

DISCUSSION

The vascular cambium in the stem of Dalbergia, Holoptelea and Syzygium occurs in the form of a ring between secondary phloem and xylem as in majority of dicotyledons. It contains two cell types: 1) elongated cells with tapering ends called the fusiform cambial cells and 2) nearly isodiametric, relatively small cells called the cambial ray cells. Two types of cambial cell arrangements occur in Angiosperms viz; storied and non storied (Bailey, 1923; Esau, 1977). Dalbergia and Holoptelea show storied cambium which is considered to be phylogenetically advanced than the nonstoried one and found only in a few dicotyledon taxa. The organization of cambium in Syzygium is nonstoried. The occurrence of storied cambium in a few tropical species including Dalbergia and Holoptelea has been reported by earlier workers (Ghouse and Yunus, 1972; Ghouse and Yunus, 1974; Sajwan and Paliwal, 1976; Rao and Dave, 1983a).

CAMBIAL ACTIVITY VIS-A-VIS PHENOLOGY AND CLIMATIC FACTORS:

Trees do not grow continuously, but rather periods of active growth will alternate with periods of inactivity and dormancy (Fritts, 1976). Dalbergia and Holoptelea show definite cambial reactivation, peak activity and cessation. In Syzygium, being an evergreen, the cambium remains active for major part of the year. Cambial activity occurs in single flush in normal and affected trees of Dalbergia. However, two flushes of cambial growth were also reported in Dalbergia sissoo (Venugopal and Krishnamurthy, 1987b). In Holoptelea, cambial activity occurs twice in normal

and once in affected trees. However, three flushes of cambial activity were reported in trees growing in Vallabh Vidyangar (Rao and Dave, 1983a). The activity of cambium usually starts below the sprouting buds from where it spreads downward. In Dalbergia, Holoptelea and Syzygium cambial activity in trunk begins few weeks after it appeared in young branches. Cambial activity in young branches occurs in one and two growth flushes in normal and affected trees of Dalbergia. Whereas in Holoptelea, it occurs thrice in both normal and affected trees. While in normal and affected trees of Syzygium, branch cambium remains active for a major part of the year. 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).

Dormancy may be defined as a state in which growth is temporarily suspended (Wareing and Philips, 1978). In Dalbergia, cambium is dormant from January to March in normal and from January to May in affected trees. In November, the activity ceases in both normal and affected trees and then it remains dormant. In Holoptelea, the duration of cambial activity is less in affected trees. Cambium remains dormant in January, February and April in normal trees. In affected trees, cambial dormancy lasts from January to August. Transient cambial dormancy occurs thrice in both normal and affected trees of Syzygium. The cambium of affected trees remains dormant in February and March in contrast to the normal trees, where the first flush of cambial activity occurs during the same period. During dormancy the cambial zone

is 4 to 7, 4 to 7, 2 to 6 layered in healthy and 2 to 7, 3 to 7, 2 to 6 layered in affected trees of Dalbergia, Holoptelea and Syzygium respectively. Leaf shedding is a noticeable morphological change that occurs in plants during dormant period of cambium.

Available literature shows that the cambial growth is greatly influenced by leaf initiation and development (Priestly, 1930; Paliwal and Prasad, 1970; Ghouse and Hashmi, 1979, Rao, 1981; Denne and Atkinson, 1987). Cambial growth is regulated by physiological activity of the crown and specifically by translocated products produced by shoots (Kozlowski, 1971). There is a relationship between the leaf fall, followed by the arrival of new crop of leaves and reactivation of cambium in Dalbergia (Paliwal and Prasad, 1970). In the present work similar relationship is also noticed in both normal and affected trees of Dalbergia. But in Syzygium, it appears that the cambial activity is not influenced by leaf initiation. Similar findings were reported in Fraxinus excelsier (Chalk, 1930) and in Psidium guajava (Chou and Chiang, 1973). Cambial activity in Holoptelea is initiated by both leaf development and fruiting in normal trees and only by leaf development in affected trees. Evert (1961) suggested that in Pyrus there may be a relationship between cambial activity and fruit production. In Holoptelea, the cambial cells close to phloem divide when the trees bear green flat fruits (Rao and Dave, 1983a).

