

## **DISCUSSION**

Like other dicotyledons, the vascular cambium in the stems of Tectona, Acacia, Azadirachta and Tamarindus occurs in the form of a ring between secondary phloem and xylem. It comprises of vertically elongated fusiform cambial cells with tapering ends and horizontally aligned nearly isodiametric, relatively small ray cambial cells. In angiosperms two types of cambia occurs viz. storied and non-storied (Bailey 1923, Esau 1977). The former is considered to be phylogenetically more advanced than later, as nonstoried cambia appears in most of the fossil pteridophytes and gymnosperms (Bailey 1923, Zimmermann and Brown 1974). However, occurrence of storied cambium is restricted to few dicotyledonous taxa (Metcalf and Chalk 1983, Rao et al. 1996) and reported in a few tropical species (Ghouse and Yunus 1973, 1974; Sajwan and Paliwal 1976, Rao and Dave 1983, Rajput and Rao 1996). The present study also reports the occurrence of storied cambium in Tamarindus indica. The organization of cambium in Tectona, Acacia and Azadirachta is nonstoried.

Growth of vascular cambium in woody plants is probably never continuous, even in the so called evergreen species of the tropical rain forest. Rather cambial activity is cyclic with periods of activity alternating with periods of rest or relatively inactivity (Kozlowski 1962). Cambium is found to be dormant for a short period in an evergreen tropical Psidium guajava (Chou and Chiang 1973) and Liquidamber formosana (Lu and Chiang 1975). But there are some tropical

plants in which cambium is reported to be active throughout the year (Fahn and Sarnet 1963, Dave and Rao 1982a, Fahn 1990). Tectona being a tropical deciduous tree show a definite cambial reactivation, peak activity and cessation (Rao and Dave 1981). The same pattern of cambial behaviour is noticed in this trees growing in both, MDF and DDF. In Acacia, Azadirachta and Tamarindus. the correlation between extension growth and cambial activity is not clear like certain evergreen trees (Chowdhury 1958, Fahn et al. 1968). In Acacia cambial growth occurs for major part of the year in MDF, throughout the year in DDF and in two growth flushes in SF. In Azadirachta cambial growth is noticed for major part of the year in MDF, in two growth flushes in DDF and throughout the year in SF. In Tamarindus cambial activity continues for major part of the year in all the three forests. Each new surge of cambial cell division starts following the arrival of new crop of leaves in young branches and thence the divisions spread downwards into main trunk.

Cambial activity in young branches of Tectona growing in both the forest occurs in one growth flush. In MDF, cambial cell division in main trunk begins in March but in young branches it is noticed in June. In DDF initiation of cambial cell divisions in the main stem and young branches commences in June. However, cessation of cambial growth in the main stem and young branches of the trees growing in MDF is noticed in October but it does not coincide in the trees of DDF.

Though cambial growth in DDF starts simultaneously, it ceases in October in the branches while in November in the main stem.

In the young branches of Acacia and Azadirachta growing in all the three forests, cambial growth occurs for major part or throughout the year. In IDDF, cambial growth in the main stem of Acacia occurs for the major part of the year except in March and May while in the young branches begins in January and ceases in November. In DDF, cambium remains active throughout the year but in branches radial growth occurs in two growth flushes. The first flush of cambial cell divisions begin in January, and ceases in April. Second flush starts in June and cambium is found dormant in November-December. Similarly in SF, cambium in the main trunk begins to divide in January and remains dormant from May to September. In branches also first flush of cambial activity starts in December and ceases for a brief spell of rest in May. Reactivation for second growth flush occurs in June and cambium remains dormant from September to November.

Similarly in Azadirachta cambium of the trees growing in MDF is dormant in April and December while in branches it remains dormant in November - December. In DDF cambium is active in main trunk and branches and are found suspended in May and November-December while in branches it is dormant only in September. In SF, cambium is active through out the year in main trunk but in branches it is inactive from November to January. In deciduous, diffuse porous

dicotyledons, frequency of cambial cell divisions were found to be rather slow and divisions in trunk might not begin until several weeks after it began in the twigs (Wareing 1951, Wilcox 1962)

In the trees of temperate regions, cambial activity is closely associated with an annual rhythms correlated with the succession of season. Normally growth starts in spring then it slows down and gradually ceases at the end of summer followed by period of dormancy which extends to the following spring. It is generally believed that in trees of tropical regions cambial activity is not correlated with seasonal changes because under tropical climates cambial cells gradually divide and develop at more or less uniform rate throughout the year. However, not all the tropical tree exhibit continuous cambial activity (Fahn 1990). There are conflicting reports about the periodicity of wood formation in tropical trees (Koriba 1958, Chowdhury 1961, Alvim 1964, Ghouse and Hanshmi 1979, Rao and Dave 1981).

