

**SEASONAL BEHAVIOUR OF VASCULAR CAMBIUM IN TEAK  
(TECTONA GRANDIS) GROWING IN MOIST DECIDUOUS AND  
DRY DECIDUOUS FORESTS**

by

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SUMMARY

Seasonal behaviour of vascular cambium in *Tectona grandis* L. f. growing in Moist Deciduous Forests (MDF) and Dry Deciduous Forests (DDF) of Gujarat State in Western India was studied for one annual cycle. In both the forests active cambial cell division and simultaneous differentiation of xylem and phloem started in June when the dormant shoot buds opened. In MDF cambial cell activity reached its peak in August–September and ceased in October; in DDF it ceased in November after reaching a peak in July–August. Maximum radial growth in trees of both forests occurred during the monsoon period. In both forests, phloem differentiation ceased before xylem differentiation. During dry months and the leafless periods the cambium remained dormant. Xylem mother cells next to the mature xylem in MDF underwent differentiation into xylem elements following the onset of periclinal divisions in March. In both forests, the seasonal anatomical changes associated with the cambium closely followed the phenology of the tree and local climatic conditions.

**Key words:** Vascular cambium, xylem, phloem, *Tectona grandis*.

INTRODUCTION

The pattern of radial growth in trees largely depends on the seasonal behaviour of the vascular cambium. The vascular cambium of different taxa varies in form and its activity depends on the genetic and physiological constitution of the plant as well as on environmental factors (Philipson et al. 1971; Iqbal & Ghouse 1987). The cambium of temperate trees has been studied more widely than that of tropical trees. Recently, the cambium of tropical trees has attracted more attention, although the structural changes that the meristem undergoes with seasonal climatic variations needs more study (Iqbal & Ghouse 1985, 1987; Eckstein et al. 1995).

*Tectona grandis* L. f. (teak) is well known for its prized wood. A few studies have been carried out on seasonal behaviour of the vascular cambium in teak (Lawton 1972; Rao & Dave 1981). Chowdhury (1940) recorded the variation in periodicity of cambium in relation to growth-ring formation in teak growing in Dehradun, Chittagong,

Nilambur of the Indian subcontinent. Recently, Priya and Bhat (1997, 1998) reported anatomical changes in juvenile wood following insect defoliation and the influence of environmental factors on the formation of false rings in teak growing in the southern part of India.

The State of Gujarat has a rich teak forest, particularly in the southern part (Dangs). The present investigation's objective is to document the seasonal anatomical changes associated with the cambium in teak growing in moist deciduous and dry deciduous forests of Gujarat State in the western part of India.

## MATERIALS AND METHODS

Samples of cambial tissue along with inner bark and outer sapwood were collected from the main trunk at breast height of *Tectona grandis* trees with diameters of 35–40 cm. The trees grew naturally in moist deciduous forests at the Waghai region of Dangs forest (20 52' N; 73 33' E) and dry deciduous forest at Pavagadh (22 30' N; 73 33' E). Collections were made from January–December 1994 in the second week of every month. Two different trees were sampled each time to obtain four blocks, no tree being sampled more than once. Blocks measuring about 60 × 20 mm were excised with the help of chisel, hammer and single-edged blade and fixed immediately in FAA (Berlyn & Miksche 1976). Trimmed blocks were sectioned in transverse, radial longitudinal and tangential longitudinal planes at a thickness of 12–15 µm on a sliding microtome. After staining with tannic acid-ferric chloride-lacmoid combination (Cheadle et al. 1953) the sections were mounted in dibutyl phthalate xylene (DPX).

The terms cambium and cambial zone are used to include the ray and fusiform cambial initials and their immediate derivatives (mother cells) between the xylem and phloem. Cambial activity was determined by counting the number of undifferentiated cell layers between the mature xylem and phloem in transverse section. One hundred random measurements of cambial cell layer thickness were made to obtain the mean and standard deviation.

Seasonal phenological changes of the trees (such as sprouting of foliar buds, full foliage, flowering, fruiting and defoliation) were recorded at the time of each sample collection. Data on air temperature, rainfall and relative humidity were obtained from the Indian Meteorological Department, Ahmedabad.