Visible symptoms of air pollution on the foliage of affected trees are occasionally noticed in Syzygium and Dalbergia. The

terminal shoots of Holoptelea, however, remain barren. The above observations are in coincidence with the earlier report on the same species growing near G.S.F.C. (Vijayan, 1987). Affected trees of Dalbergia and Holoptelea show unusual defoliation. However, flowering and fruiting occur at similar time in both affected and normal trees of all the three species studied. Partial defoliation occurs twice in affected trees of Holoptelea and Dalbergia. Unlike in normal plants, defoliation is not complete in affected trees of Dalbergia. Though Syzygium is an evergreen, the trees growing in close proximity of the source of pollutants are completely defoliated and they remained leafless for about three months. During the same period, the trees are continuously exposed by the pollutant mixtures, as these trees fall on windward direction of the emission. Soon after the change in wind direction, these trees are refoliated. Unusual defoliation and discoloration by sulfuric acid spray (Yoshitake and Masuda, 1986), reduction of lifespan of Populus by ozone (Keller, 1988) and shorter retention time of Pine needles at sites closest to sulfur source (Amundson et al., 1990) have been reported.

It is well known that environment plays a controlling part in cambial development (Larson, 1964; Kitin, 1992). Dormancy of bud and cambium and leaf shedding are responses to environmental pulsations representing temporary levels of adjustment with a minimal structural damage (Halle et al., 1978). In the present research leaf fall, sprouting of 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. Cambium is reactivated in healthy and affected trees of Dalbergia when the air temperatures is 39 C and 35 C in the months of April and May respectively. Initiation of cambial activity in normal and affected trees of Holoptelea, begins when the temperature is not high. It gives the impression that, high temperature is not necessary for the cambial reactivation in Holoptelea. Paliwal and Prasad (1970) suggested that high temperature is conducive to the initiation of cambial activity in Dalbergia sissoo. Cambial activity increases in Psidium (Chow and Chiang, 1973) and Liquidambar formosana (Lu and Chiang, 1975) when the temperature rises. In Larix, temperature increases cambial activity (Antonova and Stasova, 1988). Badola et al., (1989) reported that increase in temperature brings about an enhancement 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 initials underwent rapid cell divisions in Rhododendron arboreum (Paliwal and Paliwal, 1990). From the preceding discussion it appears that the optimum temperature required for initiation of cambial activity differs from plant to plant.

The growth of a tree probably is controlled more by water availability than any other environmental factor (Kozlowski, 1971). Rainfall seems to be responsible for the radial growth of

the normal and affected trees of Dalbergia and normal trees of Holoptelea. Maximum number of cambial cell layers with rapid divisions occurs when the rains are heavy in August in all the three species except in the affected trees of Holoptelea. During the period of rains young leaves and shoots appear in normal and affected trees of Dalbergia and normal trees of Holoptelea. Cambial activity in young plants of Zygophyllum dumosum seems to be greatly affected by water supply (Waisel et al., 1970) and it is highly sensitive to rainfall in Proustia cuneifolia (Aljaro et al., 1972). In Tectona, Gmelina and Holoptelea, rainfall enhances the activity of cambium (Rao, 1981) and precipitation is the main climatic factor influencing cambial activity in Swietenia macrophylla and Terminalia ivorensis (Silva et al., 1990).

Water supply also plays a role in the synthesis and downward translocation of hormonal growth regulators from the developing crown for increasing cell divisions and cell differentiation in the cambium. In affected trees of Holoptelea, cambial activity reaches peak in October after a prolonged suppression of growth during peak wet season. This can be attributed to the fact that the affected trees of Holoptelea are subjected to stress by pollutant mixtures during the rainy season and this leads to unusual defoliation and dormancy of cambium. During the growth period, sulfur dioxide affected trees of silver fir cambial zone is 1 to 3 cell wide, wherein normal trees, it is 5 to 10 layers of thin walled cells (Fink, 1986). Syzygium being an evergreen tree the cambial reactivation, activity and dormancy may not be under the influence of climatic factors. Similar observations have been

reported in Mangifera, a tropical evergreen tree (Rao, 1981). However, peak activity of cambium coincides with the maximum rainfall in August in both normal and affected trees.

