STUDIES ON THE ENVIRONMENTAL INFORMATION IN TREE RINGS OF SOME TREE SPECIES GROWING IN NORTH-EAST INDIA

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201

Dedicated to
The loving memory of my
Grandfather
& my beloved parents

THE NORTH-EASTERN HILL UNIVERSITY

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DECLARATION

I, Nongthombam Dhirendra Singh, hereby declare that the subject matter of the thesis is the record of the work done by me, that the contents of this thesis did not form basis of the award of any previous degree to me or to the best of my knowledge to anybody else, and the thesis has not been submitted by me for any research degree in any other University/ Institute.

This is being submitted to the North-Eastern Hill University, for the degree of Doctor of Philosophy in Botany.

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CONTENTS

Chapter-6.

Chapter-7.

Chapter-8.

Chapter-9.

CHAPTER-1

Introduction

The vascular tissue of higher plants has been an object of continuous detailed study since the invention of light microscope. Vascular tissue provides the long-distance transport system for water and nutrients within the plant, and an understanding of the structure and developmental pathways within it is essential for an understanding of growth in all higher plants, including crop plants. The whole of xylem and fibres of the phloem have been in high demand commercially for their unique properties and as the only renewable (energy source) structural material on earth.

The development of the xylem is controlled by a wide variety of factors both exogenous and endogenous, including hormones and by interaction between them. Relatively little work has been done on growth rings in dicotyledons since the early survey of Jost (1891) except for the often cited work of Chowdhury (1934, 1936, 1939, 1940a, b, 1947, 1958, 1964) and the key to ring-porous woods by Record (1919a). Chowdhury, in his papers described in detail the growth rings of eleven Indian tree species to all relevant factors: temperature, light, rainfall, relative humidity, foliar development, locality (e.g., microclimates) and "internal factors" (e.g., growth-promoting substances, hormones, reserve food materials etc.). He then attempted to compare growth rings in these species. Chowdhury concludes that factors are interrelated, and one obtains no clear cut picture of which factors are primary and which are secondary in the initiation and differential events within a growth ring. However, Chowdhury's studies were undertaken in a tropical area (but seasonal); more marked results might be obtained in a temperate area with more sharply defined seasonal events. Moreover, there are many physiological measures not included by Chowdhury that one would ideally want: transpiration rates, xylem tension, and water availability (soil moisture). Gilbert's (1940) idea that ring-porosity (growth rings demarcated by much larger vessels in earlywood) is a phylogenetically derived condition and should not be accepted as a generalization, although it may be true in particular ecological conditions. His idea that ring porosity is limited to the Northern Hemisphere has been disproved many times; that idea was merely an artifact of the lack of Southern Hemisphere wood in collections at that time.

The vascular cambium has been the subject of intense study ever since its importance in building up the plant body was felt. We owe a lot to the pioneering efforts of Karl Gustav Sanio, the great German botanists in this connection (Sanio 1872, 1873). His was perhaps the first exhaustive and methodical study on cambial activity (Carlquist 1975; Timell 1980a). Besides establishing the so-called "Sanio's laws" governing the variations in the dimensions of the cambial derivatives within a tree (Bailey and Shepard 1915), Sanio was also responsible for the detailed description of the sequence of derivation of xylem and phloem cells from the uniseriate cambial initial layer. The group of four cells, consisting of an initial, a mother cell and two daughter cells, first observed by Sanio, is now known as "Sanio's Four" (Mahmood 1968). Subsequent to Sanio, Bailey and his school added considerable wealth of information on the cytology of cambial cells and the mechanism of cell division in cambial tissue (Bailey 1919, 1920a, 1920b, 1920c, 1923, 1930; Bailey and Kerr 1934). These works described the seasonal changes in the vacuolation pattern in the fusiform initials and also elucidated the mechanism of additive and multiplicative cell divisions in the cambium. So accurate were the observations of Bailey that later examinations of cambium with sophisticated techniques and instruments confirmed his descriptions admirably. In the recent past, our knowledge of cambial cytology has been greatly extended by the several studies using the techniques of transmission electron microscopy (Srivastava 1966; Srivastava and O'Brien 1966; Kidwai and Robards 1969; Robards and Kidwai 1968; Evert and Deshpande 1970; Mia 1970; Murmanis 1970, 1971, 1977; Itoh 1971; Barnett 1973, 1975; Timell 1973, 1979, 1980b; Catesson 1974; Tsuda 1975; Farooqui and Robards 1979; Barnett 1992; Farrer and Evert 1997). More information has been provided on the seasonal changes in cambial activity in relation to environmental factors, the mechanism of cell plate formation and its extension and the change during differentiation of vascular elements.

Studies on seasonal variations of cambial activity and annual rhythm of xylem and phloem differentiations in tropical trees, semi-arid and arid regions have been studied in quite a number of plants (Coster 1927; Chowdhury 1939, 1940, 1941; Koriba 1958; Alvim 1964; Reinders-Gouwentak 1965; Philipsion et al. 1971; Fahn et al. 1968; Amobi 1974; Ghouse and Hashmi 1978; Denne and Dodds 1981; Venugopal 1986; Venugopal and Krishnamurthy 1986, 1987, 1989, 1994;

Creber and Chaloner 1990; Priya and Bhat 1999; Borchart 1999; Rao and Rajput 2001). In spite of these studies, there is a lacuna in the knowledge on cambial activity, organization, cytology and duration of wood production of the trees growing in sub-tropical moist forest. Another aspect that needs to be studied in detail is about the dendroclimatic studies of Indian tree species, especially of eastern Himalayan region which will provide the environmental information on Himalayan tree ring data. Such studies will be beneficial to the scientific community (climatologist, ecologist, policy makers of both national and international level as well as public will be informed by vulgarization efforts of deforestation etc.).

The characteristic features of growth ring are affected by the activity of the vascular cambium and in turn the activity of the vascular cambium is controlled by many factors, both internal and external. Climatic factors play a significant role in the activity of cambium. Thus, based upon the relationship between the activities of cambium and the growth-ring formation, the climatic conditions of a particular site could be determined by analysis of the yearly ring-width pattern with climatic factors.

Tree ring patterns results from fluctuating cambial activity, which is sensitive to environmental changes. The Tibetan plateau, with its elevation of about five kilometers above the sea level plays a crucial role by influencing the pressure gradient which regulates the monsoon climatic regime of Indian subcontinent. It should be checked to what extent the Himalayan ecosystem reflects changes in India. A promising method is the analysis of environmental information in patterns of tree-ring width pattern, as trees are stationary living organisms responding to environmental factors during their life span. The ever-changing environmental stimuli are transformed in permanent tree structures and as such recorded over periods as long as the life time of trees (Schweingruber 1983). Thus, dendroclimatlogy should receive a lot of public attention nowadays, only a few investigations have been published sporadically in India (Pant 1979; Hughes 1992; Bhattacharyya et al. 1988 etc.)

Therefore in this thesis, three gymnospermous trees viz. *Cedrus deodara* Loudon, *Cryptomeria japonica* D.Don, *Pinus kesiya* Royle ex. Gordon and two angiospermous species viz. *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f. were studied with reference to the following aspects.

1. To study the response behaviours of the above mentioned tree species in relation to climatic factors.
2. To study the relationship between previous years ecological conditions and growth ring formation.

CHAPTER-2

Review of literature

In arborescent gymnosperms and dicotyledones two stages may be discerned in the establishment of vascular tissue. The first stage is concerned with the formation of vascular tissue in the primary plant body; which is the product of apical meristem of root and shoots. The second stage usually called secondary growth, follows the first and results in the secondary increase in girth of the axial organs due to the production of more vascular tissues outside the primary ones. Secondary growth is due to a lateral meristem, the vascular cambium.

It is not yet very clear as to when exactly the vascular cambium first arose in the evolutionary history of land plants (Barghoorn 1964). According to Brown (1971) and Morey (1973) ascribed that the vascular cambium probably first appeared in the Middle of Devonian, about 3000 million years ago or near the end of Paleozoic era. The vascular cambium develops from the pro-cambium through transformation of the derivatives of the apical meristem (Esau 1965b; Larson 1982).

Larson (1982) described that the pro-cambium and the vascular cambium are the successive developmental stages comprising pro-cambium, vascular meta cambium and cambium. In addition, Larson has suggested ~~that~~ meta cambium as an intermediate state between pro-cambium and cambium. Swamy and Krishnamurthy (1980) considered that the pro-cambium is not prerequired for the formation of cambium and that the pro-cambium must be first converted into parenchyma, which in turn give rise to cambium. Their study is related to the study of the origin of cambium in anomalous situation and in the callus. This view of Swamy and Krishnamurthy (1980) and Fahn (1982) is supported by many investigators (Salisbury and Parke 1964; Esau 1965b 1977; Gemmel 1969; Cutter 1971; Fahn 1982; Krishnamurthy and Venugopal 1984). The organization of cambium pertains into the two interwoven fusiform and ray initials. Fusiform initials are noted to be relatively short (140-210μm) in storied cambium especially in the highly specialized dicotyledons while in the non storied type the length of fusiform initials generally in between 700-500μm (Bailey 1920) and sometimes measuring up to 900μm as in *Sequoia sempervirens* (Bailey 1923).

Sanio (1872) concluded that in *Pinus sylvestris*, the length of tracheid increases from the pith through a number of annual rings until a definite size was reached. Spurr and Hyvarinen (1954) and Dinwoodie (1963) reviewed the size variations in the xylem elements and they observed two major pattern of variation viz. (i) horizontal and (ii) vertical. There is a gradient in cell length along the axis of the tree. Whereas the pattern of cell length is followed upwards in the same growth ring, the average length increases from the base upward, reaching a maximum and then decreases towards the top (Sanio 1872; Dadswell 1949).

The pioneering work of Bailey (1920a, b, c, 1930) stated that in spite of their large size the fusiform initials are, in general, uninucleate. However from the past three decades, there are several reports indicating the multinucleate conditions of the fusiform initials (Patel 1975, Ghouse and Khan 1977; Iqbal 1981, Venugopal and Krishnamurthy 1989; Dave and Rao 1989; Ghouse et al. 1979). Bailey (1920) observed differences in the rate of cyclosis of protoplast during high temperature and low temperature as well as the changes in the number of vacuoles. In other words, these changes are accompanied with active and dormant periods.

Later E.M. studies showed that the fusiform initials and ray initials are essentially alike, and both have the basic content of organelles and membranes similar to that of parenchyma cells (Rao and Catession 1987; Goosen-de Roo et al. 1983, Robards and Kidwai 1989). Farrer and Evert (1997a) studied the seasonal changes in the ultra structure of the vascular cambium of *Robinia pseudoaccacia.* The cytological details of periclinal and anticlinal divisions were described by Bailey (1919, 1920a, 1920c). The nucleus enlarged considerably before division and the chromosomal organization was evident when the nuclear membrane was still intact. The two bands like phragmoplast were noticed in tangential longitudinal section during periclinal division

Anticlinal divisions and periclinal divisions occurred in the storied and non storied cambium respectively. In pseudotransverse division new cell was laid down in the same orientation as the neighbouring cells of the cambium and reversals occur in the direction of the tilt of the pseudotransverse division from a z-type to s-type and vice versa (Bannan 1966; Hejnowicz and Krawczyszyn 1969).

Pseudo transverse divisioned cells oriented predominantly in the same direction are called domain (Hejnowicz and Romberger 1972).

Recently Farrar and Evert studied the cell divisions in the fusiform initials of *Robinia pseudoacacia* by using Transmission Electron Microscope (1997).

All these studies imparts to the mode of cell division of cambial cells which in turn gives xylem and phloem cells through the process of differentiation. The amount of wood production by a tree depends on the activity of cambium and its duration during the growth period. Thus the radial growth of a tree in a particular year is governed by the activity of cambium. Thus, it is self evident that a study of cambial activity is fundamental to our understanding of growth periodicity (Glock 1955). Studies on seasonal variations of cambial activity and annual rhythm of xylem production and phloem differentiations in tropical trees, semi-arid and arid regions have been studied in quite a number of plants (Coster 1927; Chowdhury 1939, 1940, 1941; Koriba 1958; Alvim 1964; Fahn et al. 1968; Amobi 1974; Ghouse and Hashmi 1978; Creber and Chaloner 1990; Denne and Dodds 1981; Rao and Rajput 2001; Priya and Bhat 1999; Borchart 1999; Reinders-Gouwentak 1965; Philipsion et al. 1971; Venugopal 1986; Venugopal and Krishnamurthy 1986, 1987, 1989, 1994).