In the present study radial growth in the main stem of Tectona growing in both the forests continues for six months. In both the forests, cambial growth in young branches continues for five months. Cambial activity in Acacia growing in MDF occurs for major part of the year except March and May. In DDF, cell division and differentiation in the cambial zone is continuous throughout the year. In SF, it occurs for seven to eight months in two growth flushes. However in young branches radial growth continues for nine, eight and ten months in MDF.

DDF and SF respectively. Additive divisions in the main trunk of Azadirachta growing in MDF continues for eleven months with brief spell of dormancy in April. In DDF it occurs for ten months in two growth flushes. The cambium remains active throughout the year in SF. In young branches, however, the activity is found to be for ten months in MDF, eleven months in DDF and nine months in SF. Radial growth in the main trunk of Tamarindus occurs for ten months in MDF, eight months in DDF and ten months in SF.

Trees do not grow continuously but rather periods of active growth alternate with periods of inactivity and dormancy (Fritts 1976). However, available literature shows that cambial activity is greatly influenced by leaf initiation and development of new leaves (Paliwal and Prasad 1970, Ghouse and Hasmi 1979, Rao and Dave 1981, 1982a,b, Denne and Atkinson 1987, Ajmal and Iqbal 1987a,b, Paliwal and Paliwal 1990a, Rao et al. 1996a, Srinivas 1996). Cambial growth is regulated by physiological activity of crown and specially by translocated products produced by shoots (Kozlowski 1971). There is relationship between leaf fall followed by arrival of new crop of leaves and reactivation of cambium (Paliwal and Prasad 1970) but the earlier reports on Fraxinus excelsier, (Chalk 1930) Psidium guajava (Chou and Chiang 1973) and in Courourouppita (Rao et al. 1996a) indicate that initiation and cessation of cell divisions in the cambial zone are not influenced by the arrival of new crop of leaves and defoliation respectively. In Tectona growing in MDF, cambial cells close to

mature xylem undergo periclinal divisions in March when the tree is leafless. However, active cell divisions and differentiation of xylem do not occur until June. Wareing et al. (1964) concluded that the initiation of cambial activity in ring porous wood before bud break is due to the presence of tryptophan (an auxin precursor) in the bark. Similar observations are also made by Paliwal and Paliwal (1990b). Being a ring porous species initiation of cambial cell division in MDF may be due to the presence of tryptophan and availability of ground water which seems to be sufficient enough to initiate periclinal divisions but not enough for rapid differentiation (Esau 1977, Rao and Dave 1983). Cambial cell divisions in Acacia do not show significant correlation with phenology. In MDF, it remains dormant in March and May when young leaves and flowers are noticed. This might be due to the fact that leaf emergence is accompanied by fruit setting and hence the growth hormones produced by the young leaves might be first utilised for the reproductive growth. Similar observations have also been reported in Prosopis spicigera (Iqbal and Ghouse 1985) Gmelina arborea (Dave and Rao 1982b) and Ficus rumphii (Ajmal and Iqbal 1987b). However, cambium remains active through out the year as flowering and development of new crop of leaves occur continuously. In SF, cambial activity initiates in January following sprouting of young leaves and remains dormant from May to September though development of young leaves and flowers occurs. Second flush of cambial growth commences in October when the tree possesses mature leaves. Similar to that of Acacia.

cambial growth in Azadirachta is found to be suspended in April when trees growing in MDF experience development of young leaves and flowers. In DDF, cambial cell division initiates in January and ceases in November when yellowing leaves occurs. In SF, cambial growth is continuous throughout the year though the yellowing of leaves and defoliation occur between January and March. In MDF, periclinal divisions in the cambial zone of Tamarindus ceases in February when the tree bears full foliage with mature leaves. Cambium is found inactive in May even though sprouting of new leaves begins in April. In DDF, cambial growth ceases in January when the tree bears full foliage. Periclinal divisions in cambial zone commences in May when sprouting of young leaves are noticed

