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INFLUENCE OF RAINFALL, IRRIGATION AND AGE ON THE GROWTH PERIODICITY AND WOOD STRUCTURE IN TEAK (TECTONA GRANDIS)

by

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SUMMARY

Growth periodicity was followed for two consecutive annual cycles to reveal the pattern of wood formation in plantation-grown teak at three different localities in India. Rainfall and age were the two important factors that influenced cambial activity. Cambial reactivation occurred during March–April in both years. The pre-monsoon showers broke the cambial dormancy at all three localities. Almost a month's interval was observed between bud break and initiation of radial growth. Irrespective of age and locality, a peak period of cambial activity occurred during June–July. Dormancy began during October–December, depending on the age of the trees and locality. Juvenile trees and those grown in relatively high rainfall areas had a prolonged cambial activity and retained foliage throughout the year. They produced wider rings with higher proportions of latewood. Irrigation of 5-year-old trees led to the loss of typical ring porosity of teak wood; their first three growth rings were more or less diffuse-porous. This is attributed to uninterrupted cambial activity resulting in production of rather uniform-sized vessels.

Key words: Vascular cambium, cambial reactivation, dormancy, rainfall, juvenile wood, ring porosity, *Tectona grandis*, teak.

INTRODUCTION

Knowledge of cambial activity and growth ring formation in trees is essential for determining the age and growth rate of trees in managed forest stands. Relatively little is known about the patterns of growth periodicity and wood formation in tropical trees. According to Tomlinson and Longman (1981), radial growth in tropical trees may be annual, semiannual, irregular or continuous. According to Avila et al. (1975), cambial activity is genetically controlled, and, in most plants, its rhythm is determined by evolution under certain environmental limitations. Local environment can markedly influence the initiation and cessation of cambial activity. As early as 1930, Priestley observed that the rhythmic activity of trees was modifiable by external circumstances. Cambial activity in many Indian tree species increases after rains begin (Anand 1979). Eames and MacDaniels (1947) stated cambial age, as well as tree age, affects the duration of cambial activity. Liphschitz and Lev-Yadun (1986) found rate and duration of cambial activity varied between irrigated and non-irrigated plants.

The earliest work in teak – a tropical ring-porous hardwood – dates back to 1856, when Brandis concluded that growth rings form annually (Brandis 1879). According to Troup (1921), in teak new leaves appear from April till June. Chowdhury (1940) found differences in the time of initiation and cessation of cambial activity in teak trees grown at three different locations in India. More information is needed on the effects of age, as well as the locality on the growth periodicity and wood formation in teak. Such knowledge is essential for timber management, particularly in view of the increasing number of plantation programs in the tropics. The present study investigates the influence of rainfall, irrigation and age on cambial periodicity and wood formation in teak (*Tectona grandis* L. f.) grown at three different locations in India.

MATERIALS AND METHODS

Three plantation localities were used (Table 1). Locality I (Nilambur) is considered to be the best site for growing teak as it has well-drained alluvial soil. To investigate age effects on growth periodicity, five trees each from plantations of four ages (viz. 7-, 13-, 20-, and 40-years-old) were sampled at Locality I. To investigate locality differences, five trees each of age groups 7- and 13-years-old were sampled from Localities II and III.

Periodical monthly observations of cambial activity were made during two consecutive years (1994 and 1995). Cubes (2 × 2 × 2 cm) comprising cambial tissues along with outer bark and inner sapwood were chiseled out at breast height from the selected trees. The samples were taken in four rows 2.5 cm apart in the northern cardinal direction during the first year and in the southern cardinal direction in the second year.

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

Factor	Locality I (Nilambur)	Locality II (Walayar)	Locality III (Peechi)
Elevation (m)	100	215	175
N latitude	10° 16'	10° 51'	10° 32'
E longitude	76° 15'	76° 50'	76° 20'
Soil	well drained alluvium	dark sandy loam	deep blackish sandy loam
Mean annual rainfall (mm)	2600	1200	2400
Mean temperature range (°C)	17–37	21–41	21–32
Age group (years)	7, 13, 20, 40	13	7
Mean tree height (m)	11–31	11.5	9
Mean dbh (cm)	12–47.8	18	11

Table 2. Cambial activity of the trees sampled in relation to phenology during 1994–1995 (three localities combined).

