

CAMBIAL ACTIVITY AND JUVENILE WOOD FORMATION IN TEAK

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PEECHI, THRISSUR

January 1998

Pages: 41

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Abstract

One effective silvicultural tool for improving the teak timber supply is shortening rotation period of plantations. Growth in such managed plantations would be so rapid that rotations anticipated are as short as 20-30 years in contrast to the existing practice of 60-70 years. As the trees at that age contain higher proportion of juvenile wood, knowledge of growth periodicity of relatively young trees and the pattern of juvenile wood production is crucial for timber management in teak plantations.

The specific objectives of the present study are: (a) to determine the growth (cambial) periodicity and influencing factors in juvenile wood production including false ring formation in teak (b) to determine the age at which teak trees stop producing juvenile wood and begin to form mature wood and (c) to evaluate the differences in size and proportion of different secondary xylem (wood) elements, microfibrillar angle, specific gravity and bending strength (Modulus of rupture) between the juvenile and mature wood.

Cambial periodicity was followed for two consecutive annual cycles (during 1994 and 1995), in the trees marked in each plantation of four age groups from three different locations (Nilambur, Walayar and Peechi as Locations I, II and III respectively) of diverse environmental conditions in Kerala. To determine the age of demarcation between juvenile and mature wood, timber samples were collected from 65-year-old plantations located in Nilambur, Konni and Arienkavu.

Cambial activity was influenced by the age of the tree. Cambium was active for longer period of the annual cycle in juvenile wood formation than in mature wood production of the trees. Pre-monsoon showers during March-April, influenced the cambial activity and broke dormancy earlier. Irrespective of age and location, a peak period of wood production was recorded during June-July, when the cambium was 15-20 layered, correlating with the highest amount of rain fall of the year. Narrowing of cambial zone was observed from September onwards; and by the time the cambium had attained dormancy during November-December, the zone was found to be reduced to 10 layers of radially flattened cells. Wider growth rings were produced in juvenile trees of 7- and 13-year age groups and so is the amount

growth ring. This is attributed to the prolonged period of cambial activity of juvenile trees. Thus the late onset of dormancy influenced the quality of wood as evidenced by a higher proportion of latewood in the growth ring. Artificial drought induction and field transplantations interrupted the active growth causing false ring formation in the juvenile wood of 2- and 3-year-old seedlings. Insect defoliation in 8-year-old trees did not induce false ring formation while decreasing growth rate of the trees without affecting specific gravity, size and proportion of vessels and cell wall percentage. The data obtained from both cross-dating of plantations and controlled experiments, including induced drought, showed that rain fall during dry period, drought during active growing season, polybag/field transplantation of seedlings are the important causative factors of frequent false ring formation in teak. This new information will be of particular interest to dendrochronologists in tree ring analysis. The observations on shorter duration of cambial activity in drier locality and drought/irrigation effects on cambial activity and wood formation will throw light on management strategies needed for commercial teak plantations.

The age of demarcation between juvenile and mature wood in teak trees was found around 20-25 years depending on growth rate. The fast growing trees had a tendency to prolong the period of juvenile wood formation. The current finding on maturation age of wood formation, as 20-25 years, will be useful for plantation managers in fixing rotation cycles for production of desired wood quality or manipulation of juvenile wood proportion of the timber to be harvested.

The juvenile wood in teak is characterised by wide growth rings, wide microfibrillar angle, small diameter and low percentage of vessels and high percentage of cell wall with short fibres as compared to mature wood. Because mechanical properties such as bending strength of slow grown trees and compression strength (parallel to grain) did not differ consistently between juvenile and mature wood, the former is not necessarily always inferior in timber strength to mature wood.

Keywords: *Tectona grandis*, cambium, juvenile-mature wood, false ring, wood property, tree-ring analysis, wood formation, environmental factors, timber management.

1. Introduction

It is a known fact that diameter growth of trees is brought about by the addition of new cells derived from the cambium. Knowledge of annual increment / growth ring formation in trees is essential not only to determine the tree age and growth rate but also wood production in managed forest stands. In such managed plantations, forest managers will aim at maximizing wood production by intensive silvicultural practices which accelerate the tree growth for early harvesting. The pattern of wood production and the structure of wood formed in such relatively young plantations are likely to be quite different from those of naturally grown trees. Knowledge of growth periodicity of young trees and the pattern of juvenile wood formation is therefore crucial for timber management in teak plantations.

Wood quality depends partly on wood structure (proportions of early- and latewood as well as dimensions of cambial derivatives such as vessels, fibres, rays and axial parenchyma) and partly on tree form (straightness and taper of the bole influencing grain angle; branchiness determining knot size and frequency, etc.). Both aspects of wood quality are affected by the silvicultural treatments that modify the form of the crown and the environment around it (Larson 1969).

2. Literature review

2. 1 Cambial Activity and Wood Production

Most of the research on cambial growth and wood production has gone to the trees of temperate zones (Brown 1971). Investigations of the cambial physiology of temperate trees reveal a close relationship between bud activity and cambial activity (Tomlinson and 1981). Cambial activity commences in the opening of buds and then spreads basipetally over the old wood of branches and trunks (Priestley 1932; 1935; Priestley et al. 1933). However, in many ring-porous species, cambial reactivation spreads so quickly that it appears simultaneous throughout the tree in twigs, branches and the main stem (Wareing 1951).

2.2 Growth Ring Formation

Annual ring formation is generally regarded as a result of periodicity in the types of cells formed by the cambium. Any environmental effect such as drought, photoperiod or temperature would affect growth ring formation indirectly through its direct effects on shoot growth and foliar development and subsequent levels of IAA. Larson (1960) succeeds in producing false rings in conifers by the manipulation of photoperiod and foliar development affecting hormonal regulation.

Relatively little is known about the patterns of cambial activity including both initiation and cessation of growth and hence the patterns of early- and latewood formation in tropical trees. On the other hand, available data indicate that cambial activity generally follows the foliar development initiating first in the twigs and then in the main bole in many tropical species in contrast to the simultaneous cambial reactivation in teak throughout the stem as reported for other ring porous species (Chowdhury 1939).

Radial growth in tropical trees may be annual, semiannual, irregular or continuous (Tomlinson and Longman 1981). As early as 1856, Brandis concludes that growth rings are formed annually in teak. Chowdhury (1939) states that the boundary of growth rings of teak can easily be detected by the presence of large earlywood pore zone embedded in initial parenchyma. Where as in false rings the vessels do not form a ring nor are they embedded in initial parenchyma although Venugopal and Krishnamurthy (1987) do not observe initial parenchyma in the growth rings of the teak twigs. According to Chowdhury and Rao (1949), young or juvenile wood produced in teak saplings usually show discontinuous or often continuous false growth rings.

In his observation on the progress of growth throughout the year, Chowdhury (1939) concludes that in ring-porous timbers like teak, initial growth is fast during the formation of early pores during July, then it slows down before the final rapid growth that occurs before the cessation of cambial activity sometime during the second week of November. The period of maximum growth is recorded in the months of September and October. On the other hand, extended period of xylem production for 8 months in teak is reported by Venugopal and

Krishnamurthy (1987). The cambial reactivation and xylem differentiation start generally one month after the onset of bud break during June (Rao and Dave 1981).

It is however yet to be shown in teak whether this variation in the periodicity of cambial activity is due to the result of interactions between internal hormonal and nutritional balances, age or environmental conditions affecting various physiological processes. Chowdhury (1939) has already given an indication that locality plays an important role in the progress of cambial activity particularly due to temperature differences. Cambial reactivation usually starts when the temperature is highest of the year but local temperature has no direct relation to cessation of growth. However, no immediate effect of local rainfall and temperature has been noticed in the diameter growth of teak although Anand (1979) observes enhanced cambial activity after the beginning of rains in many Indian tree species.

2.3 Juvenile vs. Mature Wood

Juvenile wood is that wood formed in proximity to the crown when the tree is young. The period of juvenile wood formation is variable for different species and between trees of a species. Compared to mature wood, juvenile wood is generally characterized by short fibres and vessel elements, thin walled and small diameter cells with large fibril angles and high proportion of fibres and lower proportions of vessels (Bendtsen 1978). The patterns of length variation of fibres within the growth rings may differ between juvenile and mature wood (Taylor 1976).

With regard to the extent of juvenile wood formation in Indian timbers, no adequate data are available. In many tropical Indian tree species including teak, the most common pattern of radial variation observed is an initial increase in fibre length during the juvenile phase of wood formation (Bhat et al. 1989). Therefore there is an urgent need to characterize the juvenile wood of Indian tree species.

It is not known how age affects the cambial periodicity of teak. Whether it will follow a different pattern in the formation of juvenile wood as compared to mature wood is yet to be established.

Estimation of the differences in size and proportion of different cambial derivatives between juvenile and mature wood will be useful in assessing the wood quality and utilisation potential of juvenile wood. Knowledge of rhythm of cambial activity and the influencing factors (both external and internal) is too limited to show why more than one ring per year is formed often in teak as false rings which would make the procedure of age and growth rate determination rather difficult.