High relative humidity may also augment the activity of cambium in Dalbergia and Holoptelea. Duration of sunshine hours shows inverse relationship with the rainfall. The number of daily sunshine hour is minimum when the cambium is fairly active. Like in temperate regions, the effect of day length on cambial activity cannot be comparable with the effect of duration of sunshine hours in tropical region.

Cambium shows periods of activity and rest in Dalbergia and Holoptelea. Whereas, in Syzygium the changes are less conspicuous. In comparison with normal trees of Holoptelea, the affected trees have a longer period of dormancy. Cambial reactivation is delayed in affected trees of Syzygium and the duration of cambial activity is more in normal trees than that of affected trees in Dalbergia. Prolonged suppression of cambial growth in affected silver fir is reported by Shortle and Bauch (1986). The response of cambium may vary considerably between the species and their location. Cambial growth retardation in Abies alba in Germany is much more pronounced than in Abies balsamea (Shortle and Bauch, 1986). Similarly affected trees of Holoptelea show much reduced cambial activity in comparison to Dalbergia and Syzygium. Trees with low cambial growth potential determined electrically had reduced mitotic activity in the cambium (Smith, 1984) and died quickly when acute pollution stress was applied (Shortle, 1983).

The growth reduction in Douglas fir is a possible indication that the increased levels of air pollution is due to industrial emissions and ammonia (Ingrid de Kort, 1986). Though micro climatic variations are negligible at both normal and affected sites, much alterations in cambial behavior are found between normal and affected trees of all the three species studied. The reduction of cambial activity in affected trees of Dalbergia, Holoptelea and Syzygium, may be due to the oxides of sulfur, oxides of nitrogen, ammonia etc., present in the mixture of combined air pollutants.

FUSIFORM CAMBIAL CELLS:

Fusiform cambial cells are elongated and they give rise to axial system of secondary xylem and phloem. The vertical ends of nonstoried fusiform cambial cells in Syzygium are gradually narrower while the storied cells (at times semistoried) in Dalbergia and Holoptelea are abruptly tapered. Semistoried cambium in Dalbergia has been reported by Venugopal and Krishnamurthy (1989) and disrupted storied nature of cambium in Holoptelea by Rao and Dave (1981). Thick and beaded radial cell walls are much prominent during dormant period in the affected trees of three species studied. This could be attributed to the delayed and much suppressed activity of cambium in affected trees.

DIVISIONAL ACTIVITY:

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

both the normal and affected trees of all the three species begin with the formation of phragmoplast ring which gradually extends from the centre to the tips of fusiform cambial cells. Anticlinical divisions occur predominantly at the end of the growth season in all the three species. In Dalbergia and Holoptelea anticlinal divisions are radial and in Syzygium, they are pseudotransverse. In Syzygium, the fusiform cambial cells are long due to the intrusive growth and they usually undergo forking at the tips. Such forking of cell tips has also been reported in the cambium of Juglans and Liriodendron (Esau, 1977) and Mangifera, Tectona and Gmelina (Rao and Dave, 1981).

DIMENSIONAL CHANGES:

Changes in the length of fusiform cambial cells are just one aspect of the profound modifications which takes place in the cambial zone during the life span of plants (Catesson, 1974). The mean length of fusiform cambial cells for the year in both normal and affected trees is 162 μm , 160 μm in Dalbergia, 246 μm , 246 μm in Holoptelea and 815 μm , 805 μm in Syzygium respectively. The mean width of fusiform cambial cells for the year in both normal and affected trees is 15 μm , 15 μm in Dalbergia, 13 μm , 13 μm in Holoptelea and 26 μm , 23 μm in Syzygium respectively. The mean length and width of the cells of affected trees of Syzygium is less in comparison to normal trees. Wherein Dalbergia and Holoptelea the variation in mean length and width are negligible.

During the year the fusiform cambial cells and cambial zone show wide range of structural and dimensional variations. In

affected trees of Syzygium, the number of fusiform cell layers is less than that of normal ones in all the seasons. The number of cell layers is less in affected trees of Holoptelea during the second flush of cambial activity while in Dalbergia it is more or less similar in normal and affected trees.

