INTRODUCTION

Man has been interested in plants since time immemorial which forms a green mantle over the earth in the form of forests. Forests, besides having direct effect on man's economic position, tend to have a moderating influence on the local climate. They form a buffer for the earth against the full impact of sun, wind and precipitation. Forest litter adds a great deal to the enrichment of soil, the nutrient being recycled into living plants or else leached away by run off water Apart from the natural filters of air purification, timber, paper pulp, fertilizers, food and fuel are the precious products of the trees. Among these, wood is the most abundant biomass produced by trees on terrestrial ecosystem, which arises through cell division activity in the vascular cambium (Philipson et al. 1971, Fahn 1990, Savidge 1996) but our understanding of how trees make wood in terms of physiology and genetics remains far from clear.

The vascular cambium probably had its origin in the middle Devonian, some 300 million years ago. During this period, the genus Schizopodium formed radially aligned xylem elements around the periphery of lobed xylem core, which appear to reflect primitive cambial activity. From the middle Devonian on, however, cambial activity became common place and by the upper Devonian extensive secondary activity is found in all phylletic lines which make up the rich flora of carboniferous period (Barghoorn 1964).

Researchers have not always agreed upon what constitute the radial dimensions of the vascular cambium. Theodor Hartig (1853) came to the conclusion that cambium was a biseriate layer of cells in which two initials lay adjacent to each other, of that one produced xylem cells in one direction and the other produced phloem derivatives in the opposite direction. Later Sanio (1873) suggested that the cambium itself consisted of only a single layer of cells. Each time a division occurred in the cambial cells, one of the daughter cell remained as cambial initial, while the other cell became either a xylem or phloem mother cell It is difficult to point out the exact location of cambial cells because of frequent cell division on either side by xylem and phloem mother cells. Hence from time to time objections have been raised concerning the validity of assuming the cambium to be only one cell in thickness. Bailey (1923) pointed out however, that if the cambium were not uniseriate the radial continuity of differentiating xylem and phloem cells across this lateral meristem could no longer exist. For example if xylem mother cell rather than cambial mother cell underwent a pseudotransverse division to increase the girth of the cambium, then there would be no phloem counterpart and a new tire of discontinuous cells would arise on the xylem side of the cambium.

Most workers today consider the cambium as a functionally uniseriate layer, but the width of xylem and phloem mother cell zone varies with seasonal activity, vigor and cycle of periclinal divisions. Therefore, frequently, the term cambial zone is used to describe the entire radial width of actively dividing xylem and phloem mother cells including the layer of cambial initials.

The vascular cambium is initially derived from procambial cells which differentiate acropetally from pre-existing strands into the apex of the elongating primary shoots. Following the maturation of primary xylem and phloem the central portion of vascular bundle remain meristematic and function as vascular cambium. The cambium becomes a continuous cylinder in the maturing portion of elongating woody shoots by the tangential differentiation of new cambial cells through the ground meristem connecting the vascular bundles.

The vascular cambium is made up of two types of initials i) Fusiform initial and ii) Ray initial. The former is an elongated cell with tapering ends and gives rise to xylem and phloem derivatives of axial system where as the ray initial is much smaller, almost isodiametric in shape and gives xylem and phloem derivatives of radial system. Although the fusiform initials may appear to be four to six sided to the experimental observer, but Dodd (1948) observed in Pinus sylvestris to have an average of 18 different faces. The dimensions and volume of cambial initials show a wide range of variation within the same species with age, location as well as among the species (Zimmermann and Brown 1974, Furqan and Ahmad 1981, Iqbal and Ghouse 1983)

In tangential view, by the arrangement of cambial initials two types of cambia may be distinguished viz, storied and nonstoried. In the storied type, the fusiform initials are relatively short and occur in horizontal tiers, so that their end walls form essentially a straight row. In non storied type the end walls overlap, a common feature of species with long fusiform initials. The nonstoried type is more primitive than the storied type, being a common feature of fossil pteridophytes and gymnosperms. It is also present in all living gymnosperms and primitive angiosperms (Bailey 1923, Paliwal and Prasad 1970, Ghouse and Yunus 1976, Yunus et al. 1978; Rao and Dave 1983). The storied type of cambium is restricted to the more highly specialised dicotyledons (Zimmermann and Brown 1974, Metcalfe and Chalk 1983, Rao et al. 1996, Rajput and Rao 1996).