3. Objectives

The specific objectives of the present study are:

- (a) to determine the cambial periodicity and influencing factors in juvenile wood production including false growth ring formation
- (b) to determine the exact age at which teak trees stop producing juvenile wood and begin to form mature cambial derivatives
- (c) to evaluate the differences in size and proportion of different secondary xylem elements, microfibrillar angle, specific gravity and bending strength (modulus of rupture) between the juvenile and mature wood.

4. Materials and Methods

4.1 Field Experiments

To study the periodicity of cambial activity during two consecutive years (1994 and 1995), five trees were marked in each plantation of known age at three different locations (Nilambur , Walayar and Peechi as Locations I, II and III respectively) of diverse environmental conditions in Kerala. From Location I, 7-, 13-, 20- and 40-year-old plantations were selected while Locations II and III were represented by 13 - and 7-year-old plantations respectively. This sampling method was followed so as to enable comparison of juvenile and mature trees within and between geographic locations (Table 1).

To study the structure of false rings and their influencing factors, cross sectional discs of 8- and 12-year-old juvenile trees from Location I were also examined. To bring out the effect of rainfall on false ring formation, rainfall data were recorded for the corresponding years of growth. To study the effects of insect defoliation on false ring

formation and wood anatomy of juvenile teak, materials were obtained from 8-year-old plantation in Location I. When the trees were 4-year-old, some of the experimental plots had been given artificial protection against insect defoliation by spraying an insecticide (protected trees), while some other plots (control trees) had been left unprotected (Nair *et.al.* 1985). At the end of the eighth year, the trees were felled. About 10 cm thick cross sectional discs were cut at breast height, from 102 trees representing the protected as well as the control populations of which thirty discs were selected at random from each treatment for the study.

To bring out the effect of drought on false ring formation, artificial drought was induced for 1-year-old seedlings during the peak period of growth, by keeping them in a glass house without watering for 40 days, and then followed by resumption of irrigation.

To determine the age of demarcation between juvenile and mature wood, materials were collected from 65 year-old plantations from Locations I, IV and V (Table 1). From each location two each of the fast and slow grown trees were selected. This was done with a view to determining the effects of both location and growth rate on the period of juvenility.

After drawing a demarcation point of age between juvenile and mature wood, the differences in size and proportion of different anatomical, physical and mechanical properties were evaluated between the two.

Table 1. Environmental conditions and ages of trees sampled from different locations for the study

Factor	Location I (Nilambur)	Location II (Walayar)	Location III (Peechi)	Location IV (Konni)	Location V (Aryankavu)
Elevation, m	100	215	175	300	310
Soil	Well drained alluvial	Black sandy loam	Deep blackish sandy loam	Sandy loam rich in organic matter	Sandy loam
Mean annual rainfall, mm	2600	1200	2400	2900	2700
Temperature range, °C	17-37	21-41	21-32	12-35	12-33
Age Group, yr	7,8, 12, 13,	13	7	65	65

4.2 Laboratory Procedure

To follow the periodicity of cambial activity, cubical samples of cambial tissues along with the outer bark and inner sapwood were chiseled out at breast height from the selected trees at monthly intervals for two consecutive years. These samples were fixed in FAA in the field itself. After 3 days the samples were transferred to 70% ethyl alcohol for preservation. Transverse sections of 20 micrometer thickness were cut on a Reichert sliding microtome. The sections were double stained using Achrydin - Chrysoidin and Astra blue and after dehydration, in an alcoholic series, sections were transferred to xylene and mounted in DPX. To bring out the relationships between cambial

periodicity and wood formation, parameters such as ring width and early wood and late wood proportions were quantified with the help of a Video Image Analyzer (Leica Quantimet 500+).

To study the pattern of false ring formation, the cross sectional discs were sanded and observed under dissection microscope. False rings were distinguished from true annual rings and confirmed further by observing transections of each annual ring taken from two opposite radii of the discs, under light microscope. The incidence of false ring formation was then correlated to the rainfall of the corresponding year's growth.

To bring out the effect of insect defoliation on juvenile wood anatomy, various properties such as vessel diameter, vessel %, cell wall %, ring width and specific gravity were compared between the 'protected and 'control' samples. The anatomical parameters were quantified from 20 micrometer thick transections using Leica Image Analysis System. Specific gravity was determined by gravimetry. While estimating ring width, the early- and latewood proportions were first determined after making an arbitrary demarcation between the two. The earlywood was identified with wide vessels, parenchyma and thin walled fibres and the latewood with narrower vessels and thick walled fibres. Ring-wise microscopic examination was carried out in both the 'protected' and 'control' samples to determine whether insect defoliation had caused the false ring formation.

To determine the demarcation point of juvenile wood from mature wood, various anatomical, physical and mechanical properties were quantified and analysed. A 2 cm.- wide radial segment was cut from the selected discs. Quantifications were made in eight positions corresponding to the annual rings 1,5,10,15,20,25,30 and 60 from pith. 20 micrometer thick transverse section of each annual ring was cut on a Reichert sliding microtome. The sections were stained, dehydrated and mounted in DPX. Anatomical properties, viz. microfibrillar angle, vessel diameter, vessel %, cell wall %, ray % and ring width were quantified on the image analyser. Fibre length variation was determined for trees from locations I and IV after macerating the fibres by Franklin's method (1945). Microfibrillar angle was determined by Senft and Bendtsen's technique (1985).

4.3 Mechanical Testing

The basal billets of 1.4 m length were converted into pieces of 3 x 3 cm cross section to prepare test samples from pith to periphery in one radial direction selected randomly just below the breast height. From each radius, samples (with the size of 2 x 2 x 30 cm) were tested for static bending (fibre stress at elastic limit-FS-EL, modulus of rupture-MOR, modulus of elasticity -MOE) and compression parallel to grain (maximum crushing stress - MCS). The sample size of 2 x 2 x 8 cm has been used for compression test. Small pieces from tested samples were cut to determine the wood density in air dried condition. Mechanical testing has been done using a Universal Testing Machine.

4.4 Statistical Analysis

To study the effect of insect defoliation on juvenile wood, the quantitative features were compared between the protected and control trees by “t” tests. To demarcate the juvenile wood from mature wood, segmented regression analyses were used to describe the relation between the measured properties as dependant variables and cambial age (rings from pith) as independant variable. Various models were fitted to the data depending on the pattern^{ns} of radial variation in the properties studied. The analyses were carried out using spss/pc+ NLIN procedure (SAS Institute Inc. 1985). Significant models with only those properties showing definite radial patterns of variation were used to determine the critical age of demarcation. A quadratic model with plateau was fitted to the data for variables viz. vessel diameter (fast grown trees of Locality III, microfibril angle of fast and slow grown trees of Localities II and III) The model is,

$$Y = a + b x + c x^2 \quad \text{if } x < x_0$$
$$Y = p \quad \text{if } x > x_0$$

where,

Y = property of interest

x = age

x₀ = age of demarcation

a, b, c = parameters

p = plateau

For variable viz. microfibrillar angle (fast and slow grown trees of Locality I) an exponential model with plateau was fitted to the data. The model is,

$$Y = a.e^{bx} \quad \text{if } x < x_0$$

$$Y = p \quad \text{if } x > x_0$$

A reciprocal model with plateau was fitted to the data for the variables such as fibre length (fast and slow grown trees of Localities I and II) The model is,

$$Y = a + b/x \quad \text{if } x < x_0$$

$$Y = p \quad \text{if } x > x_0$$

A linear model with plateau was fitted to the data for fibre length (for slow-grown, locality-I). The model is given as,

$$Y = a + b x \quad \text{if } x < x_0$$

$$Y = p \quad \text{if } x > x_0$$

Thus for the ages less than the critical age (x_0), the equation expressing the relationship of the measured properties and the age is quadratic, exponential, reciprocal or linear and for the ages greater than or equal to the critical value (x_0) the equation is plateau.

After demarcating the juvenile wood from mature wood, the mean values for selected properties of juvenile and mature wood were estimated.

5. Results and Discussion

5.1 Seasonal activity of the cambium

The cambium in teak consists of 6-10 layers of radially flattened cells with thick radial walls during the dormancy state (Fig. 1). At the onset of cell divisions, the cambial cells swell, the radial walls become thin (Fig. 2) and the bark separates easily from wood. The tendency of bark slippage is maximum during the period of expansion of the zone of periclinal divisions as Bannan (1955) observed in *Thuja occidentalis*. The actual line of separation in teak lies immediately to the xylem side of the cambium as it is the zone of greatest weakness where the newly formed xylem elements have not begun the secondary wall formation. It was observed that after a period of dormancy, cambium resumed activity during March-April. Irrespective of age and location, a peak period of cambial activity was seen during June-July, when the cambium was 15-20 layered (Fig. 3). The narrowing of the zone of periclinal division was found from September onwards and by the time the cambium had attained dormancy, the zone was found to be reduced to 6-10 layers of cells.