It is well known that cambial growth is influenced by environmental factors (Larson 1964, Rao and Dave 1981, Dave and Rao 1982a, b, Paliwal and Paliwal 1990a,b, Kitin 1992, Rao et al. 1996b). Dormancy of bud and cambium and leaf shedding are in response to environmental pulsation representing temporary levels of adjustment with a minimal structural damage (Halle et al. 1978). There are reports that cambial activity is even influenced by direction of windflow and light, and also by paleoecological northpole in fossil trees (Zimmermann and Brown 1974). Leaf fall, sprouting of young leaves and cambial activity are correlated with environmental factors like temperature, rainfall and relative humidity. Of all the environmental factors, the effect of temperature is considered as a factor of primary importance for breaking of dormancy in cambium. Waisel and Fahn

(1965) observed that at relatively high temperature the activity of cambium increases whereas low temperature induces dormancy in Robinia pseudoacacia. Cambial cell divisions in Tectona growing in MDF, initiates in March when the temperature is relatively low. In DDF, it begins in June though the air temperature is maximum in May. Paliwal and Prasad (1970) suggested that high temperature is conducive for the initiation of cambial activity in Dalbergia sissoo. Cambial activity increases in Psidium guajava (Chou and Chiang 1973) and Liquidambar formosana (Lu and Chiang 1975) when temperature rises. In Larix temperature increases cambial activity (Antonova and Stasova 1988). Badola et al (1989) reported that increase in temperature brings about an increment in the rate of cambial activity as the bud scale initiation starts in some Himalayan tree species. With the increase in temperature and day length the fusiform cambial cell division augmented in Rhododendron arboreum (Paliwal and Paliwal 1990b). The initiation of cambial activity. Cambial cell division in Tectona growing at Vallabh Vidyanagar initiates in June when the temperature is 35°C (Rao and Dave 1981). In the present study also cambial activity commences in June when the air temperature is 36°C. In Acacia growing in all the three forests cambium remains active in December and January when the temperature is minimum of the year. In MDF and DDF, cambium is found to be dormant in May when the maximum or minimum temperature recorded is maximum of the year. However, similar to that of Acacia cambial growth in Azadirachta growing in MDF, and DDF is found

suspended in April and May in MDF and DDF respectively. The cambium remains active throughout the year in SF, even in December-January when the temperature is minimum compared to the other regions. Tamarindus growing in MDF, cambium is active in February when the air temperature is minimum and cell division ceases in March where the temperature is relatively high. The cambial activity is suspended until April even though the temperature is high. In DDF, cambial activity ceases in January when temperature remains minimum and reactivation occurs in June when the temperature is relatively high. Unlike other two forests, in SF, cambial cell division ceases in December during the period of minimum temperature and reactivates in March when the temperature is relatively higher. Cambial activity in Holoptelea begins when the temperature is not high (Srinivas 1996). Similarly in the present study also high temperature is not necessary for the cambial reactivation in Acacia and Tamarindus. Here it seems true that the optimum temperature is required for initiation of cambial activity and which differs from plant to plant (Srinivas 1996). Initiation of cambial activity varies even in the same species growing under the influence of different climatic conditions and it appears that reactivation of cambial growth is rather dependant on physiological state of the individual plants.

The growth of tree probably is controlled more by water availability than any other environmental factors (Kozłowski 1971). Maximum number of cambial cell layers with rapid cell divisions occur when the rains are heavy between July

and September in all the species studied, growing in all the three forests except Acacia growing in SF. In this region cambial growth in Acacia remains suspended from June to September, a major part of rainy season. Cambial activity in young plants of Zygophyllum dumosum is greatly influenced by water supply and it may be true that plant which have entered in dormancy, could not be reactivated for several weeks, even with the supply ample water (Waisel et al. 1970). Water supply also plays an important role in the synthesis and downward translocation of hormonal growth regulators from the developing crown and increasing divisions and differentiation in cambium (Rao and Dave 1981, Paliwal and Paliwal 1990a, b, Rao et al. 1996a, Srinivas 1996). Though cambial activity in Tectona growing in MDF initiates in March but rapid cell division and differentiation occur only after the onset of rains in June. As there is no sharp demarcation of time between defoliation and sprouting of young leaves in Acacia and Azadirachta, cambial reactivation, peak activity and dormancy in these trees may not be under direct influence of phenology. Similar observations have also been reported in tropical evergreen tree Mangifera indica (Rao 1981) and in Syzygium (Srinivas 1996). Tamarindus shows initiation of cambial activity in May in MDF and in June in DDF and March in SF. The activity reaches peak in September-October, August and September-October in MDF, DDF and SF respectively. The occurrence of peak activity at the end of rainy season in MDF and SF may be associated with the availability of ample water from soil. In Ficus rumphii (Ajmal and Iqbal 1987b)

leaf emergence is accompanied by fruit setting till early March and hence the growth hormones produced by the young leaves might be at first utilised in the reproductive phase of the growth and be available to reactivate the lateral meristem only afterwards. Similar observations are also made on Prosopis spiciqera (Iqbal and Ghouse 1985) and Gmelina arborea (Dave and Rao 1982b). It seems that growth hormones are first utilised for reproductive growth and they are just sufficient for cambial cell division but not enough for cell differentiation in the main stem.