LENGTH VARIATION IN RELATION TO XYLEM FIBRE LENGTH:

Sequence of cell divisions and changes in size of the cambial cells can be obtained by studying the secondary xylem, since divisions in cambium are more frequent on the xylem side. Studies on size relationship between cambial cells and their derivative elements in phloem and xylem have been carried out in Triplochiton, Scleroxylon, Aeschynomene (Philipson et al., 1971), Polyalthia (Sharma et al., 1979) Tectona and Mangifera (Rao and Dave, 1981; Dave and Rao, 1982a). There is definite correlation between the lengths of fusiform cambial cells and xylem fibres in Dalbergia, Holoptelea and Syzygium. This correlation exists throughout the year as the cambial derivatives leave a record of their activities. The xylem fibres are 1.7 to 2.3, 4.2 to 5.6, and 6 to 8 times longer in normal and 1.6 to 2, 3.6 to 5.1 and 5 to 9 times longer than fusiform cambial cells in affected trees of Syzygium, Holoptelea and Dalbergia respectively. The seasonal length variation of fusiform cambial cells and xylem fibres is less in affected trees of Syzygium and Holoptelea and it is more in Dalbergia.

CAMBIAL RAY CELLS:

Cambial ray cells are small isodiametric cells which produce

the horizontal rays in secondary xylem and secondary phloem. Cambial rays are storied in Dalbergia and Holoptelea and non-storied in Syzygium. Uni to multiseriate cambial rays are found in all the three species.

DIVISIONAL ACTIVITY:

Periclinal divisions in cambial ray cells lead to the formation of phloem and xylem rays. Cambial rays also increase in their height and width by 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 fusiform cambial cell. In Dalbergia and Holoptelea new rays originate by all the patterns as reported in previous studies (Bannan, 1953; Rao, 1988). An interesting feature in Syzygium is that fusiform cambial cells do not show positive staining for tannin contents. However, the cambial ray cell initials which are recently cut off from them become filled with abundant catechol type of phenolic contents.

The vertical and lateral fusion of cambial ray is of common occurrence in Syzygium. Fusion of rays is brought about by the elimination of fusiform cambial cells intervening between the groups of cambial ray cells. Height and width of ray increase by the fusion of rays. Fusion of cambial rays is less frequent in Dalbergia and Holoptelea.

DIMENSIONAL CHANGES:

The aspect of cambial ray dimensional variations in relation to pollution stress is not sufficiently investigated. In the present study, variations in dimensions and number of cambial rays per 1 mm tangential width of cambium of affected trees are compared with those of normal trees. The dimensions of cambial rays undergo alterations during annual growth of cambium. In the affected trees annual mean height of cambial rays increases modestly in Dalbergia and sharply in Syzygium. However, the variations in average cambial ray height is negligible in Holoptelea. The yearly averages of cambial ray heights of normal and affected trees of Dalbergia, Holoptelea and Syzygium are 113 to 119 μm , 161 to 159 μm and 323 to 342 μm respectively. In affected trees the average width of the cambial rays is more in Dalbergia and less in Syzygium than in normal trees. In Holoptelea, the variation in ray height and width of normal and affected trees is negligible. The average cambial ray cell diameter is same in normal and affected trees of the three species.

The average cambial ray population per 1 mm tangential width of cambium in normal and affected trees is 211 and 190 in Dalbergia, 145 and 165 in Holoptelea and 119 and 134 in Syzygium. A correlation between increase in ray width with decrease in ray population and vice versa is noted. In Dalbergia, the ray width is more and number of rays is less in affected trees. Whereas in affected trees of Syzygium and Holoptelea, the average number of rays is more and ray width is less than that in normal trees. 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 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 in affected trees of Syzygium and Holoptelea, where in which the cambial activity is suppressed. However, a decrease in frequency of rays in Mango trees at polluted site has been reported by Kalimullah and Ahmad (1987).

DEVELOPMENT OF VASCULAR TISSUES:

The various patterns of cambial growth reported in available literature indicate 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; Rao and Dave, 1981, Dave and Rao, 1982b; Venugopal and Krishnamurthy, 1987a, 1987b). In the present study, the tree species growing at different locations showed variation in the development of vascular tissues. In normal trees of Dalbergia, both the xylem and phloem differentiation begins simultaneously in April. However in affected trees, the differentiation process starts in June. In normal trees of Holoptelea, during the first flush of cambial activity both the xylem and phloem differentiate simultaneously. The xylem differentiation precedes that of phloem during the second flush of cambial growth. In affected trees of Holoptelea xylem differentiation precedes that of phloem by one month. In

Syzygium, during the second flush of cambial activity differentiation of xylem precedes that of phloem and it is simultaneous in the remaining flushes of cambial growth.