Months	Cambial layers in transection (average value)	Phenology
Jan	8–10	Leaf fall
Feb	6–10	Leafless (mature trees)
Mar	10–13	Leaf emergence (in Localities I & III during 1994)
Apr	12–14	Leaf emergence (in Locality II during 1994 and all three localities in 1995)
May	12–15	Full foliage
June	15–20	Full foliage + flowering (except 13-years-old trees in 1995 and 7-years-old trees)
July	15–20	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

The samples were fixed in FAA in the field. After three days, the samples were transferred to 70% EtOH for preservation. Twenty μm thick transverse sections were cut with a Reichert sliding microtome. Sections were double-stained used Achrydin-Chrysoidin and Astra Blue. After dehydration in an alcohol series, they were mounted in DPX.

Cambial activity was determined by counting the number of cell layers in the cambial zone (comprising cambium and undifferentiated cells lying between xylem and phloem); the greater the number of cell layers, the greater the cambial activity. The terms 'cambium' and 'cambial zone' are used in this study to designate the entire meristematic zone including portions of the phloem and xylem where the cells were enlarging, but were still able to divide, as described by Wilson et al. (1966). A video image analyser (Leica Quantimet 500+) was used to quantify ring width and earlywood and latewood proportions of growth rings of the years 1994 and 1995; values for the two years were compared by a t-test. Earlywood was distinguished from latewood by its wider vessels and parenchyma and thinner-walled fibres.

Phenological observations, such as leaf emergence, full foliage, flowering, fruiting and defoliation were made along with the monthly collections (Table 2). For each locality data on monthly rainfall were recorded.

To investigate the effect of irrigation on wood formation, cross-sectional discs were collected at breast height from nine 5-year-old plantation-grown trees at

Table 3. Environmental conditions of Ramamangalam and Nilambur.

Factor	Ramamangalam	Nilambur
N latitude	9° 56'	11° 16'
E longitude	76° 30'	76° 15'
Soil	Sandy loam	Well drained alluvium
Mean annual rainfall (mm)	2000	2600
Mean temperature range (°C)	16–34	17–37

Ramamangalam (Kerala), India (Table 3), where the plantations were continuously irrigated. These trees were compared with nine plantation-grown trees of the same age from Nilambur (Locality I) that were not irrigated (control). Transverse sections (20 μm thick) were cut for ring-wise microscopic examination.

RESULTS AND DISCUSSION

Cambial structure and seasonal periodicity

The dormant cambium of teak consists of 6–10 layers of radially flattened cells with relatively thick radial walls (Fig. 1). At the onset of cell divisions, the cambial cells swell, the radial walls become thin and the bark separates easily from the wood. The tendency for 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 the teak lies in the weak zone of newly formed xylem elements where the secondary wall formation has not begun.

The cambium remains quiescent for a period of 2–5 months annually, and the duration of the dormancy depends upon the age of the tree, as well as the local environ-

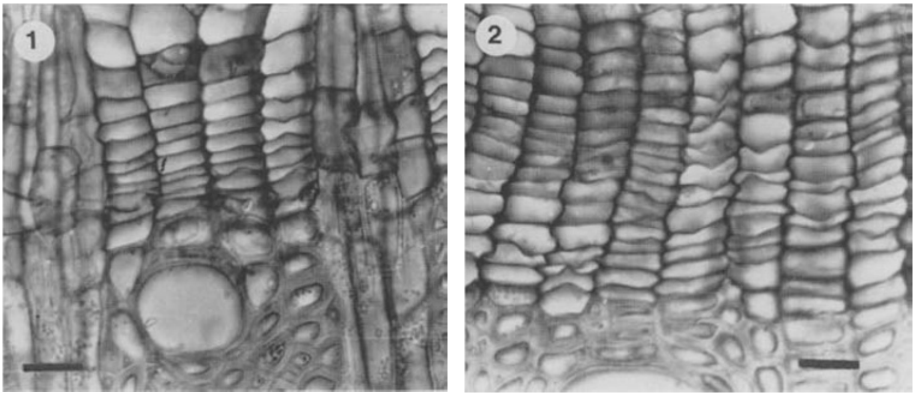


Fig. 1 & 2. Transverse sections of cambial zone of teak. – 1: Dormant cambium of 7-years-old tree. – 2: Cambium during peak period of activity. — Scale bar for 1 & 2 = 32 μm.