Kramer (1943) stated that: “Variations in the environment can produce variations in tree behavior or growth only in so far as they affect internal physiological processes and conditions of the tree”. More over the effect of climatic factors on the wood formation needs to be investigated properly. Chowdhury (1940) detected multiple periods of cambial activity in one species of ring porous wood from India.

Freisner and Freisner (1941) recognized the importance of all factors on the formation of annual rings. Although some factors are internal and hereditary, whereas others are external and environmental, “variation in growth from year to year within the same individual are related more definitely to environmental than to internal factors”. Temperature and light among the external factors are commonly adequate for growth and available water is common the limiting factor. Thus “growth curves of trees will more often show a relation to rainfall curves than to those for any other single factor”. But rainfall used alone has its problems because “the relation of growth curve to rainfall is not a simple one”. Such factor as the following enter to make the relation complex: the time of year when the rains come, the proportion which comes during the growing season, how well they are distributed over the growing season, the topography and its relation to runoff, the character of the soil and its ability to store water from times of abundant to times of inadequate rainfall. The storage of water depends upon climate, depth and nature of the water table, and the local geology, in relation to the root habits of the tree concerned. Thus it is not always prudent to base small annual rings or variations upon climatic conditions. Hansan (1941) discussed that, since, "climate is probably the most unstable factor of the environment, and it is only natural to expect some correlation between climatic fluctuations and tree growth". There are nevertheless, many characteristics of rainfall and soil which in part determine the amount of soil moisture present when trees need it. Therefore "it is apparent that the total rainfall in an area is not necessarily an index to the amount available for tree growth". Lyon (1949) points "to the accumulation of considerable evidence that the secondary growth of many conifers is determined to a large degree by the supply available to their roots during the growing season. Thus he offers the following, "When the annual growth increment does not agree well with the precipitation record, the relative ring width is a better index of the water supply available to the root system than are the records of weather bureau stations, due to the complexities of runoff, evaporation, interception by crowns and water holding properties of soils".

Chowdhury (1940) working with growth rings in India, attempted to compare growth ring from eleven trees and their activity to any particular factor. Millet (1944) studied the growth increments of Monterey pine in Australia in relation to rainfall and concluded that "the problem of growth of a forest and climate will not be near to a satisfactory solution until much more of the environmental complex is taken into account". Working on hemlock, Meyer (1941) said that "it remains unsolved question what meteorological factors or combination of factors influence the annual growth of trees in northern Pennsylvania, where rainfall is not a limiting factor". A very similar conclusion is stated by Friesner (1943b): "The problem of sorting out the different factors of the environment and determining just what role each plays in the matter of growth is well nigh unsolvable because the behaviour of the individual is its response to its total environment".

Thus in respect to radial growth it was not possible to designate specific factors as having dominant effects on tree growth (Byram and Doolittle 1950). It becomes highly need to get more precise information on the relation of diameter growth of trees as influenced by environmental conditions and with information of this character available the possibilities of dendrochronology will be very great indeed (Lutz 1945). The lack of experimental and observational work on tree growth has also been emphasized by Glock (1942a).

Because of the significant role played by water in Indian economy, it is natural to seek all possible information on rainfall. Briegleb (1950) noted that wide periodic variations in rainfall and corresponding variations in tree growth characterize the pendoresa pine type and vigour, crown size and site have great influence on growth. He further stated that trees on poor sites react to precipitation cycles by variations of increment in a more pronounced fashion than do those on good sites. During spring, growth was at a maximum when light, moisture and temperature were at an optimum; limiting effects may have been exerted by available nutrients or by internal characteristics of the trees, or on warm sunny days by a transpiration rate greater than the vertical transport of water, even with an excess of soil moisture (Byram and Doolittle 1950). Daubenmire (1945-46) measured radial growth of trees at various altitudes in Idaho by dendrometer and found growth related to the interaction of temperature and soil moisture modified by altitude.

Defoliation of spruce and balsam fir by the spruce budworm caused different degrees of retardation of growth in different parts of the crown; severe reduction in the top of tree, no change in the middle and dreaded increase near the base and when the budworm stop feeding, a second depression of growth might occur because of heavy production of cones (Church 1949). The problem of multiple growth layers in a single a year is a difficult one, and its proper solution bears directly upon the validity of much tree-ring work and such difficulty is highly important because so much of current work uses trees grown under the variable ecologic conditions of forest zones adjacent to the arid regions. Moreover it is self evident that a study of cambial activity is fundamental to our understanding of its periodicity, whether intra or inter-seasonal (Glock 1955). Among those who have detected a single period of cambial activity are Byram and Doolittle (1950) in the shortleaf pine of the South, Friesner (1941) in the beech of Indiana, Friesner and Walden (1946) in *Pinus strobes* of Maine, and Chowdhury (1940) on three species of diffuse porous wood in India. Brown (1915) found two periodic optima of growth in *Pinus strobes* of central New York, one during May and early June and the other in July and August. Other researcher's concentrating on the growth layers themselves, have observed double absent or rare: Hustich (1948b, 1949), among conifers at the polar border in Finland; Marr (1948), among conifers at the polar border on the east coast of Hudson Bay; Moseley (1941), among hardwoods of the Northern States; and Will (1946), in an oak near Bismarck, North Dacota. Thus double rings might lead to miscalculation as to the age.

Illick (1915) stated that growth rings have a physiological origin. The length of the growing season varies all the way from 12 months in the tropics (Shirley 1945) to two months or so above 56° north latitude (Marr 1948). Annual rings are found only in regions with clearly demarcated climatic periodicity, such as an alternation between cold and warm, or rainy and dry periods (Hustich 1948a). Fluctuations in growth factors are not necessarily on an annual basis; moreover, temperature and rainfall are not the sole factors having to do with tree growth. Perhaps growth does not wholly cease throughout the entire body of a tree during any part of a year (Bell 1940). Fluctuations in any one of the host growth factors or changes in their inter relationships may well cause variations in cambial activity and in rate of growth, amount of growth and times of growth (Glock 1955). Thus many of the environmental factors are in avoidable while taking to consider the exact relationship between climate and growth rings.

Growth ring studies have developed apparently along several trends: gathering of large collections of samples which cut across hundreds of miles of diverse topography, climate and soil in order to detect possible general fluctuations of climate, lessening reliance on long-time dating, lessening emphasis on growth layers as exact rain gauges and increasing emphasis on the study of growth layers through botanical methods. A layer of wood cells produced by a tree or shrub in one year, usually consisting of thin-walled cells formed early in the growing season (called early wood) and thicker-walled cells produced later in the growing season (called late wood). The beginning of early wood formation and the end of late wood formation form one annual ring, which usually extends around the circumference of the tree.

Douglass, an astronomer working in Arizona who worked to understand the interrelationship between tree growth ring ,climate and sun spot, is credited with developing tree-ring dating (1919, 1928, and 1936) and is considered the founder of the discipline of dendrochronology (Webb 1983). Dendro refers to the Greek root word meaning tree and chronology to the study of time.

The discipline is most appropriately characterized as the systematic use of tree-ring “crossdating”, a procedure that uses variability of ring characteristics to establish the exact year in which each ring was formed. Cross dating was first used to date beams or charcoal fragments from archeological and historical structures in the south western United States, and the technique provides archeologist with the most precise time control ever devised spanning the last two thousand years (Douglas 1935, 1937; Dean 1986). The term dendroecology refers to applications of dendrochronological techniques to problems in ecology. There are four basic ways that dated tree-ring information can be applied to ecological studies: (1) specific ecological events can be dated by their association with dated ring structures or injuries; (2) past forest disturbances can be dated and their importance can be evaluated by distinctive changes in ring widths or other ring factors; (3) climatic or hydrologic conditions can be calibrated and reconstructed by using the variations in ring structure and (4) climatically related variations in animal populations and behaviour can be identified and reconstructed. The terms dendroclimatology and dendrohydrology are commonly used to refer to dendrochronological studies of climatic and hydrologic phenomena. Similar tree-ring width sequences have also been used to reconstruct records of past climatic changes (Douglass 1914; Schulman 1947, 1951, 1956; Fritts 1976; Hughes et al. 1982) and to study past hydrologic history (Cook and Jacoby 1983; Stockton et al. 1985).

In the first application, all associated tree-ring materials are carefully dated to place all growth rings in their correct time sequence (Douglass 1941, 1946; Stokes and Smiley 1968; Baillie 1982; Holmes 1983). Unusual ring features or evidence of injury are dated by their association with rings in formed in a particular growing season. Thus, Sigafoos (1964) used the rings in flood-damaged trees to date scares and to deduce past flooding history. Shroder (1978, 1980), Alestalo (1971) and Giardino et al. (1984) dated the scars of trees growing on steep slopes to study rock slides and other types of geomorphic changes.

Deiterich (1980), Ahlstrand (1980) and Swetnam and Deiterich (1985) used tree ring dated fire scars to reconstruct fire history. Madany et al. (1982) and Deiterich and Swetnam (1984) demonstrated that dendrochronological dating is considerably more reliable and can be used to establish the exact fire history sequences. The uses of tree-ring dating techniques in the study of tree death and dynamics of woody debris in forest ecosystems also has considerable potential (Gore et al.1985), but has been infrequently applied in this important and developing the field of forest ecology (Harmon et al.1986; Franklin et al.1987).

Yves Bergeron and Daniel Gagnon (1987), described the age structure of red pine (*Pinus resinosa* Ait.) at its northern limit in Quebec and found that fire may be of critical importance in determining the persistence of red pine and its restriction to the islands and shores of lakes. Red pine may be restricted to lake landscape because of the abundance of sites protected from lethal fires. The application of dendrochronology in the past forest disturbances that may leave no scar but affect the ring character by influencing the tree's productivity and growth (Fritts, 1976). Marchan (1984) dated rings and analyzed their characteristics to evaluate wood production efficiency in wave regenerated fir forest (*Abies balsamea* L. Mills.). Lamarch (1966) identified periods of accelerated stream erosion by observing growth reduction effect in trees that have sustained a rapid uncovering of their roots. Lamarch (1968) dated exposed roots and used their age and depth to estimate the rate of slope degradation. Smiley (1958) and Yamaguchi (1983, 1985) dated eruptions of volcanoes by observing distinctive ring patterns of trees that had grown within the ash-fall zone. Brubaker and Greene (1979), Ferrel (1980) and Swetnam et al. (1985) work on the effects of insect defoliation on tree growth by dendrochronological dating of the annual rings, and by comparing the differences in ring growth of host trees and non host trees. Accurate dating is especially important in studies of insect defoliation and related forest disturbances, because many rings can be locally missing in severely defoliated or suppressed trees (Keen 1937; Evenden 1940; Wagener 1961) and this condition would be undetected by simple ring counting. The characteristics of the dated rings are used to reconstruct past variations in drought (Stockton and Meko 1975, 1983; Cook and Jacoby 1977), temperature and precipitation (Fritts et al. 1979), stream flow (Phipps 1972; Stockton and Jacoby 1976; Holmes et al. 1979; Cook and Jacoby 1983) and water levels (Stockton and Fritts 1973; Phipps et al. 1979). Tylor (1981) and Graumlich and Brubaker (1987) have also used dendrochronological methods in studies of forest productivity.

Watson and Luckman (2001) reconstructed precipitation for sites in the Southern Canadian Rockies by using dendrochronology of Douglass fir (*Pseudotsuga menzeisii*) and found periods of reduced precipitation occurred over this region in A.D. 1760-1775, the 1790's, the 1840's, 1890,s, 1920s and 1920-1945.

There were periods of greater precipitation during the 1880's-1920's and in the latter half of the twentieth century. Kirchhefer (2001) reconstructed summer temperature from the rings of Scots pine (*Pinus sylvestris* L.) in coastal northern Norway and all chronologies reflect July-August temperatures. At the most northern site, the response was more confined to July temperature, resulting in a strong tree-ring and climate signal. D' Arrigo et al. (2000) used Mongolia tree-rings for reconstruction of Northern hemisphere temperature and their indications of unusual warming during the twentieth century.

Legeard et al., (1999) studied sub fossil wood of Scots pine (*Pinus sylvestris* L.) and found detailed dendrochronological information, such as fire episodes and periods of environmental stress indicated in the tree-ring records, have been assigned, precisely and accurately, to calendar years in prehistory. The detailed data show the potential for both dendrochronological and wider paleoclimatic and paleo environmental information that may become available from prehistoric bog-pine chronologies, which might then permit precise correlation and comparisons of proxy-climate data between sites. Esper (2000) studied ring-width series of *Juniperous excelsa* M. Beib and *Juniperous tukestanica* Kom. from six different sites, in the Hunza-Karakorum range and were used in reconstruction of modes of regional climate over the past 500 years. Woodhouse (1999) used artificial neural network for dendroclimatic reconstruction and found that artificial neural network offer an alternative approach to linear regression techniques and may provide improved dendroclimatic reconstruction in other areas. Malcolm Grant et al. (1998) used *Pinus sylvestris* L. ring widths for dendrochronological analysis and its significance for the study of sub fossil pine layer.