With reference to the cessation of vascular tissue development, it is simultaneous in normal and affected trees of Dalbergia, Syzygium and in affected trees of Holoptelea. Whereas in normal trees of Holoptelea, phloem development ceases first followed by xylem. Developing vessel elements are noticed from the cells of cambial zone that are adjacent to mature thick walled xylem fibres in all the species studied. Initial expansion in developing vessel elements is far greater in tangential direction than that in radial direction in Dalbergia and Holoptelea.

Though much changes are not found in the development of vascular tissues, variation in the amount during one growth season between normal and affected trees has been observed. The amount of radial extent of phloem produced in affected trees is greatly reduced in Syzygium and Holoptelea. Annual production of phloem is marked due to the presence of narrow sieve elements with partially differentiated sieve plates, compressed parenchymatous layer and sieve plates with callose between current and last year's phloem tissue. Reduction in the amount of conducting phloem and increase in nonconducting phloem and rhytidome have been reported in Mangifera, Delonix and Tamarindus growing in pollution environment. The increase in the depth of nonconducting phloem zone and rhytidome is considered as an additional protective measure against pollution threat (Ahmad and Kalimullah, 1986, 1988). High callose deposition in sieve tube elements in

affected trees of Holoptelea may be correlated to the reduced translocation of food materials through phloem. Reduced phloem loading and reduced speed of translocation in two cereals by the effect of pollutants has been reported (Gould et al., 1988).

The influence of air pollution on assimilatory tissue was considered early to be reflected by tree growth. Later on, physiological and morphological responses of plants to sulfur dioxide are well documented. Such responses like decrease in growth may manifest themselves within a tree as reduced tree xylem ring widths. Reduced ring widths have been found in several areas where elevated concentration of sulfur dioxide occurs (Linzon, 1971; Keller, 1980; Thompson, 1981; Fox et al., 1986; Yokobori, 1986; Schweingruber, 1986; Jagels, 1986; Ingrid de Kort, 1986; Kagamimori et al., 1990). Though combined air pollutants are responsible for damage for the vegetation, there is ample evidence to show that sulfur dioxide is the principle pollutant causing damage in the present study area (Vijayan, 1987; Krishnayya, 1989).

Although the occurrence of growth rings in tropical trees is rare, they are distinct in Holoptelea , Dalbergia and Syzygium. The width of annual xylem increment is reduced considerably in affected trees of Holoptelea and Syzygium. In all sulfur dioxide treatments the seedlings of Ponderosa pine and Douglas fir showed decrease in diameter growth (Michalk and Siekierski, 1991). Industrial emissions and mining are considered the factors causing changes in growth rate at breast height diameter in the stems of 150 pines (Dudzinska, 1990). Visser and Molenaar (1992) studied

the strong relationship between ring width signal and sulfur dioxide emission in Abies alba. Mc Clenahem and Vimmerstedt (1993) have investigated the effect of soil properties, climate and atmospheric pollutant (especially sulfur dioxide) on tree rings and elemental concentration in them. It became a well documented fact that high sulfur dioxide concentration may impede carbon dioxide uptake by green plants without leading to visible symptoms of injury. The reduced photosynthetic activity is reflected by reduced cambial growth. Therefore the production of wood may drop drastically (Keller, 1980). In Dalbergia, however the annual ring width is more in affected trees than that of normal ones. The possible reason for the greater xylem ring width in Dalbergia is unknown. However, similar observations were reported in Spruce by Zach and Drapela (1991). The reduced width of growth rings in pollution affected trees can be attributed to the stress caused by pollutants on duration of cambial activity and differentiation of secondary vascular tissues.