5.2 Tree age vs cambial periodicity

From Fig. 4, it is evident that the 7- and 13-year-old juvenile trees in location I showed prolonged period of cambial activity exhibiting only 2-3 months of dormancy. But the 20- and 40-year-old trees had a comparatively long dormancy period. Here it is obvious that the age of the tree influences the duration of cambial activity; greater the age, shorter the duration. This is in agreement with the results discussed by Eames and Mac Daniels (1947) in temperate tree species. Further, observations made on a 147-year-old tree in Location I revealed that the cambium was active only for a short period (April-October), thus having about five months of dormancy period. When 1-year-old seedlings of teak were observed it was found that a total state of dormancy was lacking in them, rather, the cambium was active but to a lesser degree during January and February. A distinct ring porosity was not evident in the first formed ring which also could be considered as a criterion to decide the absence of a complete cambial resting period in

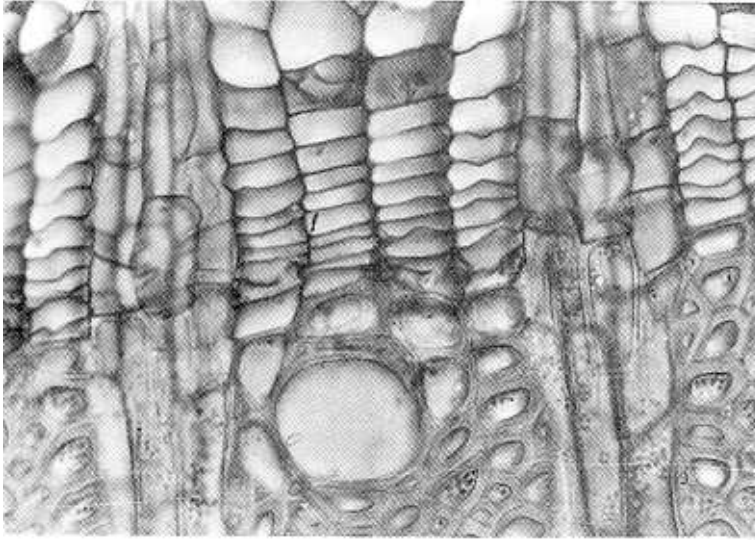


Fig.1 Dormant cambium of 7-year-old teak, x 30

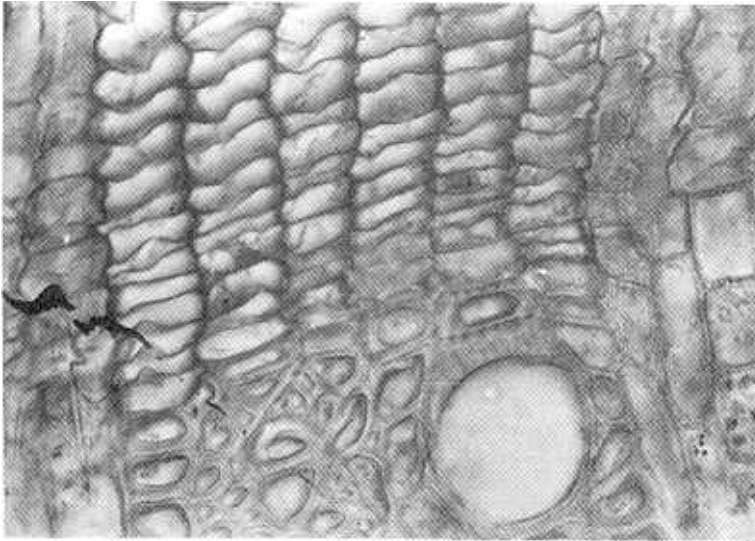


Fig.2 Reactivation of cambium after a period of dormancy, x 30

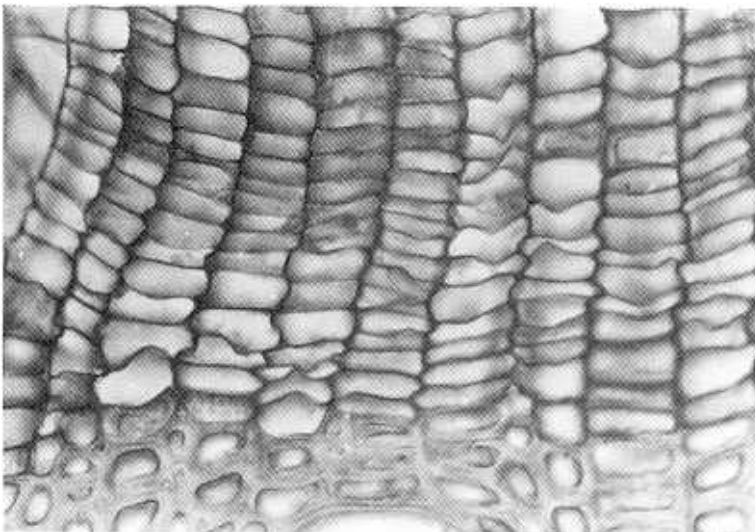
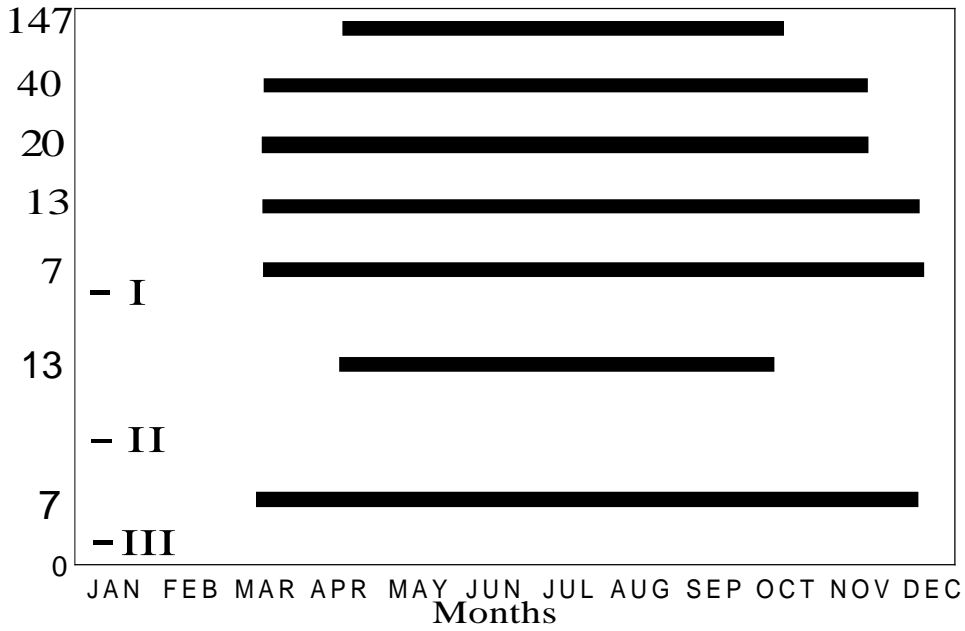


