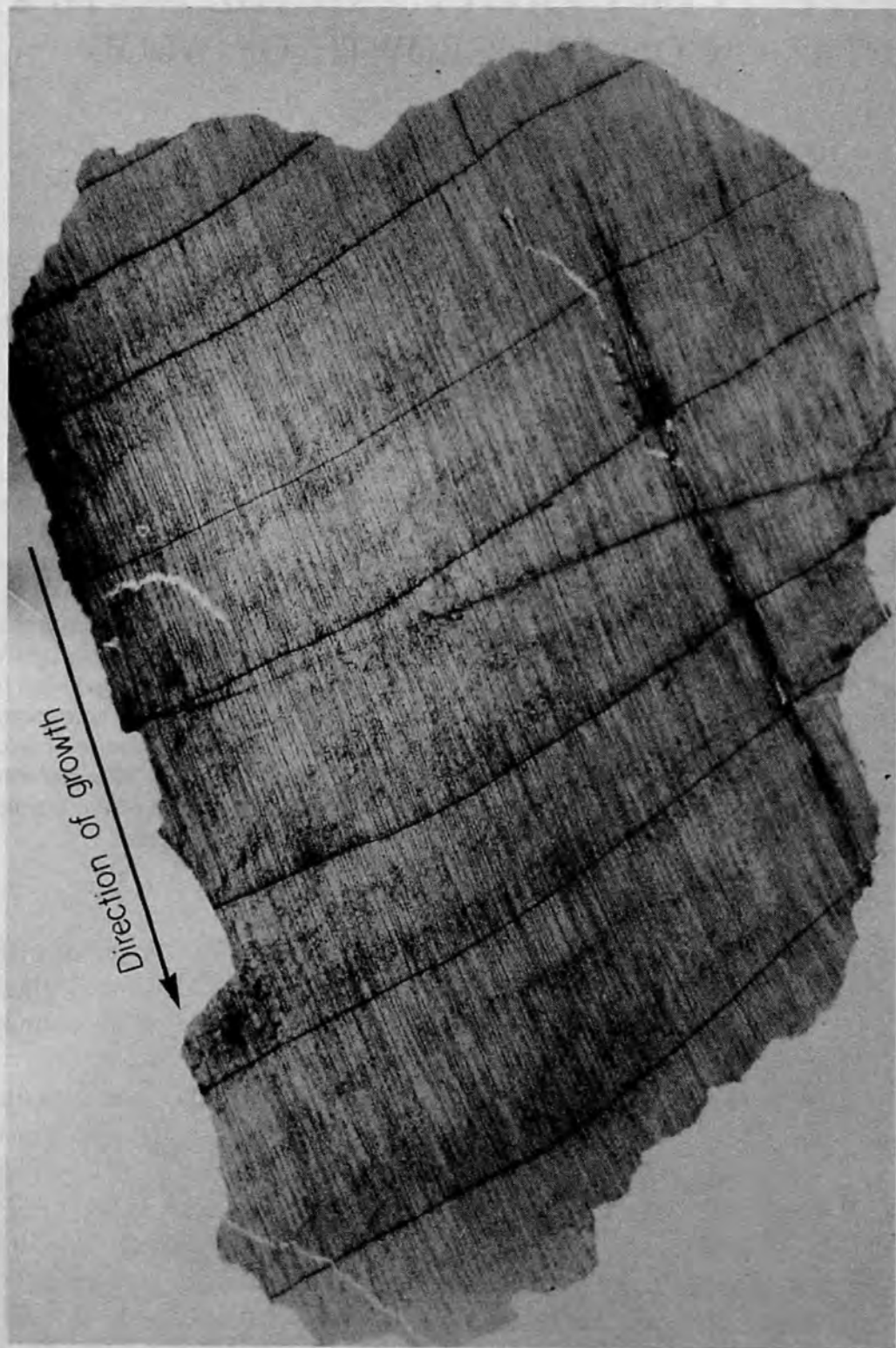
FIGURE 1. A transverse section of *Xenoxylon latiporosum*, fossil gymnosperm wood from the Upper Jurassic of Franz Joseph Land, showing the homogeneity of this type of wood. (×4·9)
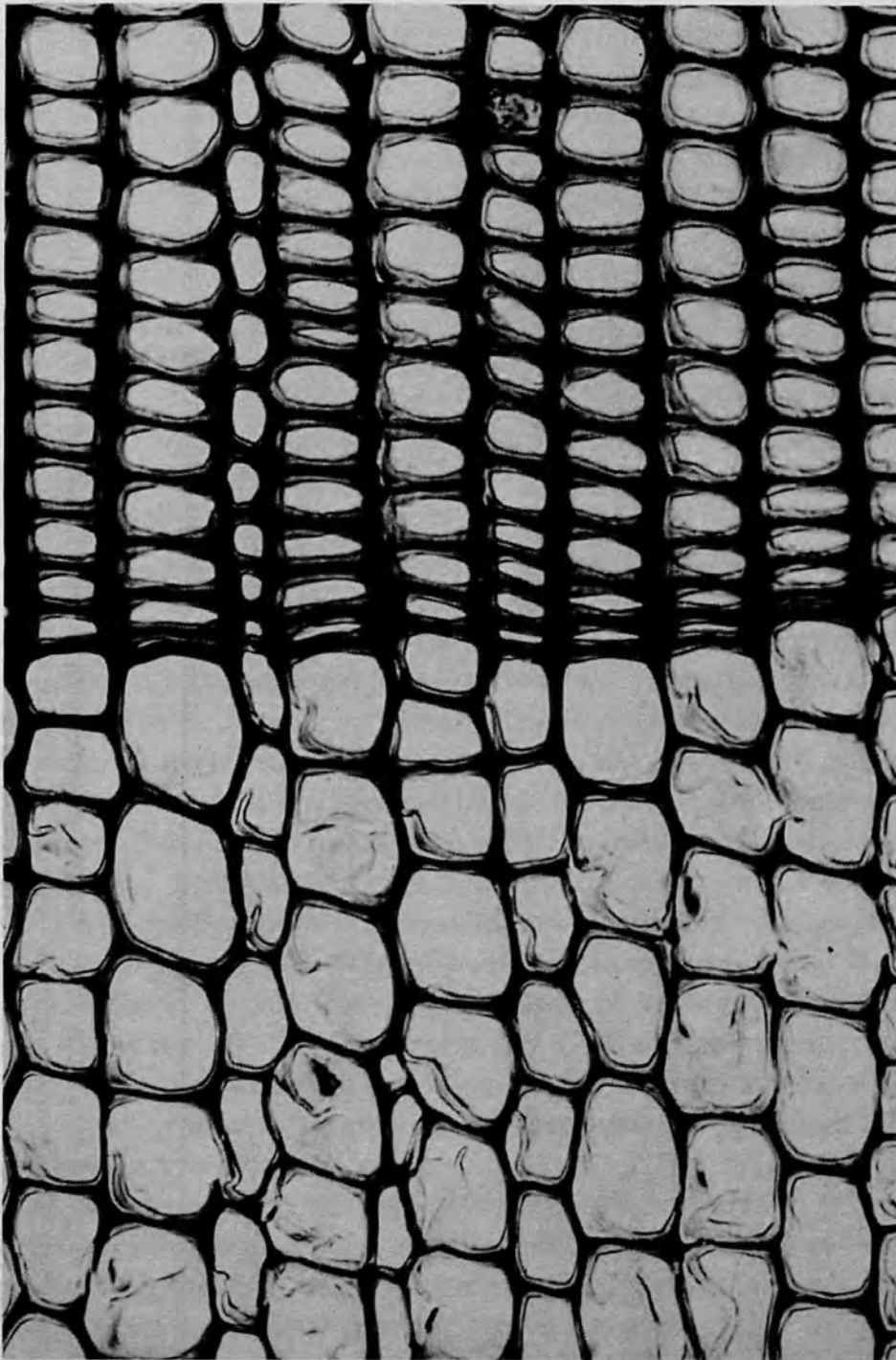
FIGURE 2. A transverse section of the wood of *Pinus strobus* showing the regular arrangement of the tracheids. The point at which cell development stopped during the winter is marked by the zone of small thick-walled cells. (× 200)
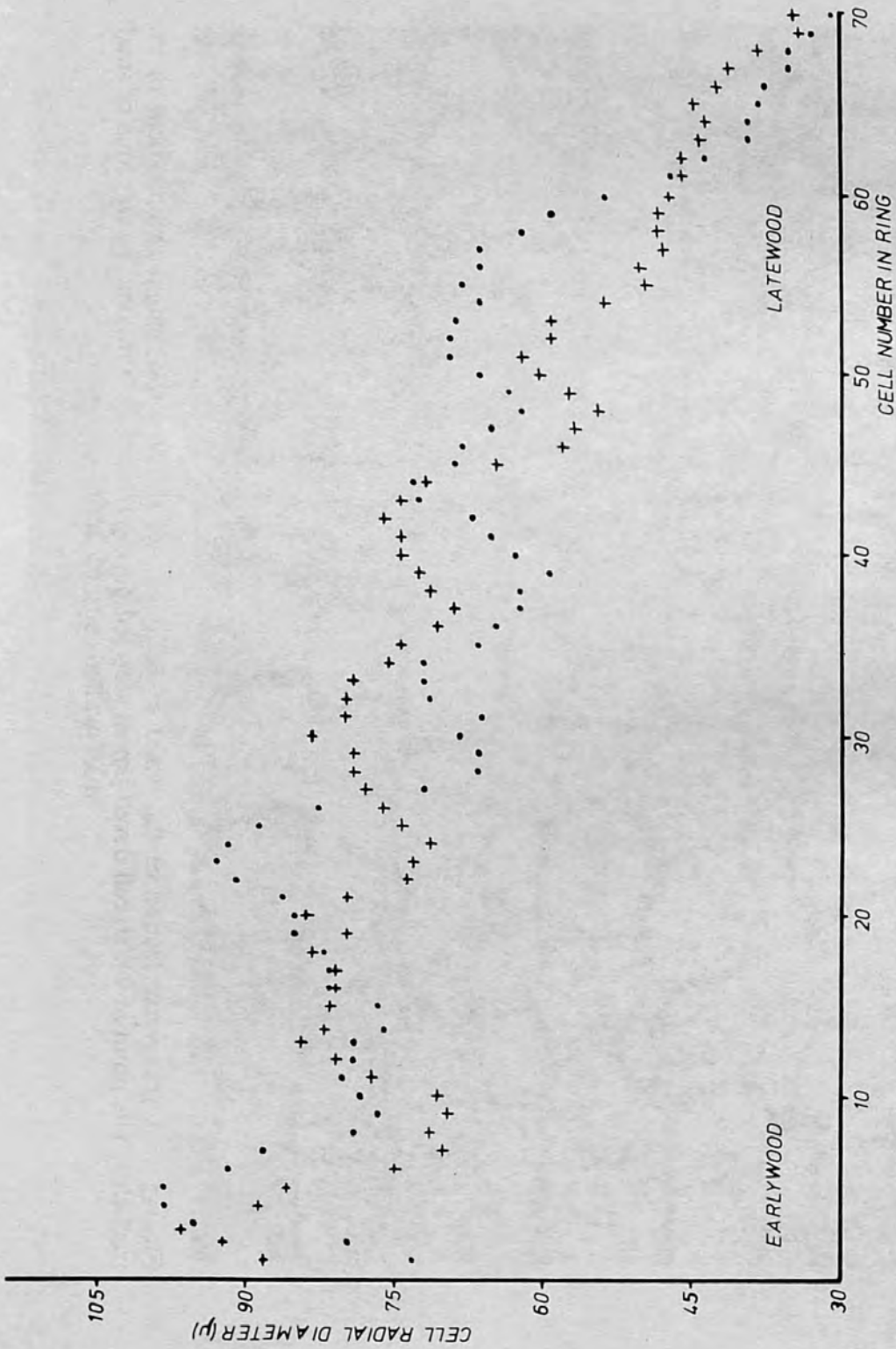
FIGURE 3. A graph of data from a late Jurassic gymnosperm to show the diminution in cell radial diameter through one growth ring. The measurements of one row of cells are shown (dots) superimposed upon the readings from the next row but one (crosses). Out-of-phase relationships can be seen at various points along the curves. The data have been smoothed with a five-point moving average

number of environmental factors. The growth rings owe their existence, through seasonality, to the inclination of the Earth's axis of rotation. The intensity of the growth rings will be influenced by the latitude of the place of growth. The force of gravity will cause asymmetries in the growth rings. Comparison of successive growth rings reflects some aspects of the totality of each growing season, as far as that particular tree is concerned; whereas the pattern of cell size within each ring is to some extent a function of environmental conditions through the duration of that particular growing season. In temperate latitudes, an exceptionally cold or exceptionally dry summer will generally produce a smaller growth increment than a milder one with adequate rainfall. Fossil wood obviously offers the potential of yielding information bearing on past climate and climatic change (Chaloner and Creber, 1973). In order to attempt an interpretation of the environmental significance of growth ring structure, the present author started a study of cell size within individual growth rings. It soon became evident that within the simple seasonal periodicity referred to, there exists a more complicated 'internal' rhythm of cell size increase.

Although there is, in general, a decline in radial diameter from the first cells to the last in a growth ring, there is not by any means a continuous diminution in size. Plotting a graph of the cell radial diameters reveals a cyclic pattern superimposed upon the slope (Figure 3). The cause of the cyclicity is difficult to determine; for the moment it is assumed that it results from the interaction of the xylem initials, each competing with its neighbours for space as expansion proceeds. That the cyclicity is a purely internal matter, and not one determined externally, can be shown by superimposing the measurements of one row upon another (Figure 3). It is evident that while the cells of one row are passing through an ascending phase, in the other row they are descending. Fourier analysis, too, has shown that there is little or no similarity in the periodicities of adjacent rows. Both the cyclicity and the out-of-phase relationships have so far been observed in gymnosperm woods from a wide range of geological time from the Upper Jurassic (Creber, 1972) to the present day. Furthermore, the effects are observable in genera that are not closely related. In the absence, as yet, of observations to the contrary it is assumed that these phenomena are fundamental to the growth of gymnosperm secondary xylem.

The wood structure of angiosperms (flowering plants) is generally not as homogeneous as that of the gymnosperms. The presence of vessels (Figure 4) distorts the pattern of cells but, nevertheless, wood that has developed in temperate latitudes will show growth rings in just as marked a fashion as in gymnosperms (Figure 4).