Xylem shows much variation in vessel elements length, width and lumen diameter in affected trees in comparison to normal trees. The yearly average length of vessel elements is decreased in Holoptelea and Syzygium, whereas, no variation is found in Dalbergia. Though annual growth shows reduction since several years, the trachied lengths were not affected significantly (Fruhwald et al., 1984; Grosser et al., 1985) which confirms the findings on affected trees of Dalbergia. Lower annual increase in length of trachieds is reported in Abies (Bauch et al., 1979) and spruce (Bosshard et al., 1986). Aszimutat et al., (1986) and De

Kort (1986) found some reduction in trachied length of affected Douglas fir. Contrastingly the annual increase of trachied length was significantly higher in affected fir trees (Bosshard et al., 1986). The annual average vessel element width is more in affected trees of Dalbergia and less in Syzygium and Holoptelea. However, in all the species studied the vessel lumen diameter is decreased in comparison to normal ones. Considerable decrease in cross sectional area of trachieds is reported in affected spruce and fir (Bauch, 1986) and Abies alba (Shortle and Bauch, 1986). Narrow trachieds arranged in less regular files (Ingrid de Kort, 1986) have also been reported in trees under the effect of pollutant mixture (Ammonia, Sulfur dioxide and oxides of Nitrogen).

Larson (1973) found that trachied diameter was primarily determined by the amount of auxin reaching a developing trachied. Trachied length reduction in relation to extremely slow radial growth is not a specific response to pollution induced decline but may result from other stress situations as well (Bass et al., 1984).

The average number of vessels per 0.5 mm² cross sectional area in affected trees is found to be more than that of normal trees of Holoptelea and Syzygium. Increase in number of trachieds per cross sectional area has been reported in affected trees of silver fir (Bauch et al., 1979). However Eckstein et al., (1981) and Krapfenbauer et al., (1985) reported a decrease in number of trachiedal cells in spruce. The increase in average number of vessels per unit cross sectional area in affected trees is possibly due to the transverse dimensional decrease in vessel

members. To mitigate the physiological stress on conduction of water and mineral nutrients, the average number of vessels might have been increased in pollution affected trees. The structural alterations of cell size, lumen and wall dimensions and density will be of greater interest for the understanding of physiological responses in affected trees and constraints on hydraulic conductivity (Ingrid de Kort, 1986).

HISTOCHEMISTRY:

Studies on histochemical changes occurring in the cambial tissue during seasonal cycle in pollution affected trees are meagre. Esau (1948) suggested that starch and tannins may occur in the cambial ray initials. Starch is the most abundant reserve carbohydrates in many woody plants. The starch content is clearly dependent on the season with maximum in spring and it declines during summer and autumn, leading to a minimum in winter in evergreen trees (Forschner, 1989). Whereas, in deciduous trees starch content depends upon different growth seasons of a year (Essiamah and Eschrich, 1985).

Starch content fluctuates parallel to the cambial activity in Dalbergia and Holoptelea. During the active period, starch content is negligible however high amount of starch accumulates during the period between cessation and initiation of cambial growth. However, in storage tissues of Syzygium such correlation is not found. Tsuda and Shimaji (1971) studied the seasonal changes of cambial activity and starch content in Pinus densiflora and noticed that the starch content does not fluctuate

parallel to the cambial activity.

Starch accumulates in higher amounts in phloem tissue of Dalbergia when normal and affected trees are with full foliage. In normal and affected trees of Holoptelea, phloem starch accumulation occurs according to the phenological variations. i.e., starch accumulation is more when trees are with full foliage and less during bud break. Less phloic starch content is correlated with active cambial cell divisions in normal trees of Holoptelea. Starch content in phloem axial parenchyma of Syzygium is higher in active period and lower in dormant period. The phloem starch is significantly high in affected trees of Dalbergia and Holoptelea whereas, low content is observed in Syzygium. Evergreen species accumulate carbohydrates much later in winter but seasonal reserves in evergreen species are much smaller than in deciduous trees (Krammer and Kozlowski, 1979).

Starch grains are observed only in cambial ray cells and are not found in fusiform cambial cells under light microscope. Presence of large starch grains in the cambium of affected trees of Dalbergia and Holoptelea indicates high amount of carbohydrate is being translocated to the storage tissues. The reason for the appearance of starch grains in cambial ray cells in Tectona and Gmelina is possibly the result of translocation of photosynthates from developing leaves (Rao and Dave, 1983b). Cambial ray cells and its derivatives in Syzygium are filled with dark tanniniferous contents. Few starch grains embedded in dark phenolic contents indicate that major reserve metabolites in this species is not in the form of starch. Low content of starch and high lipid

accumulation in Syzygium is the result of starch conversion into lipids (Patel and Devi, 1986).