Fig.3 Cambium showing peak period of activity, x 30

Age & Locality



Age(yr) ,Locality

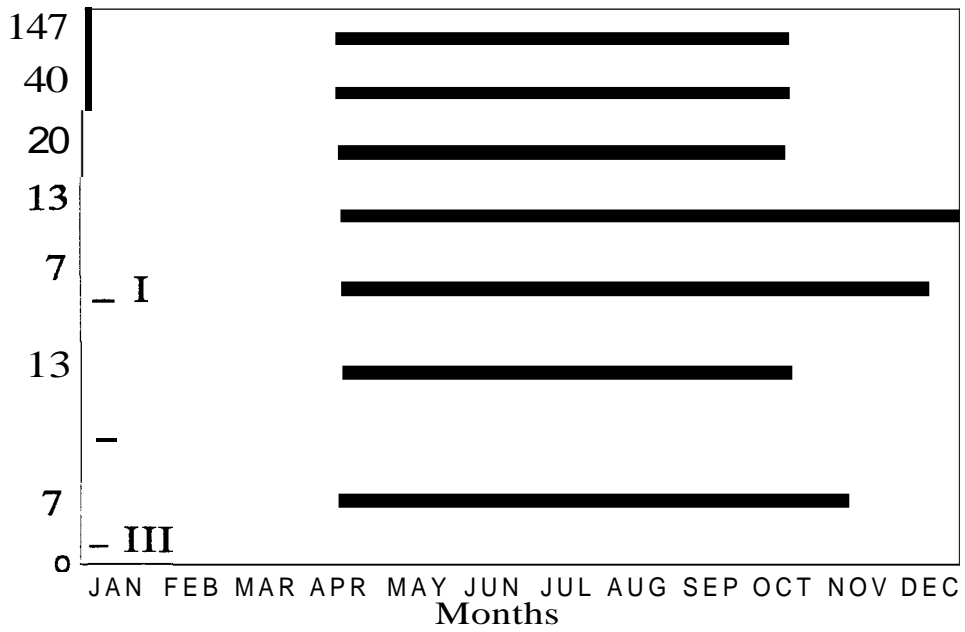
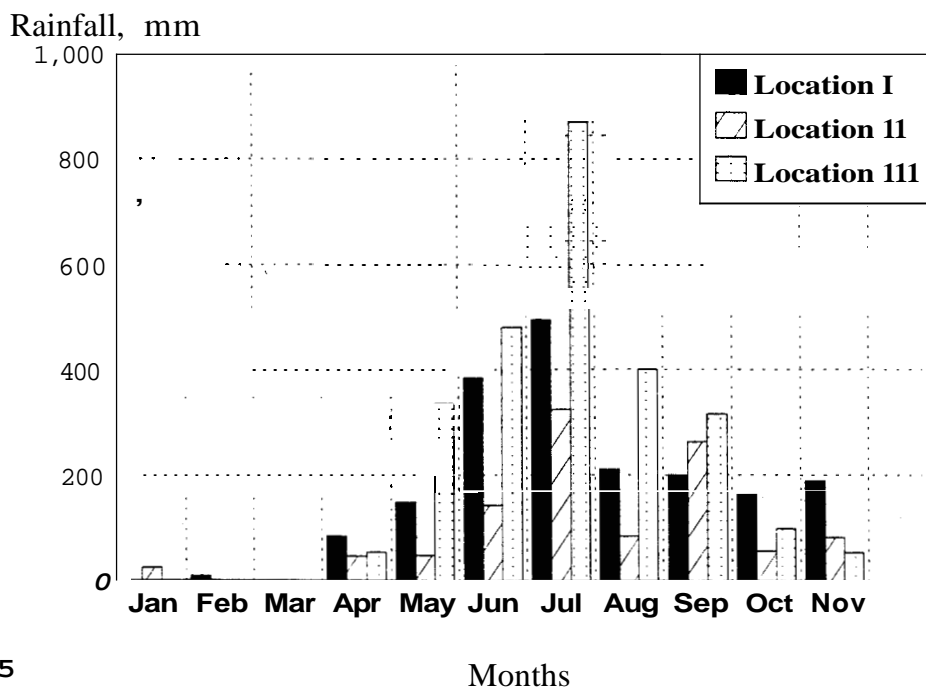
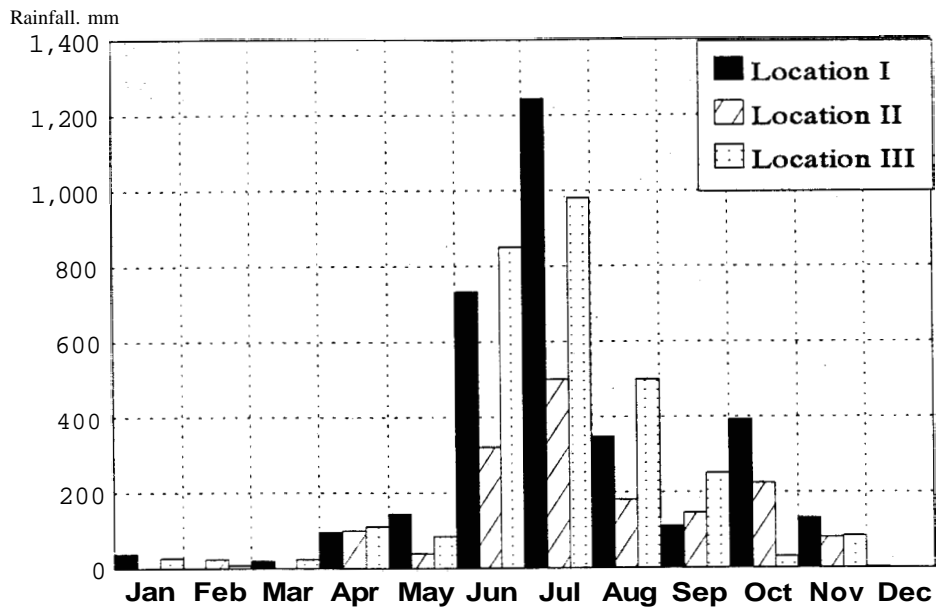


Fig 4 Cambial periodicity in the years 1994 (top) and 1995 (bottom)



1995

Months

Fig 5. Monthly rainfall in three locations in the years 1994 and 1995

1-year-old seedlings. Similarly, extended period of xylem production was reported in the twigs of teak although age was unknown (Venugopal and Krishnamurthy 1987).

5.3 Rainfall vs cambial periodicity

The effect of the local environmental factor especially the mean annual rainfall on cambial activity is clear from the observations in the 13-year-old juvenile trees of location II (where the mean annual rain fall was less than half of location I or III), where they had only a brief period of activity as compared to the same aged trees in location I. In location II, cambial activity commenced in April and continued until the end of October thus remaining quiescent for the rest of five months. Here it deserves mention that pre-monsoon showers during the onset months initiated the cambial activity in the different localities studied. During the year 1994, cambial activity commenced in the trees in locations I and III in March itself after the first rains but in 1995, the dormancy was broken only in April, after the onset of rains (Fig 5). In location II, the cambium became active only after receiving the first showers in April in both the years observed .

5.4 Cambial activity and wood formation

New xylem with large vessels was formed during the two months after cambial reactivation. In the younger trees earlywood formation was completed in the second month itself after cambial reactivation, whereas in the older trees (40-year-old) it extended up to the end of the third month. Latewood formation was very rapid in the younger trees. Widest rings were produced in 7-year-old trees in location I. They also exhibited the maximum latewood in their annual rings followed by the 13-year-old trees (Table 2). This can be attributed to the prolonged period of cambial activity in the younger trees. Thus the late onset of dormancy influences the quality of wood as evidenced by a higher proportion of latewood in the growth ring. This is reflected in the trees in location II where there was earlier onset of dormancy as compared to the same aged trees in location I. The mean latewood proportion built up during 1995 was 76 % as against 90% in Nilambur trees. Similarly the trees in location III had a lower latewood percentage than the same aged trees in location I, which is again the result of an earlier onset of cambial

dormancy in the former. The 7- and 13-year-old trees in location I exhibited faster growth than their counterparts in locations II and III which is evident from the maximum width of their annual rings. This may be due to the influence of the local environment and differences in the genetic constitution of the trees.

Table 2. Mean ring width with earlywood and latewood proportions of selected trees

Location	Location I					Location II	Location III
	7	13	20	40	147	13	7
Tree age, yr	7	13	20	40	147	13	7
Ring width (mm)	4.55	4.24	0.95	1.33	0.99	1.88	1.47
Earlywood width (mm)	0.38	0.43	0.49	0.74	0.30	0.45	0.33
Earlywood %	8	10	52	56	30	24	22
Latewood width (mm)	4.17	3.81	0.46	0.59	0.69	1.43	1.14
Latewood %	92	90	48	44	70	76	78

5.5 Cambial periodicity vs phenology

Teak being a tropical deciduous tree does not bear leaves throughout the year. The annual leaf fall in teak commenced by the first week of November. The processes of leaf fall continued till February; the mature trees were almost leafless in February. The younger (7- and 13-year-old) trees witnessed only partial defoliation by retaining some of the foliage throughout the year while the mature trees lost their leaves completely (Table 3). Proportionately, the manifestation of the annual resting period of the cambium was prolonged in the mature trees. Leaf emergence was noticed in early March and the breaking of cambial dormancy in March-April. Thus there was almost a month's interval between leaf emergence and cambial reactivation as reported by Rao and Dave (1981) from Gujarat.

By the end of May, the trees were in full foliage. Peak activity was recorded in June-July. The trees were seen in flower in June and to set fruits in July. The 7-year-old trees were not found to flower in both the years observed. The cambial activity slows down during September and the attainment of dormancy almost coincides with the loss of leaves from November onwards.