ment. We observed that the cambium resumed activity during March–April, as evidenced by the swelling of cambial cells with thinning of the radial walls and by formation of new xylem and phloem cells. Irrespective of age and locality, a peak period of cambial activity was seen during June–July, when the cambial zone had 15–20 layers of cells (Fig. 2). The zone of periclinal division narrowed from September onwards and dormancy was attained in October–December, depending upon the age of the tree and local environmental conditions. By the time the cambium had attained dormancy, the cambial zone was reduced to 6–10 layers. Our observations on cambial reactivation during March–April in Nilambur (Locality I) agree with the findings of Chowdhury (1940). According to him, in Dehradun and Kaptai (North India) radial growth started a little later (during June and May) than in Nilambur. Further, Rao and Dave (1981) recorded that in teak grown in the Calcutta region (India), cambial activity began in the first week of June, reaching a peak in July before declining slowly.

Cambial activity vs phenology

Teak does not bear leaves throughout the year. We observed that, irrespective of the locality, the annual leaf fall in teak began by the first week of November during both years. Leaf fall continued until February. Juvenile (7- and 13-year-old) trees retained some foliage throughout the year, but the mature trees lost their leaves completely. The retention of foliage by the juvenile trees was accompanied by a prolonged period of cambial activity as discussed by Wilcox (1962).

Bud break was observed in March in the trees of Localities I and III during 1994, and in April in Locality II. During 1995, bud break occurred in April in all three localities. Irrespective of tree age and influence of local environmental factors, almost a month's interval was observed between bud break and initiation of radial growth in all three localities. This agrees with the observations of Chowdhury (1940), Rao and Dave (1981), and Venugopal and Krishnamurthy (1987). By the end of May, the trees were in full foliage. Peak cambial activity was in June–July. The 13-year-old trees flowered in June and set fruits in July; the 7-year-old trees did not flower in either 1994 or 1995. Cambial activity slowed during September and the attainment of dormancy almost coincided with the loss of leaves from November onwards.

Factors influencing cambial activity

Rainfall — The effect of the local mean annual rainfall (Fig. 4a & b) on cambial activity is clear from our observations in the 13-year-old juvenile trees of Locality II, where they had only a brief period of activity as compared to the same aged trees in Locality I.

In Locality II, cambial activity began in April and continued until the end of October and then was quiescent for five months. Pre-monsoon showers broke cambial dormancy in all three localities. For Localities I and III, during 1994, cambial activity began in March after the first rains; during 1995, cambial activity began in April, also after the first rains. For Locality II, during 1994 and 1995, cambial activity began in

April, after the first rains there (Fig. 3). Chowdhury (1940) observed cambial reactivation during May in Nilambur (South India), and during June in Dehradun (North India). The difference he observed in time of cambial reactivation might be attributed to the earlier onset of the monsoon in the South compared to the North, where normally the monsoon begins 3–4 weeks later.