## OBSERVATIONS

### *Structure of cambium*

Cambium was nonstoried (Fig. 1) with vertically elongated fusiform cambial cells and horizontally arranged ray cambial cells. Fusiform cambial cells in the trees from Moist Deciduous Forest tended towards local storied structure (Fig. 2). During dormancy the radial walls of fusiform cambial cells were thick and beaded due to the presence of numerous primary pit fields. With the onset of periclinal divisions the radial walls became thin and the beaded pattern disappeared. Cambial rays were uni- to multiseriate and heterocellular. Cambial ray cells also showed nodding during the inactive period.

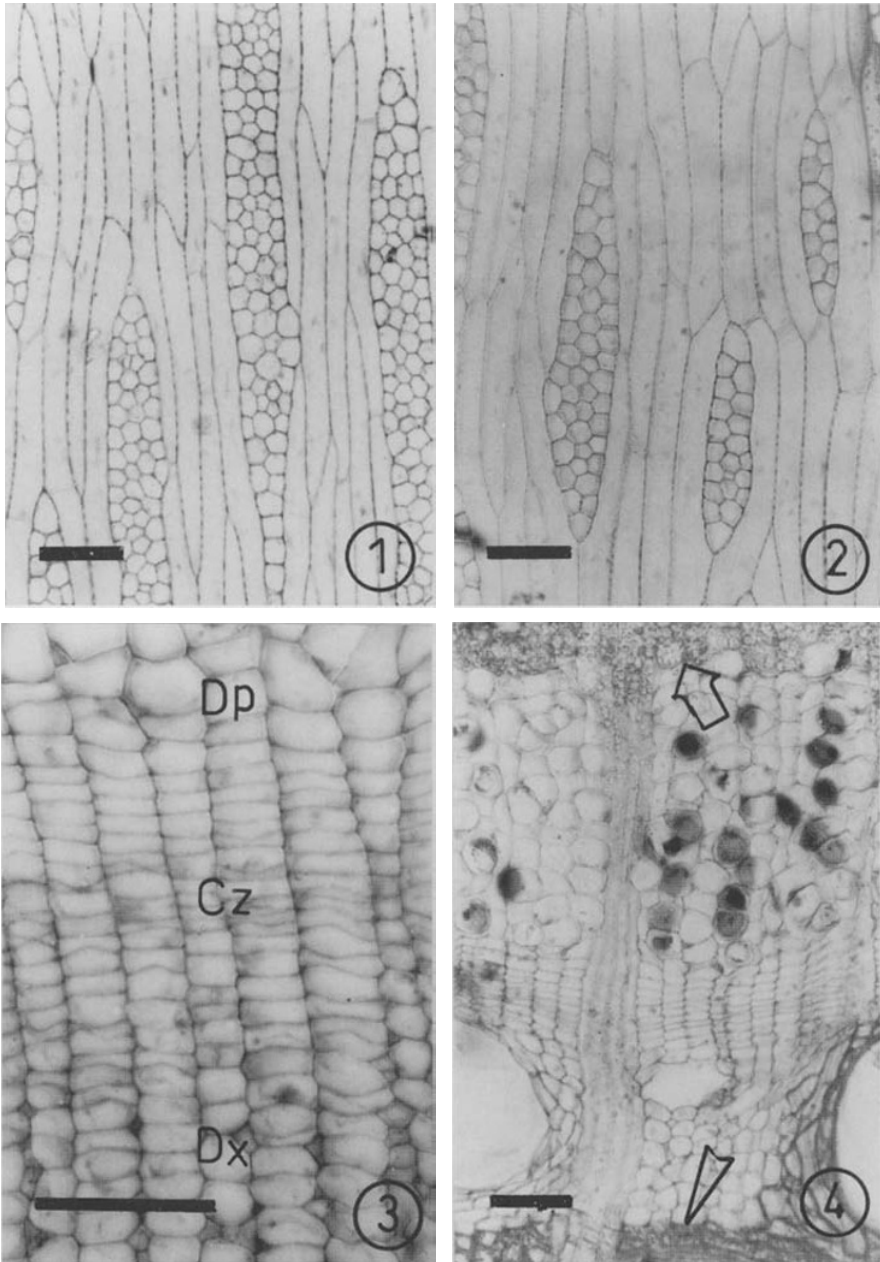


Fig. 1–4. *Tectona grandis*. – 1: Nonstoried fusiform cambial cells. Dry Deciduous Forest (DDF). – 2: Storied fusiform cambial cells. Moist Deciduous Forest (MDF). – 3: Active cambial zone in August. DDF. – 4: Cambial zone surrounded by current years xylem and phloem elements in July. Note the relatively high amount of phloem tissue. Arrow and arrowhead indicate the growth ring boundary in phloem and xylem, respectively. MDF. — Cz = cambial zone, Dp = differentiating phloem, Dx = differentiating xylem. — Scale bars in 1, 2 = 100  $\mu$ m; in 3, 4 = 75  $\mu$ m.