Table 3. Cambial activity in relation to phenology

Months	Cambial layers in transection	Phenology
JAN	8-10	Leaf fall
FEB	6-10	Leafless (Mature trees)
MAR	10-13	Leaf emergence
APR	12-14	Leaf emergence
MAY	12-15	Full foliage
JUN	15-20	Full foliage+Flowering except 7-yr- old
JUL	15-17	Full foliage+Flowering+Fruit set
AUG	14-17	Full foliage
SEP	14-15	Full foliage
OCT	11-13	Full foliage
NOV	10-11	Beginning of leaf fall
DEC	9-10	Leaf fall

5.6 Factors Influencing False Ring Formation

From the observations of cross sectional discs in sixty trees at the age of 8 years, 73% of the trees had false rings in their second annual increment. No false rings were produced in the first and the eighth year of growth. In the rest of the years, some 5-10 trees exhibited false rings (Fig. 6). The false rings in the second annual increment were confined to the early wood zone in all the trees (Fig. 7a). Anatomically they resembled true annual rings (Fig. 7b) in the sense that they comprised a zone resembling earlywood, which had one or two rows of parenchyma, large vessels and thin walled fibres which merged with the true latewood zone. This early wood-like zone was preceded by thick walled fibres characteristic of late wood fibres but produced in the true early wood zone. Yet another feature of interest was that, some trees had even double and multiple rings in the early wood zone

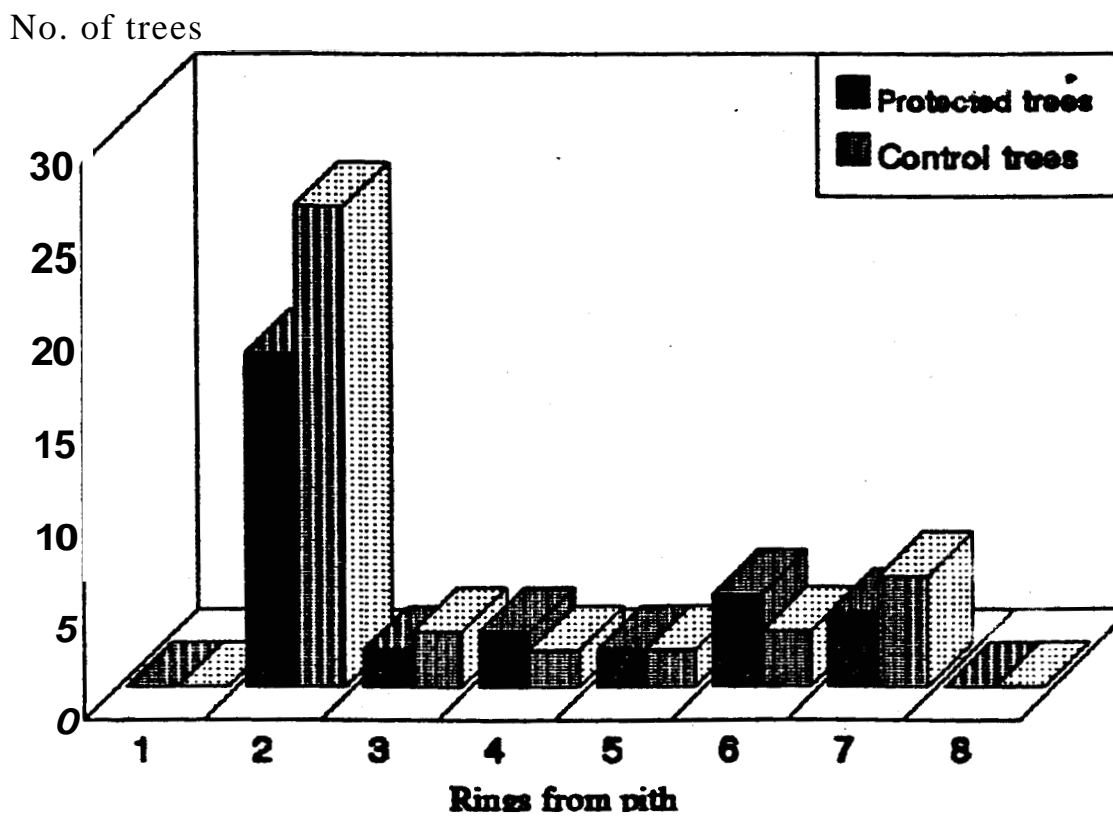


Fig 6 Distribution of false rings in 8-year-old trees

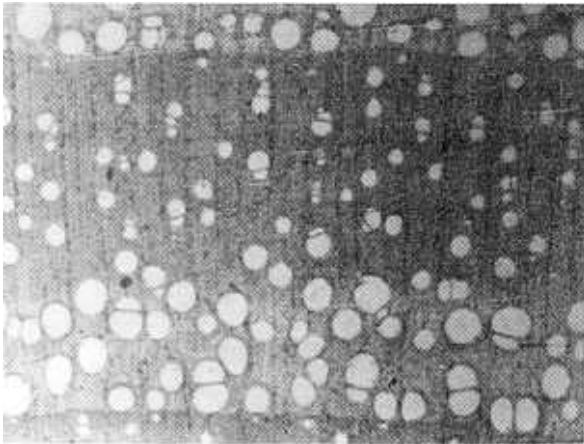


Fig.7 a. Second (normal) annual ring, x 18

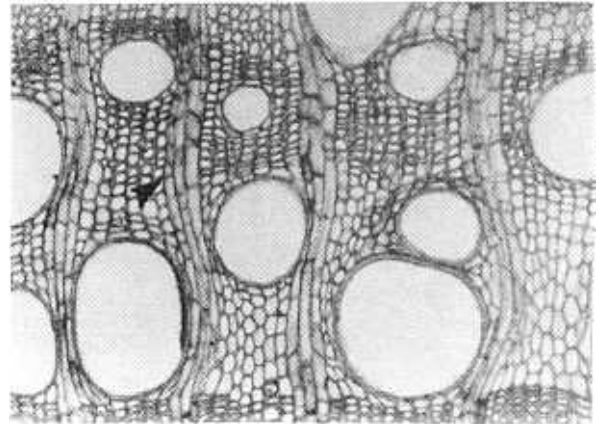


Fig. 7 b. False ring in the earlywood zone (see arrow), x 28

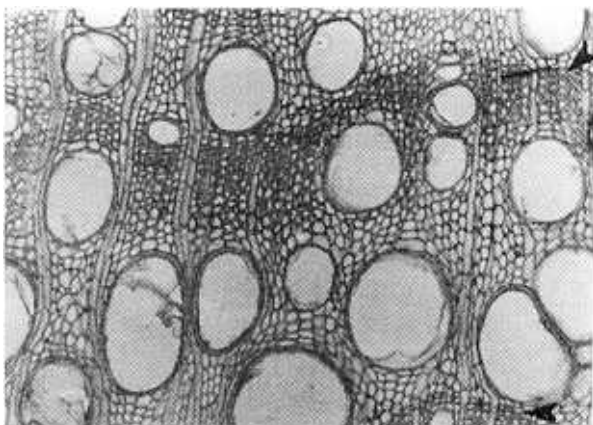


Fig.8 Double ring in the annual growth increment (see arrow), x 28

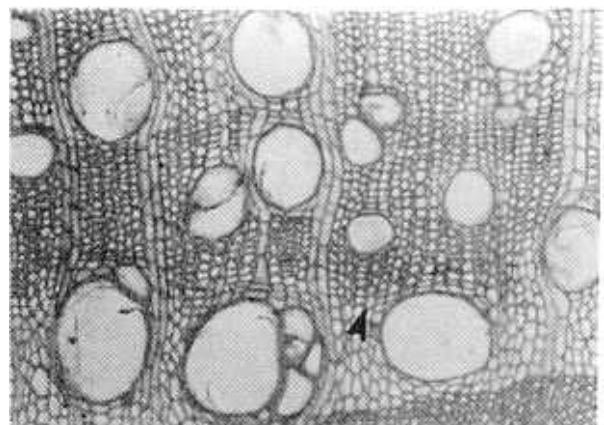


Fig.9 False ring showing and abrupt change from thin to thick walled fibres (see arrow), x 28

of their second increment (Fig. 8). Some of the false rings produced in the rest of the increments had the same anatomy as mentioned above, while some others exhibited different features (Priya and Bhat 1998). In these increments the false rings were found to be produced either in the early- wood or the latewood zones. Some of them confined to the earlywood zone consisted of an abrupt change from the usual thin walled fibres to a band of thick walled fibres without parenchyma and vessels (Fig. 9). Some false rings produced in the latewood zone were in the form of one or two rows of parenchyma cells with small vessels scattered nearby or an aggregation of vessels in a row with surrounding parenchyma. The latter type of false rings were difficult to be distinguished macroscopically.

5.7 Tree ring response to rainfall

Since almost 73 % of the trees exhibited false rings in their second growth increment, an attempt was made to correlate their formation with the rainfall of the corresponding year, i.e. 1976 (Fig.10). The trees must have commenced active growth after a period of dormancy, in the month of April, after receiving the first summer showers. Heavy rains in April must have rendered the formation of wide vessels in the earlywood zone. But the month of May witnessed unusually less rains which must have decreased the pace or led to partial cessation of growth. This was evident in the earlywood zone of the growth increment in the form of thick walled fibres characteristic of latewood. Later with the advent of heavy rains in June, active growth must have resumed once again, leading to the formation of wide vessels characteristic of early wood which was depicted in the form of a false ring in the annual growth increment. Double and multiple rings formed in some trees must be due to the partial resumption followed by cessation of growth with respect to the fluctuations in daily rainfall during May. Regarding false ring formation in the rest of the annual increments, no specific reason could be attributed, since only 5-10 trees exhibited them. So the reason may be some physiological disturbances affecting the growth of only those particular trees. From our observations, it is clear that the intervention of a dry spell during active growing season, followed by favourable conditions is capable of producing a false ring, provided it is intense enough to cease or reduce