Hormonal control of xylem development

The growth in diameter of developing xylem cells is controlled by hormones diffusing down from the foliar crown of the tree. This hormone flow in the early
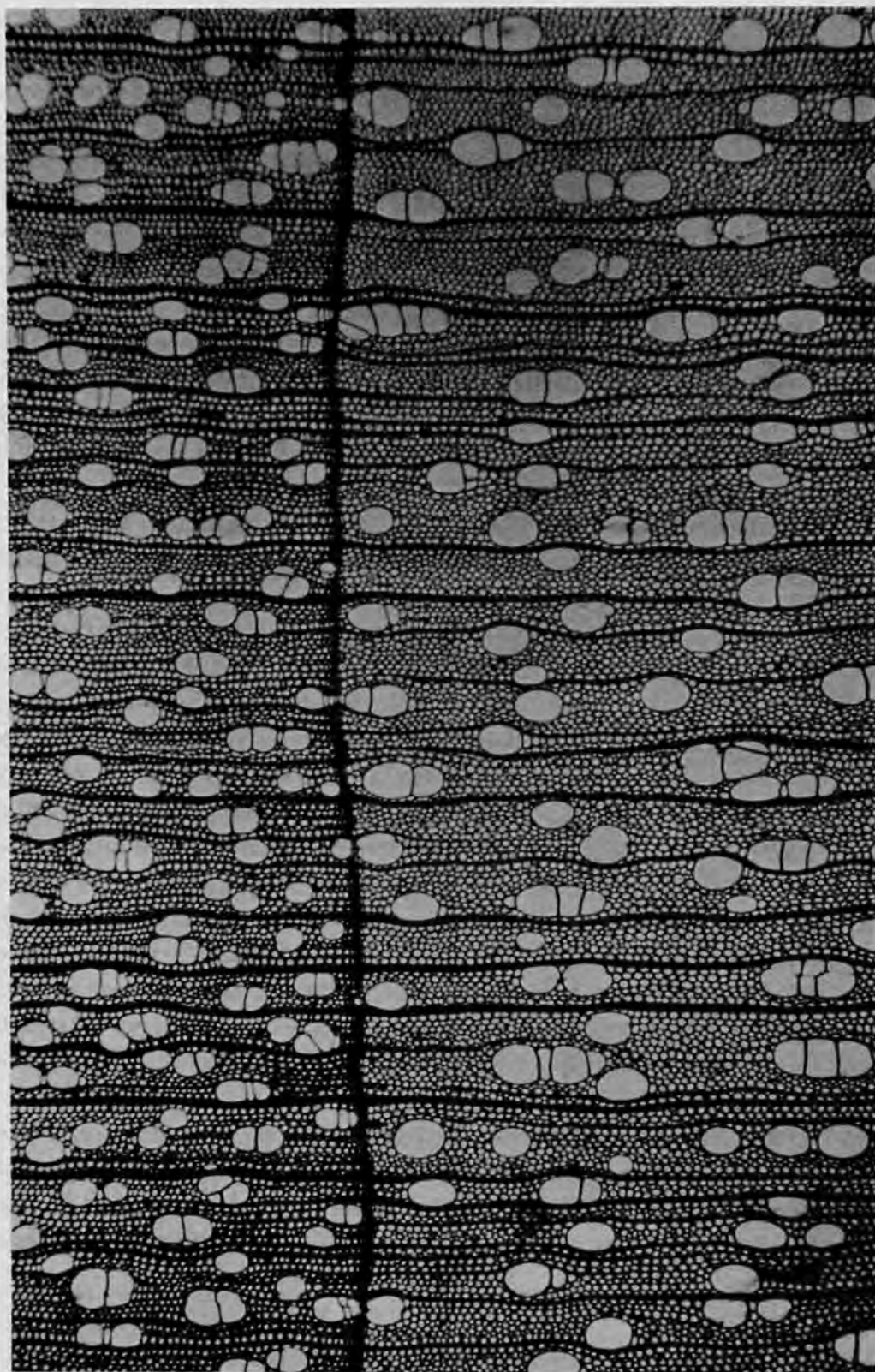
FIGURE 4. A transverse section of the wood of *Populus alba* showing the disturbance of the other elements of the wood caused by the expansion of the large vessels. The narrow zone of small cells across the photograph marks a growth ring boundary where the development of cells ceased during the winter. (× 42)

summer (in temperate latitudes) results in the formation of large cells in the early part of the growth ring. Although it has been shown (Wareing *et al.*, 1964) that indolyl acetic acid and gibberellic acid are the principal growth substances that control xylem formation, it has also been pointed out that not too much emphasis should be placed on these two substances (Robards *et al.*, 1969). They have shown that an array of substances is probably involved.

Although controlled by hormones, the actual onset of new wood formation in temperate latitudes is, however, determined by a phenomenon known as photoperiodism. This involves the perception by the plant of changes in the length of the daylight hours (day-length). As this increases during spring, the buds burst and leaves develop; the latter activity then releases the hormones which stimulate the cambium. It would seem that the evolution of photoperiodic control reflects the biological success of this method rather than one based on the seasonal rise in temperature which is often rather haphazard. Much work has been done on this control mechanism; for instance Larson (1964) has shown that a sequence of artificial growth rings may be induced by subjecting trees to a succession of varied photoperiods. Although most of the work on photoperiodic control has been carried out on temperate species some interesting work by Njoku (1963, 1964) in Nigeria has established that it may also operate in tropical conditions where the day-length variation may be only between $11\frac{1}{2}$–$12\frac{1}{2}$ hr.

It is exceedingly doubtful whether there is any evidence to show exactly when photoperiodic control of wood growth evolved in geological time. However, the existence of growth rings in wood since the Upper Devonian and the evolution of a photoperiodic mechanism involved in their formation both provide supporting evidence for the inclination of the Earth's axis of rotation for a considerable period of time.

The occurrence of considerable growth rings in the wood of trees which grew apparently very close to the contemporaneous pole raises some major problems. In particular, Schopf (1961) described growth rings of substantial proportions in some Permian woods which at the time of growth must have been within a few degrees of the Permian pole. This represents a biological paradox which is not overcome by invoking drift or polar movement.

Gravitational effects

Much of the trunk wood of trees develops with the line of action of the force of gravity passing vertically through the axis of the trunk cylinder. Provided that the trunk does not lean, the axis of symmetry is vertical and the force of gravity does not have any asymmetric effect on it. However, in the case of leaning trunks, and also, of course, of branches, gravity has a marked asymmetric effect and leads to the production of what is known as *reaction wood*. Angiosperms and gymnosperms differ as to the position of the reaction wood in the affected parts. In angiosperms it is known as *tension wood* and it develops on the upper sides of

branches and leaning trunks. Conversely, the *compression wood* of gymnosperms forms on the lower sides of branches and leaning trunks. It must be recorded, however, that there are exceptions to these general rules (White, 1962; Robards, 1965).

Reaction wood differs both macroscopically and microscopically from normal wood. To the unaided eye it is obvious that the pith is not central and the growth rings are elliptical (Figure 5). With the microscope it can be seen that the cells of reaction wood are atypical. In tension wood in angiosperms the vessels are smaller and there are fewer of them per unit volume of the wood (White, 1965). It is, however, the presence of so-called gelatinous fibres that really characterizes tension wood. These cells can be recognized because they are thicker walled than normal fibres and the innermost parts of their walls remain unlignified. That is to say, part of the original cellulose wall does not become impregnated with the
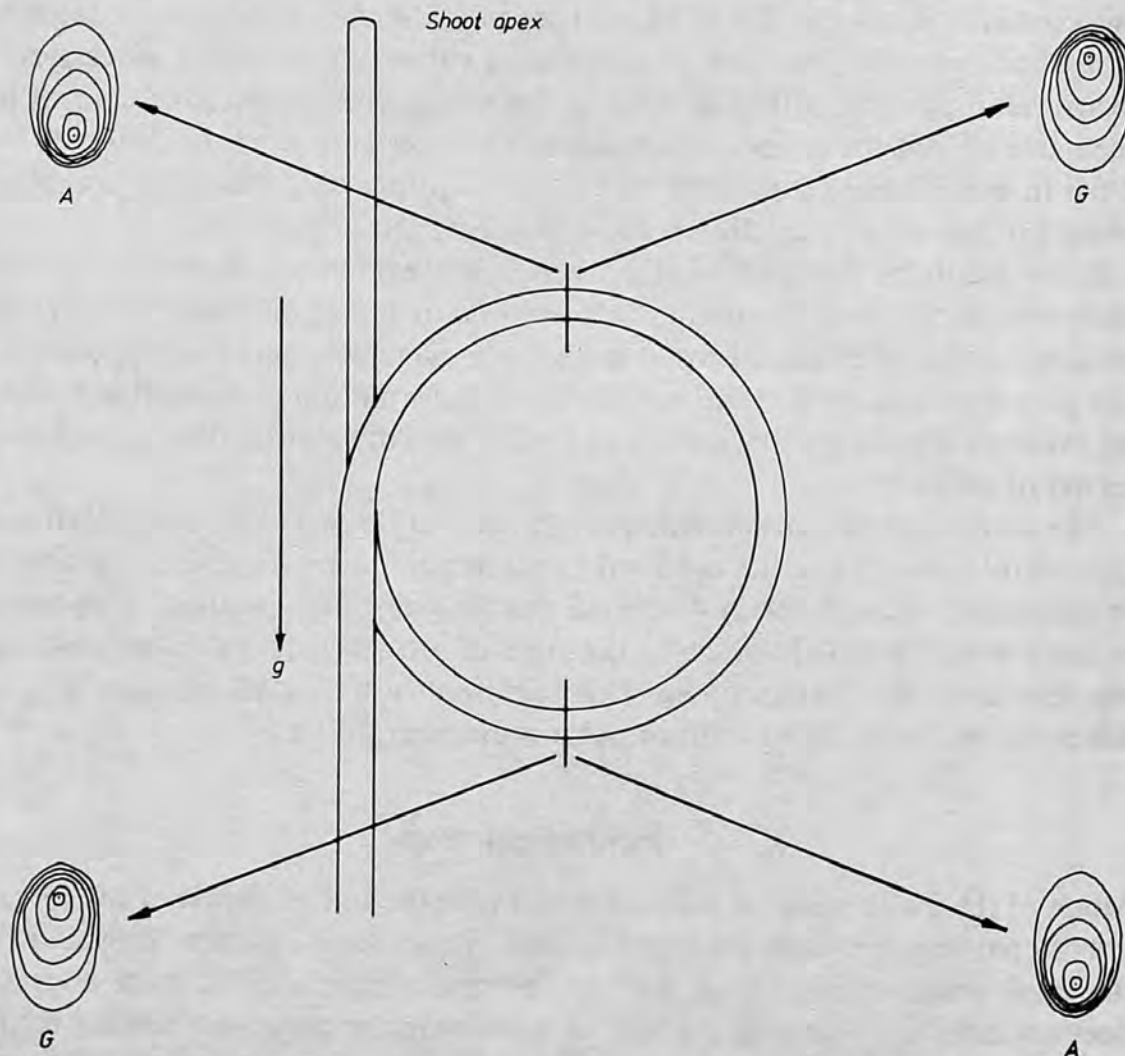
FIGURE 5. A diagrammatic representation of the distribution of reaction wood in a loop made in a stem. The asymmetry of the growth rings in angiosperms (*A*) is opposite in direction to that of gymnosperms (*G*). *g*: the line of action of the force of gravity

hardening substance, lignin, as would normally occur. Indeed, the hardness of wood is due to the fact that in general the majority of the cells become lignified. These partially lignified cells in tension wood are therefore particularly noticeable and can be shown up by various staining techniques. Tension wood has a high tensile strength on account of the large amount of cellulose present. Although this is easily demonstrated in living wood, it would probably be difficult to identify gelatinous fibres in fossil wood, owing to the changes that inevitably take place during the process of fossilization.

In gymnosperms, compression wood is also recognizable by the excentric pith and elliptical growth rings; with the further point that it is often tinged with a red tone; the German authors use the term 'rotholz'. Microscopically its special feature is that the tracheids of which it is largely composed are round in transverse section and there are consequently large intercellular spaces between them. They are also usually much thicker walled and more heavily lignified than in normal wood, making it much heavier in bulk. Timber for commercial use may be severely reduced in value if it contains compression wood on account of its considerable longitudinal shrinkage on drying. Planks may be distorted or even split as a result and the high ratio of lignin to cellulose causes brittleness. It would be unwise, however, to assume that compression wood functions by means of these distortions in the living tree.

Much experimental work has been carried out over the last 70 years since the pioneer studies of Hartig (1901). This work has shown that gravity is the primary stimulus for the production of reaction wood and that this stimulus results in changes in the distribution of growth substances diffusing down from the apex to points lower in the stem. In testing the hypothesis that the compression wood on the under sides of the branches in gymnosperms develops in response to high concentrations of indolyl acetic acid in those regions, Wershing and Bailey (1942) were able to induce compression wood formation in Pine seedlings by applying high concentrations of this auxin. Nečesaný (1958) has shown that in *Populus alba* auxin also accumulates on the lower sides of horizontal angiosperm branches. Here, however, it suppresses the formation of tension wood on the lower sides. Furthermore, he found that application of high concentrations of auxin to the upper sides of horizontal angiosperm branches suppressed tension wood formation. Reaction wood in angiosperms forms therefore in the presence of lower than normal concentrations of auxin whilst in gymnosperms it is the higher concentrations that induce its formation.