A comparative study of the climatic signal on the annual growth variation is damaged and healthy stands of Norway spruce showed that, high temperature in May increased radial growth in the healthy stands whereas summer temperature was negatively correlated in the damaged tree stands. In addition, high temperature during the previous summer decreased tree growth in the next. Tree-ring indices showed a strong positive correlation with June precipitation in the damaged stands whereas precipitation showed much reduced correlation in healthy stand suggesting the damaged is connected by drought as well as rocky or stony site. It was reported that flooding was a determinant in the periodicity of growth rhythm in *T.cassinoids*; photoperiod was indirectly responsible for radial growth rhythm in *T.umbellata*, and endogenous rhythms accounted for the radial growth rhythm of *S. globulifera* and *A. sidifolia*, from the flood-prone trees of the Atlantic rain forest in Rio de Janeiro, Brazil (Catia Henriques Callado 2001). Esper et al. (2002) analyzed tree-rings of Juniper (*Juniperus*) to reconstruct regional climatic variations in Western Central Asia since AD 618. Yuliya Savva et al. (2002) reported the influence of local ecological condition and regional climate on the growth of *Pinus sylvestris* L. along with the influence of genetic components in the Southern Taiga, Central Siberia. The climate of the early and late growing seasons provided the most consistent influences to cambial growth in *Pinus taeda* and *Pinus achinata* from central North Carolina (Alexander and William 1989). Based upon the climate sensivity of wood-anatomical features along with climatic variables, Woodcock (1989) reconstructed precipitation over a 9-month period (October-June) by using latewood vessel diameter of *Quercus macrocarpa* in Southern Nebraska.

Automatic image analysis technique showed very useful tool in obtaining vessel chronologies from teak (*Tectona grandis*) which in turn was used for the analysis of climatic signal (Nathsuda Pumijumnong and Wonkyu Park 1999). Drought sensitive tree stands in Southern Tibet showed a good potential for the reconstruction of monsoonal activity in Asia (Achim Brauning 1999). Besides these tree-ring series of Miambo woodland of Eastern Africa correlated significantly with monthly SOI-value (Southern Oscillation Index), (Valerie Trouet et al. 2001).

Trees growing in the Himalayan Zone have shown its suitability for dendroclimatic purposes because of their well-defined growth rings and its response to temperature (Pant 1979, 1983). Bilham et al. (1983) have shown that tree ring width series of Juniperous, collected from Karakoram had the same climate sensitivity with the ring width pattern of conifers growing in temperate regions.

Thus, the growth of Chir pines (*Pinus roxhburghii*) growing in

Kumaon region was controlled mainly by temperature (Pant 1983; Pant and Borgaonkar 1984). Likewise ring width sequences of *Cedrus deodara* and *Pinus gerardiana* at lower altitudes of Pirpanjal Range, South of Kasmir, exhibits a high mean sensitivity, good intra and inter species correlation among the chronologies (Bhattacharyya et al. 1988). Bhattacharyya et al. (1992) reported the Dendroclimatic potential of *Tectona grandis* and *Cedrela toona* growing in tropical forests of peninsular India. A climatic reconstruction of August-September mean temperature of Kashmir way back to late 18th Century was carried out by Hughes and Davies (1986) by using the tree ring width sequences of *Abies pindora*. Similarly a reconstruction of summer precipitation for Kashmir way back to 17 A.D. was presented by Borgaonkar et al. (1994). *Cedrus deodara* from Western Himalaya showed a significant relationship between the ring width and pre-monsoon summer temperature and precipitation (Borgaonkar, et al. 1996). Whereas tree ring chronologies from eastern Himalaya showed little response to climate and growth relationship and stated that it may be due to less ring chronology (Vandana Choudhary et al. 1999). They also have suggested that further addition of more samples and extensive collection from undisturbed forest sites may solve the problem of low signal to noise ratios. Therefore, tree species growing in the Indian subcontinent have shown the potentiality of dendroclimatic study. Thus the present study analyses the response of growth to the climatic factors on three gymnospermous trees and two angiospermous trees growing in North-East India.

CHAPTER-3

Materials, Methods and General climate of the Study area

The following plants were selected for the present study:

Gymnospermous trees:

1. *Cedrus deodara* Loudon.
2. *Cryptomeria japonica* D.Don
3. *Pinus kesiya* Royle ex. Gordon

Angiosperm trees:

4. Michelia *champaca* Linn.
5. *Shorea robusta* Gaertn.f.

To study the cambial activity, samples were collected from plants growing in the Central upland area of Shillong, Tura (Meghalaya), Nameri (Assam) and Bhalukpong (Arunachal Pradesh). Cambium with intact xylem was collected on every fortnight interval for three consecutive years (1998-2000). The timing of the different phenophases such as formation of new needles and leaves, formation of male and female cones, pollen dispersal, initiation of flowering and maturation, maturation of female cone, seed dispersal, needle and leaf fall were recorded. Climatic data such as monthly mean temperature, monthly mean maximum, monthly mean minimum, monthly mean rainfall and monthly mean relative humidity were recorded for three years 1998-2000 to study the role of above mentioned environmental factors on the activity of cambium and production of xylem in these plants. A variety of fixatives were tried but better results were obtained with materials fixed in FAA (Formalin 5cc: Acetic acid 5cc: 70 percent alcohol 90cc) and 2-3 per cent glutaraldehyde in 7.2 phosphate buffer. Fixation was done in the field itself. Because of the difficulties in sectioning the cambial tissue intact (Catession 1974; Goosen-de Roo and van Spronsen 1978), as it is sandwiched between the thick-walled xylem cells on one side and bast fibers on the other side and as it is subjected to radial and tangential tensions, the material to be sectioned was trimmed to a size as small as possible using the methods suggested by Newman (1956) and followed by Goosen-de Roo and Spronsen (1978). The materials were processed through customary methods of dehydration and paraffin (Berlyn and Miksche 1976) and glycol methacrylate embedding (Technovit 7100).

Paraffin and glycol methacrylate embedded materials were sectioned in the three planes: Transverse Section (T.S.), Tangential Longitudinal Section (T.L.S.), Radial Longitudinal Section (R.L.S.) at a thickness of 8-15 µm using a Leitz rotary microtome. These were supplemented with thin hand sections as well as sliding microtome. The last were especially made on fresh materials for purposes of histochemical studies. The sections were stained according to any one of the following staining procedures:

1. Acid Fuchsin (Feder and O' Brien 1968).
2. Lugol's iodine (Johnsen 1940)
3. Mercuric Bromophenol Blue (Mazia et al. 1953)
4. Methyl Green and Pyronin G (Jensen 1962)
5. Ninhydrin-Schiff's reagent (Yasuma and Ichikawa 1953)
6. Perioidic Acid and Schiff's reagent (PAS) (Jensen 1962)
7. Safranin and Hematoxylin (Johnsen 1940)
8. Toludine Blue (Fedder and O'Brien 1968)

For microscopic measurements, both sections and macerated preparations were used. Recently formed xylem tissue adjacent to the cambium were very carefully separated and macerated according to Jaffrey's and Schultz's *methods* (Sass 1958) *for determining* the dimensions of different vascular elements in all the months of the study period. In all measurements, which were made with ocular and stage micrometers, a minimum of 100 random readings were taken and the mean values and standard deviations were worked out. All photomicrographs were taken using a Nikon Photo micrographic unit (E 600).

To study the relationship between previous year's climatic and ecological conditions with the growth-ring of these plants, samples were collected at breast height by using increment corer. The collections of core samples and methodology have been described in detail in chapter 6 and 7. Increment bore is an auger-like instrument with a hallow shaft that is screwed into the trunk of a tree and from which an increment core is extracted using an extractor (a long spoon inserted into the shaft that pulls out the core). The extracted cores were kept in straws in the field itself. Two cores per tree on opposite directions were extracted.

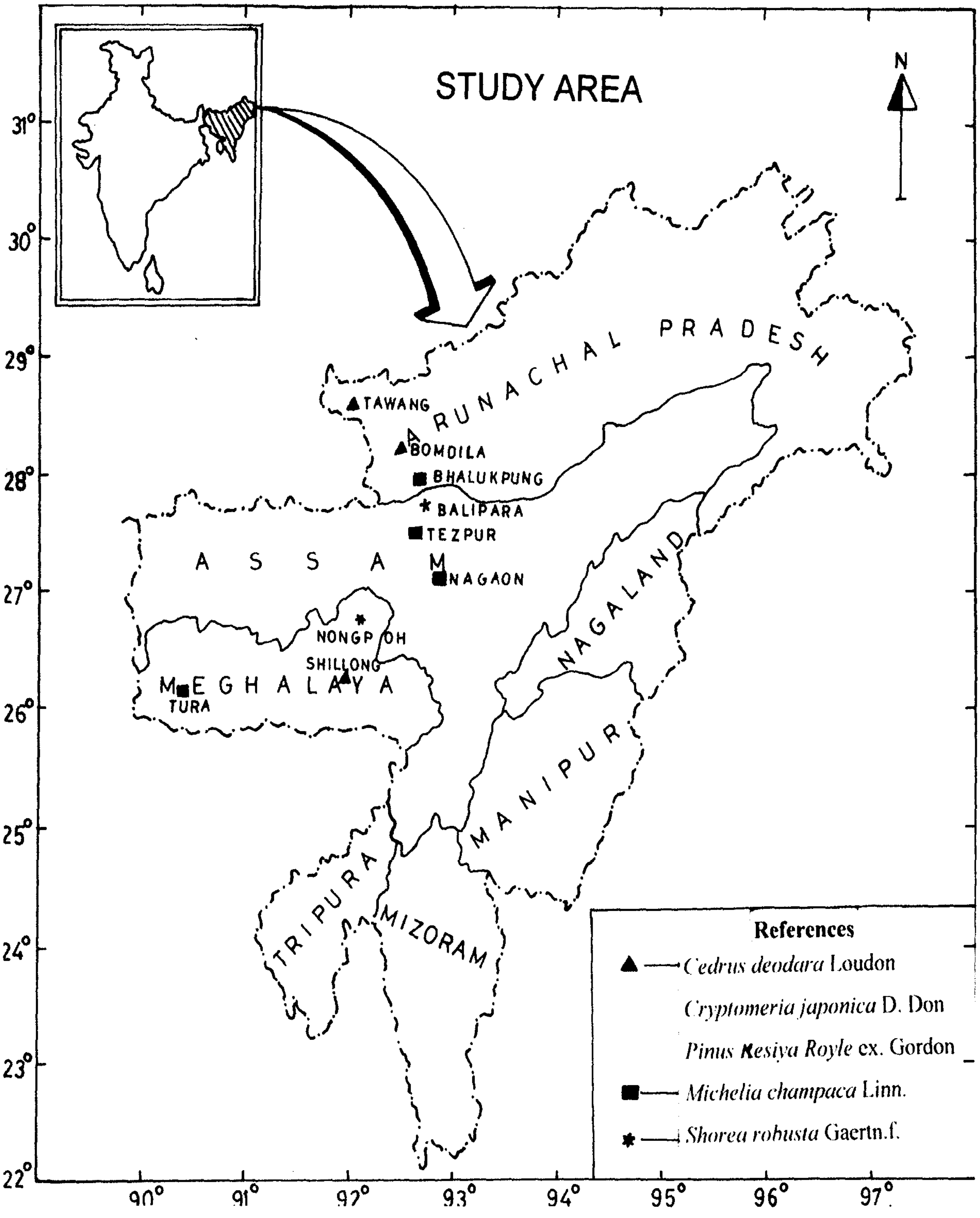
Besides these cores, wood discs were also collected from wind fallen and felled trees at the field and the date on which the tree were felled down were procured from department of forest (Arunachal Pradesh, Assam and Meghalaya). Conifer samples were smoothened first using a sharp knife and afterwards the cores were sanded using sand paper. For the wood disc, hand planer and electric planer were used and sanding was done on each wood disc to get glass like finishing. The following methods were used for dendrochronological studies which include crossdating which refers to both a principle and a practice. The principle refers to the general year-year agreement or synchrony between variations in ring characteristics of different trees. This synchrony can be shown to be the limiting effects of variations in climate on tree growth (Fritts 1976). The practice involves detecting and correcting for any lack of synchrony in ring features when the patterns are out of sequence. Thus, in the process of developing ring-width series of individual samples and the preparation of site chronologies, all samples of each site were cross-dated using the visual method (Eckstein et al. 1984; Pilcher 1990). Ring width measurements were done using a lens with 20 x 30 standard magnifications with a fitted increment scale. The ring data were passed on to the computer program CASE where they are processed to the standard ITRDB (International Tree-Ring Data Bank) format. All ring measurements were checked for possible measurement or dating errors using the computer program COFECHA (Holmes et al. 1983). Problems indicated by this program due to the ambiguous nature of a core segment or a core group of a particular site might be the result of measurement or dating errors.