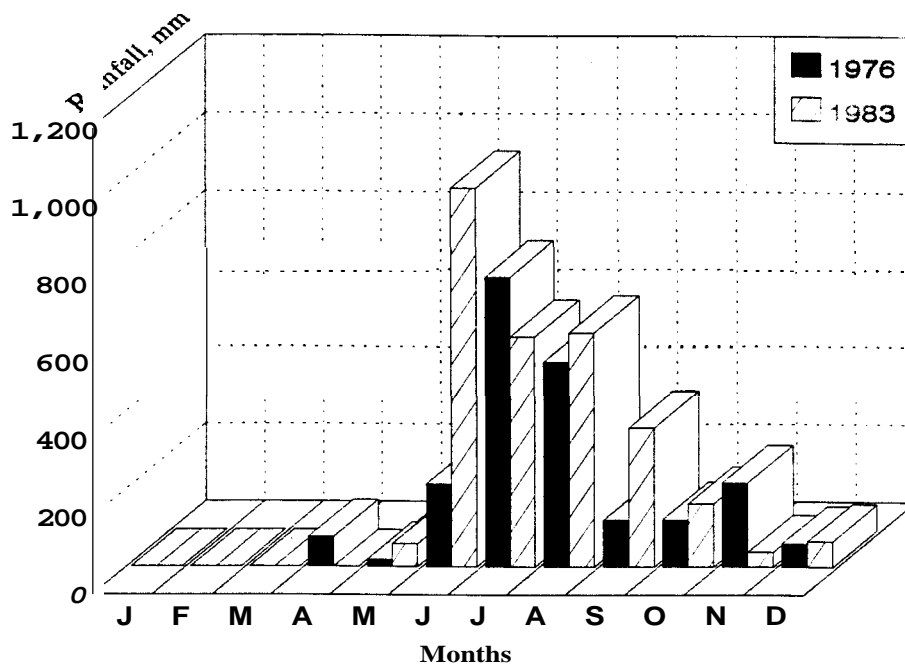


Fig 10 Monthly rainfall in mm in location I during 1976 and 1983

the pace of growth for some time prior to the resumption of active growth. To confirm this, nine discs of 12-year old trees planted in 1981 were analysed. With the exception of four annual increments, all the trees exhibited false rings in any one of their annual rings (Fig.11). Maximum number of trees had false rings in the early- wood zone of their third annual ring, which was again correlated with the rainfall of the corresponding year i. e. 1983 (Fig.10). In this year there was no rainfall during April, when active growth resumed normally in the trees. After producing a few layers of early wood, growth must have slowed down or ceased partially due to lack of rains, ultimately leading to the production of thick walled fibres. At the onset of rains in May, active growth must have resumed with the production of a zone characteristic of early wood which was evident as a false ring close to the early wood zone of the corresponding annual increment.

5.8 Effect of insect defoliation

No interrelationship could be established between insect defoliation and formation of false rings in sampled trees, although insect defoliation has been stated to be one of the causes of the latter (Haygreen and Bowyer 1989, Panshin and de Zeeuw 1980). The trees which were given artificial protection against insect defoliation also displayed false rings in the wood formed during protection period . Therefore, some physiological disturbance other than defoliation must have led to the false ring formation. Also, observations were made on trees from another location (Peechi), which had lost their foliage soon after flushing due to acute insect defoliation and resurgence of new foliage after a brief period of one week. When the growth ring of that year was observed microscopically, no false ring was. The probable reason is that either the cessation of radial growth resulted by the insect defoliation may not be of sufficient duration to produce cells characteristic of latewood. Another possible explanation is that there might have been only slight resumption of radial growth which might have led to the formation of earlywood cells characteristic of a false ring only in the upper reaches of the crown without extending up to the base of the tree, although cambial reactivation is known to be almost simultaneous throughout the tree of ring-porous species (Wareing 1951).

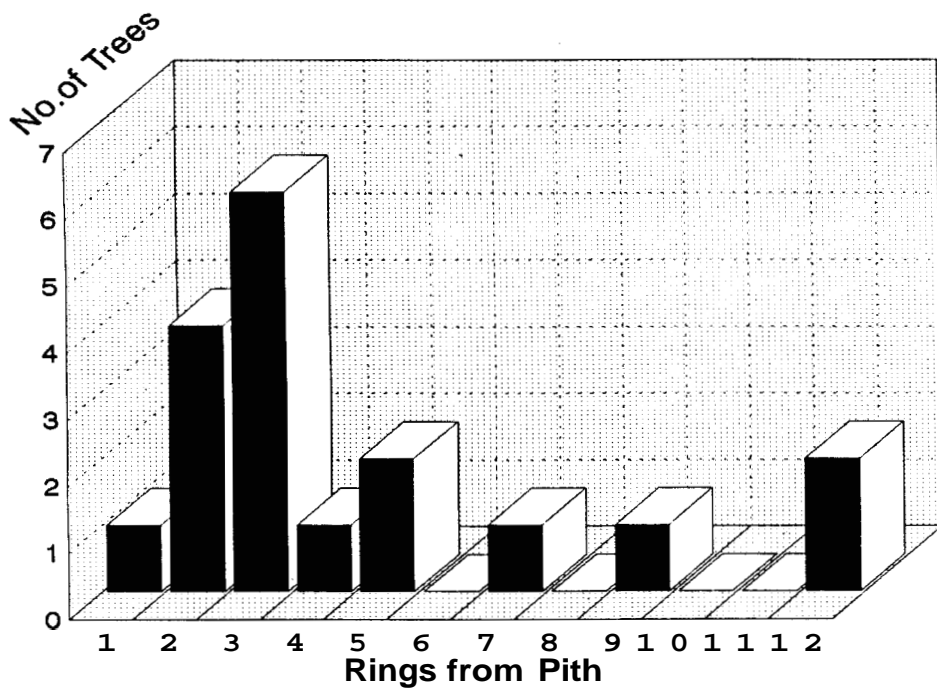


Fig 11 Distribution of false rings in 12-year-old trees

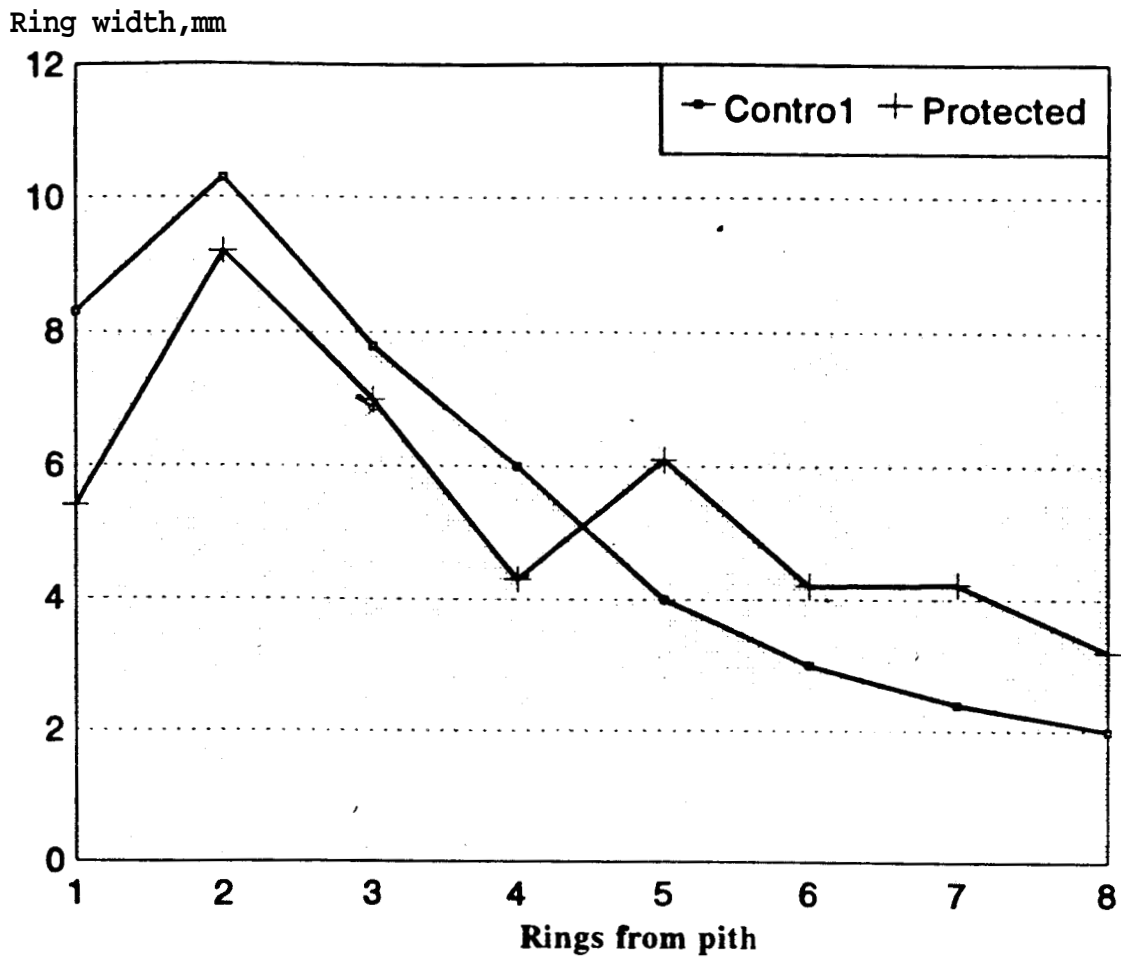


Fig 12. Ring width in relation to cambial age in control and protected trees from insect defoliation

Our observations of higher incidence of false rings in second annual ring (Fig. 11) suggest that field transplantation of 1-year-old nursery-raised seedlings interrupt the cambial activity to cause false rings in teak.