The opposite behaviour of gymnosperms and angiosperms to the same concentration of auxin does not in any way cast doubt on the validity of the auxin theory, since a similar situation arises in the response to gravity of the roots and shoots of herbaceous plants. Here, gravity brings about a redistribution of auxin in both root and shoot but each behaves in an opposite way to the same concentration of the substance. High concentrations promote cell elongation in stems but suppress it in roots. Additional work to demonstrate gravity as the primary
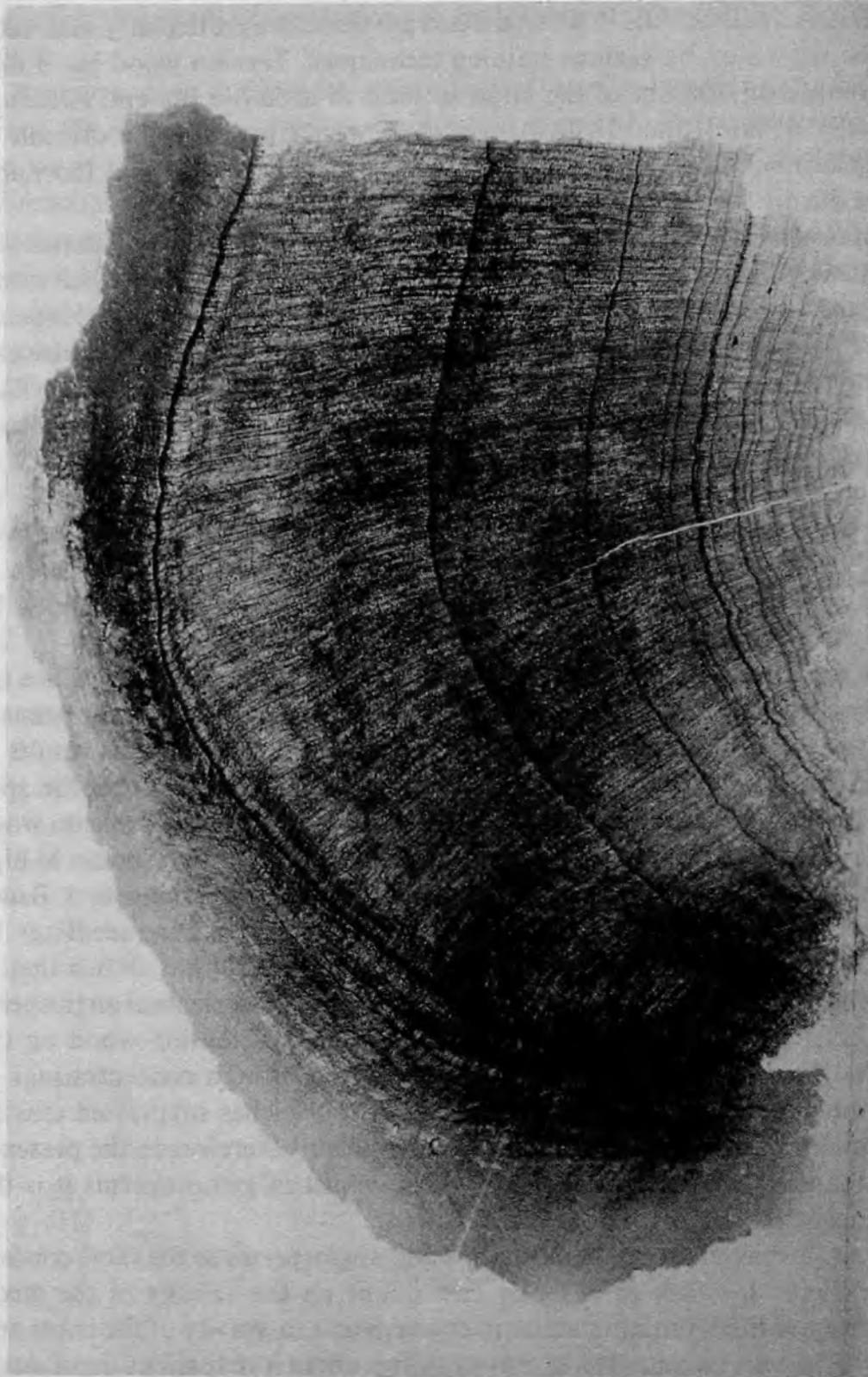
FIGURE 6. A transverse section of a piece of gymnosperm wood from the Upper Jurassic of Norfolk showing asymmetric growth rings. (× 4·2)

cause of reaction wood formation is illustrated in Figure 5. Such work has been carried out by Ewart and Mason-Jones (1906) on gymnosperms and by Onaka (1949) on angiosperms; more recently further work has been done on angiosperms by Robards (1965). It has been shown conclusively that the formation of reaction wood is not related to one particular side of the shoot experimented upon but is connected solely with the line of action of the force of gravity. By bending the shoot into a complete loop it was possible to show that in the upper part the reaction wood formed on the morphologically lower side; in the lower part of the loop the reaction wood formed on what was actually the opposite side to that higher up. Thus the reaction wood formed where the shoot was traversed by the force of gravity; parts of the shoot that experienced the force longitudinally showed no development of reaction wood.

Previous workers had suggested that the quantity of reaction wood in a leaning trunk is proportional to the sine of the displacement angle; this proportionality became known as the sine rule. Robards (1965) has, however, clearly demonstrated that this rule must now be modified. By growing a large number of willow saplings inclined at various angles to the vertical (5°–180°) he showed that the maximum amount of tension wood was produced at 120° to the vertical. It is interesting to note that this is in close agreement with Audus' work (1964) on geotropic responses in herbaceous plants. It also became clear from Robards' work that deviations of as little as 5° from the vertical were quite sufficient to cause the production of tension wood. He is of the opinion that the site of graviperception is in, or very close to, the vascular cambium.

The extent to which reaction wood develops in a trunk or branch will therefore depend on three factors; the first is *g* itself, the second is the load that the part is carrying and the third is the angle of deviation from the vertical. That is to say, there will be a considerable development of reaction wood in a trunk with a marked deviation from the vertical. Similarly there will be much reaction wood in a branch which is long and carries many smaller branches. It is likely therefore to be a very difficult task to assess, in a piece of fossil wood, the individual values of *g*, the load and the angle of deviation. As regards the occurrence of reaction wood in fossil specimens, Figure 6 shows what are apparently asymmetric growth rings in a late Jurassic gymnosperm. Such growth rings have also been observed in the lycopod genus *Lepidodendron* from the Carboniferous but in general there is little or no reference to reaction wood in fossil specimens. A re-examination of fossil material specifically to identify reaction wood might well prove to be a most useful exercise, especially if it were possible to quantify the extent of its development through a wide range of geological time.

References

Audus, L. J. (1964). Geotropism and the modified sine rule; an interpretation based on the amyloplast statolith theory. *Physiologia Pl.*, **17**, 737–745

Chaloner, W. G. and Creber, G. T. (1973). Growth rings in fossil woods as evidence of

past climates, pp. 425–437 in *Implications of Continental Drift to the Earth Sciences* (Ed. D. H. Tarling and S. K. Runcorn), Academic Press, London

Creber, G. T. (1972). Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham Sands of Norfolk. *Palaeontology*, **15**, 655–661

Ewart, A. J. and Mason-Jones, A. J. (1906). The formation of red wood in conifers. *Ann. Bot.*, **20**, 201–203

Hartig, L. (1901). *Holzuntersuchungen. Altes und Neues*, Springer-Verlag, Berlin, 99 pp.

Larson, P. R. (1964). Some indirect effects of environment on wood formation, pp. 345–365 in *The Formation of Wood in Forest Trees* (Ed. M. H. Zimmermann), Academic Press, New York

Nečesaný, V. (1958). Effect of B-indole-acetic acid on the formation of reaction wood. *Phyton, B. Aires*, **11**, 117–127

Njoku, E. (1963). Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees. *J. Ecol.*, **51**, 617–624

Njoku, E. (1964). *Ibid*. II. Observations on seedlings. *J. Ecol.*, **52**, 19–26

Onaka, F. (1949). Studies on compression and tension wood. *Bull. Wood Res. Inst. Kyoto*, **1**, 1–83

Robards, A. W. (1965). Tension wood and eccentric growth in crack willow (*Salix fragilis* L.). *Ann. Bot.*, **29**, 419–431

Robards, A. W. (1966). The application of the modified sine rule to tension wood production and eccentric growth in the stem of crack willow (*Salix fragilis* L.). *Ann. Bot.*, **30**, 513–523

Robards, A. W. (1969). The effect of gravity on the formation of wood. *Sci. Prog., Oxf.*, **57**, 513–532

Robards, A. W., Davidson, E. and Kidwai, P. (1969). Short-term effects of some chemicals on Cambial activity. *J. exp. Bot.*, **20**, 912–920

Schopf, J. M. (1961). A preliminary report on plant remains and coal of the sedimentary section in the central range of the Horlick Mountains, Antarctica. *Inst. Polar Studies*, Rept. 2, 61 pp.

Wareing, P. F., Hanney, C. E. A. and Digby, J. (1964). The role of endogenous hormones in Cambial activity and xylem differentiation, pp. 323–344 in *The Formation of Wood in Forest Trees* (Ed. M. H. Zimmermann), Academic Press, New York

Wershing, H. F. and Bailey, I. W. (1942). Seedlings as experimental material in the study of 'red-wood' in conifers. *J. For.*, **40**, 411–414

White D. J. B. (1962). Tension wood in a branch of sassafras. *J. Inst. Wood Sci.*, **10**, 74–80

White, D. J. B. (1965). The anatomy of reaction tissues in plants, pp. 54–82 in *Viewpoints in Biology*, 4 (Ed. J. D. Carthy and C. L. Duddington), Butterworth, London

DISCUSSION

TARLING: If you wish to see a change in *g* reflected in the growth of trees, you should see this in trees growing at different elevations.

CREBER: Yes, and the effect in a single tree would be maximum in the giant Sequoias. It would be a different matter comparing these observations with fossil trees whose life orientation and elevation one was uncertain of.

BUDDEMEIER: Some of the more optimistic researchers in the field might even be able to correlate the rhythm in cell size of trees with tidal cycles.

EVANS: Is it possible for fluctuations in size of cells to reflect variations in cell cross-section through different parts of the tree?

CREBER: The pattern of tapering of the cells and the position of the cross-section through them might give apparent periodicities, but much more research needed to be done in this regard.

HIPKIN: How long does it take for the tree to add one growth increment?

CREBER: It varies with locality. I believe May–October was a reasonable growing season for British plants.

BUDDEMEIER: Photoperiodic growth rhythms demonstrated to be important in plants should be considered more seriously by marine biolgists in relation to their organisms.

ROSENBERG: I recommend researchers distinguish between the variations in seasonal length of daylight (l.o.dl.) and the variable geophysical parameter, length of day (l.o.d.). Both vary with the changing rate of the Earth's rotation, and the distinction would seem especially significant to plant evolution in the distant past.

Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham Sands of Norfolk

BY

G. T. CREBER

THE PALAEONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations, and publishes the quarterly journal *Palaeontology* and *Special Papers in Palaeontology*. Membership is open to individuals, institutions, libraries, etc., on payment of the appropriate annual subscription:

Institute membership . . . . . £10·00 (U.S. $26.00)
Ordinary membership . . . . . £5·00 (U.S. $13.00)
Student membership . . . . . £3·00 (U.S. $8.00)

There is no admission fee. Institute membership is only available by direct application, not through agents. Student members are persons receiving full-time instruction at educational institutions recognized by the Council; on first applying for membership, they should obtain an application form from the Membership Treasurer. All subscriptions are due each January, and should be sent to the Membership Treasurer, Dr. A. J. Lloyd, Department of Geology, University College, Gower Street, London, WC1E 6BT, England.

COUNCIL 1972–3

President: Professor M. R. House, The University, Kingston upon Hull, Yorkshire

Vice-Presidents: Dr. Gwyn Thomas, Department of Geology, Imperial College, London, S.W. 7
Mr. N. F. Hughes, Sedgwick Museum, Cambridge

Treasurer: Dr. J. M. Hancock, Department of Geology, King's College, London, W.C. 2

Membership Treasurer: Dr. A. J. Lloyd, Department of Geology, University College, Gower Street, London, WC1E 6BT

Secretary: Dr. W. D. I. Rolfe, Hunterian Museum, The University, Glasgow, W. 2

Editors

Dr. Isles Strachan, Department of Geology, The University, Birmingham, B15 2TT
Dr. R. Goldring, Department of Geology, The University, Reading, RG6 2AB, Berks.
Dr. J. D. Hudson, Department of Geology, The University, Leicester
Dr. D. J. Gobbett, Sedgwick Museum, Cambridge
Dr. L. R. M. Cocks, Department of Palaeontology, British Museum (Natural History), London, S.W.7

Other members of Council

Dr. M. G. Bassett, Cardiff
Dr. E. N. K. Clarkson, Edinburgh
Dr. R. H. Cummings, Abergele
Prof. D. C. Dineley, Bristol
Dr. Julia A. E. B. Hubbard, London
Dr. J. K. Ingham, Glasgow
Mr. M. Mitchell, Leeds

Dr. Marjorie D. Muir, London
Dr. B. Owens, Leeds
Dr. W. H. C. Ramsbottom, Leeds
Dr. P. Rawson, London
Dr. Pamela L. Robinson, London
Dr. A. D. Wright, Belfast

Overseas Representatives

Australia: Professor Dorothy Hill, Department of Geology, University of Queensland, Brisbane
Canada: Dr. B. S. Norford, Institute of Sedimentary and Petroleum Geology, 3303–33rd Street NW., Calgary, Alberta
India: Professor M. R. Sahni, 98 The Mall, Lucknow (U.P.), India
New Zealand: Dr. C. A. Fleming, New Zealand Geological Survey, P.O. Box 30368, Lower Hutt
West Indies and Central America: Mr. John B. Saunders, Geological Laboratory, Texaco Trinidad, Inc., Pointe-à-Pierre, Trinidad, West Indies
Western U.S.A.: Professor J. Wyatt Durham, Department of Paleontology, University of California, Berkeley 4, California.
Eastern U.S.A.: Professor J. W. Wells, Department of Geology, Cornell University, Ithaca, New York

GYMNOSPERMOUS WOOD FROM THE KIMMERIDGIAN OF EAST SUTHERLAND AND FROM THE SANDRINGHAM SANDS OF NORFOLK

by G. T. CREBER

ABSTRACT. A description is given of the types of gymnospermous wood occurring in material collected from the Kimmeridgian of the East Sutherland coast. These types are compared with those collected from the Sandringham Sands of Norfolk. All of the material is described in terms of *biorecords* and *events*: references are made to previously described species in the form of *comparison records*. In traditional taxonomy some of the specimens are referable to *Cedroxylon* Kraus and the remainder to *Pityoxylon* Kraus. A close similarity is found between the two collections of wood providing a useful rough correlation of the base of the Sandringham Sands with the Kimmeridgian.

THE present work is based on two collections of gymnospermous wood; one from the Kimmeridgian of the East Sutherland coast and the other from the base of the Lower Portlandian of Norfolk (Sandringham Sands). The Scottish material consists of large calcareous petrifications from the shore at Helmsdale. The material from Norfolk is calcified in a highly ferruginous matrix and was obtained during the excavation of a drainage channel near West Dereham. The differing natures of the materials led to the use of two distinct techniques. Cellulose peels were made from the Helmsdale material but rock sections were prepared in studying the Sandringham Sands specimens as they required excessive etching time in attempts at making peels.