Such problems have been taken into account to improve dating quality by measuring or re-checking particular core segments or core groups. The growth potential of the seedling and its capacity to respond to climate changes slowly as the seedling grows, matures and attains a dominant position in the canopy of the forest. These changes affect the character of the rings in young trees, creating the well-known ring-width sequences of (Duff and Nolan 1953). Some of the techniques of Duff and Nolan were applied to older chronologies or trees used for dendrochronology by comparing 20-year mean ring characteristics rather than comparing the yearly ring-width values (Fritts et al. 1965a). They showed that the ring width decreases with increasing age of the cambium, with increasing height in the young stem, and with decreasing amounts of apical growth. These changes produce a downward trend in ring width and variance that are due to intrinsic factors such as ageing and changes in bole geometry. To study changes in the extrinsic environmental factors of trees, the time series of these measurements must be transformed before applying most statistical analyses. The procedure of standardization is designed to make this transformation. It usually involves the fitting of a curve or straight line to correspond to the average growth potential as it changes over time (Fritts et al. 1969). Age trends following a negative exponential curve were observed for most of the ring-width series. Also suppression and release of tree growth were seen in many series. This may be due to natural survival competition among the trees. Therefore selection of the detrending method was done at the individual tree level for optimum performance.

Detrending of individual series and preparation of site chronologies were carried out with the computer program ARSTAN (Cook 1985). Index series of individual series of individual samples were obtained by the quotient method and site chronologies were formed by calculating the biweight mean. For studying the relationship between the climate and tree ring width sequences the climatic data on monthly mean temperature, precipitation and relative humidity were collected from the respective meteorological stations from where the tree ring samples collection was executed. Computer program RESPO (DPL, Arizona) was used for the response function analysis. Program RESPO computes response functions of tree growth to climate by means of principal components using two methods for selecting the principal components for the regression analysis. It involves principal component and multiple regression analysis, with climatic parameters on monthly basis as predictors and the tree-ring index as the predictant. A set of 45 variables were used as predictors which means 15 for mean temperature, 5 for mean rainfall and 15 for mean relative humidity from September current year to August previous year. Selections of the starting month for the response analysis were made depending upon the date of collection of individual tree.

Study area and general climate

The central upland areas where most of the sub-tropical wet forests exists has been selected for the present study in and around Shillong (Latitude 25° 34′ N and Longitude 91° 53′ E) with elevation 1,500m above sea level. The soil is a loam, reddish brown in colour and lateritic in origin. The pH ranges from 5.9-6.2. Climatologically, this study area belongs to the sub-


STUDY AREA
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28°
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22°
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93°
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96°
97°
ARUNACHAL PRADESH
ASSAM
MEGHALAYA
NAGALAND
MANIPUR
TRIPURA
MIZORAM
TAWANG
BOMDILA
BHALUKPUNG
BALIPARA
TEZPUR
NAGAON
NONGPOH
SHILLONG
TURA
References
▲ Cedrus deodara Loudon
Cryptomeria japonica D. Don
Pinus Kesiya Royle ex. Gordon
■ Michelia champaca Linn.
✱ Shorea robusta Gaertn.f.

tropical wet climatic regions. This region receives abundant south-west monsoon from July to September and during winter in the month of December to the middle of February the region receives northeast monsoon. In the month of April the region receives rainfall of over 900mm per year. Highest rainfall is in July and August i.e. above 1,000mm per year. In winter, temperature ranges from 7°C to 10°C and during summer mean temperature ranges from 18°C to 22°C.

Tura is relatively at low elevation of the Western Meghalaya characterize by fairly high temperature for most part of the year, i.e. from February to October with April as the warmest month having the mean maximum and mean minimum as 34.9°C and 22.1°C respectively. The second highest temperature in the year with 33.1°C and 22.8°C as the mean maximum and mean minimum respectively in spite of its heavy rainfall (513mm). The temperature of the coldest months, December and January, records a mean maximum of 24.9°C and the mean minimum as low as 11.6°C and 11.1°C respectively. The average annual rainfall in western Meghalaya (Tura) is 2,689mm of which more than two-thirds are received in the four months, May to August. Winter is conspicuously dry with less than 50mm of rainfall in four months, November to February.

The climate of Nameri (Assam) located in 27°34′ N and 93°31′ E , with an elevation of about (128m-130m) above sea level is controlled by five factors: (a) the orographic, (b) the alternating pressure cells of North - West India and the Bay of Bengal, their eastern and north-eastern periodic oscillations, (c) the predominance of maritime tropical air-mass (d) the periodic western disturbances and (e) the local mountain and valley winds. On the basis of variations of temperature, rainfall and directions of winds, the year in the region may be divided into four distinct seasons: (a) winter, (b) pre-monsoon or summer, (c) monsoon and (d) retreating monsoon. Winter season months are December to February with cool weather and frequent morning fog. Temperature remains well above 12.8°C, the average diurnal range seldom exceeding 5.5°C. January is the coldest month of the season. The total amount of rainfall in this cool, fair and pleasant weather is interrupted casually by showers associated with western disturbances, which lower the temperature and bring cold spells. Pre-monsoon or summer season (March-May) is transitional between relatively dry winter and wet summer, and is characterized by a rapid rise of temperature. The advance of the pre-monsoon season is marked progressively by greater number of rainy days, e.g., 6 days in March, 12 days in April and 14 days in May. Monsoon season (June-September) is characterized by the prevailing low pressure trough draws in monsoon currents in the valley. During this period the temperature is 27.17°C with an average diurnal range of over 6°C. The total amount of rainfall is very high and there are about 18-20 rainy days each in June, July and August and about 14 days in September. Retreating monsoon season (October-November) is characterized by fair weather with weaken monsoon. The rainfall does not exceed 15.2cm in the valley and the rainy days are fewer with 7-9 days in October and 1-3 days in November.

Bhalukpong in Kameng district of Arunachal Pradesh (28°43′ N and 92°71′ E) with an elevation of 1000-1120m above sea level experienced a sudden change of temperature as the altitude raised up. The pre-monsoon showers begin towards the end of March, the monsoon proper lasting from May to the end of September. June and July are the wettest months and summer temperature registered up to 32°C and in winter the temperature drops to 4-7°C and temperature is the primary criterion for this region. Soils are alluvial in nature being either loams or sandy loams mixed with pebbles, brought down by rain from higher altitudes.

CHAPTER-4

Vascular cambium: organization, activity and xylem production in relation to climatic factors and phenology in three Gymnospermous trees; *Cedrus deodara* Loudon, *Cryptomeria japonica* D. Don and *Pinus kesiya* Royle ex. Gordon

Introduction

It is a well established fact that the activity of vascular cambium is not uniform throughout the year and that it is greatly affected by several endogenous and exogenous factors and their interactions (Reinders-Gouwentak 1965; Philipson et al. 1971; Creber and Chaloner 1990; Iqbal 1994). Majority of the past studies pertained to plants of temperate regions, where there are well defined seasons with marked climatic variations. In trees growing in temperate region, the cambium is dormant during winter resuming its activity with the onset of spring (Bailey 1923; Bannan 1951, 1955, 1956, 1957; Glock 1955; Fritts 1959, 1962; Evert 1961; Glock and Agarter 1962; Gregory 1971; Murmanis 1977).

A few comprehensive reviews have elucidated the diverse, fascinating aspects of the cambial organization and functions (Philipson et al. 1971; Catesson 1974, 1980; Berlyn 1962, Larson 1982; Iqbal and Ghouse 1990).

Recently, studies on the variations in cambial activity has been explored in trees of tropical, semi-arid and arid regions (Coster 1927; Chowdhury 1939, 1940, 1941; Koriba 1958; Alvim 1964; Fahn et al. 1968; Paliwal and Prasad 1972; Amobi 1974; Ghouse and Yunus 1976; Ghouse and Hashmi 1978, 1979; Venugopal and Krishnamurthy 1987, a, b; 1989, 1994; Borchert 1999; Rao and Rajput 1999, 2001). However, in sub-tropical wet forest, the behaviours of cambium in relation to climatic factors and phenology have been explored very little (Coster 1927 in *Taxodium mucronatum*; Carlquist 1975; Tomlinson and Craighead 1972). Therefore, in this chapter the interrelationship between climatic factors, phenology, periodicity of cambial activity and duration of xylem production are examined in detail in three gymnospermous trees viz. *Cedrus deodara* Loudon, *Cryptomeria japonica* D.Don and *Pinus kesiya* Royle ex. Gordon. Because, the climatic control of tree development and of cambial activity are the basis of dendrochronology.

Phenology of *Cedrus deodara* *Loudon,* ***Cryptomeria japonica*** D. Don and ***Pinus kesiya*** Royle ex. Gordon.

The annual growth in terms of elongation of the branch apices commonly consists of new apical buds being formed from February end to November in both *Cedrus deodara* and *Cryptomeria japonica.* Thus, *C. deodara* and *C. japonica* exhibited recurrent flushing behaviour of new needles and branches throughout the year except during December and January (dormant period). The formation of male cones occurred simultaneously along the first flush of needle formation during February after dormancy in *C. japonica* and this was continued up to July end. The pollen dispersal also continued as and when the male cones were matured. But the last formed male cones during July only contributed, mainly the pollen grains for fertilization. Whereas, in *Cedrus deodara* the male cone formation took place in May and the mature male cones were ready for pollen dispersal during July last week to September end. The female cone formation occurred during March first week and it took seven months i.e. up to September to attain maturity and ready for fertilization in *Cedrus.* An interesting feature in *Cedrus* is the formation of female cones in alternate years. The dispersal of seeds occurred during December middle week in *Cedrus*. This phenomenon is similar to that of *P. kesiya.* Seed dispersal took place from November end to the middle of December in *Cedrus*, but in *Cryptomeria* the dispersal of seed took place from March to April in subsequent year (Table 4.1).

In *P. kesiya*, three growth flushes with new apical buds being formed between two flushes was exhibited. Three whorls of shoots were thus formed in one year, one each in the end of months of February and June and third one in the middle of October. Thus *P. kesiya* exhibited recurrent flushing behaviour of needles and branches thrice in a year. The formation of needle in three flushes appearing in different time in a year as different patterns of falls and life expectancy. The needles which appear in February falls in October of the current year to March next year; the needles which appear in June were lost in the following January to June next year and those appeared in October were lost in March to October of next year.

The formation of male cones occurred simultaneously along with the first flush of needle formation during February. The dispersal of pollen grains took place from the middle of March to the end of April.

Table 4.1 Different phenophases of *Cedrus deodara* Loudon and *Cryptomeria japonica* D.Don

Different phenophases	***Cedrus deoadra*** Loudon	***Cryptomeria japonica*** D. Don
Formation of new needle	February end	February end
Needle fall	March to April in Subsequent year	March to April in Subsequent year
Male cone formation	June end	June end
Maturation of male cone and pollen dispersal	September to October	September to October
Female cone formation	February	February
Seed dispersal	November end to middle of December	March to April, subsequent year

The interesting feature in *P. kesiya* is the formation of female cones during March in alternate years. The maturation of female cone and dispersal of seeds took place from May to June in subsequent year (Table 4.2).

Vascular cambium: organization, activity and xylem production

In *C. deodara* the vascular cambium was non-storied with axially elongated fusiform initials and more or less isodiametric, horizontally oriented ray initials. Cambial rays were predominantly uni-biseriate but unicellular ray initials were also noticed occasionally and multiseriate rays were very rare (Plate-4.1 b, c). During the active period the cambial zone was wider and cell walls of both fusiform and ray initials were thin and surrounded by differentiating xylem and phloem elements (Plates-4.1 a & 4.2 b). But during the dormant period, cambial zone was narrow consisting of 3-4 layers with relatively thick radial walls (Plate-4.2 a, c). The initiation of cambial activity was marked by radial swelling of fusiform initials and the active vacuolation followed by periclinal divisions in the fusiform initials (Plate-4.1 a). Consequently, the number of layers in the cambial zone and width of the cambial zone increased considerably (Plate-4.2 b). The fusiform initials contained 3-4 nucleoli in each nucleus. The average data pertaining to the length of fusiform initials

Table 4.2 Different phenophases of *Pinus kesiya* Royle ex. Gordon.