High relative humidity may also augment the activity of cambium. Duration of sunshine hours shows inverse relationship with the rainfall. The number of daily sunshine hours is maximum when the cambium is fairly active. Like in temperate regions the effect of day length of cambial activity can not be comparable with the effect of duration of sunshine hours in tropical region.

In all the species studied from the three forests, maximal growth occurs during July to September (except Acacia growing in SF), when the rains are heavy. In Tectona, Gmelina and Holoptelea rainfall enhances the activity of cambium (Rao 1981) and precipitation is the main climatic factor influencing cambial activity in Switenia macrophylla and Terminalia ivorensis (Silva et al 1990). Periodicity of cambial growth varies among the species growing under the influence of different climatic condition and these variations may be coupled with

the physiology of the trees. Shortle and Bauch (1986) concluded that the response of cambium may vary considerably between the species and their location

The fusiform cambial cells are vertically elongated and give rise to axial elements of secondary xylem and phloem. The morphology and dimensions of these cells undergo variation following changes in the periodicity of cambium. Semistoried nature of cambium in Dalbergia has been reported by Venugopal and Krishnamurthy (1989) and disrupted storied nature in Holoptelea by Rao (1981) and Srinivas (1996). The thick and beaded radial walls of the dormant fusiform cambial cells are less conspicuous when the activity starts. This indicates that the cells undergo elongation with the beginning of activity. Beaded radial walls were first observed by Bailey (1930) and figured by Kerr and Bailey (1934). Bailey (1930) attributed the beadings to the unequal thickening of portions of radial walls. Barnett and Harries (1975) and Barnett (1981) doubted the presence of beads in true cambial initials and stated that the beaded cells belonged to enlarging derivatives. In all the species studied fusiform cambial cells are conspicuous beaded during dormant period. A careful review of previous literature and illustrations provided therein revealed that true fusiform cambial cells were, in fact, characterised by beaded radial walls (Evert and Kozlowski 1967, Paliwal and Prasad 1970, Ghouse and Yunus 1974, Goosen de Roo and Van spronsen 1978, Timell 1980, Venugopal and Krishnamurthy 1989).

Nucleus in the fusiform cambial cells, undergo considerable variation in their size during the seasonal activity of cambium. In active cells, nucleus appears round to oval and larger in size while in nondividing cells it becomes elongated and fusiform shaped. These variations may be related to the turgidity of cambial cells.

Periclinal and anticlinal divisions in the cambial zone lead to an increment in the amount of vascular tissues and number of cells in the cambial zone respectively. Periclinal divisions in all the four species growing in different forest types begins with the formation of phragmoplast ring which gradually extends from the centre to the tip of fusiform cambial cells. Anticlinal divisions occur predominantly at the end of growth season in all the four species. In Tectona, Acacia and Azadirachta, anticlinal divisions are pseudotransverse and in Tamarindus they are radial longitudinal. However, in Tectona both the types of cell divisions are reported by Rao (1981). In the present study also both the types of cell divisions are encountered. However, inclination toward storiedness in Tectona growing in MDF may be due to occurrence of more radial longitudinal divisions and delayed elongation of derivative cells. Fusiform cambial cell undergo intrusive growth during active period resulting forking of cell tips and splitting of rays. Compared with other three species forking of cell tips is noticed frequently in Tamarindus growing in all the three forests. Such forking cell tips

has also been reported in the cambium of Juglans and Liriodendron (Esau 1977), in Mangifera, Tectona and Gmelina (Rao 1981) and Syzygium (Srinivas 1996)

Changes in the length of fusiform cambial cells is just one aspect of the profound modifications which takes place in the cambial zone during life span of plants (Catesson 1974). From the observations it is clear that the yearly average of fusiform cambial cells is relatively more in MDF and less SF in all the species. This indicates that cell elongation is more in the species growing in MDF which may be due to more availability of water.

During the year, cambial zone cells also show a wide range of structural and dimensional variations. In Tectona and Tamarindus the number of layers in the cambial zone are more in MDF while in Acacia and Azadirachta the layers are more in DDF and SF respectively. These findings indicate that the width of cambial zone of a species may vary depending on the local environmental conditions.