STRATIGRAPHY

The Sutherland material was collected mainly from the shore near Helmsdale where it is abundant; specimens occur with decreasing frequency northwards and southwards from Helmsdale along most of the outcrop of the Kimmeridgian from Kintradwell to Dun Glas. These wood specimens are most frequently encountered where there are outcrops of the boulder beds (Pl. 129, fig. 1). These remarkable beds consist of 'immense angular blocks and smaller waterworn stones of Middle Old Red Sandstone rocks embedded in a matrix of gritty, shelly limestone' (Phemister 1960). This matrix yields plant megafossil compression remains, a fauna of a littoral marine type with typical Kimmeridgian fossils and also some ammonites. Bailey and Weir (1933) considered that the breccias or boulder beds collected at the base of a submarine fault-scarp, the littoral shells and plant debris being swept down from the upthrow side together with Old Red Sandstone material by tsunamis or tidal waves energized by earthquakes along the fault.

It is only in comparatively recent years that the exact age of the Sandringham Sands of Norfolk has been worked out. Various excavations in the county have been of great assistance in providing exposures with ample fossil material. Larwood (1961) mentions the site where the Norfolk material described in this paper was found. Excavations

(TL 655997) immediately south-west of Abbey and West Dereham Station, about two miles to the east-north-east of Fordham, exposed part of the Sandringham Sands. The section exposed was about 6·5 m deep. The lower beds consisted of a conglomerate passing down into very pebbly dark grey sands; these rested on 1·5 m of blue-grey silty sands which formed the bottom of the section. Contractors' bore-logs for this locality show that the blue-grey silty sands, with occasional beds of harder cemented sandstone, continue below the visible base of the excavated section for at least 8 m, giving a thickness of about 16 m for the sands at this point. The blue-grey silty sands contained a layer of nodules; in the latter were large fragments of wood and phosphatized casts and moulds of many bivalves, some belemnites and occasional ammonites. Of the fossils Casey (1961) said that this part of the excavation revealed a suite indicative of a Berriasian (Infra-Valanginian) fauna new to Britain. He described the occurrence of the fossils in nodular masses of hard grey-brown glauconitic sandstone with carbonized plant debris about 10 m above the base of the formation. Included were species of *Hartwellia*, *Isocyprina* and *Isodonta* which have their closest parallels in the Upper Jurassic.

Further evidence for the age of the Sandringham Sands was provided by a section exposed by an excavation for a North Sea Gas pipeline near King's Lynn (TF 65 15). Casey and Gallois (1968) describe a previously unrecorded sequence of ammonite faunas in a facies of glauconitic sand and phosphate nodules. The genus *Subcraspedites* was succeeded by forms of the group of *Garniericeras tolijense* (Nikitin), diagnostic of the Uppermost Volgian of the Northern U.S.S.R., in turn succeeded by similar ammonites accompanied by an undescribed genus ancestral to the basal Cretaceous (Ryazanian) *Hectoroceras*; the sequence continued with *Hectoroceras* and *Surites*. In addition, Ager (1971) has strengthened the correlation of the Sandringham Sands with the Volgian of the U.S.S.R. in studies on the brachiopod genus *Rouilleria*.

The present work therefore lends considerable support to an Upper Jurassic age for the base of the Sandringham Sands, by showing that there is a very high degree of correlation between the gymnospermous woods of these beds and those of the Kimmeridgian of East Sutherland. The possibility has to be faced that in both the Sandringham Sands and in the Helmsdale Kimmeridgian the wood material might have been re-worked. However, in the case of the Norfolk material one piece of wood (MGC/T) shows borings by xylophagous crustacea (or mollusca) which are fresh and do not appear to have suffered the abrasion likely to have occurred in re-working. The largest pieces of wood seen at the Helmsdale locality measured 40 cm by 25 cm (Pl. 129, fig. 3). Associated with

---

EXPLANATION OF PLATE 129

Fig. 1. About eight square metres of the boulder beds on the shore at Helmsdale, polished by the sea and showing numerous clasts.

Figs. 2, 6. Biorecord 1 TRACHEIDOXYL *MS*. 2, Specimen MGC/T, a portion of a tangential longitudinal section with transverse sections of a number of rays, some of which are partially biseriate; × 150. 6, Specimen MGC/A, cross-field pits in a radial longitudinal section, the ray cells are filled with resin; × 150.

Fig. 3. Two large pieces of calcified wood, drilled by Recent rock-boring molluscs, on the storm beach at Helmsdale; length of hammer 30 cm.

Fig. 4. cfA 2 TRACHEIDOXYL *RC*. Specimen B 34/17, part of a tangential longitudinal section showing a fusiform ray with resin canal; × 150.

Fig. 5. cfA 1 TRACHEIDOXYL *MS*. Specimen B 34/9, large cross-fields pits seen in a radial longitudinal section passing along a ray; × 150.
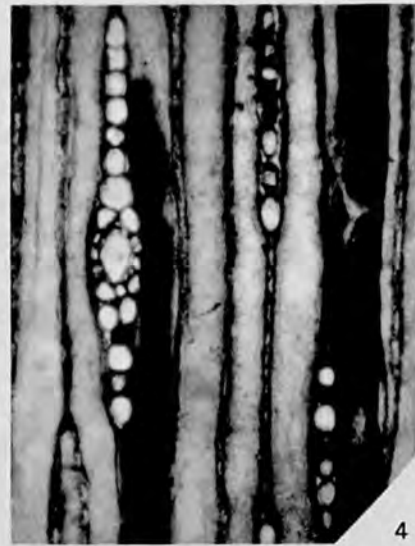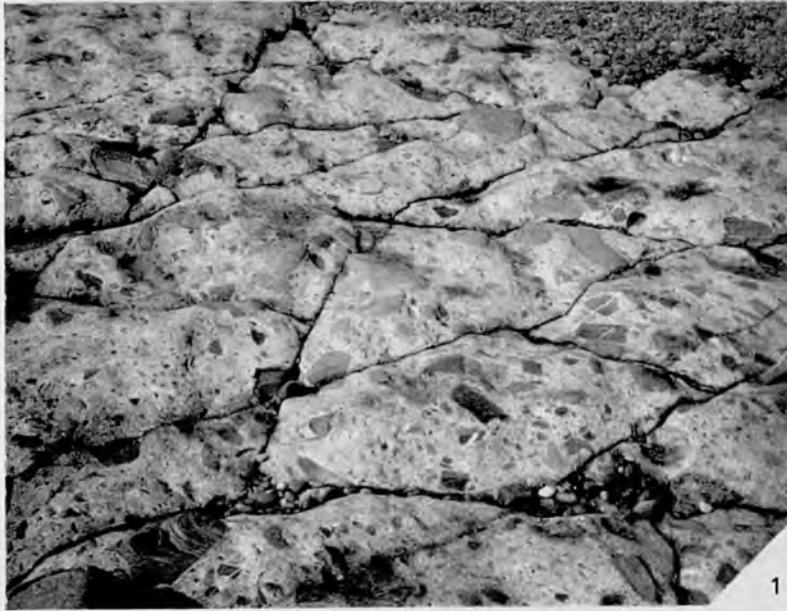
CREBER, Late Jurassic petrified wood

the fossil corals referred to above is a large quantity of carbonized wood fragments up to 3 cm in diameter; connection between this wood and the petrified wood has not yet been demonstrated.

SYSTEMATIC SECTION

For description of the material use is made of the biorecord system of Hughes and Moody-Stuart (1969). A biorecord is defined as a conceptual taxon based on a specimen from a stated locality. The biorecord is not in essence different from a palaeontologic species at the stage of description by its originator, but differs in the use that can subsequently be made of it; virtually no literature search is involved and description priorities are not considered. The title heading and reference line for a biorecord (e.g. 1 TRACHEIDOXYL *MS*) consists of (*a*) a serial number which outside this paper would be preceded by an identifier such as author's initials, (*b*) an informal (but stored) classification guide, and (*c*) an author's working reference printed in italics to indicate that it is a 'non-search' item. The term TRACHEIDOXYL is used to indicate that the specimen involved is a detached portion of wood characteristically composed of tracheids with only a minor proportion of other tissues.

Additional specimens are listed as comparison records; those which cannot readily be distinguished from the biorecord are designated 'cfA'. Specimens of progressively lower grades of comparability then receive the prefix 'cfB' if there is one quantitative difference and 'cfC' in the case of further divergence.

BIORECORDS JUR 28 27 GB XYL

The above heading, in a form suitable for data storage, indicates that the biorecords are wood specimens from localities in the British Jurassic. The Ages/Stages are those used in the Fossil Record (Harland *et al.* 1967), numbered consecutively back from Recent. Thus 28 and 27 are the Oxfordian and Kimmeridgian, respectively. All specimens are lodged at the Sedgwick Museum, Cambridge.

1 TRACHEIDOXYL *MS*

Diagnosis. Growth rings well marked, 0·5 cm broad. Early wood tracheids cross-section 50 μm × 50 μm, reducing only slightly through the season which terminates with a few rows of very small elements. Bordered pits, 15 μm diameter, on the radial walls of the tracheids, uniseriate arrangement, sometimes contiguous and compressed. Rays uniseriate or partially biseriate, 2 to 20 cells in height, average 11 (Pl. 129, fig. 2). Cross-field with a solitary, large, oblique pit.

Record Specimens. MGC/A, MGC/B, MGC/Q and MGC/T from the Flood Relief Channel cut in the Sandringham Sands to the south and east of Abbey and West Dereham Station (TL/655997).

Description. This biorecord is readily distinguished by its highly characteristic cross-field pitting (Pl. 129, figs. 5 and 6), the 'eiporen' of the German authors.

Comparison Records. cfA 1 TRACHEIDOXYL *MS*: (1) *Metacedroxylon scoticum* described by Holden (1915) from the Kimmeridgian of Loth, East Sutherland; Sedgwick Museum Specimen No. K613. (2) Specimens B34/9 and B34/20 from Helmsdale, East Sutherland.

2 TRACHEIDOXYL *RC*

Diagnosis. Growth rings very variable in breadth, 1–3 mm. Early wood tracheid cross-section 40 μm × 40 μm. Marked zone of late wood, 12 rows of smaller dense elements. Bordered pits on tracheid radial walls 10–12 μm in diameter, bars of Sanio. Pits generally uniseriate but smaller and biseriate at ends of tracheids. Vertical (Pl. 130, fig. 1) and horizontal resin canals. Rays uniseriate or fusiform with resin canal, 2–20 cells in height, average 8. Cross-field with one to two small bordered pits.

Record Specimen. MGC/R from the Sandringham Sands (TL/655997).

Description. This biorecord is of considerable interest in that it possesses rays with fusiform cross-sections (Pl. 129, fig. 4) and bars of Sanio (Pl. 130, fig. 2) on the radial walls of the tracheids. It would appear that there is no other undoubted record of such a wood as early as the Kimmeridgian.

Comparison Records. cfA 2 TRACHEIDOXYL *RC*: Specimen B34/17 from Helmsdale, East Sutherland and 3 TRACHEIDOXYL *RD* (Specimen MGC/O) from the Sandringham Sands (TL/655997). cfB 2 TRACHEIDOXYL *RC*: *Piceoxylon scleromedullosum*, described by Shimakura (1937) from the Senonian of Sakhalin has many similar features to 2 TRACHEIDOXYL *RC*; a much closer comparison could be made if the preservation of 2 TRACHEIDOXYL *RC* would allow the certain determination of the existence of ray tracheids (there is some evidence of their presence but insufficient to include as an item in the diagnosis).

3 TRACHEIDOXYL *RD*

Diagnosis. Growth rings uniform, 0·5 cm broad. Early wood tracheids cross-section 60 μm (Rad) × 50 μm (Tan). Gradual transition to late wood through the ring. Bordered pits on tracheid radial walls 17 μm in diameter. Bars of Sanio. Pits generally uniseriate but occasionally biseriate at ends of tracheids. Vertical (Pl. 130, figs. 3 and 4) and horizontal resin canals. Rays uniseriate or fusiform with resin canal, 2–17 cells in height, average 9 (Pl. 130, fig. 5). Cross-field with one to two small bordered pits.

Record Specimen. MGC/O from the Sandringham Sands (TL/655997).

Distinction. This is very similar to biorecord 2 above. In order to avoid conflicting items in the diagnosis they are being maintained separately for the time being. It is fully realized that the differences may only be such as one might expect between pieces of wood from the inner and outer parts of the trunk or between branch and trunk. Collection of further material may elucidate the matter.

EXPLANATION OF PLATE 130

Figs. 1, 2. cfA 2 TRACHEIDOXYL *RC*. 1, Specimen B 34/17, a vertical resin canal seen in transverse section; × 150. 2, Specimen B 34/17, a portion of a radial longitudinal section showing bordered pits with bars of Sanio; × 150.

Figs. 3–5. Biorecord 3 TRACHEIDOXYL *RD*. Specimen MGC/O. 3, 4, vertical resin canals seen in transverse section; × 150. 5, part of a tangential longitudinal section showing a fusiform ray with resin canal; × 150.