From ring width measurements in the 8-year-old 'protected' and 'control' trees, it was evident that protection from insect defoliation at the age of four years accelerated the growth rate in the following year with an increase of about 28% ring width (Fig.12). The extent of growth acceleration (increased ring width) due to protection remained more or less constant for rest of the period up to eighth year. Obviously, insect defoliation reduced the growth rate of the trees in the corresponding years appreciably, without altering the specific gravity. There was a significant increase in the latewood width of the 'protected' samples corresponding to the increase in ring width, while earlywood width remained fairly constant. However, the effects of wider latewood on other anatomical features were too little to cause any change in specific gravity. This is probably because the relative proportions of latewood and fibre wall substance are smaller in wider rings of juvenile wood than in mature wood.

Table 4. Comparison of mean values of anatomical properties in control and 'protected' trees from insect defoliation.

Parameters	Growth ring no. from pith	Control Mean	Protected Mean	t-value
Specific gravity	1-4	0.539	0.548	-0.63ns
	5-8	0.553	0.563	-1.03ns
Vessel diameter (mm)	6	0.178	0.180	0.48ns
	7	0.187	0.176	1.67ns
	8	0.170	0.176	-1.62ns
Vessel area (%)	6	23.6	23.8	-0.19ns
	7	21.9	19.1	2.18ns
	8	22.4	19.9	1.67ns
Cell wall area(%)	6	44.3	44.9	-0.67ns
	7	45.2	45.5	-0.33ns
	8	45.4	47.4	-1.91ns
Ring width (mm)	6	2.5	3.5	-2.57*
	7	2.6	3.7	-2.68*
	8	2.5	3.6	-3.33**
Earlywood width (mm)	6	0.927	0.775	-0.28ns
	7	0.809	0.898	-1.81ns
	8	0.735	0.939	
Latewood width (mm)	6	1.604	2.732	-2.29*
	7	1.821	2.807	-2.77*
	8	1.807	2.637	-3.56**

* = Significant at 5% level

** = Significant at 1% level

ns = Not significant

5.9 Effect of induced drought

From the observations made on seedlings, it was noticed that any changes affecting their growing conditions had pronounced bearing on their active growth, obviously producing a false ring. Fluctuations in the rainfall, field transplantation of the seedlings, irregular irrigation treatments etc. resulting in partial or complete loss of leaves were found to produce false rings in seedlings. Thus they were more susceptible to the changes in the environment than mature trees, which is obvious from the higher frequency of false ring formation in the former. It was observed that induction of drought during active growing season produced false rings in the seedlings. During the treatment period, growth was brought to a stand still, with the formation of thick walled fibres as characteristic of late wood. When watering was resumed, large vessels and parenchyma characteristics of the early wood were noticed, appearing as a false ring in the annual growth increment.

5.10 Age effect

When a comparison was made between locations, based on visual interpretation by combining both fast and slow grown trees of each location, we observed that all the anatomical properties showed definite trends of variation with age, with the exception of the percentage of cell wall material and rays. The mechanical properties and specific gravity did not display any definite pattern of variation.

Microfibrillar angle was maximum in the rings near the pith and gradually decreased with age up to 20 years in location IV and up to 25 years in locations I and V and stabilised thereafter (Fig. 13). Vessel diameter increased steadily up to 20 years, then decreased during a brief transition phase and stabilised around 25 years (Fig. 14). Vessel percentage gradually increased initially for about 20-25 years and thereafter showed a rapid increase in all the locations. Ring width was maximum in all the rings formed during the first 20 years and then decreased steadily up to 25 years and thereafter exhibited different trends in all the locations. Fibre length increased initially up to 15 or 25 years before stabilising in mature wood zone depending on growth rate and location (Fig. 15).

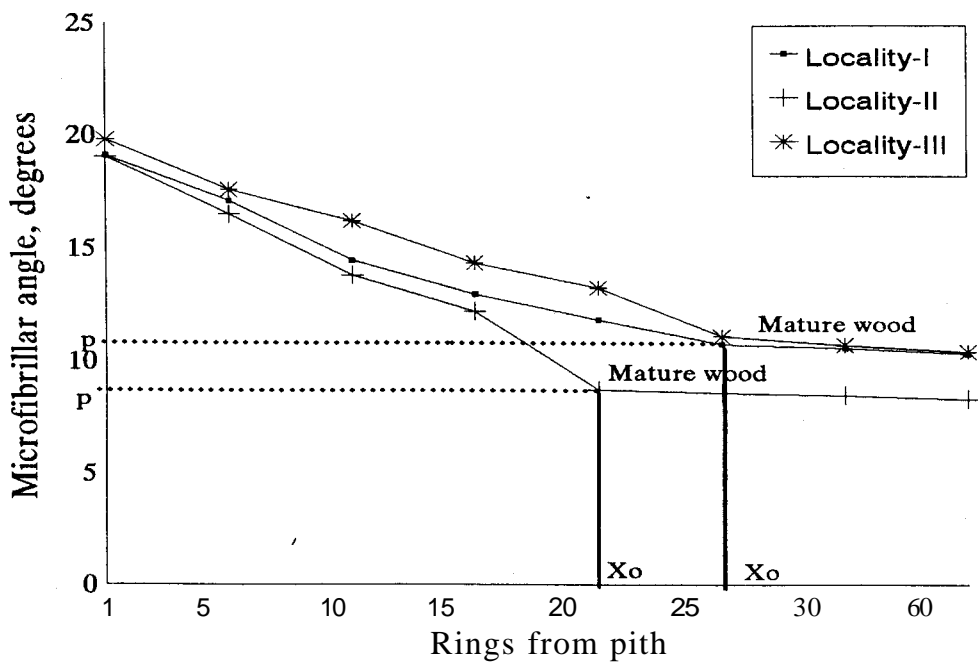


Fig 13. Radial variation in microfibrillar angle in relation to cambial age (note the age demaraction between juvenile and mature wood)