Sequence of cell division and changes in size of cambial cells can be obtained by studying the secondary xylem, since divisions are more frequent on xylem side. Studies on size relationship between cambial cells and their derivatives elements are rare and have been carried out in Triplochiton, Scleroxylon, Aeschynomene (Philipson et al. 1971), Polyalthia (Sharma et al 1979), Tectona and Gmelina (Rao and Dave 1981, Dave and Rao 1982b) and Syzygium, Dalbergia and Holoptelea (Srinivas 1996). The xylem fibres are 2.8 to

6.5 times longer than the fusiform cambial cells in Tectona, Acacia, Azadirachta and Tamarindus growing in all the three forests. Chattaway (1936) has observed that fibres in dicotyledonous wood 1.1 to 9.5 times longer than the fusiform cambial initials. The xylem fibres in the present study fall under the range given by Chattaway (1936). However, wood fibres exhibit more length among all the xylem derivatives as they undergo more intrusive growth than the rest of the axial elements.

Cambial rays are nonstoried and heterocellular in Tectona, Acacia and Azadirachta and storied, homocellular in Tamarindus. They are unimultiseriate in Tectona, Acacia and Azadirachta while exclusively uni-biseriate and rarely triseriate in Tamarindus growing in all the three forests.

Cambial rays are characterised by the presence of large intercellular spaces among the cells in Tectona, Azadirachta and Tamarindus during the dormant period of cambium in all the three forests. However, no such intercellular spaces are present in Azadirachta growing in SF, as the cambium remains active throughout the year. Although in the majority of tree species, large intercellular spaces are lacking in the cambium, such opening do exist in some species (Hook et al. 1972, Hook and Brown 1972). It has been suggested that cambium forms a impervious sheath for free gas exchange (Krammer and Kozłowski 1960) but observations by Sledge (1930) on cambial layers of dormant shoots cut under glycerin showed air streaks in both the uniseriate and multiseriate rays from

phloem across the cambium into the xylem. However, in actively growing cambium air streaks were absent across the cambium. Large intercellular air spaces are found continuous in the rays from phloem to xylem via cambium during leafless period in Tectona growing in both the forests. The air spaces are found in Azadirachta growing in MDF, and DDF in April and May respectively when the cambial growth is suspended. Similarly in Tectona and Tamarindus air spaces are absent among ray cambial cells during active growth.

In mesophytic tree species, the transpiration stream undoubtedly plays a vital role in supplying oxygen and removing carbondioxide from actively dividing and differentiating cells of xylem side of relatively impervious cambium. Conversely in halophytes where air is often limiting to the roots and water is plentiful, the cambium is more permiable to air (Hook and Brown 1972). Trees develop intercellular air spaces in flooded region while those species are nonadaptive to flooded condition does not develop intercellular spaces (Hook and Brown 1972). The trees of Tectona growing in MDF and DDF bear leaves until December and January respectively. However, during this vegetative phase, transpiration stream may provide oxygen and remove carbondioxide. while during the leafless phase development of intercellular spaces may be associated with the exchange of gas for the metabolic activities. Intercellular spaces in the xylem rays of Tectona, Azadirachta and Tamarindus are very small and inconspicuous due to the development of secondary walls.

In dormant cambium, ray cambial cells undergo shrinkage and become oval to oblong which leads to the formation of large intercellular air spaces. In active cambium ray cambial cells become turgid and polygonal which leaves no spaces between adjacent cells. Turgidity of the cells hinder from being spherical while loss of water results in the formation of intercellular air spaces which essentially become continuous within all parenchymatous tissues (Hook et al 1972)

Periclinal divisions in the cambial ray cells lead to the formation of phloem and xylem rays. Cambial rays also increase in their height and width by the transverse and vertical anticlinal divisions respectively. The origin of secondary rays occurs by the division of fusiform cambial cells. These divisions are the lateral anticlinal or transverse. Transverse divisions occur at the tip or the entire length of the cells. The pattern of cambial ray development in Tectona growing in both the forests is similar to the earlier report (Rao 1988). In Acacia, Azadirachta and Tamarindus new rays originate by all the patterns as reported in previous studies (Bannan 1953, Rao 1988, Srinivas 1996). An interesting feature in Acacia is that fusiform cambial cells do not show positive staining for tannin contents. However, the ray cambial cells which are recently cut off from them become filled with abundant dark brown phenolic contents. Similar features has also been reported in Syzygium (Srinivas 1996).