Fig. 6. cfA TRACHEIDOXYL *CH*. Specimen K 571, a portion of a tangential longitudinal section showing one of the deep rays; × 150.
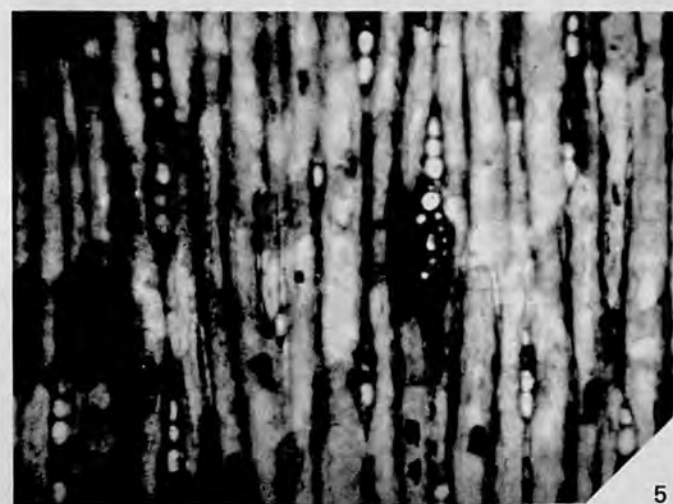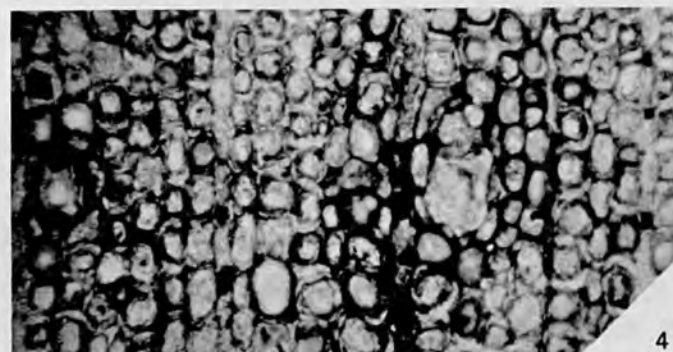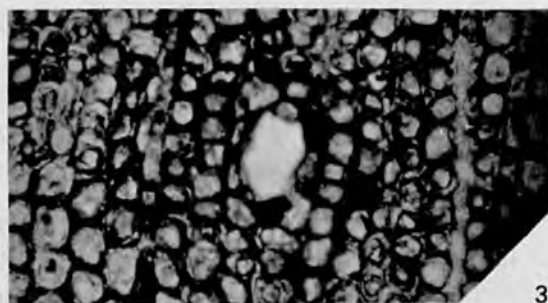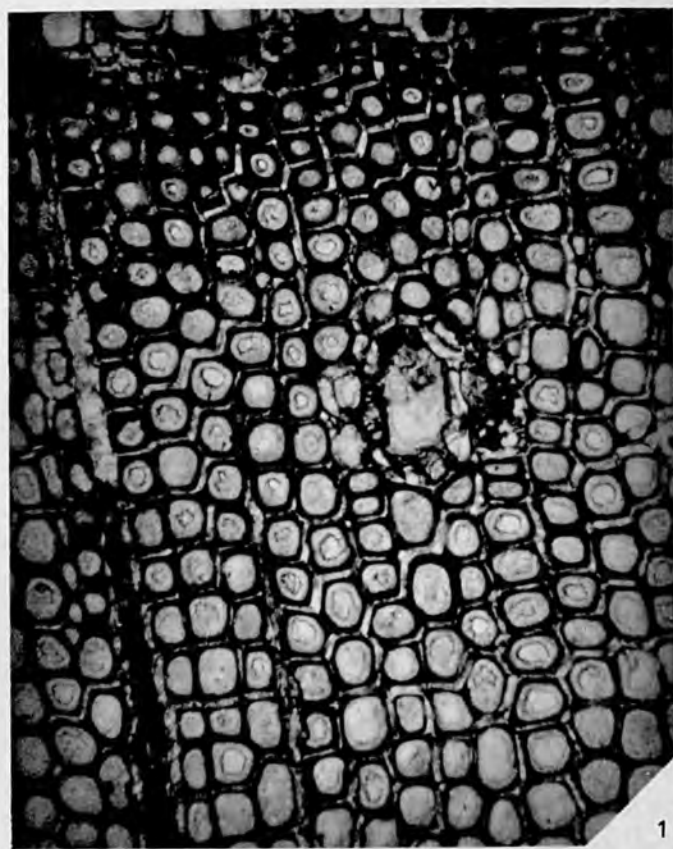
CREBER, Late Jurassic petrified wood

4 TRACHEIDOXYL *CH*

Diagnosis. Growth rings well marked, 0·1–0·5 cm broad. Rings sometimes subdivided by bands of smaller tracheids. Bordered pits on tracheid radial walls 17 μm in diameter, generally uniseriate but not infrequently biseriate and opposite (Pl. 131, fig. 1). Rays uniseriate, sometimes very large (Pl. 130, fig. 6), one to 34 cells high, average 16. Cross-field pitting one to four small pits, most frequently two.

Record Specimens. MGC/H and MGC/U from the Sandringham Sands (TL/655997).

Comparison Records. cfA 4 TRACHEIDOXYL *CH*: (1) *Cedroxylon hornei* described by Seward and Bancroft (1913) from Helmsdale shows clearly the characteristic cross-field pitting (Pl. 131, figs. 2 and 5) and curious variability in the growth rings (Pl. 131, fig. 4) which are such special features of this biorecord. (2) Sedgwick Museum Specimen No. K 571 from Helmsdale. (3) Specimens B 41/2 and B 34/13 from Helmsdale, East Sutherland.

5 TRACHEIDOXYL *GR*

Diagnosis. Very broad growth rings, 0·9 cm wide. Early wood tracheid cross-section 50 μm × 50 μm. Wide zone of late wood, about 1/3 of the ring, distorted and collapsed (Pl. 131, fig. 3). Bordered pits on radial tracheid walls 13 μm in diameter. Uniseriate arrangement, sometimes contiguous. Rays uniseriate 6–29 cells in height, average 15.

Description. This material is not very well preserved but it is represented in the Helmsdale collection by such striking hand specimens that it demands recognition. The most noticeable feature is the width of the growth rings some of which are nearly one centimetre wide. The most likely explanation is that the material originated from the heartwood of a very large trunk; sections of the modern *Sequoia gigantea* show at the centre growth rings of the calibre of this biorecord. Such fine detail as can be observed in the specimens would indicate that they are probably the central portions of trunks of 4 TRACHEIDOXYL *CH*.

Record Specimens. B34/1 and B41/1 from Helmsdale, East Sutherland.

GENERAL REMARKS

Although a number of attempts have been made to systematize the very large number of published species of fossil gymnospermous wood, exquisitely preserved material is often required for successful identification in the complicated keys involved. For example Kräusel (1949) published a key separating the various woods into 25 genera, many of the 27 dichotomies requiring the presence in the specimens of minute details. Further keys follow, dividing the genera into species: in some genera there are upwards of 20 species. Many of the latter have names which imply supposed relationships with modern species; the evidence for these relationships is frequently very scanty.

The aim of the present work is to depart as far as possible from the purely taxonomic approach and to attempt to use the material as a means of geological correlation. In this initial essay there would appear to have been considerable success. By using the biorecord system of Hughes and Moody-Stuart (1969) it has been possible, with material not especially well preserved, to show an essential similarity between the assemblages of gymnospermous wood from two widely separated localities. Further support has been provided for the correlation previously carried out by other workers on these localities.

However, if this technique is to be applied to a number of localities a certain measure of taxonomy may be desirable in order to appreciate the relative proportions of broadly different types of wood occurring in each. The following is proposed:

A. Wood with resin ducts normally present. This would comprise the species previously described under the generic names *Pityoxylon, Piceoxylon, Pinuxylon,* and further subdivisions of these as proposed by subsequent authors. The modern genera that fall unto this group are: *Pinus, Larix, Picea* and *Pseudotsuga.*

B. Wood with resin ducts only of traumatic origin, pits on the radial walls of the tracheids separate and circular and, if in two or more rows, opposite. Contiguous and more or less flattened pits may occur but never as a general rule. This would comprise the species previously described under the generic names *Cedroxylon, Cupressinoxylon, Mesembrioxylon,* and the various later sub-divisions of these genera. Modern genera in this category are: *Cedrus, Abies, Juniperus* and *Sequoia.*

C. Wood in which the pits on the radial walls of the tracheids are normally contiguous with their mutual boundaries flattened to form a polygonal pattern. These pits are usually multiseriate and alternate. This would comprise *Dadoxylon* and its later subdivisions. Examples of modern genera: *Agathis* and *Araucaria.*

This classification implies a considerable amount of 'lumping' as compared to the more complicated ones extant in the literature but for present purposes it would have a number of advantages. First, virtually all the available material could be classified; only the very lowest grade of preservation would fail to preserve the relatively major features necessary to place a specimen in its proper category. The relative proportions of the numbers of specimens in each group would serve as useful data in the process of correlating strata. A further advantage lies in the fact that it may prove possible to apply this method to wood preserved other than by petrification; that is to say, lignitic fragments and fusain.

EVENTS AND TIME-CORRELATION

Event: H — Helmsdale.
        Woods of Type A: cfA 2 TRACHEIDOXYL *RC* (B 34/17).
        Woods of Type B: Biorecord 5 TRACHEIDOXYL *GR* (B 34/1 and B 41/1).
                      cfA 1 TRACHEIDOXYL *MS* (B 34/9, B 34/20 and K613).
                      cfA 4 TRACHEIDOXYL *CH* (B 41/2, B 34/13 and K571).
        Woods of Type C: None.
        Woods indeterminate: 16 specimens.

Figs. 1, 2, 4. Biorecord 4 TRACHEIDOXYL *CH*. 1, Specimen MGC/U, biseriate pitting on the radial walls of a group of tracheids; ×150. 2, Specimen MGC/U, cross-field pitting seen in a radial longitudinal section passing through a ray; ×150. 4, Specimen MGC/H, a transverse section showing three 'false rings' produced in one season; the section shows the effect of drilling by xylophagous animals; ×90.

Fig. 3. Biorecord 5 TRACHEIDOXYL *GR*. Specimen 41/1, a transverse section showing a sector of one complete growth ring with the late wood collapsed and distorted; ×45.

Fig. 5. cfA 4 TRACHEIDOXYL *CH*. Specimen K 571, cross-field pitting seen in a radial longitudinal section; ×150.
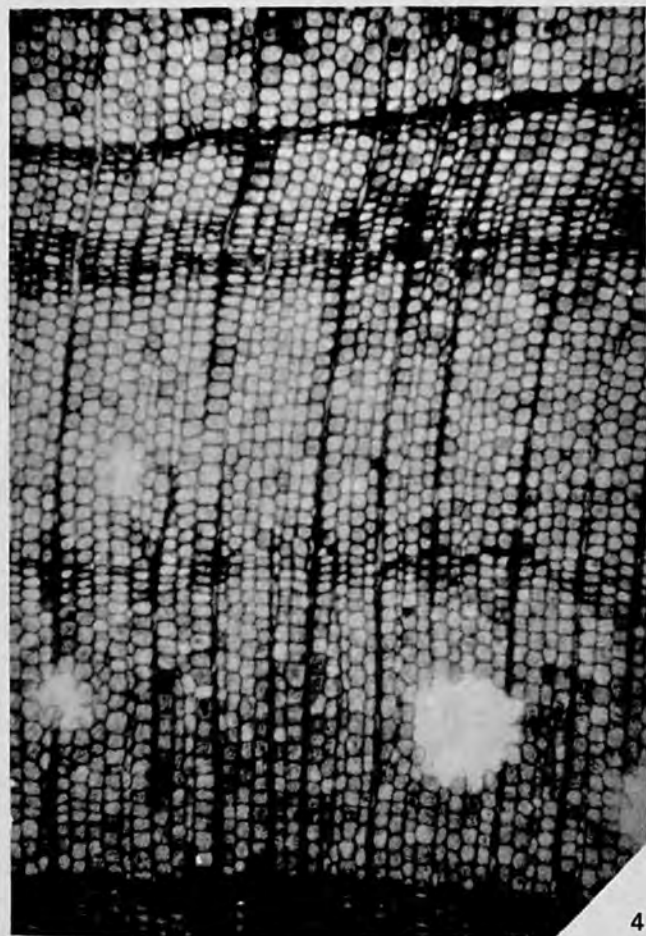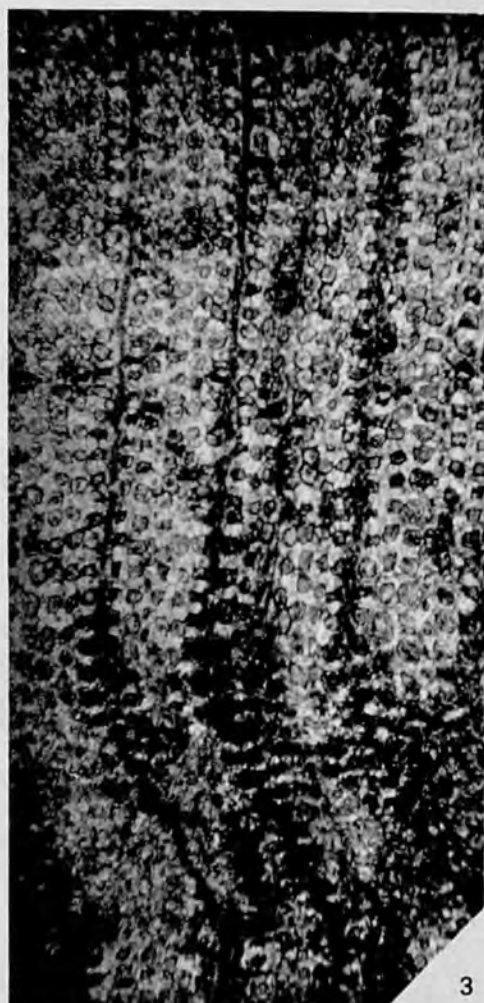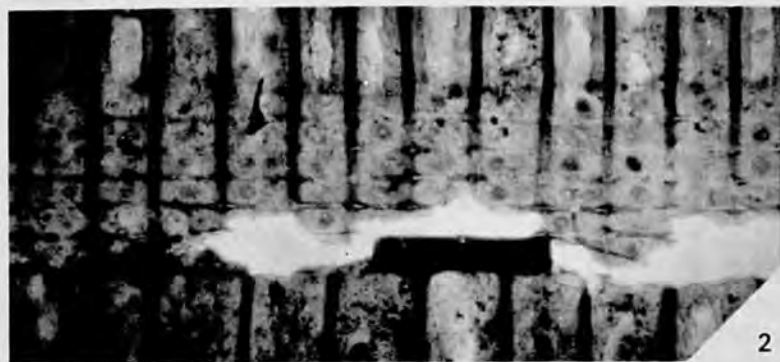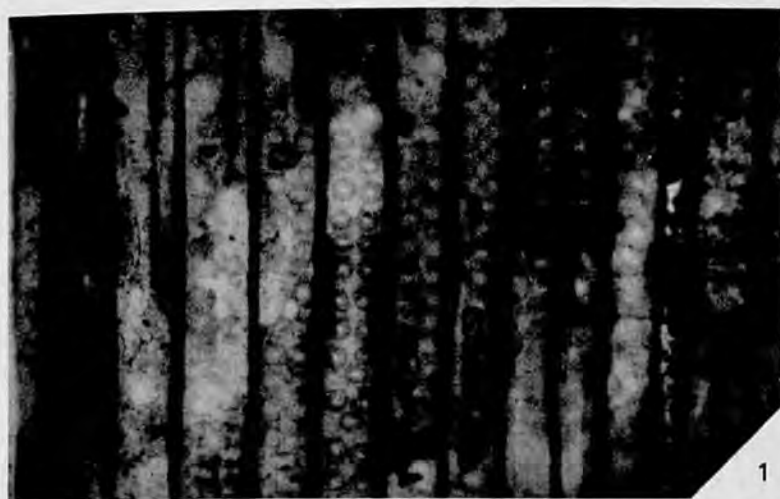
Event: N — Norfolk.
   Woods of Type A: Biorecord 2 TRACHEIDOXYL *RC* (MGC/R).
                    Biorecord 3 TRACHEIDOXYL *RD* (MGC/O).
   Woods of Type B: Biorecord 1 TRACHEIDOXYL *MS* (MGC/A, MGC/B,
                    MGC/Q and MGC/T).
                    Biorecord 4 TRACHEIDOXYL *CH* (MGC/H and MGC/U).
   Woods of Type C: None.
   Woods indeterminate: 5 specimens.