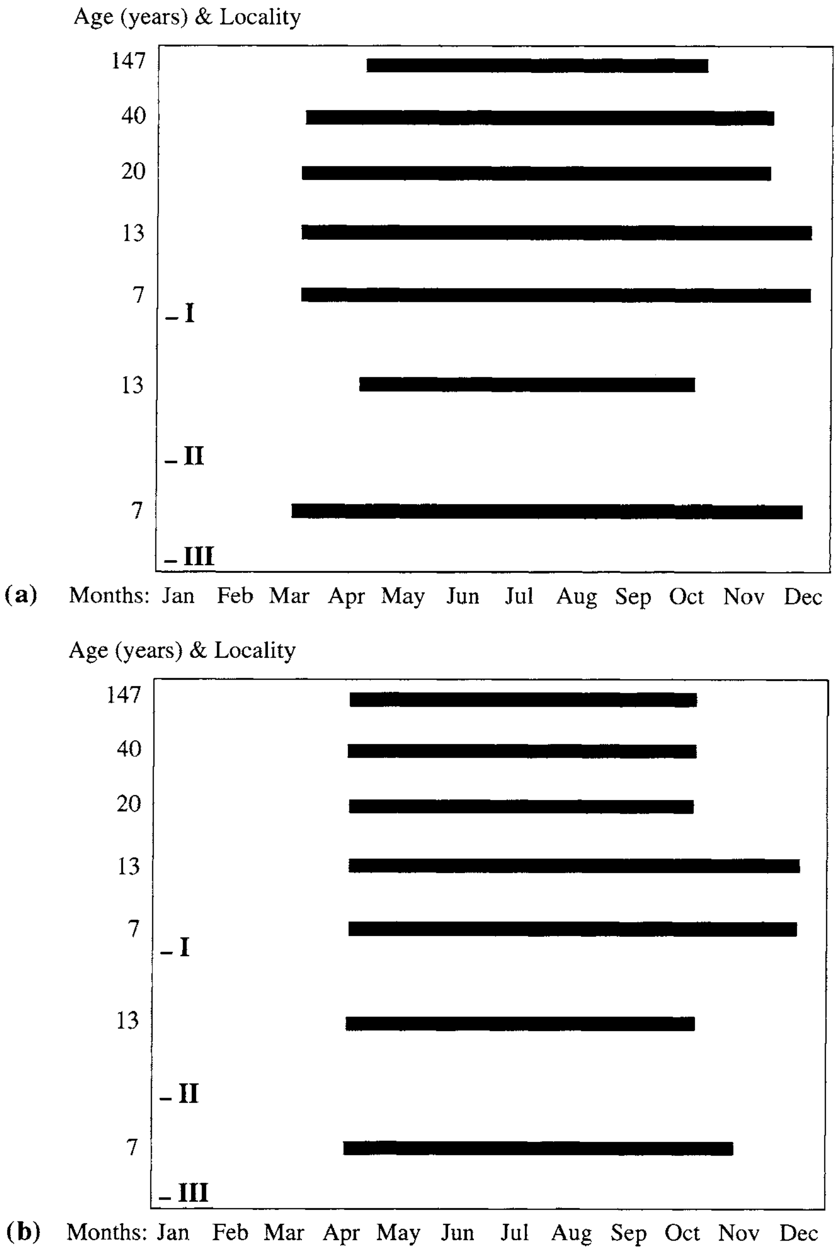


Fig. 3. Cambial periodicity during 1994 (a) and 1995 (b).

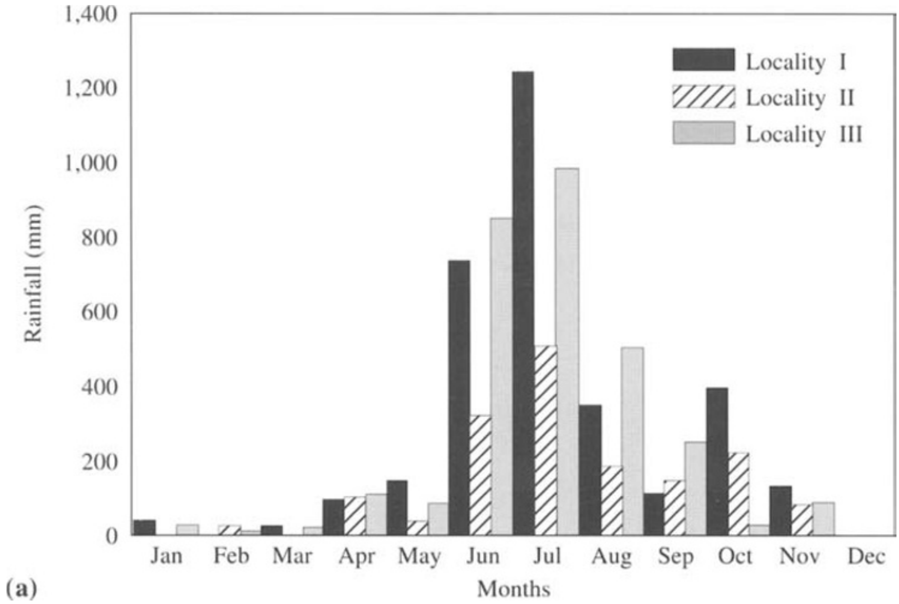
Table 4. Comparison of average values of ring width, earlywood and latewood percentages of five selected trees during 1994 and 1995.