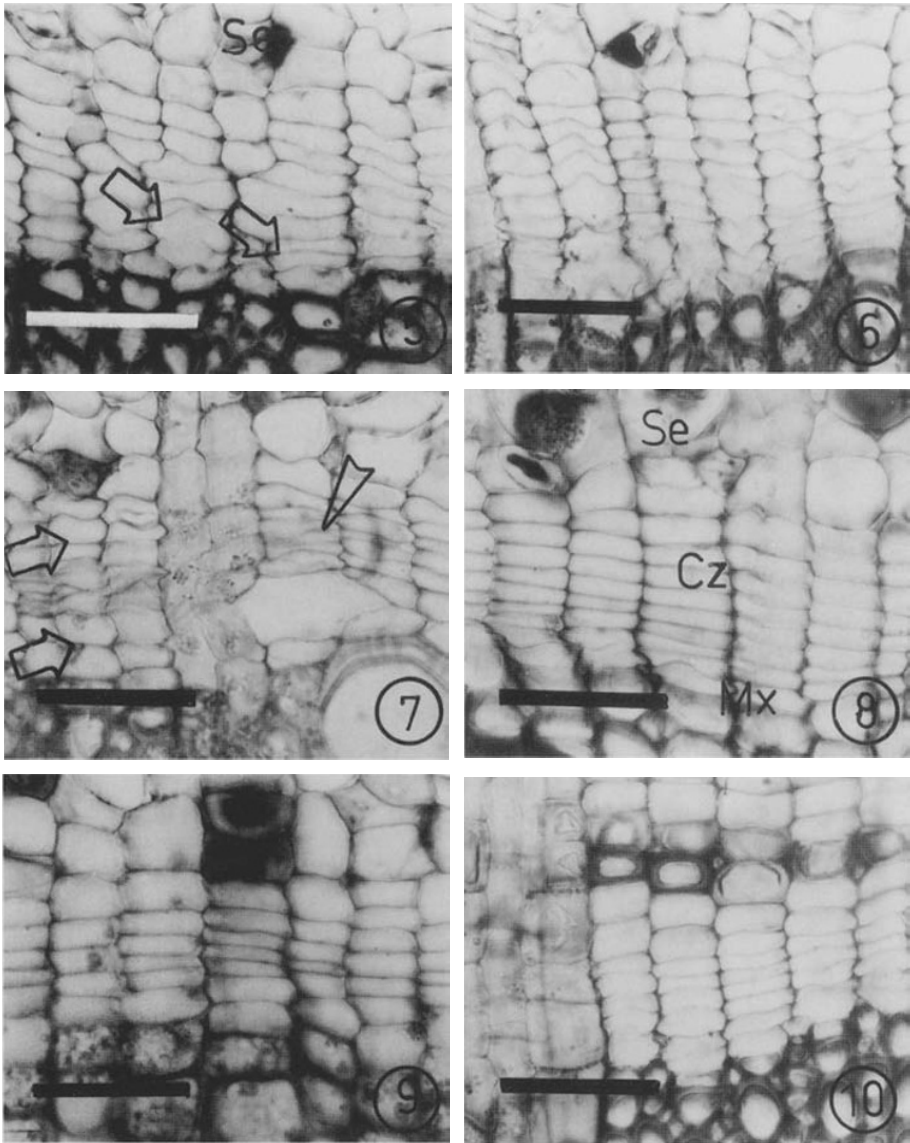


Fig. 5–10. *Tectona grandis*. – 5: Cambial zone showing initiation of activity (arrows) in March. MDF. – 6: Periclinally dividing cambial cells close to the xylem in March with few differentiating xylem derivatives. MDF. – 7: Initiation of cambial activity in June (arrowhead). Note the simultaneous differentiation of xylem and phloem (arrows). – 8: Cessation of cambial activity in October. Note the maturing xylem elements while there is no phloem development. MDF. – 9: Cambial zone showing initiation of activity in June. DDF. – 10: Dormant cambial zone in December surrounded by completely mature xylem and phloem. — Se = sieve element, Cz = cambial zone, Mx = maturing xylem. — All scale bars = 75  $\mu$ m.

### ***Cambial activity***

In some of the samples collected in March from Moist Deciduous Forest, the xylem mother cells next to the mature xylem showed periclinal divisions (Fig. 5). A few differentiating vessels were also observed at some places along the cambial zone. However, no cell divisions or vessel differentiation were observed in the samples collected in April and May. In June, periclinal divisions began in the cells at the middle of the cambial zone (Fig. 7) leading to the simultaneous differentiation of xylem and phloem. The divisions reached a peak in August–September forming a wide cambial zone with 11–16 layers of cells in each radial file, then declined, and stopped in October (Fig. 8). During the other months, the cambial zone remained narrow surrounded by mature xylem and phloem elements. Cambial cell divisions in Dry Deciduous Forests began in June (Fig. 9) and reached a peak in July–August (Fig. 3) with 13–20 layers of cells in the cambial zone. Cell division declined gradually and stopped in November. The cambial zone was narrow with 5–8 layers of cells (Fig. 10) in the other months.