In both events woods of Type A are rare, especially at Helmsdale where only one out of 25 specimens is of this type. Of the 16 indeterminate specimens the preservation was at least sufficient to show that they were not of Type A. The proportion in the Norfolk event seems to be slightly larger with two out of 13 specimens.

It will be seen that these two wood-events are very similar but that there is no evidence to indicate which is earlier in time. However, the external evidence of time-correlation suggests that the Norfolk locality is Volgian whilst the Scottish one is probably Lower-Middle Kimmeridgian. The situation as regards the latter is much confused by considerable folding and faulting but the northernmost part of the outcrop (i.e. the Helmsdale area) is usually regarded as containing the higher beds.

REFERENCES

AGER, D. V. 1971. The Brachiopods of the Erratic Blocks of Spilsby Sandstone in Norfolk and Suffolk. *Proc. Geol. Ass.* **82**, 393–401.

BAILEY, E. B. and WEIR, J. 1933. Submarine Faulting in Kimmeridgian Times: East Sutherland. *Trans. Roy. Soc. Edin.* **57**, 429.

CASEY, R. 1961b. The Geological Age of the Sandringham Sands. *Nature*, London, **190**, 1100.

—— 1967. in Annual Report (for 1966). *Inst. of Geol. Sciences*, London, 90–91.

—— and GALLOIS, R. W. 1968. in Annual Report (for 1967). *Inst. of Geol. Sciences*, London, 104–105.

HARLAND, W. B. *et al.* (Eds.). 1967. The Fossil Record. London (Geological Society), xii+828 pp.

HOLDEN, R. 1915. A Jurassic Wood from Scotland. *New Phytologist*, **14**, 205–209.

HUGHES, N. F. and MOODY-STUART, J. C. 1969. A method of stratigraphic correlation using early Cretaceous spores. *Palaeontology*, **12**, 84–111.

KRÄUSEL, R. 1949. Die fossilen Koniferenhölzer; Teil II. *Palaeontographica* **B 89**, 83–203.

LARWOOD, G. P. and FUNNELL, B. M. (Eds.). 1961. The Geology of Norfolk. *Trans. Norfolk and Norwich Nat. Hist. Soc.* **19**, Pt. 6, 270–375.

PHEMISTER, J. 1960. Scotland: The Northern Highlands. *Inst. of Geol. Sciences*, London, 89–90.

SEWARD, A. C. and BANCROFT, N. 1913. Jurassic plants from Cromarty and Sutherland, Scotland. *Trans. Roy. Soc. Edin.* **48**, 867.

SHIMAKURA, M. 1937. Studies on fossil woods from Japan and adjacent lands. *Sci. Rep. Tohoku Imp. University*, 2 Geol., **19**, No. 1, 28.

G. T. CREBER
University College School
Hampstead
London

Implications of Continental Drift to the Earth Sciences

VOLUME 1

NATO Advanced Study Institute, April 1972,
The University of Newcastle upon Tyne

Edited by

D. H. TARLING AND S. K. RUNCORN

School of Physics, The University,
Newcastle upon Tyne,
England

3.14

W. G. CHALONER and G. T. CREBER

Department of Botany & Microbiology,
University College, Gower St,
London, England

Growth Rings in Fossil Woods as Evidence of Past Climates

Introduction

The wood forming the trunks of forest trees growing in temperate latitudes generally shows a banded structure, reflecting the seasonal character of the climate under which it grew. Wood of trees grown within the humid parts of the tropics, particularly in tropical rain forest, generally shows either only very obscure growth rings, or no perceptible periodicity of structure at all (Richards, 1952). Although this general statement needs to be qualified in detail, it appears that a study of growth rings in petrified woods might offer a basis for deductions concerning palaeoclimate, and hence of palaeolatitude and palaeo-pole positions. Unlike much other biological evidence bearing on palaeoclimate, observations on the character of growth rings (or lack of them) represents an observable parameter in fossil woods independent of any recognition of identity or of supposed relationship between taxa.

Unger (1847) is reported to have been the first palaeobotanist to draw attention to the absence of growth rings in Palaeozoic woods, and to interpret it as indicating an equable and seasonless climate (Antevs, 1953). H. Potonié and Walter Gothan subsequently pursued this theme; they regarded the absence of growth rings in certain fossil woods as evidence of a humid seasonless (and so by implication, tropical) climate at the time of growth (see Gothan, 1911). Other authors (e.g. Seward, 1892) were more cautious, emphasizing the many problems in interpreting growth rings in terms of direct climatic causation. The possibility of seeing past climate reflected in growth rings was further reviewed by Frentzen (1931) and Antevs (1917, 1925, 1953), while several authors reviewing the general relationship between fossil plants and palaeoclimate have incidently touched on the growth ring aspect (e.g. Arnold, 1947; Schwarzbach, 1963; Mägdefrau, 1968 and Kräusel, 1961, 1964).

While the palaeoclimatic interpretation of growth rings in fossil woods remains controversial, research in two rather remote fields over the last twenty years makes a renewed study of this problem particularly desirable. Firstly, the geophysical evidence for the occurrence of major movements of the continents with respect to the climatic belts has encouraged an impartial re-examination of all biological evidence relating to palaeoclimate. Secondly, the study of the biochemical and biophysical basis of plant growth has thrown a good deal of light on the mechanism by which plants control wood formation, and hence the development of growth rings.

Terminology

Before pursuing this topic further, it is appropriate to comment on some of the terms used in describing growth rings in woods. The secondary xylem ('wood' of normal usage), which constitutes the bulk of a woody gymnosperm or angiosperm tree-trunk, is formed by the activity of a thin layer of living tissue, the vascular cambium, just beneath the bark. A wide range of features of the environment—both physical and biological—may cause a cessation or slowing down of cambial activity and result in a recognizable feature in the texture of the wood, which may or may not be continuous around the circumference. The most obvious and widespread cause of such banding is of course seasonal change, especially where this is associated with considerable fluctuation in temperature or availability of water; but under some circumstances (for example a double annual wet season) two growth rings may be formed in each year's growth. For this reason the indiscriminate use of the term 'annual rings' for all features of periodic growth in woody plants is inappropriate. However, in temperate latitudes each growth ring generally represents a single year's growth. In a conifer grown under such temperate climatic conditions there is commonly discernible within each year's growth, a zone of secondary wood formed early in the growing season in which the conducting cells show a relatively large diameter ('early wood', Fig. 1A). This is followed by a zone in which the cells become successively of smaller radial diameter, and with a narrower bore, which were laid down during the latter part of the growing season ('late wood'). The change from early wood to late wood formation is usually fairly gradual, and contrasts with the cessation of late wood formation, followed in abrupt juxtaposition by the renewed formation of early wood the following spring. This gives a strikingly asymmetrical character to each growth ring. Of course the extent to which successive growth rings are clearly demarcated, and the relative proportions of early and late wood, vary greatly, even between plants grown under similar circumstances, according to the inherent characters of a given species. There is similarly great variation in the expression of the growth rings in a given specimen of wood in relation to its position on the tree. In the conifers, which represents the major surviving group of gymnosperms (the most primitive of extant forest trees), the distinction between early and late wood is relatively simple. Generally speaking, the secondary wood of the more advanced angiosperms (flowering plants) is anatomically more complex, and the change from early to late wood may be expressed in a changing ratio of water conducting cells to other types of wood constituents, or to a changing pattern in their internal distribution. However, since angiosperm woods are abundant only from the Late Cretaceous onwards, their particular complexities will not be pursued further, and we shall concentrate mainly on the comparison between living gymnosperm wood (principally conifers) and that of analogous fossil woods of the Palaeozoic.

Our interest in fossil woods centres on the question of whether the character of the wood is reflecting the general features of the climate in which it grew, to the extent that we can 'read back' the palaeoclimate from features of the wood anatomy, as Unger and Gothan believed. It is perhaps worth emphasizing that this has little to do with the science of dendrochronology or 'tree-ring dating'—a means of using sub-fossil wood or wooden artifacts for both relative and absolute dating in an archaeological context. This method was pioneered by the American worker, Douglas, and is particularly effective if applied to wood specimens in which the growth took place under con-

ditions in which aridity was the principal limiting factor. Dendrochronology depends on recognizing the idiosyncrasies of a given sequence of years, resulting principally from the vagaries of rainfall; this makes it possible to assemble the partial sequences offered by individual wood specimens, much as seasonally banded (varved) clays may be correlated over short distances. Sequences of such tree ring-counts may be pieced together to give an absolute chronological scale on to which both naturally occurring wood specimens and wooden artifacts may be fitted. This method is of course applicable only to the last few thousand years of the post-glacial period. Recent reviews of this field, which is of the utmost importance in the Pleistocene geochronology of the American southwest, are given by Stokes & Smiley (1968) and Fritts (1972). Dendrochronology is mentioned here only since it involves growth ring study of (at least sub-) fossil wood, and since the controlling factor underlying the method is climatic. It has little bearing on the more controversial ground of trying to interpret the broad features of palaeoclimate from growth ring characteristics of much older petrified wood specimens. However, dendrochronology has also given a stimulus to the study of the extent to which climate regulates the formation of growth rings (see for example Fritts, 1966, 1972), and this is an essential part of the present discussion.

The Mechanism of Environmental Control of Wood Formation

The range of factors which may effect growth increments of trees includes water supply to the roots, atmospheric humidity, mineral nutrients, temperature and light. The operation of these factors, varying through a seasonal pattern, interacting on one another and on the genetically controlled growth potential of any individual tree, produces a situation of some complexity (see Zimmermann *et al.*, 1964; Fritts, 1966; Kozlowski, 1971 and Wareing & Phillips, 1970). The activity of the vascular cambium in a tree trunk, laying down the current year's growth increment, is controlled primarily by growth substances (plant hormones in the broad sense) being produced in the young leaves and shoots at the crown of the tree. The decisive role that the seasonal character of the environment plays in wood formation is therefore indirect so far as the wood of the tree trunk is concerned. The direct effect of the climatic environment acts on the crown of the tree, controlling both the production of carbohydrate as raw material, and the formation of growth substances, which in turn govern the thickness and character of the secondary wood laid down (Larson in Zimmermann, 1964).

The situation is further complicated by the fact that the actual time of onset of new elongation growth in the spring (and the transition from early wood to late wood production) is not controlled primarily either by the ambient temperature and water availability or by the rate of photosynthesis occurring in the young shoots. In evolutionary terms, it has evidently proved unsatisfactory to use the sporadic occurrence of warm weather or high light intensity in the spring as a triggering mechanism for the onset of renewed rapid growth of young shoots and the formation of the year's production of leaves. As with the onset of flowering in many angiosperms, the process called photoperiodism, which involves in effect the measurement of day-length by the plant, has been evolved as the mechanism controlling the irreversible onset of new leaf formation. From the limited evidence at present available, the onset of early wood formation in conifers, and the subsequent change to late wood production, appears to be—at least in the temperate species investigated—largely controlled by day-length

rather than the more or less seasonally linked (but unpredictable) light intensity, temperature and water-availability cycle (see Kozlowski, 1971, chapter 3, and references there cited).

The onset of a growth ring shown by a typical temperate tree trunk (whether gymnosperm or angiosperm) has been to some extent, therefore, programmed for induction by an increase in day-length, while the amount of both early wood and late wood is controlled by the environment to which the crown of the tree is exposed. This influence of day-length may be demonstrated by subjecting a temperate plant or leafy shoot to a period of longer days (corresponding to the onset of spring) followed by a period of short days. This produces a flush of new leaf formation, with ensuing hormone release, which in turn causes a band of 'early wood' formation by the cambium; in this way several false growth rings may be artificially induced in a single season's growth.

The precision of this photoperiodic adaptation is shown by the fact that some species of conifers with a wide latitudinal range may have races with different photo-periods, matching the spring-time day lengths appropriate to their latitudes (Wareing & Phillips, 1970, p. 229). These authors conclude that 'this fact suggests that woody plants are rather closely adapted to natural day-length conditions, and that the latter probably play an important controlling role in the seasonal cycle of growth and dormancy'.

In examining the record of fossil woods it may reasonably be supposed that at any time in the past, a given species of tree would have been adapted to its environment not merely in a climatic sense but also in terms of photoperiod. The establishment of forest in a new climatic situation (migration), or actual climatic change affecting a species within its existing range would both presumably have been slow enough for the species to have had time to adapt to the new situation (or, failing to do so, to have been ousted by competition). The presence of a sequence of growth rings in a fossil—as in a living wood—must be construed as normally reflecting climatic periodicity to which the tree is not merely responding, but to which it was adapted in terms of a photoperiodic response, if one was involved.