Locality:		I				II	III
Tree age (in years):		7	13	20	40	13	7
Ring width (mm)	**1994**	5.83	5.38	1.78	1.91	3.47	1.97
	1995	4.92	4.15	1.70	1.59	2.39	1.89
t-value		6.66**	3.37*	0.37^{ns}	1.07^{ns}	–4.01*	0.50^{ns}
Earlywood width (mm)	**1994**	0.44	0.44	0.45	0.37	0.45	0.39
	1995	0.48	0.46	0.39	0.49	0.47	0.37
t-value		–1.47^{ns}	–0.43^{ns}	0.95^{ns}	–1.56^{ns}	–0.35^{ns}	0.53^{ns}
Earlywood (%)	**1994**	7.55	8.18	25.3	19.4	13.0	19.8
	1995	9.76	11.1	22.9	30.8	19.7	19.6
Latewood width (mm)	**1994**	5.39	4.94	1.33	1.54	3.02	1.58
	1995	4.44	3.69	1.31	1.10	1.92	1.52
t-value		6.64**	3.28*	0.07^{ns}	1.80^{ns}	4.50*	0.33^{ns}
Latewood (%)	**1994**	92.45	91.82	74.7	80.6	87.0	80.2
	1995	90.24	88.9	77.1	69.2	80.3	80.4

ns = not significant at 0.05 level; * = significant at 0.05 level; ** = significant at 0.01 level.

Average growth rate (ring width) for the trees from all three localities, irrespective of age, was higher in 1994 than in 1995 (Table 4). There was more latewood in the 1994 growth rings, whereas the earlywood width did not vary significantly. The juvenile trees in Localities I and II had significantly higher growth rates during 1994, but for the mature trees and the juvenile trees of Locality II, the difference was not statistically significant. The significantly higher ring width values for Localities I and II during 1994 could partially be attributed to the greater amount of rainfall during that year, especially during the active growing season (June–July) (Fig. 4). Jacoby (1989) observed that the radial growth of teak in India and Java was influenced by the amount of rainfall during the dry season. Pumijumnong et al. (1995) observed that the growth of teak in Northern Thailand correlated with the rainfall during the first half of the wet season (April–July).

Irrigation — Wood produced by nine 5-year-old trees (in Ramamangalam), which were irrigated throughout their growing period, tended to be diffuse-porous in the first three years of growth (Fig. 5). There was little distinction between earlywood and latewood making demarcation between successive growth rings difficult. From the fourth year onwards, ring porosity developed gradually. On the other hand, the



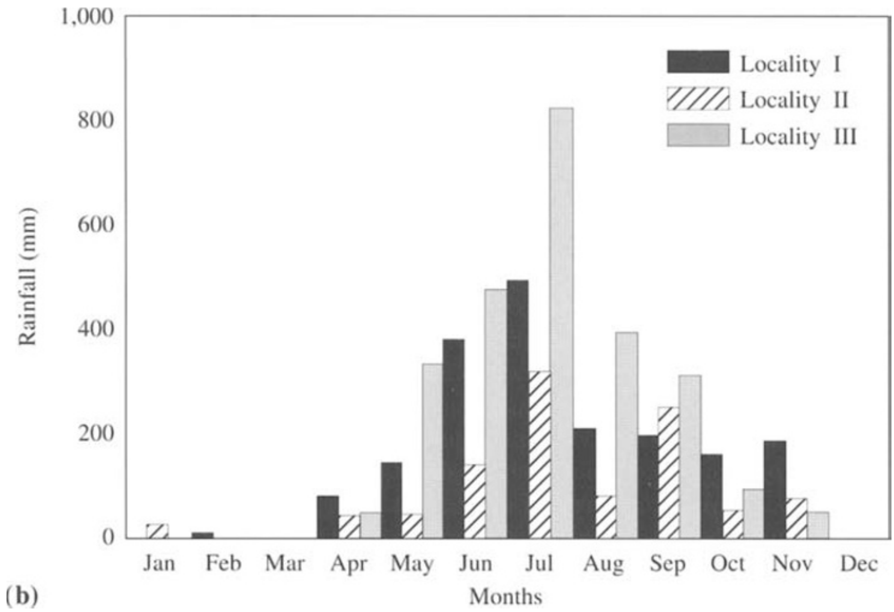
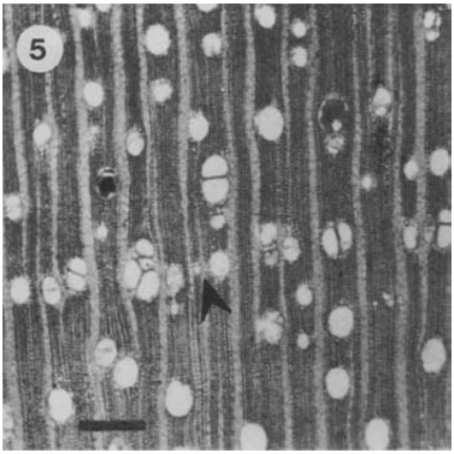