Different Phenophases	Time period
Formation of new needle, three flush in a year.	First flush: February end Second flush: June second week Third flush: October
Needle fall	1. Needles which flushed in the month of February end, falls in the month of October first year to March second year. 2. Needles which flushed in second week June during first year falls in the months January to June next year. 3. Needles which flushed in the month of October in the first year falls during the months March to October on the second year.
Male cone formation	Second week of February
Maturation of male cone and pollen dispersal	Middle of March to the end of April.
Female cone formation	During the first week of March in alternate years.
Seed dispersal	Next year April to May.

in *C. deodara, Cryptomeria japonica* and *P. kesiya* are shown for different months of the years 1998 and 1999 in Tables 4.3 (*Cedrus*), 4.4 (*Cryptomeria*) and 4.5 (*Pinus*). In *Cedrus* cambial cells began to divide in the first week of March and reached its peak activity during April with 8-12 cells in each radial file and in the cell walls the beads were not distinct (Plates-4.1 b & 4.2 b). The cambial activity was then slowed down during May and June due to higher wind speed (6.9 & 4.7 km/h) as well as higher needle fall and then remained more or less constant from July to the end of November. During the month of November, the cambial zone exhibited predominantly anticlinal division. The cessation in the activity of cambium and its dormancy were observed from the end of December to the end of February. During dormancy, the fusiform initials had distinct beaded cell walls (Plate-4.1 c).

In *Cryptomeria japonica* also the vascular cambium was non-storied with axially elongated fusiform initials and radially isodiametric ray initials. Cambial rays are predominantly uniseriate and occasionally biseriate rays were also noticed. Multiseriate rays were found to be absent (Plate-4.3 b, c). During the dormant period cambial zone was narrow consisting of 3-4 layers with relatively thick radial wall and abundant of

Table 4.3 Average Qantitative data of vascular cambial cells and their derivatives in *Cedrus deodara* Gaertn.f. in different months of the years 1999-2000. (* For plotting the graph during November to January months the length of fusiform initials and tracheids has been used based on the average minimum values of the concerned dormant periods).

Months	Average number of cambial layers	Average cambial zone width in µm.	Average width of Differentiating xylem zone in µm.	Average length of fusiform initial in µm.	Average length of tracheid in µm.
March	7	105.2 (7.8)	100.3 (8.1)	1974.7 (167.8)	1619.4 (121.4)
April	8-12	105.2 (7.8)	125.5 (9.4)	2592.8 (207.4)	1620.5 (129.6)
May	8.12	142.5 (11.4)	320.4 (22.4)	2592.8 (181.4)	1979.4 (128.6)
June	9-10	142.5 (8.5)	330.2 (28.0)	2592.8 (207.4)	1979.5 (142.5)
July	9-10	142.5 (8.5)	360.5 (25.2)	2646.7 (224.9)	1980.5 (128.7)
August	7-9	112.5 (9.5)	215.2 (17.2)	2819.4 (253.7)	2081.1 (145.6)
September	7-9	112.5 (9.5)	90.5 (6.3)	2502.1 (212.6)	2084.5 (145.9)
October	5-6	82.5 (5.4)	85.4 (7.6)	2173.6 (187.6)	1769.0 (141.5)
November	5-6	82.5 (5.4)	60.5 (60.5)	1789.8 (173.7)	1760.9 (123.2)
December	3-4	45.6 (3.2)	0	1392.3 * (90.4)	1650.5 * (148.5)
January	3-4	45.6 (3.2)	0	1392.3 * (90.4)	1650.5 * (148.5)
February	5-6	82.5 (6.6)	13.0 (0.5)	1852.5 (129.6)	1712.1 (128.4)

Table 4.4 Data of cambium, fusiform initials and tracheids of *Cryptomeria japonica* D.Don. Figures in the parenthesis indicate standard deviation. (* For plotting the graph during November to January months the length of fusiform initials and tracheids has been used based on the average minimum values of the concerned dormant periods).

Months	Average number of cambial layers.	Average width of cambial zone in µm.	Average width of differentiating xylem zone in µm.	Average length of fusiform initial in µm.	Average length of tracheid in µm.
March	6-7	97.5 (5.8)	60.5 (3.3)	1780.1 (133.5)	1958.9 (137.1)
April	6-7	97.5 (5.8)	80.3 (4.0)	1783.1 (124.8)	1961.4 (127.4)
May	8-9	127.5 (7.01)	196.1 (11.7)	1799.4 (116.9)	2069.3 (124.1)
June	9-10	142.5 (9.9)	360.3 (25.2)	1828.3 (127.9)	2102.6 (147.1)
July	9-10	142.5 (9.9)	362.4 (28.9)	1810.2 (126.7)	2081.7 (156.1)
August	7-8	112.5 (6.7)	190.1 (9.5)	1805.1 (144.4)	2166.2 (140.8)
September	7-8	112.5 (7.8)	173.2 (8.6)	1805.6 (108.3)	2165.5 (129.9)
October	5-6	82.5 (3.3)	90.2 (3.6)	1778.5 (133.3)	1956.4 (107.6)
November	5-6	82.5 (3.2)	85.3 (3.4)	1778.5 (115.6)	1956.3 (88.0)
December	3-4	52.5 (2.6)	0	1107.2 * (60.8)	1195.8 * (95.6)
January	3-4	52.5 (2.6)	0	1107.2 * (68.5)	1195.8 * (95.6)
February	5-6	82.5 (3.3)	17.2 (0.3)	1779.8 (115.6)	1867.7 (121.4)

Table 4.5 Data of cambium, fusiform initials and tracheids of *Pinus kesiya* Royle ex. Gordon. Figures in the parenthesis indicates standard deviation. (* For plotting the graph during November to January months the length of fusiform initials and tracheids has been used based on the average minimum values of the concerned dormant periods).

Months	Average number of cambial layers	Average width of cambial zone in µm.	Average width of differentiating xylem zone in µm.	Average length of fusiform initial in µm.	Average length of tracheid in µm.
March	9-10	135.0 (5.4)	300.2 (15.0)	2089.1 (146.2)	2298.6 (160.8)
April	9-10	135.0 (5.4)	296.3 (11.8)	2690.2 (174.8)	3093.7 (247.5)
May	7-8	112.5 (3.3)	250.6 (8.0)	2688.1 (188.1)	3225.8 (241.9)
June	7-8	112.5 (3.3)	215.7 (8.6)	2744.6 (233.2)	3293.5 (230.5)
July	8-9	127.5 (3.8)	196.1 (5.8)	2994.0 (209.5)	3592.8 (287.4)
August	8-9	127.5 (3.3)	160.5 (6.4)	2905.6 (203.3)	3341.4 (200.4)
September	7-8	112.5 (4.5)	110.2 (3.3)	2807.6 (224.6)	3228.7 (242.1)
October	6-7	97.5 (2.9)	80.3 (2.4)	2526.8 (101.0)	2779.5 (166.7)
November	5-6	82.5 (3.3)	60.6 (2.4)	1985.0 (119.1)	2143.8 (150.0)
December	3-4	52.5 (1.5)	0	1562.4 (110.8)	1710.7 (119.7)
January	3-4	52.5 (1.5)	0	1562.4 (109.4)	1710.7 (11.4)
February	4-5	52.5 (1.5)	15.0 (0.3)	2086.6 (166.9)	2190.9 (131.4)

storage reserved product accumulated in the fusiform initials and ray initials (Plate-4.4 a), but during the active period cambial zone was wider consisting of 7-10 layers (Plate-4.4 b, c), the cell walls of both fusiform initials and ray initials were thin and surrounded by differentiating xylem and phloem elements. The initiation of cambial activity was marked by radial wall swelling of fusiform initials and active vacuolation and followed by pariclinal division in the fusiform initial with disappearance of storage reserve food materials (Plate-4.3 a). Consequently the number of cells in the cambial zone and width of the cambial zone increased considerably. The fusiform initials contained 3-4 nucleoli in each nucleus, but the nuclei of the ray initials were invariably always globular (Plates-4.3 b, c & 4.5 a). The average data pertaining to the number of cambial layers, cambial zone width, differentiating xylem zone width, length of fusiform initial and tracheid length were shown for different months of the years 1998-1999 from March to February (Table 4.4). Cambial cells began to divide in the first week of March and reached peak activity in May to July, and then the activity of cambium was slowed down from August to November. Towards the end of dormancy as well as at the time of formation of late wood, cambial zone predominantly exhibited anticlinal division especially during November (Plate-4.5 b). The cessation in the activity of cambium and its dormancy were observed from the middle of December to the end of February.

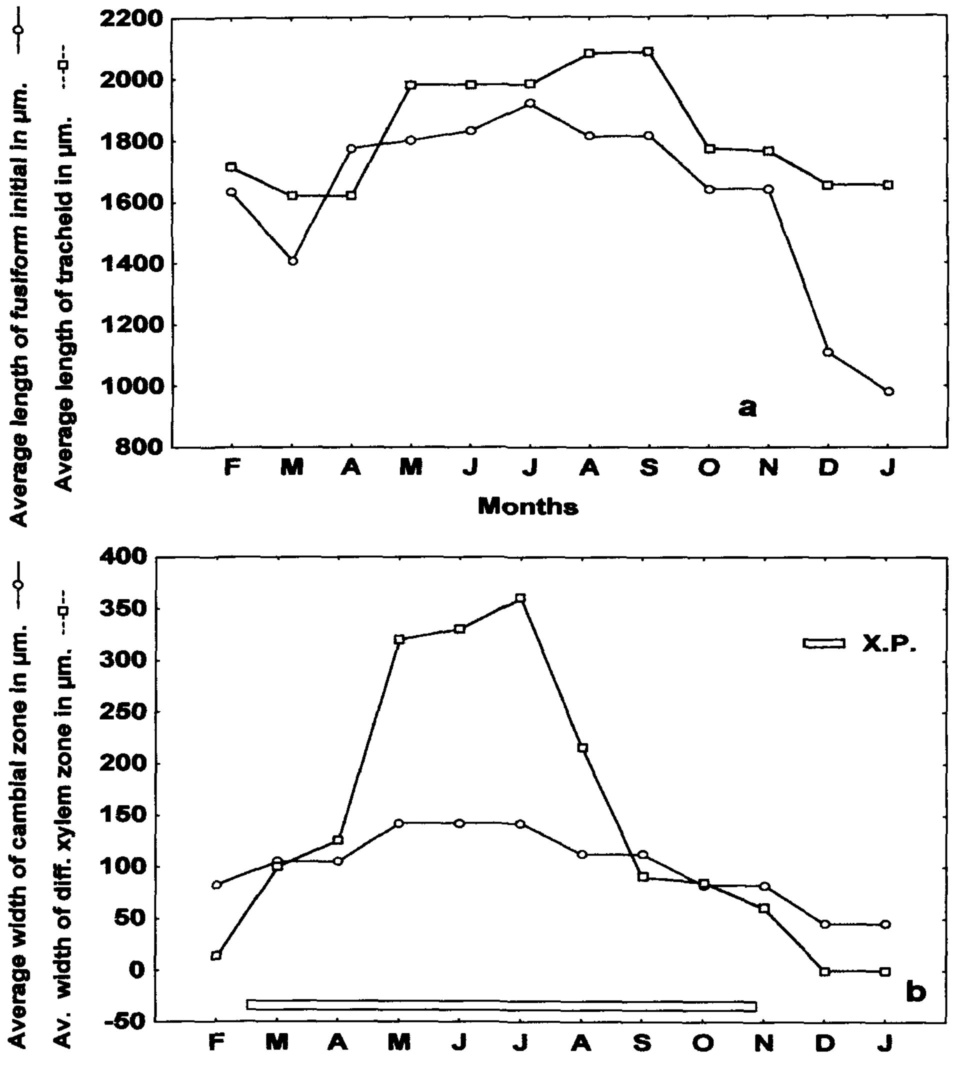
In *P. kesiya* the vascular cambium was non-storied with axially elongated fusiform initials and consists of more or less horizontally oriented isodiametric ray initials. Cambial rays were predominantly uni-biseriate but unicellular and multiseriate rays were also noticed occasionally (Plate-4.6 b). During the active period the cambial zone was wider and cell walls of both fusiform and ray initials were thin and surrounded by differentiating xylem and phloem elements (Plates-4.6 a & 4.7 b). Whereas during the dormant period, cambial zone was narrow with relatively thick radial walls and surrounded by matured xylem and phloem (Plates-4.6 c & 4.8 a). The initiation of cambial activity was marked by radial swelling of fusiform initials and the active vacuolation and followed by periclinal divisions in the fusiform initials (Plate-4.8 a, b). Consequently the number of cells in the cambial zone and width of the cambial zone increased considerably (Plates-4.6 a & 4.8 b). The fusiform initials showed binucleate condition with 3-4 nucleoli in each nucleus (Plate-4.9 a, b). The average data pertaining to them are shown for different months of the years 1998 and 1999 in the Table 4.5. Cambial cells began to divide in the middle of the first week of March and reached peak in April with 8-12 cells in each radial file (Plate-4.6 a). The cambial activity was then slowed down during May and June due to higher wind speed (6.9-4.7 km/h) and higher needle fall and it was more or less remain constant continuously from July to the end of November. During November, the cambial zone exhibited predominant anticlinal division (Plate-4.9 c). The cessation and dormancy of cambial activity were observed from the end of December to the end of February. The crystals, starch and protein bodies were observed during the dormancy of the cambium (Plates-4.6 c & 4.7 a).