Vascular cambium of different taxa varies in form and function and depends for its derivatives on the generic constitution and physiological phenomena of the plant as well as on environmental factors (Philipson et al. 1971, Iqbal and Ghouse 1987). However, Savidge (1996) classified these generic constitution, physiological phenomena and environmental factors as extrinsic and intrinsic factors which ,regulate the cambial growth and development. These extrinsic factors viz. temperature, water (Rain fall), relative humidity, photoperiod, gravity, geographic location, growing season, directional effects etc , act indirectly on the cambium by controlling the timing and extent of metabolism and primary and secondary growth in plants. The intrinsic factors like genomic content, phytoharmones, reserved food material and physiological state of the plant directly influence the cambial behavior (Kozlowski 1962) and in short supply they limit seasonal activity of cambium (Savidge and Wareing 1981, Savidge 1991)

Dormancy of bud and cambium and leaf shedding are response to environmental pulsation representing temporary level of adjustment (Halle et al. 1978). The relationship between the bud break and the onset of activity has been known since long (Priestly 1930, Wareing 1951, Rao and Dave 1981, Denne and Atkinson 1987, Paliwal and Paliwal 1990a,b, Rao et al. 1996). Developing leaves produce harmones necessary for cambial activity (Hess and Sachs 1972, Rao and Dave 1981, 1983, Paliwal and Paliwal 1990a,b, Savidge 1996) and attributes to the development of its derivatives.

Various environmental and physiological factors have been observed by various authors as controlling the cambial periodicity. The effect of temperature is considered as a factor of primary importance for activating the cambium (Paliwal and Prasad 1970, Philipson et al. 1971, Tsuda and Shimaji 1971, Chou and Chiang 1973, Krammer and Kozlowski 1979, Rao and Dave 1983, Iqbal and Ghouse 1985, Antonova et al. 1988, Badola 1989, Paliwal and Paliwal 1990a, Srinivas 1996, Rao et al. 1996a,b). Temperature influences shoot growth through its effect on bud formation and bud dormancy and the initiation of seasonal distribution of bud expansion into shoot (Krammer and Kozlowski 1979). Trees will not continue growing in dry season if water is not adequate. However, cambial activity is also dependent on the availability of water. Voegeli and Reinhart (1956) found that drought year had greatest effect on the amount of wood formation. In tropical environment it is thought to be onset of dry season which brings about dormancy (Fahn 1990) and rainfall is considered as an important factor controlling the cambial activity (Waisel and Fahn 1965, Waisel et al. 1970, Rao and Dave 1981, 1983, Kozlowski 1982, Silva et al. 1990, Savidge 1996). Perhaps for the first time Glock and Argerter (1962) proposed that rainfall has direct bearing on cambial activity by increasing water in the soil as well as the metabolic process of the tissues. Later, Little (1975) stated that the water stress directly inhibit it by lowering the turgor pressure of the cell and indirectly by reducing the growth of leaves and supply of hormones Alongwith this, photoperiod has also been having significant contribution in initiation and extent of cell division in cambium (Wareing and Roberts 1956, Waisel and Fahn 1965, Fahn et al. 1968, Waisel et al. 1970, Wodzicki 1968, Paliwal and Paliwal 1990a,b, Srinivas 1996). The effect of light intensity on cambial growth is complicated and mediated chiefly through export from leaves of carbohydrates and hormonal growth regulators. In many species of trees the continuation of cambial growth is linked to continued shoot expansion and ceases soon after shoot elongation stops. This relationship is the result of stimulation of cell division in the cambium by hormones produced by actively growing shoots. Hence the effect of photoperiod on shoot growth also influence the duration of cambial growth. Short day stops shoot expansion and causes development of dormant state, where as long days delay or prevent dormancy. Experimental evidences showed that cambial growth is much influenced by days longer than normal one (Wareing 1951, Wareing and Roberts 1956, Krammer and Kozlowski 1979, Paliwal 1981). In addition to controlling the duration of cambial growth the photoperiod greatly influences the specific gravity of wood by controlling the proportion of large diameter to small diameter cells in the annual xylem ring. Decline in cambial growth due to short day length and low temperature and rainfall has also been reported by Paliwal and Paliwal (1990b). The initiation of cambial activity and radial expansion of xylem cells is auxin related phenomena originating from developing buds. Studies on cambial activity in relation to hormones both in-vitro and in-vivo have also been carried out (Little and Wareing 1981, Little and Savidge 1987, Savidge and Wareing 1984, Savidge 1989, Sundberge et al. 1987, 1990, 1991, Gersani and Sachs 1990, Aloni et al. 1990, Zhong and Savidge 1995, Larson 1994, Savidge 1993, 1996).

From the perusal of above literature it is clear that the rise in temperature and day length enhance the cambial activity through increasing hormonal level and the rate of metabolic activity, with bud break tends to augment the hormonal synthesis and may cause further enhancement in this phenomena. Ultimately rainfall, which improve the soil moisture leads to an additional absorption of water by roots, bringing about increased turgidity of cells. This allow them to become more active accompanied by other factors, for higher production of metabolites and hormones for cell division and differentiation leading to maximal cambial activity.

In the temperate regions of the world, the resumption of cambial growth, each spring is correlated with the renewed activity of buds and development of leaves, which produce distinct growth rings. In tropical and subtropical regions, however, the cambium may remain active throughout the year (Dave and Rao 1982a, Fahn 1990) or for a major part of the year (Chowdhury 1958, Fahn and Sarnet 1963, Chou and Chiang 1973, Iqbal and Ghouse 1983, Dave and Rao 1982b). Because of the wide variations in the pattern of shoot growth due to the fluctuations in environmental conditions growth rings are not distinct. Certainly much less about the pattern of cambial activity in tropical trees are known compared to the abundant literature on the seasonal activity of cambium of temperate zone species (Evert and Kozlowski 1967, Philipson et al. 1971, Catesson 1974).