Fig. 4. Monthly rainfall in mm for Localities I, II, III during 1994 (a) and 1995 (b).

control trees were ring-porous from the first year of growth. The probable explanation is that continuous availability of water might cause more or less uninterrupted cambial activity, with scarcely any dormant period, and production of vessels of more or less uniform diameter through the year.



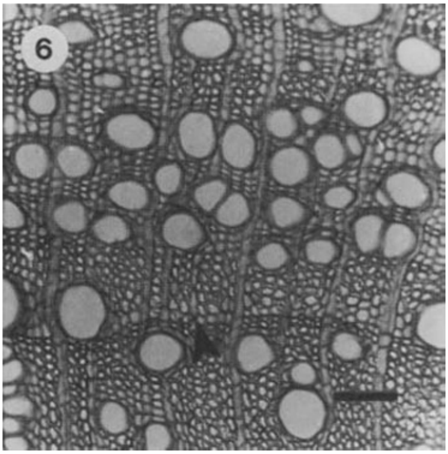
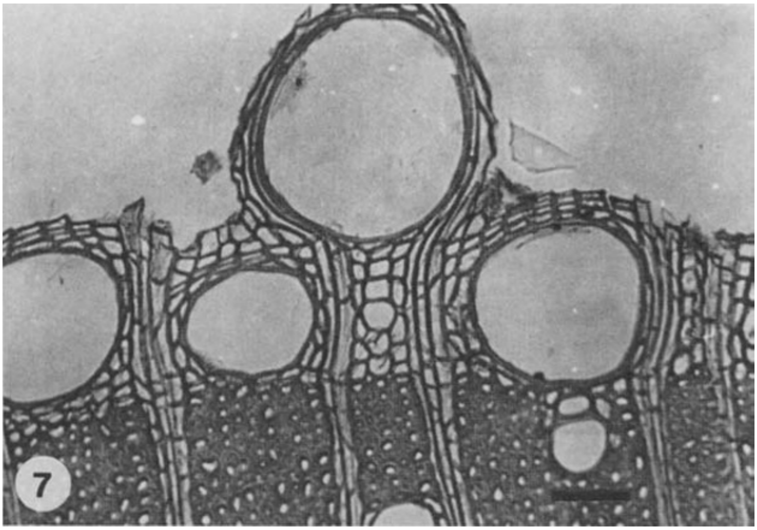


Fig. 5 & 6. Transverse sections of teak wood. – 5: Irrigation effect, altering ring-porous wood to diffuse-porous in the third growth ring; arrow at boundary. – 6: One-year-old teak seedling with less pronounced ring porosity; arrow at ring boundary. — Scale bar for 1 = 40 μm, for 2 = 90 μm.

The effect of irrigation seems to decrease with increasing age, as very young seedlings are more responsive to even minute changes in the external environment (Priya & Bhat 1998). Similar observations were made for *Quercus ithaburensis* and *Olea europaea* by Liphschitz (1995) who found that an unfavourable water supply resulted in low rates of cambial activity and ring-porous wood, while ample water supply resulted in prolonged periods of cambial activity and diffuse-porous wood. Waisel et al. (1970) found that cambial activity in the desert shrub *Zygophyllum dumosum* was prolonged by irrigation. Liphschitz et al. (1985) observed that in irrigated plants of *Pistacia lentiscus* the cambium was continuously active throughout the spring. Based on experiments conducted in *Populus euphratica*, Lipschitz and Waisel (1970) concluded that an unfavourable water supply caused either by a water shortage or by a high concentration of salts in the soil solution resulted in short periods and low rates of cambial activity, narrow rings, and ring-porous wood.