Differentiation of Xylem tissue

The secondary xylem of *C. deodara* consisted of tracheids, rays and axial parenchyma cells. The rays were homogenous consisting of only procumbent cells. The bordered pits were dispersed in biseriate in the wider region whereas uniseriate in the narrow part of the tracheids (Plate-4.1 d). Axial parenchyma cells are scanty. Details regarding the timing of initiation and cessation of xylem production in terms of average differentiating xylem zone width and length of tracheid for different months of the study period (1998-1999) as well as their duration are illustrated in (Fig. 4.1 a, b). Xylem production was noticed for a total period of about eight and half months in *C. deodara* and it was started with the formation of tracheids in the middle of March, nearly two weeks after the sprouting of new needles and branches. It was continued up to the last week of November. Tracheids produced during March were thin walled (average cell wall thickness, 8-10μm) and the number of bordered pits per unit area (120-150/mm^2) which was more than that of late wood elements (10-20/mm^2). However those tracheids abutting with xylem rays had half bordered pits. The late wood elements were more compressed radially and thick walled than those produced in other months (Plate-4.2 a).

A comparison was made to find out changes in length between the average lengths of fusiform initials with that of the tracheids in different months of the year (Fig. 4.1 a). The average length of xylem tracheids had showed the same trend of variation as that of fusiform initials in *Cedrus*. The tangential lumen diameter of tracheid was high during the initial production of it in March and April (80-100μm). Deposition of starch grains and crystals in tracheids were found during the pre-dormancy and

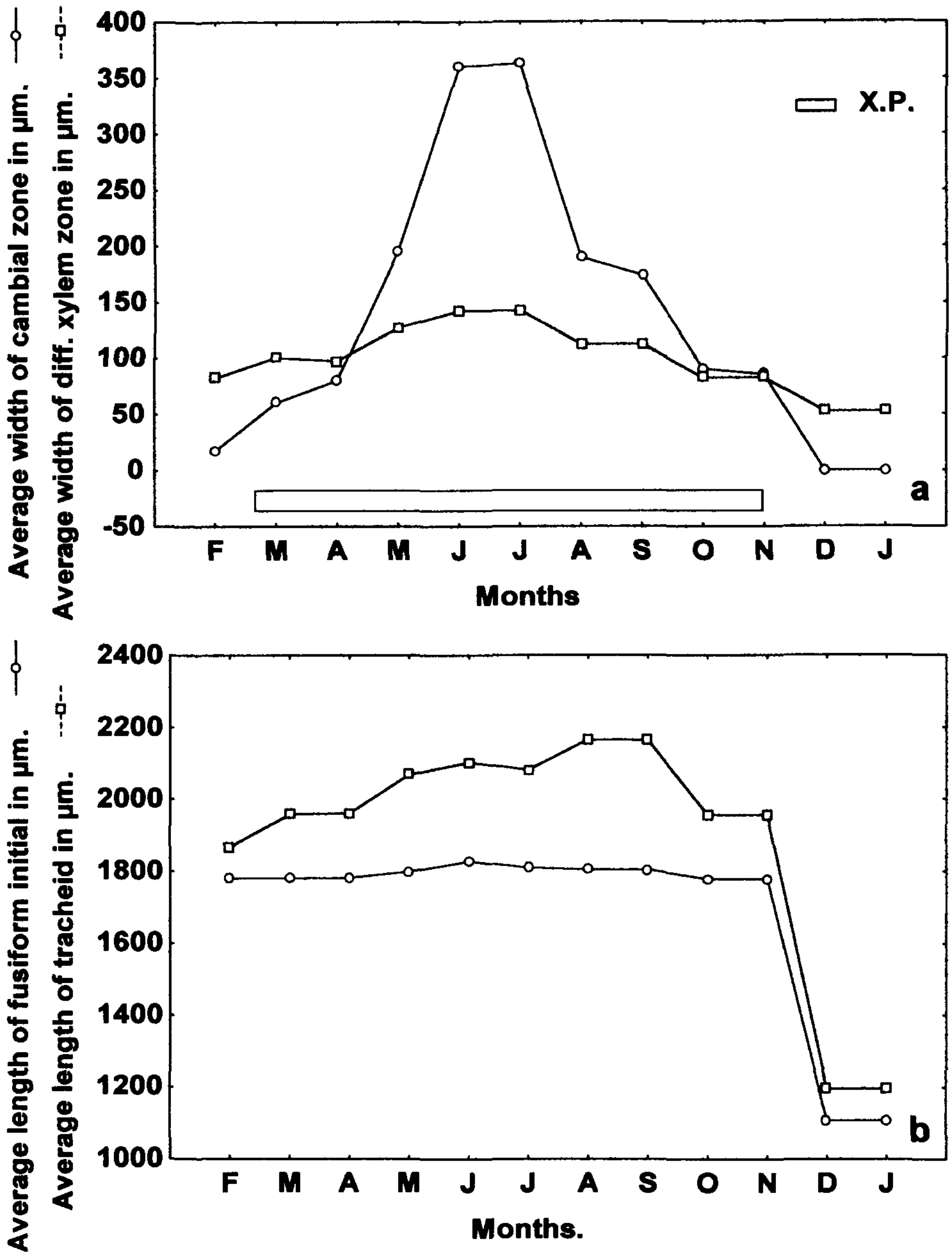
Fig. 4.1 Average data of two years 1998-1999 of *Cedrus deodara* Loudon. X.P= xylem production, Av= Average



fully during the dormant stages of the cambium. During the onset of cambial activity these ergastic substances characteristically were reduced in amount and totally lost.

The secondary xylem of *Cryptomeria japonica* consisted of tracheids, rays, resin cells and axial parenchyma cells. The rays were homogeneous consisting of only procumbent cells (Plates-4.4 b & 4.5 c). The bordered pits were dispersed more or less in the uniseriate pattern (Plate-4.5 c). The resin cells were mostly restricted in the late wood (Plate-4.4 b). Axial parenchyma cells were scanty. Details regarding the timing of initiation and cessation of xylem production as well as the duration are represented in (Fig. 4.2 a, b). Xylem production was noticed for a total period of about nine months in *Cryptomeria japonica* and it was started with the differentiation of tracheids in the first week of March which continued up to the last week of November. Tracheids produced during March were thin walled (cell wall thickness is 7-10μm) and number of bordered pit per unit area (80-100/mm^2) which is more than the late wood elements (Plate-4.4 b). Generally resin cells were formed in the beginning of differentiation of late wood xylem elements during the end of September and continued up to the end of November (Plate 4.4 b). Those tracheids adjacent with xylem

Fig. 4.2 Average data of two years 1998-1999 of *Cryptomeria japonica* D.Don. X.P= xylem production

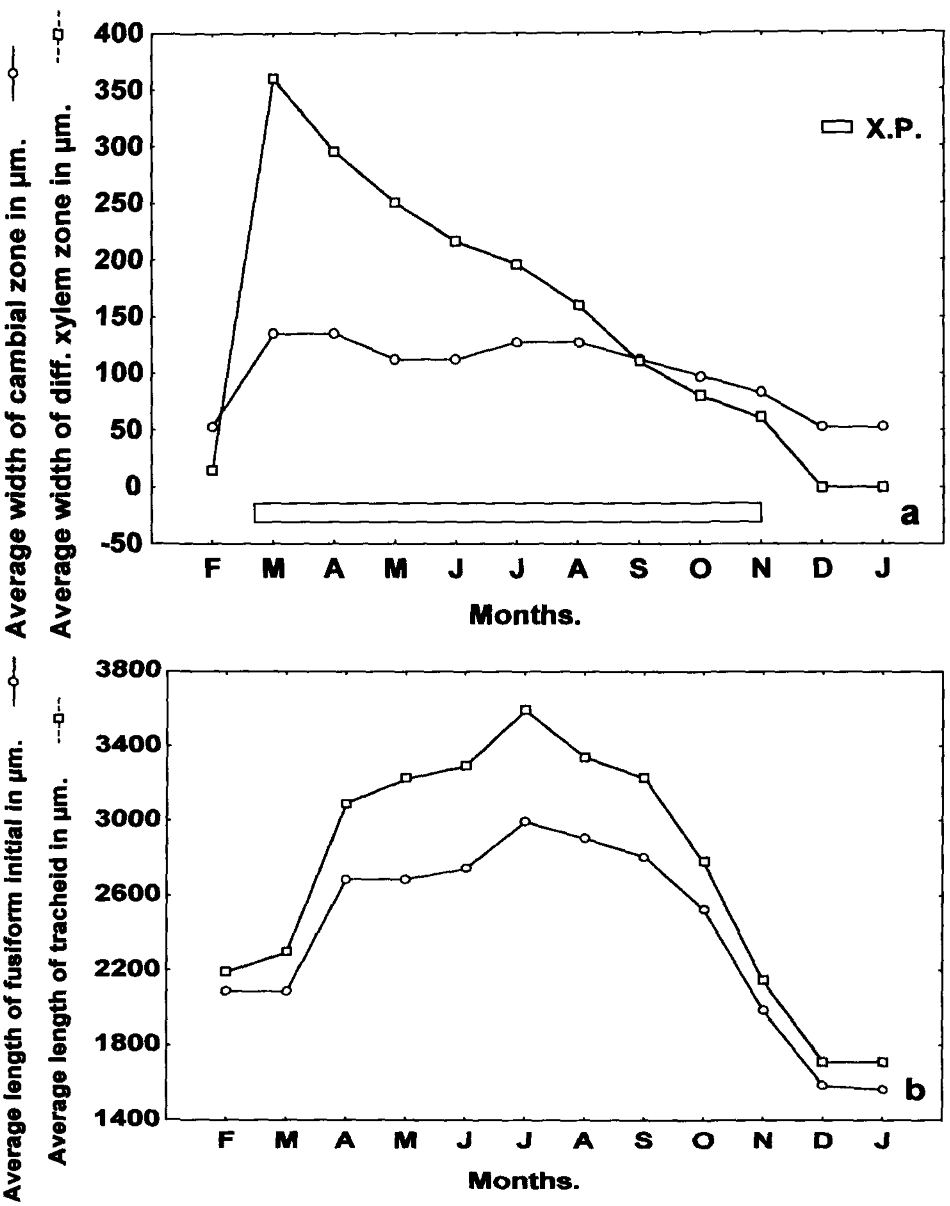


rays were half bordered pits and the late wood elements are radially compressed and thick walled (cell wall thickness 15-20μm) than those produced during other months (Plate-4.4 a, c).

A comparison was made between the average lengths of fusiform initial with that of the tracheid in different months of the year to find out changes in length (Fig. 4.2 a, b). The average length of xylem tracheid has showed the same trend of variations as that of fusiform initials in *Cryptomeria* also (Fig. 2 b). The tangential lumen diameter of tracheid was high during the initial production of it in March and April (80-100μm). Starch grains crystals and lots of storage reserve materials were observed in the fusiform initial of dormant cambium (Plate-4.4 a). During the onset of cambial activity these ergastic substance characteristically were reduced in amount and totally lost.