The seasonal pattern of cambial activity varies within and among the species growing on the same site at various latitudes. Almost a century ago, Robert Hartig (1885) noted differences in the initiation and cessation of diameter growth in spruce on the northern slopes versus those on the warmer sunny south slopes in central Germany. Trees on the latter sites had completed one fourth of their annual increment, 30 days or more before any cambial activity could be detected in those only a 100 paces away on the cooler north slopes However, reports on the comparative study of same species growing at different sites are available on the trees of temperate regions (Eggler 1955). On the otherhand, apart from the work by Chowdhury (1940) no information is available on tropical trees growing under the influence of different climatic conditions.

The pattern of growth, both primary and secondary of species growing in different climatic regions may not be similar. A species growing under onset of local climatic conditions may yield more biomass compared to the same species from other regions. Therefore it was considered worthy to study the pattern of cambial cell division and its differentiation during annual growth in different forest regions of Gujarat state.

The state of Gujarat is situated on the West coast of India between 20° and 25° North latitude and 68° and 75° East latitude. Its boundaries are defined by the Arabian Sea on West, the state of Rajasthan on North-east and the states of Madhya Pradesh and Maharashtra on Southern east and South respectively On the North-western fringes it has a common border with Pakistan.

From the point of view of forest distribution and description the whole of the state can be divided into three distinct zones.

i. The area South of the river Narmada consisting of moist deciduous forest with teak as a main economic species.

ii. The area between the river Narmada and extreme North excluding Saurashtra and Kutch covering dry deciduous forest with or without teak and

iii. The area of Saurashtra and Kutch with poor teak forest in Junagadh, scrublands, mangroove forest and desert areas.

To extreme south-east of Gujarat are the hills of Sahyadri. These hills add a great deal to the forest wealth of the state. Kutch is practically undulating rocky area with many small hills and with the rann of Kutch lying on the Northern end consisting of vast expense of tidal mud flats with saline efflorescence As the tropic of cancer passes through the Northern border of Gujarat, winters are severe and summers oppressively hot with wide range in diurnal temperature except in the coastal tract. The hottest months of the year are April-May throughout the state The maximum temperature is varying in different parts of the state being lowest in the Southern part (average 37°C) than in central and northern parts (average 40.5°C). The state experiences winter from November to February with December and January being the coldest months.

Regarding rains, however, the monsoon heralds with a few thunder showers by about the middle of May in Ghat regions, followed by torrential rains in the month of June. The monsoon months are from June to September in the state, with maximum rains in July closely followed by August and with a few light showers some times in the first week of October. November to May are rainless months though a few showers are sometimes experienced by the end of December In general the average rainfall is more in South Gujarat (1252-3162mm, average 2205 mm) than the other parts of the state and the lowest in Kutch (80-1153 mm. average 420mm). The average rainfall is highest in the Southern most part of the state and it gradually decreases from South to North. The rains are more in the hilly regions than plains, heaviest in Ghat regions of Balsar and Dangs district.

Since last two decades due attention has been given for the studies on structure and seasonal activity of Cambium in tropical trees (Paliwal et al 1976. Amobi 1973, 1974, Ghouse and Hashmi 1979, 1983, Rao and Dave 1981, 1984, 1985, Dave and Rao 1982a,b, Krishnamurthy and Venugopal 1983, Ajmal and Iqbal 1987a,b, Paliwal and Paliwal 1990a,b, Srinivas 1996, Rao et al. 1996a,b) because the answer for what controls the duration of cambial activity and rate of xylem differentiation are still incomplete and yet they are of critical importance for wood production and wood quality.

For many reasons, studies on general structure, amount and quality of wood have been concentrated in temperate region trees and there is an urgent need for similar information in tropical trees from developing countries. Therefore, the studies described in this thesis were carried out in an attempt to understand the influence of varying climatic conditions on seasonal anatomy and histochemistry of cambium and its derivative tissues.

For the comparative study of cambium and its derivatives four timber yielding tree species, Tectona grandis, Acacia nilotica, Azadirachta indica and Tamarindus indica were selected. The following aspects have been considered for investigation in the present thesis.

i Seasonal behaviour of vascular cambium of species growing in different forest regions.

ii Comparision of cambial growth between the main stem and young branch

iii Relation between cambial activity and foliar development.

iv Relation between cambial activity and climatic conditions.

v Initiation and cessation of xylem and phloem development.

vi Extent and duration of xylem development.

vii Structural and dimensional changes in cambial cells and their derivatives

viii Histochemical changes in cambial cells and their derivatives

I used the terms fusiform cambial cells and ray cambial cells for representing fusiform initials and ray initials, as the cambial initials can not be identified from their immediate derivatives. For the sake of brevity Moist deciduous forest, Dry deciduous forest and scrubland forest are represented in this thesis as MDF, DDF and SF respectively