Tree age — We observed that the 7- and 13-year-old juvenile trees in Locality I showed a prolonged period of cambial activity at bh level, with only 2–3 months of dormancy (Fig. 3). On the other hand, the 20- and 40-year-old trees had a comparatively long dormancy period. Tree age influences the duration of cambial activity; the greater the age, the shorter the duration. This agrees with others' observations (e.g., see Büsgen & Münch 1929; Eames & MacDaniels 1949; Zimmermann & Brown 1971). Further, we observed in a 147-year-old tree in Locality I that the cambium was active only for seven months (April–October). In 1-year-old seedlings complete dormancy was absent, and the cambium was active to a lesser extent during January and February. Thereby, distinct ring porosity was lacking in the next growth increment, probably due to the absence of a complete cambial resting period (Fig. 6).



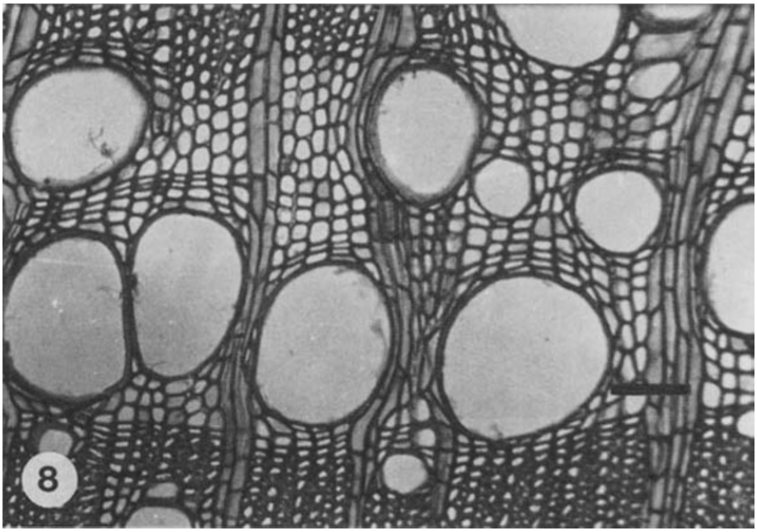


Fig. 7 & 8. Transverse sections of teak wood. – 7: Earlywood formation still in progress in a 40-years-old tree in the second month after cambial reactivation. – 8: Completion of earlywood formation in a 7-years-old tree in the second month after cambial reactivation. — Scale bar for 7 & 8 = 90 μm.

Cambial activity and wood structure

In trees aged 7, 13, and 20 years, earlywood formed during the two months after cambial reactivation, while in the older trees (40 years), earlywood formation extended until the end of the third month (Fig. 7, 8). During both 1994 and 1995, at Locality I, juvenile trees (7- and 13-years-old) had wider rings with more latewood than mature trees (Table 4). This difference in latewood amount can partially be attributed to the prolonged period of cambial activity observed in younger trees. A late onset of dormancy influences wood quality as there is a higher proportion of latewood, also observed by Denne (1985). Trees at Localities II and III had an earlier onset of dormancy and comparatively less latewood than their counterparts at Locality I (Table 4). The 7- and 13-years-old trees at Locality I had wider growth rings (likely also indicating more rapid growth) than their counterparts at other localities. This may be due to the influence of variations in environmental factors, especially a higher rainfall and soil conditions (teak is known to grow faster at Locality I due to the well-drained alluvial soil), and also due to differences in the genetic constitution of the trees.

CONCLUSIONS

From the results of the present study, we draw the following conclusions:

1) Rainfall influences cambial activity in teak; pre-monsoon showers break cambial dormancy, and higher rainfall contributes to a greater amount of wood formation.

2) Irrespective of age and locality, after cambial reactivation during March–April, a peak period of cambial activity occurs during June–July, when the cambium has 15–20 layers, coinciding with the highest amount of rainfall of the year in South India.