The secondary xylem of *P. kesiya* consisted of tracheids and xylem rays and the later were homogenous consisting of only procumbent cells. The bordered pits were dispersed in biseriate in the wider region whereas uniseriate in the narrow part of the tracheids and bars of Sanio were also distinct in between the bordered pits (Plate-4.10 c). The resin canals are mostly restricted in the late wood in *Pinus* (Plate-4.10 a). Axial and ray parenchyma cells were absent. Details regarding the timing of initiation and cessation of xylem production as well as their duration are illustrated in (Fig. 4.3 a, b). Xylem production was noticed for a total period of about 9 months in *P. kesiya* as in *Cryptomeria* and it was started with the formation of tracheids in the middle of March, nearly twenty days after the sprouting of new needles and branches. It was continued up to the last week of November. Those tracheids and resin canals produce during November remained in the partially differentiated state, over wintered and completed their development from the second weak of March to the last week of March. Tracheids produced during March were thin walled (cell wall thickness 8-10μm) and the number of bordered pits per unit area (average of 180/mm^2) is more than the late wood elements (Plates-4.9 a, b, c; & 4.10 b). Resin canals were generally formed in the beginning of the differentiation of late wood elements and continued up to the end of November (Plate-4.10 a). The numbers of bordered pit were less on the radial walls in the late wood elements (10/mm^2). However, those tracheids abutting with xylem rays had half bordered pits (Plate-4.7 a). The late wood elements were more compressed radially and thick walled than those produced during other months (Plates-4.8 a, b & 4.11 a).

Fig.4.3 Average data of two years 1998-1999 of *Pinus kesiya* Royle ex. Gordon. X.P= xylem production



The average length of xylem tracheids showed the same trend of variation as that of fusiform initials in *P. kesiya* (Fig. 4.3 b). The tangential lumen diameter of tracheid was high during the initial production of it in March and April (70-80μm) (Plate-4.9 a). Starch grain crystals and deposition of resin in the epithelial cells of resin canals and occasionally in tracheids were found during the pre-dormancy and fully during the dormant stages of the cambium. During the onset of cambial activity these ergastic substances characteristically were reduced in amount and totally lost (Plates-4.6 a & 4.7 b).

Cambial activity and xylem production in relation to climatic factors.

In *Cedrus deodara,* average width of cambial zone and monthly mean temperature showed a close relationship (r=+0.85) in the response function analyses (Fig.4.4 a). As well as average length of fusiform initials also showed a very close relationship with monthly mean temperature (r=+0.86) (Table 4.6). Whereas, a lesser relationship was observed between precipitation (r=+0.47) and relative humidity (r=+0.35) (Fig. 4.4 b, c) with the cambial zone width. The relationship between the average width of differentiating xylem zone and average length of tracheid also

Fig. 4.4 Regression line along with regression equation. r value is significant at $p< 0.005$ in *Cedrus deodara* Loudon.

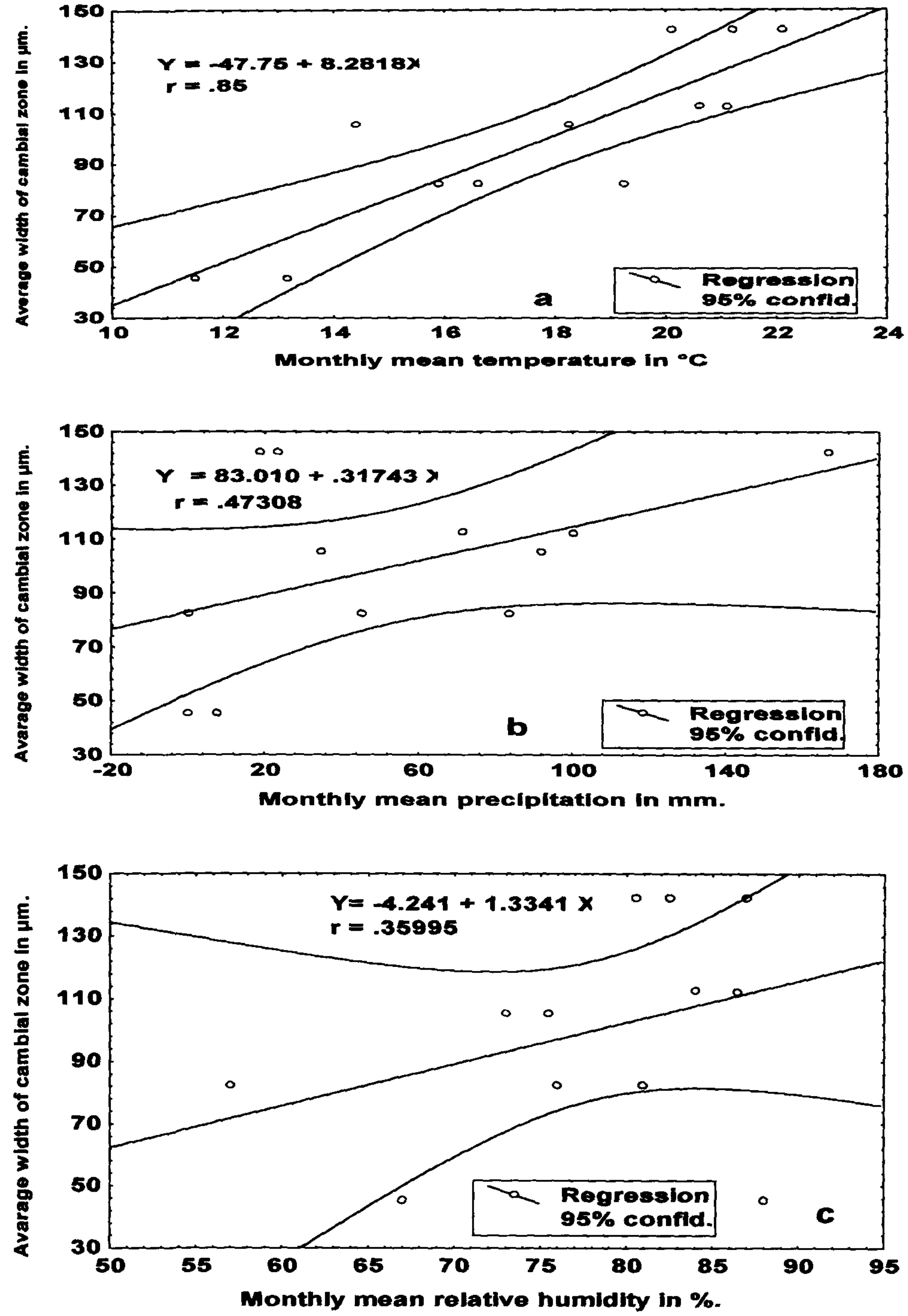


Table 4.6 Showing the correlation coefficients r values. All r values are significant at $p<0.05$ in *Cedrus deodara* Loudon.

Climatic factor Anatomical variables	Monthly mean temperature in °C.	Monthly mean maximum temperature in °C.	Monthly mean minimum temperature in °C.	Monthly mean precipitation in mm.	Monthly mean relative humidity in %.
Average length of fusiform initial in µm.	0.86	0.85	0.86	0.75	0.34
Average length of tracheid in µm.	0.84	0.86	0.81	0.5	0.16
Average cambial zone width in µm.	0.85	0.86	0.83	0.47	0.35
Average differentiating xylem zone width in µm.	0.86	0.83	0.86	0.53	0.54

showed a very close relationship with monthly mean temperature (r=+0.86; r=+0.84) (Fig. 4.5 a, b). Response to the monthly mean precipitation and relative humidity were less (Table. 4.6).

In *Cryptomeria* also, response function analysis was done to find the response of cambial activity and xylem production to the monthly mean temperature, monthly mean maximum temperature, monthly mean minimum temperature, monthly mean precipitation and monthly mean relative humidity. Average width of cambial zone showed a high relationship with monthly mean temperature (r=0.91) (Fig. 4.6a), whereas in the case of precipitation and relative humidity, the relationship were decreased (Fig. 4.6 b, c). The width of xylem differentiation zone also showed a good relationship with monthly mean temperature (r=0.84) (Fig. 4.8 a) and precipitation, relative humidity showed the decreased relationship (r=0.53; r=0.54) (Fig. 4.8 b, c). In all these response function analysis, the activity of cambium and the size variations of fusiform initials and tracheids responded positively to temperature than the monthly mean precipitation and relative humidity (Fig. 4.7 a, b) (Table. 4.7). Moreover the region of study is a sub-tropical wet forest area. Thus the

Fig. 4.5 Regression line along with regression equation. r value is significant at p< 0.005 in *Cedrus deodara* Loudon.

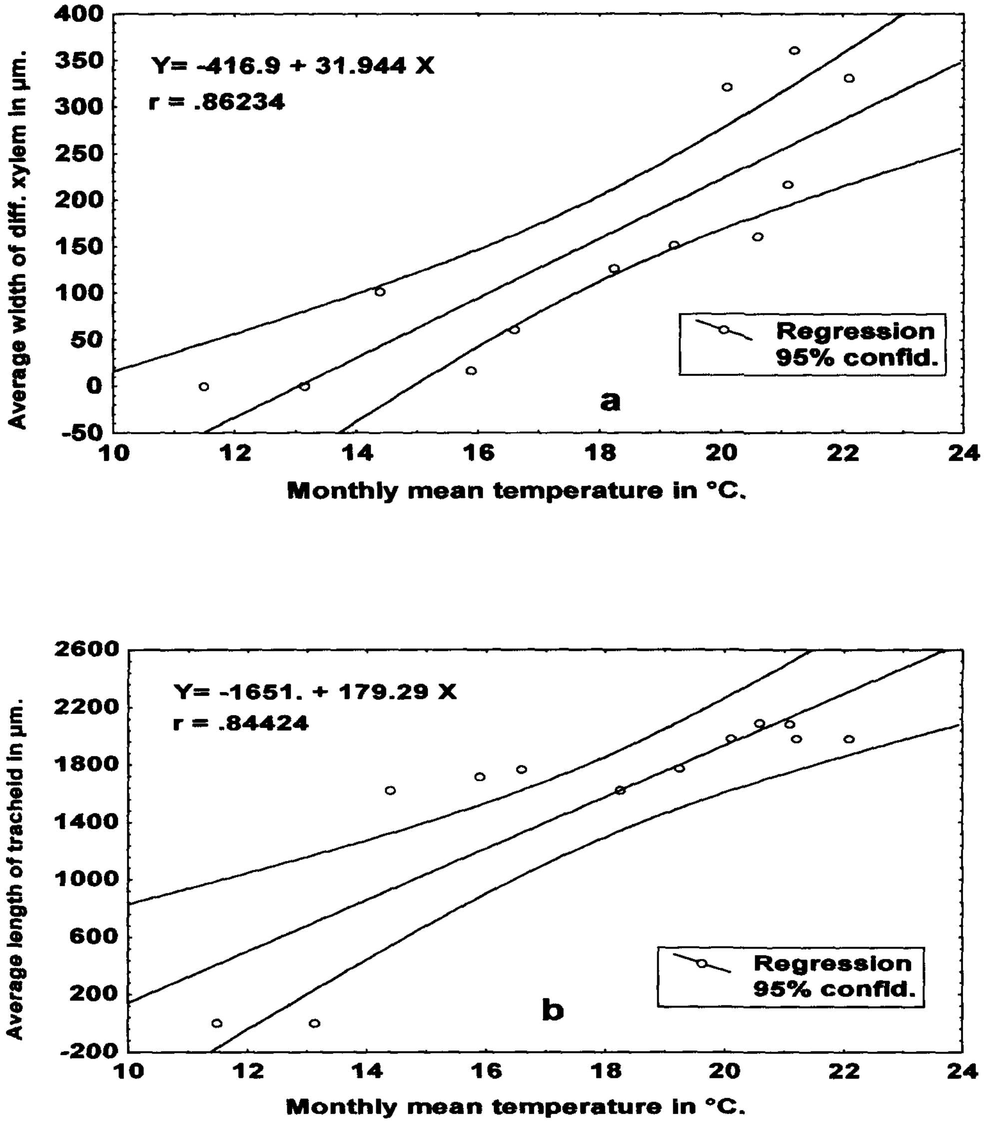


Fig. 4.6 Regression line along with regression equation. r value is significant at $p < 0.005$ in *Cryptomeria japonica* D. Don.