The vertical and lateral fusion of cambial ray is also encountered in Acacia. Fusion of rays is brought about by the elimination of fusiform cambial cells

intervening the group of ray cambial cells Height and width increases by the fusion of rays

Variations in the dimensions of cambial rays and their number per one cm tangential width of cambium are compared among the tree species growing in different forests. The dimensions of the rays undergo alterations during the annual growth of cambium variations in height of cambial rays in Tectona growing in both the forests are negligible. The yearly mean height of cambial ray is relatively more in MDF. The mean height of the ray is more in Acacia and Azadirachta growing in SF and in Tamarindus growing in MDF. The average width of the ray is more in Tectona growing in DDF, Acacia, Azadirachta and Tamarindus in SF The variations in ray cambial cell diameter are found negligible in all the species studied.

Cambial ray population is more in Tectona, Acacia and Azadirachta growing in DDF and Tamarindus growing in MDF. An increase in ray width coincides with decrease in ray population and vice-versa In DDF cambial ray width and number of rays per one cm are also more in Tectona, while in Acacia, Azadirachta and Tamarindus, cambial ray width is more in SF, while number of rays are less. The reason for the inverse relationship between width and number of cambial rays is to maintain the relative proportion of cambial rays with fusiform cambial cells The high average of ray population in the cambial zone may be related to the increase in area of the ray channels for radial translocation of water.

metabolites and growth regulators between xylem and phloem of trees growing in SF

Perusal of literature shows that the time factor varies for phloem and xylem differentiation. Phloem differentiation may precede or follow xylem differentiation or differentiation of both the conducting tissues may begin simultaneously in different species (Davis and Evert 1965, Derr and Evert 1967, Philipson et al 1971, Rao and Dave 1981, Dave and Rao 1982b, Venugopal and Krishnamurthy 1987a, 1987b, Rao et al 1996a). In the present study, the tree species growing at different forests showed variations in the development of vascular tissues. The development of xylem in Tectona growing in MDF starts in March. However, the divisions are sluggish and observed only in those cells close to the xylem during March while in June cell division starts in the middle of cambial zone leading to the differentiation of xylem and phloem simultaneously. In DDF xylem and phloem differentiation starts simultaneously. Simultaneous development of xylem and phloem has already been reported in Tectona (Rao and Dave 1981). However, development of xylem precedes that of phloem in Acacia growing in MDF and SF. Azadirachta in MDF and DDF. In Tamarindus it occurs simultaneously in all the three forests. Interestingly more phloem development occurs in the beginning of cambial growth in Tectona growing in MDF. By July, season's most of the phloem is developed from cambium while such feature has not been observed in Tectona

growing in DDF. Ajmal and Iqbal (1987b) reported more phloem production in Ficus rumplii due to low temperature and high humidity. However, development of more phloem in the beginning of cambial growth may be related with the variations in temperature and humidity between MDF and DDF. The rapid burst of phloem production in the beginning of cambial activity may lead to the rapid translocation of photosynthates to the growing organs.

The development of two sieve tube elements from each sieve tube mother cell is common in Tectona which has already been reported (Lawton 1972). However, development of 3-4 sieve tube elements from single mother cell are also observed at the end of cambial activity in both the forests. These elements are narrow with smaller diameter. Phloem functions for 8-9 months in Tectona growing in both the forests. But in Acacia, Azadirachta and Tamarindus addition of new sieve elements and cessation of their function are continuous.

It is well established that development of massive callose on sieve plate and lateral sieve area is regarded as a sign of inactivation of sieve elements in temperate as well as tropical regions (Evert 1984, Deshpande and Rajendrababu 1985, Vishwakarma 1991). In present study also all the four species show deposition of callose on sieve plates and lateral sieve areas followed by obliteration of sieve elements.

With reference to the cessation of vascular tissue development, cessation of phloem development precedes that of xylem in all the four species studied. Except

in Acacia and Azadirachta growing in DDF and SF respectively where the cambium is found active throughout the year.

Though much significant changes in structure are not observed in the vascular tissues, variations in the amount produced between the same species growing in three different forests, has been observed. Annual phloem increment is easily discernable due to the presence of narrow sieve elements with compressed parenchyma and obliterated sieve elements in last years phloem and sieve plates with callose deposition. Ray cells with distinct accumulation of starch makes the last years phloem discernable from current years one. Compared with fusiform cambial cells length of sieve tube elements decreases slightly in Tectona, Azadirachta and Tamarindus while it increases slightly than that of fusiform cambial cells in Acacia. Zahur (1959) and Den Outer (1986) also reported the presence of shorter sieve tube elements in some dicotyledonous taxa. However, slight decrease in length of sieve tube member may be due to shifting of pointed hexagonal tip of fusiform cambial derivatives to transverse position (Anand et al 1978). Similar feature has also been observed in Sterculia (Rao et al 1996). Increase in length of sieve elements compared with fusiform cambial cells in Acacia may be associated with elongation of oblique end walls during the development of compound sieve areas.