### ***Development of vascular tissues***

In both forests the cambial zone was surrounded by mature xylem and phloem elements until May. However, in Moist Deciduous Forest, a few differentiating xylem elements were observed in March (Fig. 6). The xylem and phloem differentiated simultaneously in June (Fig. 7 & 9) following the onset of periclinal divisions in the cambial zone. Phloem development stopped before xylem (Fig. 8). In both the forests, there was a rapid increase in divisions of cambial zone cells from June to July. Periclinal cell divisions were initially more frequent towards the phloem side (Fig. 4) in Moist Deciduous Forest, resulting in relatively more phloem tissue. Later, xylem formation was more rapid than phloem. As a result, a maximum number of xylem elements was produced in August–September. In Dry Deciduous Forest, however, xylem and phloem development was maximal in July–August when the cambial zone had the maximum number of dividing cells. Maturation of xylem continued until November and December in Moist Deciduous Forest and Dry Deciduous Forest, respectively.

### ***Cambial activity in relation to phenology*** (Table 1)

*Tectona* remained leafless during the drier part of the year. In Moist Deciduous Forest, floral and foliar parts began to dry in November–December. Defoliation began in January and by April the trees were leafless. New leaves began appearing in June, and in July–August trees attained full foliage and fruit setting. The development of young leaves ceased and apical buds became dormant in September. During this period the cambium was active. Cambial growth ceased after complete maturation of leaves and fruits. Defoliation in Dry Deciduous Forest was initiated in December and trees became completely leafless by March. Sprouting of new leaves from dormant buds was followed by initiation of cambial cell division in June. Cambial activity reached its peak when the crown attained full size with young leaves and flowers in July–August. The sprouting of new leaves ceased following resting of the apical buds in October.

Table 1. Periodic changes in number of cambial layers in relation to phenology in *Tectona grandis*, growing in Moist Deciduous Forest (MDF) and Dry Deciduous Forest (DDF) of Gujarat State.