Despite the complexity of action of these controlling factors, it is still a valid observation that the formation of uninterrupted secondary wood is generally to be correlated with a uniform, seasonless climate. Wood entirely lacking growth rings is generally confined to those areas in the tropics (especially in areas of tropical rain forest) in which the climate is relatively seasonless. The converse is not, of course, true; within the tropics, trees within the savanna belt (exposed to a highly seasonal rainfall pattern) show a more or less regular leaf shedding and leaf flushing pattern with resulting growth rings in the wood. There appears to be no recognizable distinction between wood showing rings in response to a seasonal aridity against those associated with a cessation of growth during a seasonal cold period (the winter of temperate latitudes). It is significant that even in tropical latitudes where day-length may vary only between $11\frac{1}{2}$ and $12\frac{1}{2}$ hours through the year (as in southern Nigeria, Njoku, 1963), this seemingly inconspicuous day-length difference forms the basis of the regulation of leaf flushing, and hence presumably of cambial activity. As Njoku (1964) concludes, 'the effect of small differences in day-length on the onset of dormancy indicates that tropical trees are not very different in this respect from trees of higher latitudes, in many of which day-length is known to control bud dormancy'.
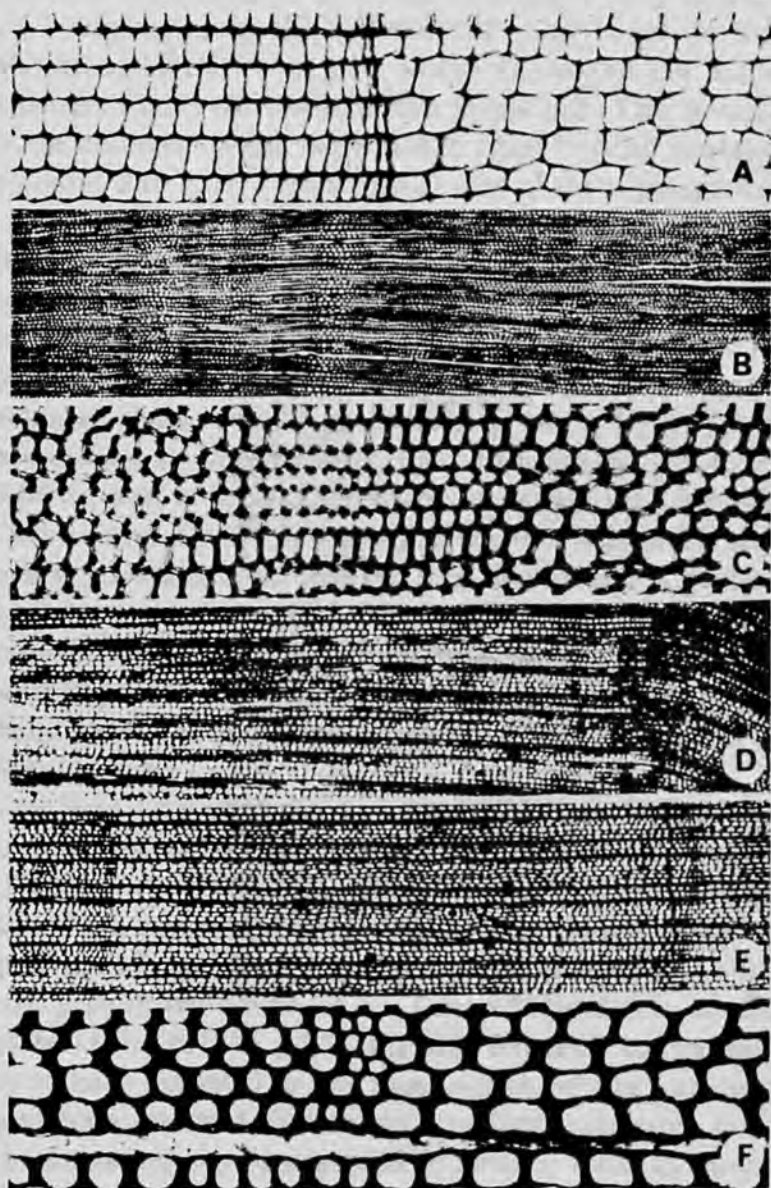
FIGURE 1   Transverse sections of extant pine wood and of North American Devonian woods. The radial direction of the wood lies across each photograph, with the centre of the stem to the left in each case.

A. *Pinus strobus*, grown in temperate latitudes, with clearly-defined seasonal growth rings, of which one is shown here; early wood at right, late wood at left. × 87.

B. *Pinus radiata*, from Hawaii (part of the specimen figured by Mirov, 1967, pl. 6–3B) with variation in tracheid diameter, but lacking clearly defined periodic growth rings. × 15.

C. Detail from the same area, a band of small-diameter tracheids, flanked by tracheids of larger diameter, with gradual transition between. × 87.

D. *Callixylon newberryi*, a progymnosperm wood from the Upper Devonian of southern Indiana (specimen kindly provided by Prof. C. A. Arnold). This specimen lacks growth rings through a radial thickness of 2 cm. × 15.

E. *Callixylon* sp., from the Upper Devonian of North America (Scott Collection, British Museum, Natural History, No. 3521), showing two of a number of weakly developed growth rings. × 15.

F. Detail of the left-hand growth ring from E. × 87.

Any experimental work leading to results that might help in the interpretation of fossil woods is complicated by the fact that the conifers are on the whole plants of temperate habitats, and the few that grow within the tropics are mainly upland plants growing at altitudes above the lowland rain forest belt. This habitat restriction probably reflects the conifers having been ousted from tropical lowland habitats during the Late Cretaceous and Early Tertiary expansion of the angiosperms. This means that we have no gymnosperms with the compact and regular wood of the conifers now growing in (and so adapted to) a humid, tropical lowland climatic pattern. So that while we can observe the behaviour of conifers planted under relatively uniform tropical climate, their response is complicated by their having been moved into a day-length environment to which they are not adapted. In spite of this, conifers grown under these circumstances show surprisingly uniform growth. Figure 1B shows part of the trunk of *Pinus radiata* (a pine endemic to California) grown in Hawaii (ca. 20° N latitude) at 1600 m, part of a specimen made available to us through the kindness of Prof. N. T. Mirov and Dr. G. Orbell. The section illustrated probably represents about three years' growth of a six year old tree. While there is evidently some fluctuation in tracheid diameter, the wood lacks clearly-defined growth rings such as those typically shown by *Pinus* species grown under a temperate seasonal climate (cf. Fig. 1A). It is of course possible that some of the growth fluctuation shown by the Hawaiian specimen reflects a residual endogenous rhythm of the type known to be operative in many biological systems.

At present we have little evidence concerning the time of appearance of hormonal and photoperiodic control in the course of plant evolution. Antevs (1953), in commenting on Palaeozoic woods lacking growth rings, suggests that 'these primitive trees might have been incapable of forming growth zones'. But those brown, marine algae which produce a large 'stem' (stipe) which increases in diameter over a period of years also show growth periodicity in the form of concentric banding of apparently seasonal character (Fritsch, 1945, p. 232, Fig. 85). Whatever mechanism is involved here, it seems likely to have operated in any algae which became sufficiently massive, and were growing under a seasonal climate, prior to land migration. In any event, in that brown algal organization can be regarded in Antevs' sense as 'more primitive' than that of gymnosperms, it seems that 'primitiveness' alone cannot be invoked to explain lack of response to a seasonal environment. It is still evidently possible that the earliest land plants with massive secondarily thickened stems, of the Late Devonian and Carboniferous, could respond to the seasonality of the environment only as a direct reaction to changing temperature, light, and moisture availability unregulated by a hormonal system involving day-length control. If this were so, then the evolution of such a photoperiodic mechanism may merely have strengthened rather than initiated the expression of a seasonal climate in the products of cambial activity.

Non-Climatic Factors in Growth Ring Formation

Against the background of an orderly mechanism governing growth ring formation in trees of higher latitudes in response to a strongly seasonal climatic pattern, a wide range of other phenomena may also influence the growth rings shown by an individual wood specimen. These include:

(*a*) The thickness of wood laid down in a given year; this is a function of the position of the sample in relation to the whole tree (see Kozlowski, 1971, chap. 3). On the trunk alone, the thickness of one year's increment is generally greatest at a short distance below the main shoot apex, after which the increment diminishes towards the base. Under closed forest conditions the annual growth increments, even under optimal climate, may become very reduced at the base of a large mature tree.

(*b*) Within a given region, local conditions of soil moisture (drainage) and other site factors (e.g. exposure to wind) influencing the microclimate will greatly affect the character of the growth increments. While this difference is of course a climatic environmental response, it means that two specimens of the same species of wood from trees within the same limits of regional climate will show different growth ring characteristics, due to such local effects.

(*c*) Various random events (either biological or physical in origin) may affect the character of wood—especially the removal of the leaves, as for example by insect attack, by forest fire or by storm damage. A young tree growing in mature forest might show sudden acceleration of growth (i.e. broader growth rings) on the death of a large neighbouring tree, by responding to removal of its shading and root competition. Destruction and the resulting opening up of forest following a major storm might similarly cause a surge of relatively broad growth rings in the surviving trees, followed by years of diminishing thickness as forest cover was once again established. All such fortuitous events would be recorded in the growth rings, superimposed, as it were, on the seasonal character of the regional climatic pattern and its idiosyncrasies from year to year.

In the case of fossil wood specimens, a further series of problems arise in trying to interpret apparent growth ring phenomena:

(*a*) The compaction of wood buried in accumulating sediment, before this is halted by the infiltration of petrifying mineral matter, may induce a series of crush structures which simulate growth rings (cf. lower dark zone in Fig. 2C). The extent and form of such crushing is also influenced by the extent of microbial degradation of the cell wall material. The occurrence of these artifact growth rings can usually be recognized by microscopic examination of thin sections; but the possibility of their being misconstrued as growth rings on casual observation or as seen under a hand lens is particularly important in assessing reports in the older literature, unsubstantiated by photomicrographs, of growth rings in fossil woods.

(*b*) A somewhat different problem in dealing with a fossil wood is the certainty with which its source may be recognized. Because of the possibility of long distance transport by water (river, or ocean currents) the source of a single wood specimen, drifted and incorporated in a sedimentary rock is inevitably uncertain. Obviously a true 'petrified forest' with tree-trunks in the position of growth is manifestly *in situ*, as for example in the succession of such occurrences in the Yellowstone National Park (Dorf, 1964). The same assumption might be made, with only marginally less confidence, for most Carboniferous coal-balls. But a single isolated petrified wood specimen in a marine sediment might well have come from some totally remote source.

(*c*) We still know relatively little about the general growth behaviour of many extinct plants. Tree-sized Carboniferous lycopods may show a zone of secondary wood which can be up to 2 or 3 cm in width, entirely free of growth rings (Fig. 2D). Before such wood is used as a basis for postulating the character of the contemporaneous
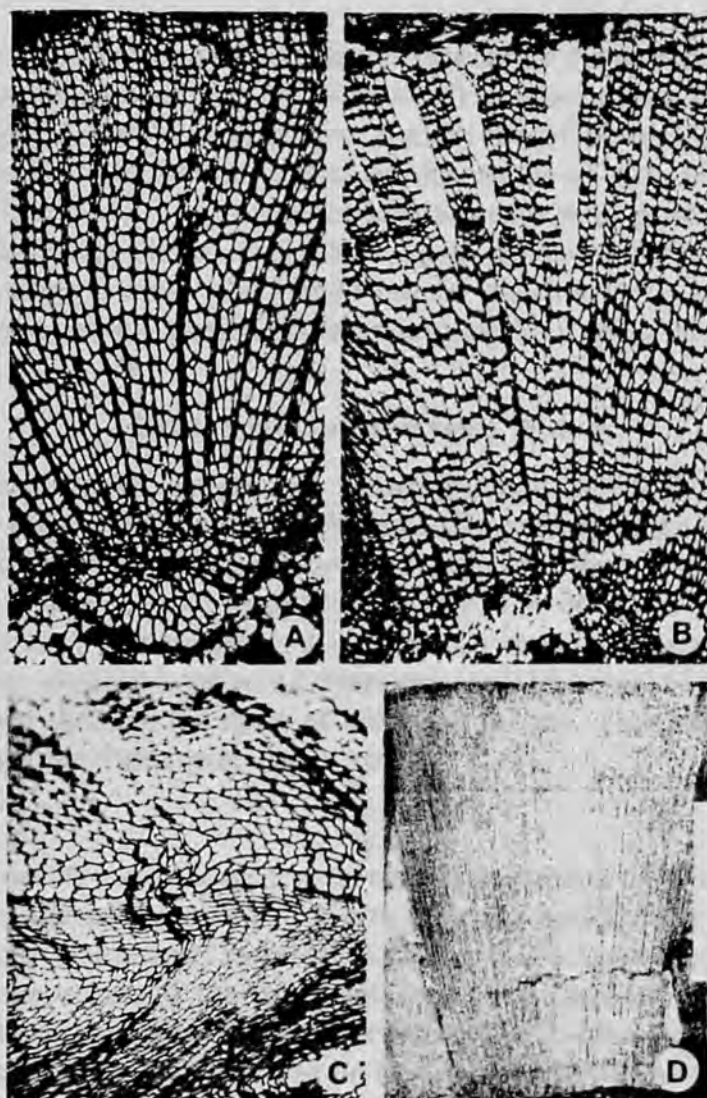
FIGURE 2   Transverse sections of Carboniferous and Permian or Triassic petrified woods. The radial direction of the wood is vertical, and the centre of the stem is directed downwards in each case.

A. A seed-fern stem, *Lyginopteris oldhamia*, from the Upper Carboniferous of Britain, showing more or less uniform secondary growth, but with some diminution of tracheid diameter towards the top of the figure. × 15.

B. Another specimen of the same species from the Upper Carboniferous of Britain, showing a clear interruption in growth, probably of traumatic nature; such features have been referred to as 'pseudo-annual rings' by Gothan (1911). The wedge-shaped gaps in the upper part of the figure were probably occupied by soft (parenchymatous ray) tissue in the life of the plant. × 15.

C. Part of a section of *Antarcticoxylon* sp. of Permian or Triassic age from the central range of the Horlick Mountains, Antarctica, showing detail of the boundary between two growth rings; early wood occupies the upper part of the figure, and the smaller-celled late wood of the previous year, the lower half. The dark area in the lowest quarter of the figure represents intensely crushed wood cells, one of a number of 'rings' of crushed tissue which resemble the true growth rings, and in this particular specimen considerably outnumber them (see Schopf, 1961). From a photograph taken by Prof. J. M. Schopf, and reproduced by kind permission of the United States Geological Survey. × 120.

D. Wood of *Lepidodendron* sp., from the Upper Carboniferous of Kansas. This stem shows two centimeters of uniform secondary growth. × 2.

climate, it is essential to know whether this represents the growth of several years (as might be supposed by analogy with living trees) or whether this represents the attainment of a single season's growth. The occurrence of several distinct reproductive phases (shown by zones of cone scars) on the trunks of such trees (cf. Chaloner & Boureau, 1967, Fig. 433) suggests that several years were probably involved in the growth of these large plants. But this is again involving deductions based on the behaviour of living plants, which may not be valid, and on present evidence the possibility of one-season growth however improbable cannot be entirely eliminated.

Observations on Fossil Wood

In trying to 'read back' past climate from specimens of fossil wood, it is perhaps appropriate to express the problem in the pervasive contemporary jargon of electronics. In these terms one might think of the direct climatic effect as constituting a 'signal' which we are trying to read through a background of 'noise', represented by the various non-climatic phenomena and fossilization aspects considered above. We then have to consider whether fossil wood offers any readable signal of palaeoclimate which can be discerned through the noise of unknown factors. This possibility will now be briefly examined for Palaeozoic fossil woods.