Occurrence of sieve elements in the rays of secondary phloem has been reported in Cucurbitaceae (Fischer 1884) and Compositae (Chavan et al 1983). They have also been reported in mesocarpic as well as endocarpic region of fruits (Thanki 1978, Shah et al 1983). In the present study radially arranged solitary and groups sieve tube elements have been noted in the phloem rays of Tectona, Acacia and Azadirachta. They have been observed parallel or slightly oblique to axial sieve tube elements mostly in the region of ray splitting (Chavan et al. 1983). But in the present study these sieve tube elements are radially arranged like ray cells. Occurrence of simple as well as compound sieve plates has also been reported by Thanki (1978) and Chavan et al. (1983) and it appears true that even sieve plates of these elements are specialized in the utilisation of maximum area on sieve plates (Shah and Chavan 1980, Rajput and Rao 1997). Occurrence of well developed sieve plates with slime mass and their connection with the main phloem strands indicate that they are probably involved in the short distance exchange of photosynthetic material with the ray parenchyma cells (Chavan 1981) and their increasing frequency away from cambial zone confirms here with that they develop as additional translocatory path to cope with the rapid transport of photosynthates (Thanki, 1978, Chavan et al. 1983, Shah et al. 1983, Rajput and Rao 1997). Their constant association with companion cells (Esau 1969) and extensive deposition of callose in nonfunctional phloem, while open sieve pores, slime mass and their contact axial sieve elements also suggest their role in the translocation of

photosynthates. Like axial sieve elements, sieve elements in the rays also showed massive deposition of callose when they become nonfunctional.

The differentiation of either solitary or grouped sieve elements in response to injury or chemical, especially growth hormones has already been reported by earlier workers (Eschrich 1953, La Motte and Jacobs 1962, Digby and Wareing 1966a, 1966b, Aloni 1980). The sampled trees of present study were growing in deep forests and care was taken before sampling that trees were not injured earlier therefore, occurrence of these ray sieve elements are not in response to either injury or chemicals. However, occurrence of these elements may be related to the incidental development for short distance exchange of photosynthates between the axial and radial system.

Growth rings in xylem of tropical trees are not distinct. Being ring porous, xylem of Tectona exhibits distinct growth rings while diffuse porous xylem of Acacia, Azadirachta and Tamarindus show indistinct growth rings. However, the amount of wood produced in every growth season could be discerned by abruptly reduced lumen diameter and thick walled elements. Ray noding pattern also helps to distinguish the growth rings (Amobi 1973, Rao et al. 1996). Noding of vascular ray generally occurs in the region of resting cambial zone. The size of nodes varies in individual plants. In transverse sections, nodes generally appear spindle shaped. The nodes may persist distinctly in the wood. However, noding is not so distinct in some trees (Amobi 1973).

Xylem shows much variation in vessel element length, width and lumen diameter among the species. Compared with fusiform cambial cell, vessel elements have shorter length and their width increases to a greater extent in all the four species studied. The yearly mean length of vessel elements is greater in Tectona and Acacia growing in MDF, in Azadirachta in DDF and Tamarindus in MDF. However, vessel lumen diameter decreases but the cell wall thickness and number per unit area increases at the end of activity in all the species studied. During the early part of the activity, vessel lumen diameter is more and cell wall thickness and number per unit area are less. However, increase in vessel lumen diameter may be associated with the more availability of growth hormones. Increasing number of vessels per 0.5 mm<sup>2</sup> area at the end of the activity may be related with reduction in supply of water from soil and growth hormones. Comparative studies done on ecological wood anatomy have shown that plants grown in extreme habitats usually have high density of very narrow vessels in contrast to low density of wider vessels in plants grown in mesomorphic environment (Aloni 1987). This appears true in case of Acacia growing in SF. Compared to other two forests, trees of SF show more density of narrow vessels in xylem. It seems that environment controls the dimensions of vessels and their distribution pattern.

The annual average width of vessel elements is more in Tectona and Azadirachta growing in DDF, Acacia in MDF and Tamarindus in SF. Vessels

frequency in cross sectional area of xylem in Tectona growing in both the forests is found to be same. In Acacia the frequency is more in SF. In Azadirachta and Tamarindus growing in MDF, the frequency is found maximal compared with other two forest types.