3) Juvenile teak trees in irrigated plantations tend to produce diffuse-porous wood during the first 3–4 years of growth in contrast to the ring porosity displayed even in the first year of growth in the unirrigated (control) plantation.

4) Cambial periodicity in teak is influenced by tree age, as seen by the marked differences in seasonal activity between juvenile and mature trees. Juvenile (7- and 13-years-old) trees have a shorter dormancy period than mature (20- and 40-years-old) trees.

5) Wider rings, with a higher percentage of latewood, in 7- and 13-years-old trees are partially attributable to a prolonged period of cambial activity in juvenile trees.

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REFERENCES

Anand, S.K. 1979. Organisation, structure and behaviour of cambium and contiguous tissues of some tropical trees. PhD Thesis, University of Delhi.

Avila, G., M.E. Aljaro, S. Araya, G. Montenegro & J. Kummerow. 1975. The seasonal cambial activity of Chilean and California shrubs. Amer. J. Bot. 62: 473–478.

Bannan, M.W. 1955. The vascular cambium and radial growth in Thuja occidentalis. Can. J. Bot. 33: 133–138.

Brandis, D. 1879. Memorandum of the rate of growth of teak. Indian For. 4.

Büsgen, M. & E. Münch. 1929. The structure and life of forest trees. Ed. 3. Translated by T. Thompson. John Wiley & Sons, Inc., New York.

Chowdhury, K.A. 1940. The formation of growth rings in Indian trees. III. A study of the effect of locality. Indian Forest Records (NS) Utilization 2: 59–75.

Denne, M.P. 1985. Towards a model of wood production in a tree. In: L.J. Kucera (ed.), Xylorama: 51–57. Birkhauser Verlag, Basel.

Jacoby, G.G., Jr. 1989. Overview of tree ring analyses in tropical regions. IAWA Bull. n.s. 10: 99–108.

Liphschitz, N. 1995. Ecological wood anatomy: changes in xylem structure in Israeli trees. In: Wu Shuming (ed.), Wood Anatomy Research: 11–15. International Academic Publishers, Beijing.

Liphschitz, N. & S. Lev-Yadun. 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. IAWA Bull. n.s. 7: 145–153.

Liphschitz, N., S. Lev-Yadun & Y. Waisel. 1985. The annual rhythm of lateral meristems (cambium and phellogen) in Pistacia lentiscus L. IAWA Bull. n.s. 6: 239–244.

Liphschitz, N. & Y. Waisel. 1970. The effect of water stresses on radial growth of Populus euphratica Oliv. La Yaaran 20 (3): 53–63, 74–80.

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

Priya, P.B. & K.M. Bhat. 1998. False ring formation in teak (Tectona grandis L.f.) and the influence of environmental factors. Forest Ecol. Management 108: 215–222.

Pumijumnong, N., D. Eckstein & U. Sass. 1995. Tree ring research on Tectona grandis in northern Thailand. IAWA J. 16: 385–392.

Rao, K.S. & Y.S. Dave. 1981. Seasonal variations in the cambial anatomy of Tectona grandis (Verbenaceae). Nord. J. Bot. 1: 535–542.

Tomlinson, P.B. & K.A. Longman. 1981. Growth phenology of tropical trees in relation to cambial activity. In: F.H. Borman & G.P. Berlyn (eds.), Age and growth rate of tropical trees: 7–19: Yale Univ. School Environ. Studies, Bull. No. 94, New Haven, Connecticut.

Troup, R.S. 1921. The silviculture of Indian trees. Clarendon Press, Oxford.

Venugopal, N. & K.V. Krishnamurthy. 1987. Seasonal production of secondary xylem in the twigs of certain tropical trees. IAWA J. 8: 31–39.

Waisel, Y., N. Liphschitz & A. Fahn. 1970. Cambial activity in Zygophyllum dumosum Boiss. Ann. Bot. 34: 409–414.

Wilcox, H. 1962. Cambial growth characteristics. In: T.T. Kozlowski (ed.), Tree growth: 57–88. Ronald Press, New York.

Wilson, B.F., T.J. Wodzicki & R. Zahner. 1966. Differentiation of cambial derivatives: proposed terminology. For. Sci. 12: 438–440.

Zimmermann, M.H. & C.L. Brown. 1971. Trees. Structure and function. Springer-Verlag, New York..