Devonian

The earliest occurrence of large tree trunks with extensive development of secondary xylem is in the Upper Devonian of North America and Europe. Elkins & Wieland (1914) describing 'Cordaitean' wood (actually wood of progymnosperms, the probable evolutionary antecedents of the living conifers) from Indiana, USA, figure clear but subdued growth rings; in one of their specimens (*Callixylon newberryi*) six rings occur within a thickness of about 5 cm. Arnold (1947) refers to this and other species of the same genus, and remarks on the occurrence of 'rings believed to be true annual rings in some Upper Devonian woods . . . the best examples being from western New York'. Growth rings similar to those figured by Elkins & Wieland and by Arnold are shown by an American specimen of *Callixylon* in the Scott Collection, illustrated on Fig. 1E. This specimen shows clearly defined growth zonation, but with only a very narrow zone of late wood, and with a generally less sharply pronounced junction between late and early wood than that shown in most extant conifers of the temperate zones (compare Figs. A and F in Fig. 1). The growth rings reported by Beck in root wood of *Callixylon* (Beck 1953) and by Matten and Banks (1967) in *Sphenoxylon*, both from the Upper Devonian of New York, are even less clearly pronounced. Other Devonian woods from the Euramerian area (eastern USA, Europe) show no detectable growth rings; for example, the holotype of *Callixylon trifilievi* Zalessky from the Upper Devonian of the Donetz Basin shows uniform structure (lack of growth rings) through a specimen representing 2.5 cm of growth (type material made available through the kindness of Dr. A. Takhtajan, Leningrad). Høeg (1941) figures a fragment of secondary wood of gymnospermous type from the Middle or Upper Devonian of Spitsbergen, showing no trace of growth zones within the limits of this rather small specimen (8 mm × 8 mm). This is of particular interest in being probably the most northerly specimen of a petrified Devonian wood.

From this rather limited evidence, it appears that at least some of the Late Devonian

progymnosperm woods were capable of developing growth rings (presumably representing some aspect of a seasonal climate); but within the specimens studied, the growth rings, where present, are less clearly defined than in analogous conifer woods from comparable latitudes, and in some cases are entirely lacking.

Carboniferous

In the Lower Carboniferous, similar rather weakly defined growth rings are reported in woods of gymnospermous type, even in relatively high latitudes (e.g. in *Eristophyton* from Scotland; Lacey, 1953); but by Upper Carboniferous time, a great diversity of large stems known from coal-balls are found to be lacking growth rings, from Kansas eastwards across the Mid-West of the United States, and from Europe eastwards to the Donetz Basin. It is significant that this lack of growth rings is a feature not only of gynmnosperm woods (e.g. *Dadoxylon*) but also of the woods of the tree-sized lycopods (e.g. *Lepidodendron*) *Calamites* (related to the living horse-tails) and the seed-ferns. A transverse section of part of the secondary wood of an Upper Carboniferous *Lepidodendron* from Kansas is shown in Fig. 2D, with completely uniform growth through a radial width of 2 cm. Referring to the gymnosperm wood of the genus *Dadoxylon*, Frentzen (1931) states that for the Carboniferous and Permian of the northern hemisphere, 'the overwhelming majority' of specimens of that genus are free of growth rings. A very small minority of Upper Carboniferous woods have been reported showing weak but discernible growth rings, a recent instance being those reported from a wood from Kansas by Baxter and Hartman (1954). Frentzen (1931) suggests that such occasional occurrences of growth rings in Upper Carboniferous woods must be attributed to specimens transported from upland habitats, in which the seasonal character of the climate might have been more strongly expressed than in the coal-forming swamp environment.

In addition to these supposedly allochthonous specimens which occasionally show weak but regularly recurrent growth rings, some of the large stems which are ubiquitous members of the swamp flora may also show interruptions of cambial activity. Figure 2A shows a transverse section of *Lyginopteris oldhamia* (one of the commonest plants of British coal-balls, and presumably a member of the actual coal swamp association) with apparently more or less uniform growth. The steady fall-off of tracheid diameter towards the periphery may represent the diminishing cambial activity of a finite (closed) growth system (cf. the growth of extant annual plants; see also Potonié, 1953). Figure 1B shows the same species, in which some interruption of cambial activity has produced a narrow zone of small-diameter tracheids, after which more or less normal tracheid size was resumed. This type of phenomenon (which is infrequent in *Lyginopteris*) is probably a result of damage (e.g. removal of a branch higher on the plant by fall of an adjoining tree, or by the occurrence of some localized pathological condition) rather than having any seasonal significance. Gothan (1911) refers to this type of traumatic growth interruption (which frequently extends only part way round the stem, and is never repeated periodically) as 'pseudo-annual rings.' Although apparently not related to any climatic cause, such traumatic growth phenomena are of interest in showing that some presumably external factor can produce response in cambial activity which then appears as a feature of the secondary growth in these plants. This supports the supposition that the general lack of growth rings in the plants of the Upper Carboniferous coal swamps genuinely reflects a seasonless climate rather than

some innate inability of the plants to express a seasonal fluctuation of growth activity.

Permian

As in the Upper Carboniferous, the majority of northern Permian woods are lacking in growth rings (Frentzen, 1931). Lemoigne & Tyroff (1967) and Schweitzer (1968) have recently reported exceptions to this, in weakly developed growth rings in Permian woods from Europe. Schweitzer remarks that his petrified conifer wood (from the German Upper Permian) suggests a climate of less pronounced seasonality than that of present-day central Europe. That author also makes the very pertinent comment that we cannot discern from the wood whether the seasonal fluctuation was principally one of moisture or of temperature. The situation for the northern hemisphere Carboniferous and Permian remains much as it was when summarized by Gothan in 1911; for this interval, periodic growth rings of plants with secondary growth is 'lacking or at best only doubtfully developed'.

The situation regarding Palaeozoic petrified woods from Gondwanaland is significantly different from that for the northern continents. Woods from the Gondwana area ranging in age from 'Carbo-Permian' to 'Permo-Triassic' all show growth rings, in some cases with very pronounced differentiation of early and late wood. Of particular interest are records of Carbo-Permian woods showing growth rings from Antarctica, since the south pole actually fell within or close to this continent during that interval (see, for example, the Permian and Triassic palaeo-continent positions in Dietz and Holden, 1970). Schopf (1961) has published an illustration of one of the best-documented occurrences of growth rings in an Antarctic wood. One of his photographs of *Antarcticoxylon* (of undifferentiated Permo-Triassic age, from the Horlick Mountains, Antarctica) is reproduced in Fig. 2C. In addition to the crush zones (resulting from compaction in the incorporating sediment at the time of fossilization) which superficially simulate growth rings, there are also clear genuine growth rings. These true growth rings are considerably outnumbered by the crush zones. Other petrified Antarctic wood, dated more securely as Permian, is figured by the same author (Schopf, 1971, pl. 4, Fig. 13) from Mount Augusta, showing part of a clearly defined but inconspicuous growth ring in an unassigned gymnosperm stem. Schopf (1961), commenting on growth rings in the Permo-Triassic petrified wood from the Horlick Mountains, remarks that 'they show seasonal periodicity and vigorous annual increments of growth comparable to that of coniferous trees growing to-day under favourable conditions in temperate climates. The occurrence seems decidedly anomalous'.

Conclusions and Future Work

The Palaeozoic record of growth rings is one of very weak and sporadic occurrence from the Upper Devonian through Carboniferous into the Permian for Europe and North America. Antevs' (1953) suggestion that this is a result of these Palaeozoic plants being too 'primitive' to show growth rings seems implausible in the face of the occurrence of regular but subdued growth rings in a few instances and in the traumatic growth rings which may be seen in occasional specimens. The lack of growth rings in Euramerian Upper Palaeozoic woods contrasts with later Mesozoic and Tertiary woods from the same area which in general show clear growth rings. In Gondwanaland, in

contrast, clearly-defined growth rings are present in woods ranging in age from Permian to Permo-Triassic. These observations seem consistent with a Carboniferous and Permian equator (and associated humid tropical belt) passing through eastern North America and Europe, as suggested on palaeomagnetic and other evidence. The general prevalence of strong growth rings in Late Palaeozoic woods from the Gondwana continents is consistent with their position in 'temperate' latitudes through that interval. But the thickness of annual growth increments occurring in Antarctica in relative proximity to the contemporaneous south pole cannot be explained simply by relative polar and continental movement alone, superimposed on the present pattern of climatic distribution.

There is evidently much scope for further work in attempting to elucidate the relationship between palaeoclimate and growth rings in fossil woods. Only the Palaeozoic data have been briefly considered here; far more data are available for Mesozoic and Tertiary woods. The prime need is for extended knowledge of the characteristics of growth rings (in both gymnosperms and angiosperms) under a wide range of climatic conditions. For example, it would be of interest to observe the effect of a high latitude day-length regime under more uniform temperature conditions than prevail in those latitudes now. There is also need for a quantitative treatment of growth ring characteristics which could be used to effect direct comparison between Recent and fossil woods. The variance of such simple parameters as growth ring width, or the ratio of early wood to late wood width, if taken for a large number of fossil specimens, might offer a basis for discriminating between extremes of oceanic and continental climate, at the same latitude. As with other aspects of palaeobotany, the potential of the fossil material will only be adequately realized when we have fuller understanding of the corresponding features of living plants.

Acknowledgements

References

Antevs, E., 1917. Die Jahresringe der Holzgewachse und die Bedeutung derselben als Klimatischer Indikator. Eine Literaturzusammenstellung, *Progr. Rei Bot.*, **5**, 285–386.
Antevs, E., 1925. The climatological significance of annual rings in fossil woods, *Amer. J. Sci.*, **9**, 296–302.
Antevs, E., 1953. Tree rings and seasons in past geological eras, *Tree-ring Bulletin*, **1953**, 17–19.
Arnold, C. A., 1947. An Introduction to Paleobotany. New York, 433 pp.
Baxter, R. W. and Hartman, E. L., 1954. The coal-age flora of Kansas—V. A fossil coniferophyte wood, *Phytomorphology*, **4**, 316–25.
Beck, C. B., 1953. A new root species of *Callixylon*, *Amer. J. Bot.*, **40**, 226–33.
Chaloner, W. G. and Boureau, E., 1967. Lycophyta. In Traité de Paléobotanique, edited by E. Boureau, 2, 435–802. Masson et Cie, Paris.

Dietz, R. S. and Holden, J. C., 1970. The break-up of pangea, *Sci. Amer.*, **223**, 30–41.

Dorf, E., 1964. The petrified forests of Yellowstone Park, *Sci. Amer.*, **210**, 107–14.

Elkins, M. G. and Wieland, G. R., 1914. Cordaitean wood from the Indiana black shale, *Amer. J. Sci.*, **38**, 65–78.

Frentzen, K., 1931. Die palaeogeographische Bedeutung des Auftretens von Zuwachszonen (Jahresringen) bei Hölzern der Sammelgattung *Dadoxylon* Endl. aus dem Carbon und dem Rotliegenden des Oberrheingebietes, *Centralbl. Mineral., Geol. Palao., Jr.*, **1931A**, 617–24.

Fritts, H. C., 1966. Growth rings of trees: their correlation with climate, *Science*, **154**, 973–9.

Fritts, H. C., 1972. Tree rings and climate, *Sci. Amer.*, **226**, 92–100.

Fritsch, F. E., 1945. Structure and Reproduction of the Algae. II. Cambridge University Press, 939 pp.

Gothan, W., 1908. Die Frage der Klimadifferenzierung im Jura und in der Kreideformation im Lichte paläobotanischer Tatsachen, *Jb. Kongl. Preus. Geol. Landesanst.*, **29**, 220–42.

Gothan, W., 1911. Die Jahresringlosigkeit der paläozoischen Bäume und die Bedeutung dieser Erscheinung für die Beurteilung des Klimas dieser Perioden, *Naturwiss. Wochenschr.*, *N.F.*, **10**, 1–13.

Høeg, O. A., 1942. The Downtonian and Devonian Flora of Spitsbergen. Norges Svalb. Ishavs-Undersok., **83**, 1–228.

Kozlowski, T. T., 1971. Growth and Development of Trees, 2. Academic Press, New York, 514 pp.

Kräusel, R., 1961. Palaeobotanical evidence of climate. *In*: Descriptive Palaeoclimatology, edited by A. E. M. Nairn, pp. 227–254.

Kräusel, R., 1964. Introduction to the palaeoclimatic significance of coal. *In*: Problems in Palaeoclimatology, edited by A. E. M. Nairn, pp. 53–56.

Lacey, W. S., 1953. Scottish Lower Carboniferous Plants: *Eristophyton waltoni* sp. nov. and *Endoxylon zonatum* (Kidston) Scott from Dunbartonshire, *Ann. Bot. N.S.*, **17**, 579–96.

Lemoigne, Y. and Tyroff, H., 1967. Caractères anatomiques d'un fragment de bois appartenant a l'èspèce '*Walchia (Lebachia) piniformis*' du Permien d'Allemagne, *Comptes rendus Acad. Sci.*, **265**, 595–7.

Mägdefrau, K., 1968. Paläobiologie der Pflanzen. 4th ed. G. Fischer, Jena, 549 pp.

Matten, L. C., and Banks, H. P., 1967. Relationship between the Devonian progymnosperm genera *Sphenoxylon* and *Tetraxylopteris*, *Bull. Torrey Bot. Club*, **94**, 321–33.

Mirov, N. T., 1967. The Genus *Pinus*. Ronald Press, New York, 602 pp.

Njoku, E., 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. I. Observations on mature trees, *J. Ecol.*, **51**, 617–24.

Njoku, E., 1964. Ibid., II. Observations on seedlings, *J. Ecol.*, **52**, 19–26.

Potonié, R., 1953. Zur Paläobiologie der karbonischen Pflanzenwelt. Ökologische Zeugnisse der Karbonflora zur Kohlenbiogonie, *Die Naturwissenschaften*, **4**, 119–28.

Richards, P. W., 1957. The Tropical Rain Forest. Cambridge University Press, 450 pp.

Seward, A., 1892. Fossil Plants as Tests of Climate. Clay & Sons, London, 151 pp.

Schopf, J. M., 1961. A preliminary report on plant remains and coal of the sedimentary section in the Central Range of the Horlick Mountains, Antarctica. Inst. Polar Studies, Rept. 2. 61 pp.

Schopf, J. M., 1971. Notes on plant tissue preservation and mineralization in a Permian deposit of peat from Antarctica, *Amer. J. Sci.*, **271**, 522–43.

Schwarzbach, M., 1963. Climates of the Past. Van Nostrand, London, 328 pp.

Schweitzer, H.-J., 1968. Die Flora des oberen perms in Mitteleuropa, *Naturwiss. Rundschau*, **21**, 93–102.

Stokes, M. A. and Smiley, T. L., 1968. An Introduction to Tree-ring Dating. University of Chicago Press, 73 pp.

Unger, D. F., 1847. Uber den Grund der Bildung der Jahreslagen dicotyler Holzpflanzen, *Bot. Zeit.*, **5**, 265–72.

Wareing, P. F. and Phillips, I. D. J., 1970. The Control of Growth and Differentiation in Plants. Pergamon Press, Oxford, 303 pp.

Zimmermann, M. H. (Ed.), 1964. The Formation of Wood in Forest Trees. Academic Press, New York, 562 pp.