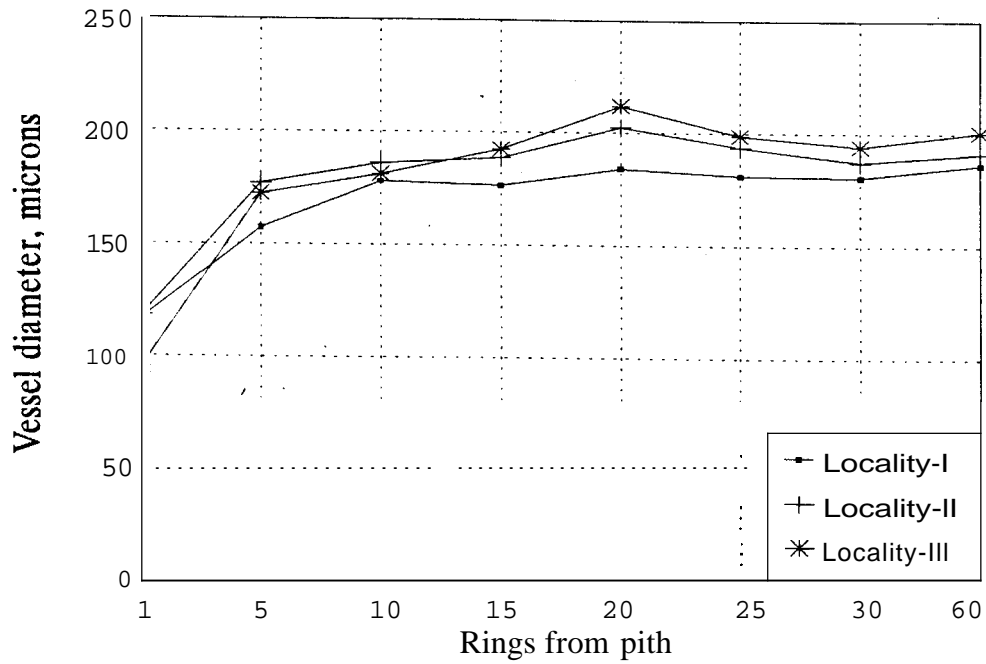


Fig 14 Radial variation in vessel diameter in three locations

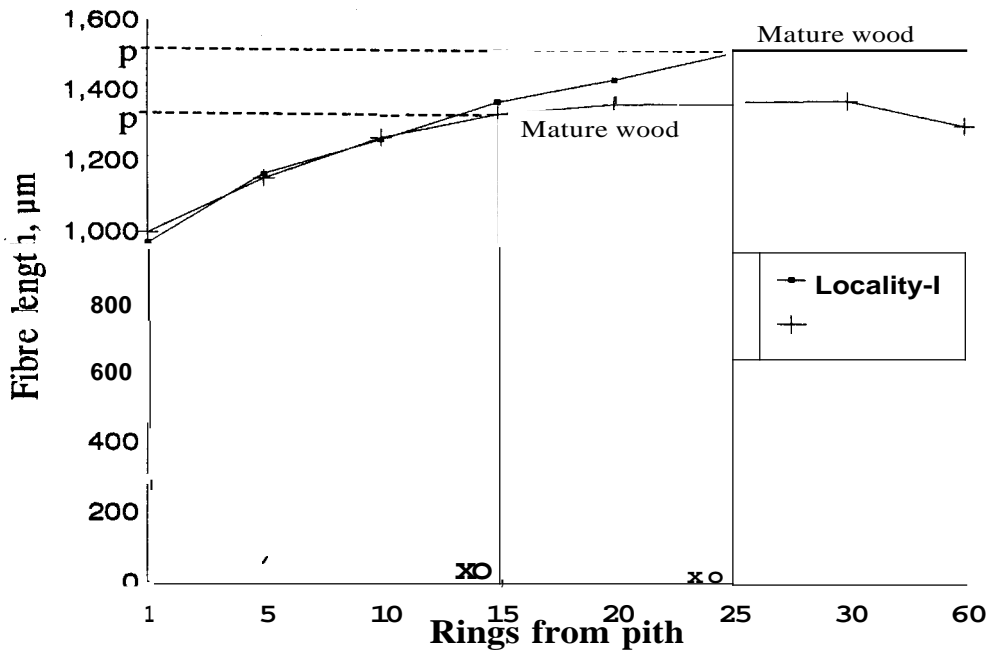


Fig 15. Radial variation in fibre length in relation to cambial age in three locations (note the age demarcation between juvenile and mature wood)

Based on the statistical analyses we conclude that the point of demarcation of juvenile and mature wood lies somewhere around 20 - 25 years of age. Of all the parameters analysed, microfibrillar angle seemed to be the best indicator, according to which the period of juvenility extended up to 20 years in Location IV and up to 25 years in locations I and V (Fig. 13). When the fast and the slow grown trees were considered separately under each location, it was found that the slow grown trees had a tendency to form mature wood from the age of about 20 years, whereas, in the fast grown trees the period of juvenility extended invariably up to the age of 25 years. While the different anatomical parameters exhibited different patterns of radial variation, physical and mechanical properties such as specific gravity and MOR varied relatively little from juvenile wood to mature wood zones and did not show definite trends (Fig. 16). It was therefore concluded that among the various wood properties, microfibrillar angle, vessel diameter/percentage and to a lesser degree fibre length were the most useful indicators of maturation age of teak wood.

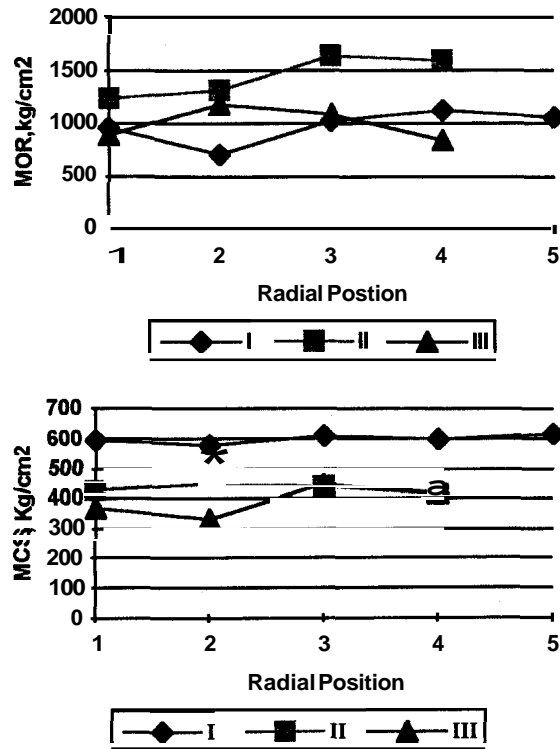


Fig. 16 Radial variations in MOR (bending strength) and MCS (compression strength parallel to grain) in 65-year-old teak from Nilambur (I), Konni (II) and Ariekavu (III) locations

The mean values of properties estimated, after the demarcation of juvenile wood from mature wood, are presented in Table 5. It is concluded that the juvenile wood of teak is generally characterised by wide growth rings, large fibril angle, small diameter and low percentage of vessels, short fibres and high percentage of cell wall and relatively low bending strength properties (MOR and MOE) as compared to mature wood. Some properties, viz. ray percentage, compression strength parallel to grain (MCS) and bending strength of slow grown trees did not show significant differences between the two (Table 5). Thus, in terms of specific gravity and strength properties, juvenile wood of teak is not necessarily always inferior to mature wood.

Table 5. Comparison of juvenile- and mature wood properties in fast-grown (Treatment-1) and slow-grown (Treatment-2) trees of three localities

Property	Treatment	Juvenile wood	Mature wood	't' value
Microfibrillar angle °s	1	15	10	10.97**
	2	16	10.1	5.94**
Vessel diameter µm	1	173.2	196.31	-3.9*
	2	160.4	186.2	-3.5*
Vessel %	1	13.8	18.5	-5.31**
	2	12.9	27.7	-4.38**
Ray %	1	18.6	20.3	-2.09 ^{ns}
	2	18.7	18.7	0.01 ^{ns}
Cell wall %	1	55.7	51.1	3.91*
	2	54.1	47.2	3.09*
Specific gravity	1	0.56	0.57	-1.14 ^{ns}
	2	0.57	0.54	2.56*
Fibre length µm	1	1281	1500	-20.33*
	2	1101	1377	-3.41 ^{ns}
MOR (N/mm ²)	1	98.3	124.2	-4.84**
	2	114	134.6	-1.97 ^{**}
MOE (N/mm ²)	1	12695	15746	-4.12**
	2	14460	16220	-1.29 ^{ns}
MCS (N/mm ²)	1	45	47	-0.74 ^{ns}
	2	54	53	-0.47 ^{ns}

^{ns} = not significant at 0.05 level
 * = significant at 0.05 level
 ** = significant at 0.01 level

6. Conclusions

- Cambial periodicity in teak is influenced by the age of the tree. Cambium is active for longer period of the year in juvenile wood formation than in mature wood production of trees.
- Pre-monsoon showers (rain fall) during March-April, influence the cambial activity and break the dormancy period earlier in certain locations.
- Irrespective of age and location, a peak period of cambial activity was seen during June-July when the cambium was 15-20 layered. Narrowing of the zone of the periclinal divisions was observed from September onwards and by the time the cambium had attained dormancy, the zone was found to be reduced to 6-10 layers of radially flattened cells.
- Wider annual rings were produced in younger (7-year-old) juvenile trees followed by 13-year-old trees and so is the amount of latewood in the growth ring, which is attributed to the prolonged period of cambial activity of juvenile trees. Thus the late onset of dormancy influences the quality of the wood as evidenced by a higher proportion of latewood in the growth ring.
- The intervention of a drought period during the active growing season, followed by favourable conditions, induces false ring formation, if it is intense enough to cease or reduce the pace of active growth for some time. Also drought induction or any other external factor such as field transplantation that interrupts the active growth causes false ring formation in the juvenile wood of 2- or 3-year-old seedlings.
- Insect defoliation does not necessarily induce false ring formation. It however reduces the growth rate of trees without affecting the specific gravity, size and proportion of vessels and cell wall Percentage of the juvenile wood.

- The age of demarcation between juvenile and mature wood in teak trees is found around 20-25 years depending on growth rate. The fast growing trees, both within and between the geographic locations, have a tendency to prolong the period of juvenile wood formation compared to slow growing trees.
- The juvenile wood of teak is characterised by wide growth rings, greater microfibrillar angle, small diameter vessels and high percentage of wall material with short fibres as compared to mature wood.
- Since the mechanical properties did not vary significantly between juvenile and mature wood, the former is not necessarily inferior in timber strength to mature wood as generally believed.

6.1 Practical significance of the results

- The results offer scope for further research in the area of growth manipulation (accelerating tree growth) for higher yield of timber without compromising the quality from short rotation teak plantations. The current findings are of particular interest to teak plantation managers, other wood anatomists and industrialists who process juvenile teak wood for various end-uses.
- The observations on shorter duration of cambial activity in drier locality and irrigation effects on reactivation will be useful to Silviculturists to adopt specific plantation management strategies for teak in commercial plantations.
- The results showing the influence of rain fall and drought during active growth season on false ring formation will be of interest to Dendrochronologists for tree ring analysis.
- The determination of age of attaining maturity of cambial derivatives and cessation of juvenile wood formation (as 20-25 years) will help the plantation managers to fix the rotation cycle for the production of desired wood quality or for manipulation of juvenile wood proportion of the timber to be harvested.

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