Month	MDF		DDF	
	Phenology	Cambial	Phenology	Cambial
January	Yellowing of leaves and initiation of defoliation	6 ± 0.94	Partial defoliation	6 ± 1.05
February	Yellowing and defoliation	6 ± 1.47	Partial defoliation	6 ± 1.33
March	Partial defoliation	7 ± 1.22	Complete defoliation	6 ± 1.23
April	Complete defoliation	7 ± 1.12	Complete defoliation	5 ± 1.18
May	Complete defoliation	7 ± 1.20	Complete defoliation	5 ± 0.99
June	Sprouting of new leaves	8 ± 0.72	Sprouting of new leaves	6 ± 0.96
July	Full foliage with young leaves	9 ± 1.42	Full foliage with young leaves, flowering	13 ± 1.56
August	Full foliage, flowering	10 ± 1.40	Full foliage, flowering fruit setting	18 ± 2.69
September	Full foliage, flowering terminal bud dormant	14 ± 1.10	Full foliage, terminal bud active	10 ± 1.35
October	Full foliage, fruit setting terminal bud dormant	10 ± 1.97	Full foliage, terminal bud dormant	10 ± 1.70
November	Mature leaves, drying of fruits	6 ± 1.10	Yellowing of leaves, drying of fruits	8 ± 1.57
December	Mature leaves, drying of fruits	6 ± 0.65	Initiation of defoliation	5 ± 0.88

### ***Cambial activity in relation to climatic factors***

Rainfall and temperature are interdependent factors. The air temperature reached its peak in May at the end of the dry season, then fell with the onset of rains in June and reached a minimum in July when the rains were heavy. Dormant shoot buds were noticed in May when the temperature was highest in the season. The opening of shoot buds began in June when the maximum temperature was about 35 °C. Cambial cell division and differentiation reached a maximum when the rains were heavy. During the dry period the cambium remained dormant (Fig. 11A & B).

## DISCUSSION

The vascular cambium in *Tectona grandis* is nonstoried (Rao & Dave 1981). The development of nonstoried cambium involves oblique anticlinal divisions and intensive intrusive growth of fusiform cells (Bailey 1923). The fusiform cambial cells from the trees of Moist Deciduous Forest often locally appear short with their tips

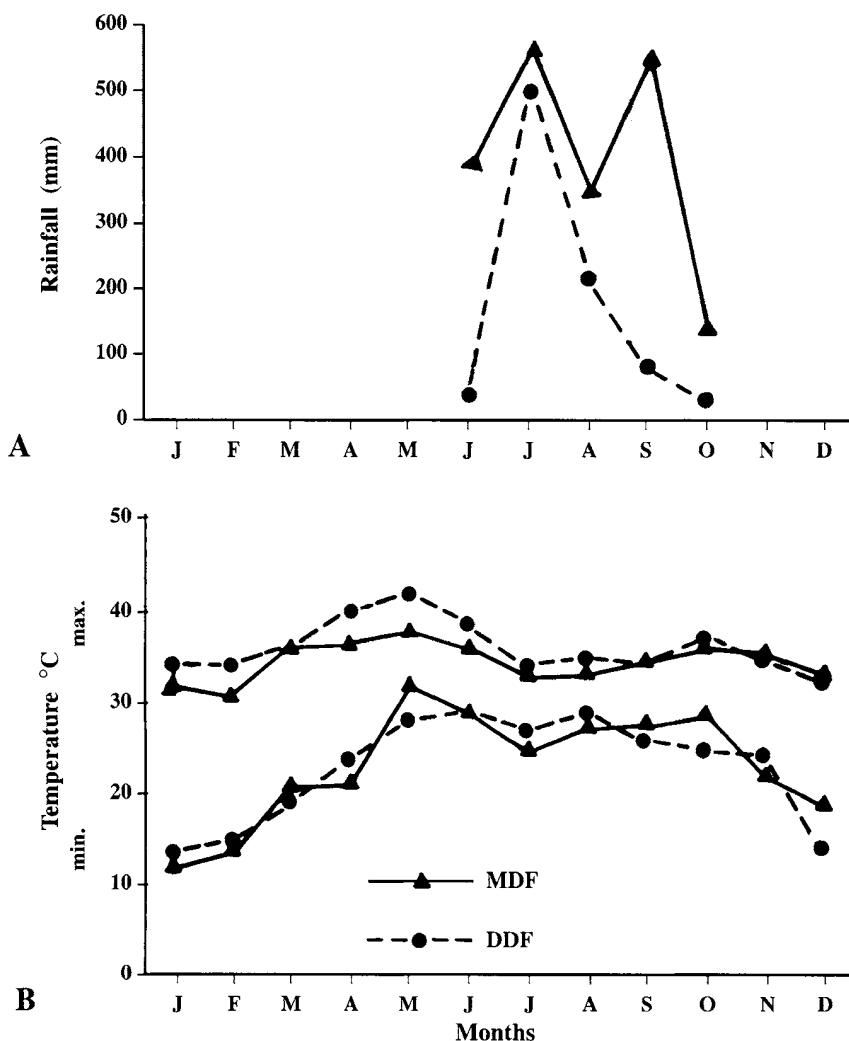


Fig. 11. Graphic representation of average rain fall (A) and temperature (B) in Moist and Dry Deciduous Forest recorded at the Indian Meteorological Center, Ahmedabad in 1994.