Abundant starch is stored in xylem parenchyma of both normal and affected trees of Dalbergia. In all the tree species studied, the accumulation of starch in xylem is high in affected trees. Less xylem starch content in May in Dalbergia and in April in Holoptelea is attributed to the more utilization of reserve starch for bud break and development of new leaves.

Phloem starch reserves are generally utilized for the activity of cambium and bud break (Drossopoulos and Niavis, 1988). The absence of starch in xylem indicates that all the starch reserves of affected trees of Dalbergia and Holptelea are completely utilized for cambial cell division and differentiation.

The mechanisms suggested for the high accumulation of starch are:

- i. The inhibition of several metabolic processes like hydrolysis of starch and sucrose as well as transport of sugar (Balsberg, 1989)
- ii. Delay in starch mobilization caused by a reduction in assimilate transport capacity of phloem (Forschner et al., 1989) and probably due to partial inhibition of starch translocation at night (Leuthy-Krausse and Landolt, 1990).
- iii. A mode of defense mechanism exhibited by tolerant species of pollution zone by converting glucose to polysaccharides under the effect of sulfur dioxide (Mejnartowicz and Lukasiak, 1985).

Higher starch accumulation, particularly during dormant season, in affected trees of Dalbergia and Holoptelea has been observed in the present study. The following workers have reported the higher amount of polysaccharides with pollution stress in various tissues. An increase in insoluble polysaccharides has been reported in secondary vascular tissues of Tamarindus indica growing under pollution stress (Patel and Devi, 1986). Starch content is significantly higher in Norway spruce needles than their undamaged counterparts (Forschner et al., 1989). While the foliage samples of Betula pubescens, B.pendula, Picea abies and Pinus sylvestris collected nearest to the pollution sources show higher concentration of starch and total sugars than control samples (Balsberg, 1989). On the other hand, Ozone fumigation induces starch accumulation in chloroplast of Norway spruce needles (Leuthy-Krausse and Landolt, 1990). The tolerant tree species growing under the effect of fluorine and sulfur dioxide show higher accumulation of polysaccharides (Mejnartowicz and Lukasiak, 1985).

It is suggested that lipid and protein bodies are organic reserve materials which are required for the reactivation and differentiation of cambium. Lipid bodies are localized in both fusiform and ray cells of cambium in Dalbergia and Holoptelea and only in fusiform cambial cells in Syzygium. Large lipid bodies are localized in dormant period i.e. prior to the initiation of cambial activity in normal trees of Dalbergia and affected trees of Holoptelea. However much variation in lipid accumulation is not found in Syzygium. Patel and Devi (1986) reported that lipid

content of wood and bark of the polluted plants of Tamarindus, Syzygium is greater than that of normal plants and it is identical in both normal and polluted plants of Mangifera indica. Lipid content may get either reduced (Grunwald, 1981) or increased (Malhotra and Khan, 1978) or remains unaltered (Patel and Devi, 1986) in pollution affected plants. Ozone is known to increase water stress, which may increase lipid content in plants (Douglas and Paleg, 1981). It is likely that under such a stress caused by pollution the starch is converted into lipids (Patel and Devi, 1986). The increased lipid content in affected trees of Holoptelea may be attributed to the pollution induced stress.

Protein bodies are considerably high in active cambial cells than in dormant cells in Dalbergia and Holoptelea. The protein accumulation is significantly high in fusiform cambial cells of affected trees of Syzygium and much variation is not found in Holoptelea and Dalbergia. Decreased protein staining is reported by Evans and Miller (1972) in Ponderosa pine fumigated with Ozone. Total protein concentration was much decreased by sulfur dioxide in Pinus needles and sulfur dioxide also induced a general decline in intensity of staining for proteins (Percy and Riding, 1981). It appears that there is no effect of pollutants on structure and hydrolysis of proteins in Holoptelea and Dalbergia. In June, there is a decrease in starch accumulation and increase in protein content in affected trees of Syzygium. The increase in protein content in Syzygium may be related to starch conversion into proteins.