Vessels are mostly solitary in Tectona, Acacia, Azadirachta and Tamarindus. However, Acacia growing in SF possess more tangential multiple vessels. Axial parenchyma in all the species is vascicentric aliform in Tectona and Azadirachta and vascicentric aliform to confluent in Acacia and Tamarindus. Occurrence of vascicentric, aliform to confluent arrangement of axial parenchyma is considered to be phylogenetically advanced character (Metcalf and Chalk 1983). No significant variation has been observed in the structure of xylem in Tectona, Azadirachta and Tamarindus growing in all the three forests. However, the structure in Acacia growing in SF differs from that of other two forest types. In MDF and DDF, distribution of axial parenchyma is aliform type while in SF it is confluent forming continuous very wide tangential bands. In addition, more number of narrow vessels in tangential or radial multiples and occurrence of G-fibres are the characteristic feature in the xylem of Acacia growing in SF.

Compared to the histological studies seasonal histochemical changes occurring in cambial tissue are meagre in temperate as well as tropical trees (Catesson 1964, Tsuda and Shimaji 1971, Rao and Dave 1983, Rao and Menon 1989, Srinivas 1996). Seasonal variations of reserve metabolites such as starch,

lipids and proteins have been studied in cambium and its derivatives. Histochemical changes in cambial cells and xylem and phloem parenchyma during the seasonal periodicity of cambium show a significant correlation with the initiation, maturation and shedding of leaves. Esau (1948) suggested that starch and tannin may occur in cambial ray initials. Starch is the most abundant reserved carbohydrates in many plants. Starch content is clearly dependant on season with maximum in spring and it declines in summer and autumn leading to the minimum in winter in evergreen trees (Forschner 1989). Where as in deciduous trees starch content depends upon different growth seasons of a year (Essiamah and Eschrich 1985).

In Tectona heavy accumulation of starch is noticed in parenchyma cells of xylem in May when the trees are leafless. The cells of xylem and phloem in both the forests are devoid of starch during peak cambial activity. At the end of cambial activity when the trees are with mature foliage starch accumulation increases in axial parenchyma of xylem and phloem.

In Acacia starch grains in vascular tissues close to cambial zone begin to decline with rapid cell divisions in June in MDF and DDF and in January in SF however no starch is observed in the tissues when the cambium is fairly active and its distribution restricted to parenchyma of xylem away from the cambial zone. Starch deposition is heavy in all the three forests when the cambium is dormant.

Depletion of starch in Azadirachta and Tamarindus commences with rapid cell divisions in cambial zone. When the cambial activity is maximal, no starch is observed in both the plants of all the three forests. The heavy deposition of starch in all the tissues of xylem and phloem and ray cambial cells before the initiation of cambial growth suggest that starch is the main reserve material stored in the trunk for rapid growth. The decline of starch with the rapid cell divisions in cambium in all the species growing in MDF, DDF and SF indicate that the large amount of reserve carbohydrates are utilized in the production of new cambial initials and accretion of xylem and phloem (Krammer and Kozlowski 1979). Similar observations are also made in Tectona and Gmelina (Rao and Dave 1984) and Holoptelea and Mangifera (Rao and Menon 1989). The accumulation of starch with the decline of cambial activity in all the species studied may be due to higher production of photosynthates which are in excess of cambial cell divisions and differentiation.

The size and distribution of lipid bodies are considerably high during dormant period of cambium in Tectona and Tamarindus and during dormancy and sluggish cambial growth in Acacia and Azadirachta. Deshpande (1967) observed disappearance of lipid bodies with the reactivation of cambium in Tilia americana such findings have also been reported in some tropical trees (Rao and Menon 1989, Srinivas 1996). In the present study also the size and distribution of lipid bodies declines with reactivation of cambium and only sparsely distributed minute

lipid droplets occur in the active cambium of all the four species in all the three forests.

Protein bodies are considerably high in all the dormant cambial cells and less in active ones in all the studied species in all the three forests. Robards and Kidwai (1969) suggested that the lipid droplets and protein bodies are storage material which are required during the first stage of differentiation at the beginning of growth period. The concentration of nutrient and the quantity of storage reserves fall during initial stages of cambial activity (Stewart 1957). While lipid and protein bodies are reserve materials in dormant cambial cells which may be supplied to the actively dividing cells (Rao and Dave 1984, Rao and Menon 1989). In the present study also proteins and lipids are considered as reserve materials since their distribution is more in dormant cambial cells.