nearly at the same level in tangential view. Such a locally storied cambium may be developed due to less elongation of daughter cells following the pseudotransverse anticlinal divisions in the adjacent fusiform cambial cells. However, no data are available in the literature on the intrusive growth of fusiform cambial cells that might follow pseudotransverse divisions.

Cambial periodicity is more closely correlated with seasonal changes in temperature than in tropical regions. The period of radical growth is relatively long in tropical conditions where it continues either throughout the year (Fahn 1982; Dave & Rao 1982a) or for a major part of the year (Fahn & Sarnet 1963; Chowdhury 1968; Dave

& Rao 1982b; Iqbal & Ghouse 1987). In the present study radial growth of *Tectona* in both the forests continued for about six months. In the young branches of teak growing at Tiruchirappalli (South India), cambial cell division begins in July and lasts for eight months (Venugopal & Krishnamurthy 1987).

Teakwood often is described as ring-porous or semi-ring-porous. The initiation of cambial activity in ring-porous wood before bud break has been suggested to be due to the presence of tryptophan (an auxin precursor) in the bark (Wareing et al. 1964). In teak, however, the initiation of cambial cell division before bud break contrasts with temperate zone ring-porous woods.

Various environmental and physiological factors contribute to plant growth and development. The effect of temperature on reactivation of cambium is considered to be one of the most important factors (Waisel & Fahn 1965; Rao & Dave 1981; Dave & Rao 1982a, b; Paliwal & Paliwal 1990). A high temperature may be necessary for opening of dormant foliar buds and inducing activity by endogenous growth hormones. On the other hand cambial activity is not affected by a fall in temperature (Rao & Dave 1981; Dave & Rao 1982a, b; Paliwal & Paliwal 1990). In Moist Deciduous Forests, cambial cell division occurred for a brief period in March when the average maximum temperature was 35 °C. Periclinal divisions in the cambial zone began in June in both forests when the temperature was 36 °C. Cambial activity in *Tectona* growing at Vallabh Vidyanagar began in June when the temperature was 35 °C (Rao & Dave 1981). These observations indicate that 34–36 °C temperature is optimal for radial growth of *Tectona*.

Cell division and differentiation of vascular elements start with the onset of rains in June. Though the cambial cells in Moist Deciduous Forest divide and differentiate before bud break, active cell division occurs following sprouting of new leaves and rain fall in June. The monthly rainfall varies for the two forests. The average rainfall is higher in Moist Deciduous Forest, though the duration of the monsoon is the same in both forests. Peak cambial activity in MDF correlates with the relatively abundant rainfall during August–September. Peak cambial activity in DDF occurs in July–August when the rainfall is fairly high during the monsoon season. We also found a relation between leaf fall and a dry atmospheric condition. Leaf fall is initiated in January and December in Moist Deciduous Forest and Dry Deciduous Forest, respectively. In this study it appears that under dry climatic conditions leaf shedding may be earlier compared to the moist localities. The cessation of cambial cell division in October and November in Moist Deciduous Forest and Dry Deciduous Forest correlates with the appearance of dormant terminal buds in the preceding months.

Xylem and phloem development is not necessarily synchronized. Phloem formation may begin before, after or simultaneously with xylem formation and cease later or simultaneously (Philipson et al. 1971). In the present study, in both the forests xylem and phloem differentiation starts simultaneously, but phloem development stops first. The development of phloem is more rapid at the beginning of the growth season in Moist Deciduous Forest. In *Ficus rumphii* phloem development is greater when the temperature is low and humidity is high (Ajmal & Iqbal 1987). Development of more phloem in teak may be associated with low temperature and high humidity in June–July.



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