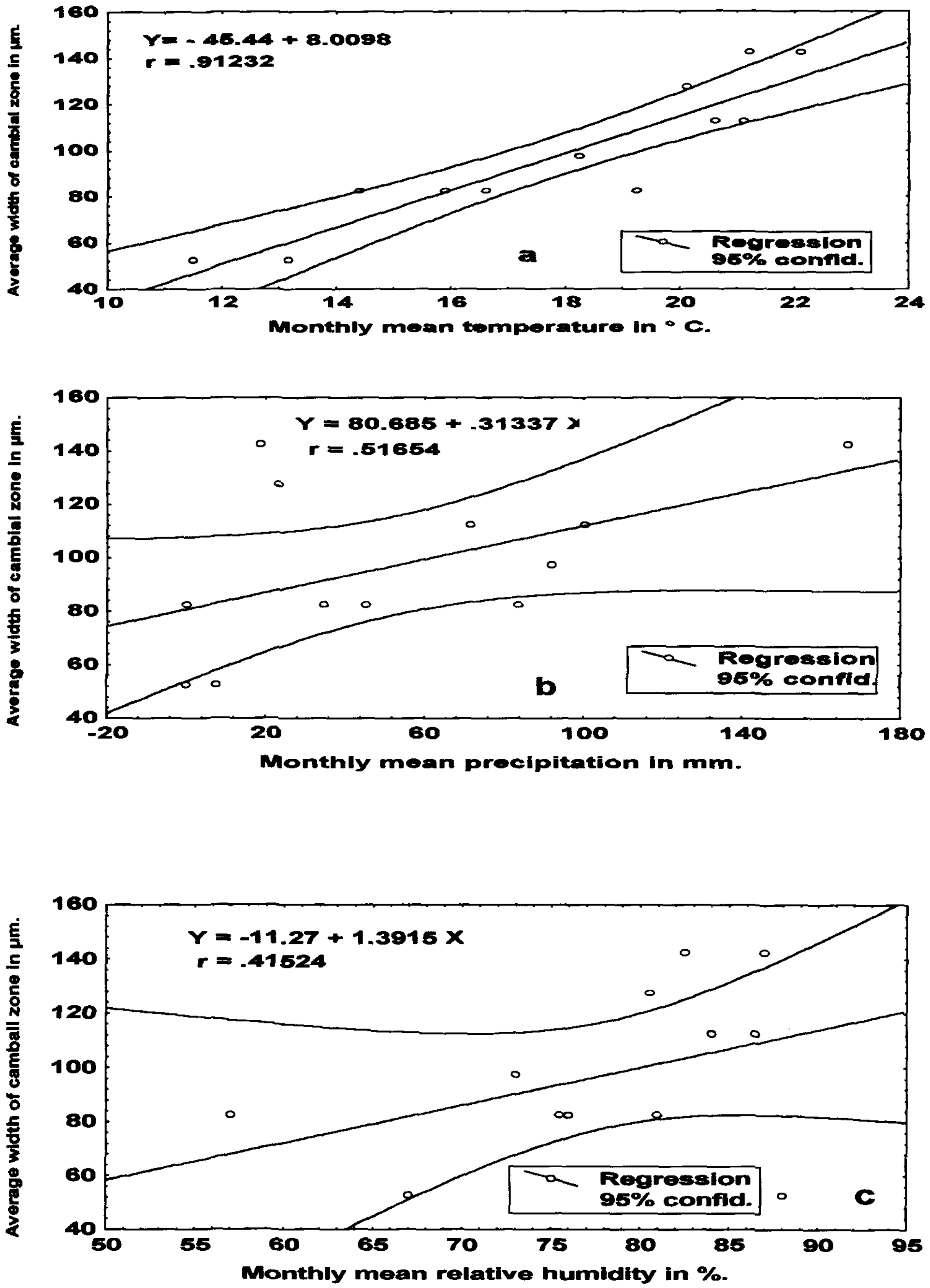


Fig. 4.7 Regression line along with regression equation. r value is significant at p< 0.005 in *Cryptomeria japonica* D.Don.

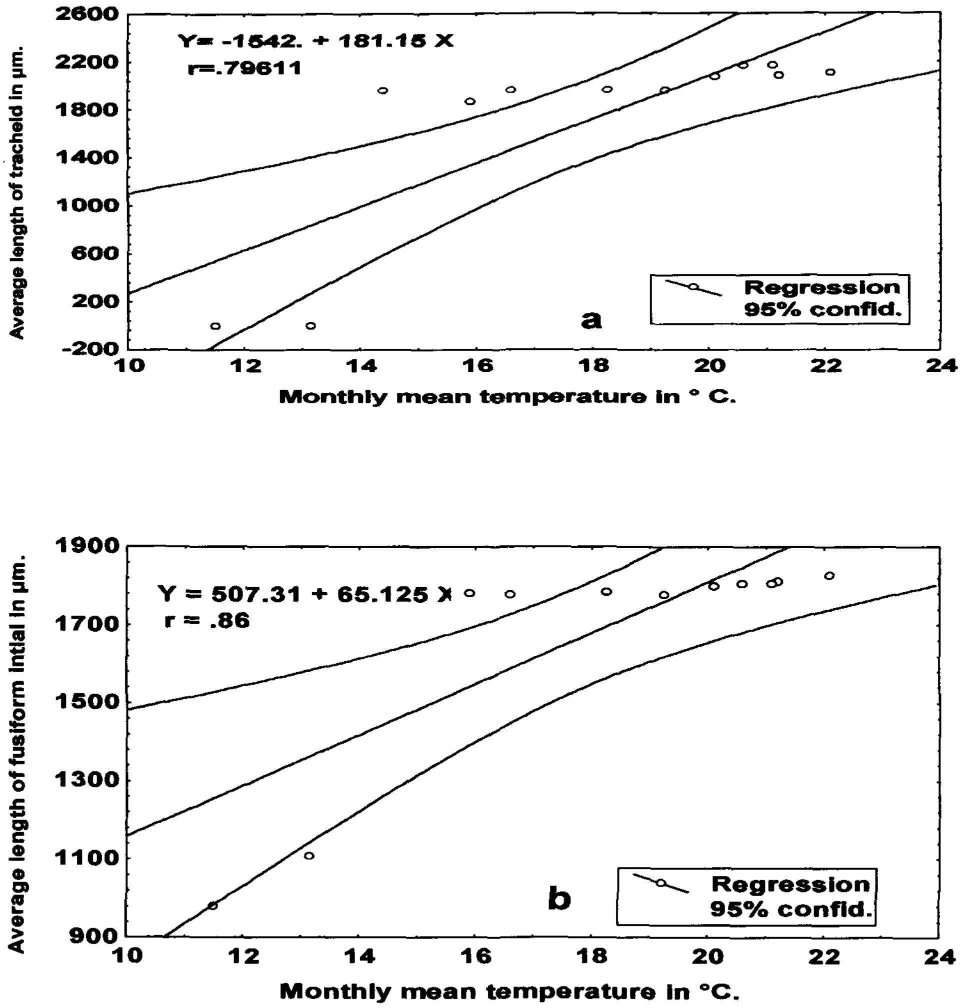


Fig. 4.8 Regression line along with regression equation. r value is significant at p< 0.005 in Cryptomeria japonica D.Don.

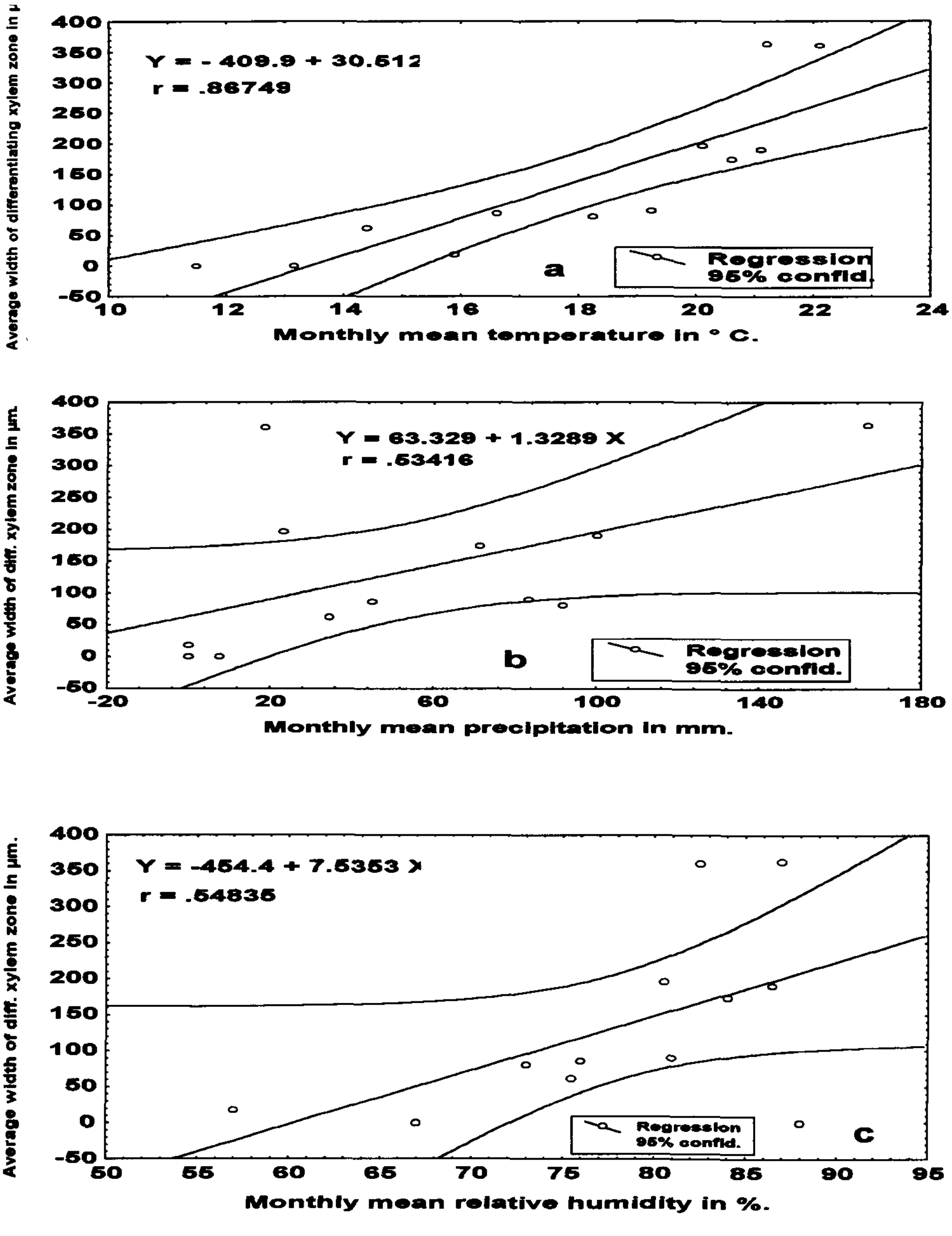


Table 4.7 Showing the correlation coefficients r values. All r values are significant at $p<0.05$ in *Cryptomeria japonica* D.Don.

Climatic factor Anatomical variable	Monthly mean temperature in °C.	Monthly mean maximum temperature in °C.	Monthly mean minimum temperature in °C.	Monthly mean precipitation in mm.	Monthly mean relative humidity in %.
Average length of fusiform initial in μm.	0.88	0.82	0.81	0.46	0.12
Average length of tracheid in μm.	0.79	0.82	0.76	0.49	0.12
Average width of cambial zone in μm.	0.91	0.92	0.89	0.51	0.41
Average width of differentiating xylem zone in μm.	0.84	0.81	0.85	0.53	0.54

soil moisture is not the limiting factor for the growth of the plant and they are not affected from soil moisture stress.

In *P. kesiya* during the onset of cambial reactivation and differentiation of xylem elements, a positive relationship was shown with the monthly mean temperature as revealed by cambial zone width response(r=0.67) (Fig.4.11 a), increased length of fusiform initials (r=0.95) (Fig. 4.9 a) as the temperature increased and decreased as the temperature decreased towards dormancy from the response function analysis.

The response function analysis revealed that the correlation coefficient of the cambial activity to monthly mean temperature was high enough than monthly mean maximum and minimum temperature respectively (r=+0.65; r=+0.66) (Table 4.8). Similarly, the fusiform initials length correlated more with monthly mean temperature (r=+0.95) (Fig. 4.9 a). A similar correlation was also existed between the mean monthly temperature and average lengths of tracheid (r=+0.90) (Fig. 4.10 a) as well as differentiating xylem zone width(r=+0.4) (Table 4.8). Whereas, the effect of rainfall and relative humidity on both the cambial activity and xylem production was secondary in nature (Table 4.8) (Figs. 4.9 b, c; 4.10 b, c ; 4.11 b, c).

Table 4.8 Showing the correlation coefficients r values. All r values are significant at $p<0.05$ *Pinus kesiya* Royle ex. Gordon.

Climatic factor Anatomical variable	Monthly mean temperature in °C	Monthly mean maximum Temperature in °C	Monthly mean minimum temperature in °C	Monthly mean precipitation in mm.	Monthly mean relative humidity in %
Average length of fusiform initial in µm.	0.95	0.94	0.94	0.71	0.44
Average length of tracheid in µm.	0.90	0.87	0.91	0.68	0.56
Average width of cambial zone in µm.	0.67	0.65	0.66	0.66	0.44
Average width of differentiating xylem zone in µm.	0.4	0.43	0.37	0.33	0.20

Fig. 4.9 Regression line along with regression equation. r value is significant at $p < 0.005$ in *Pinus kesiya* Royle ex. Gordon.

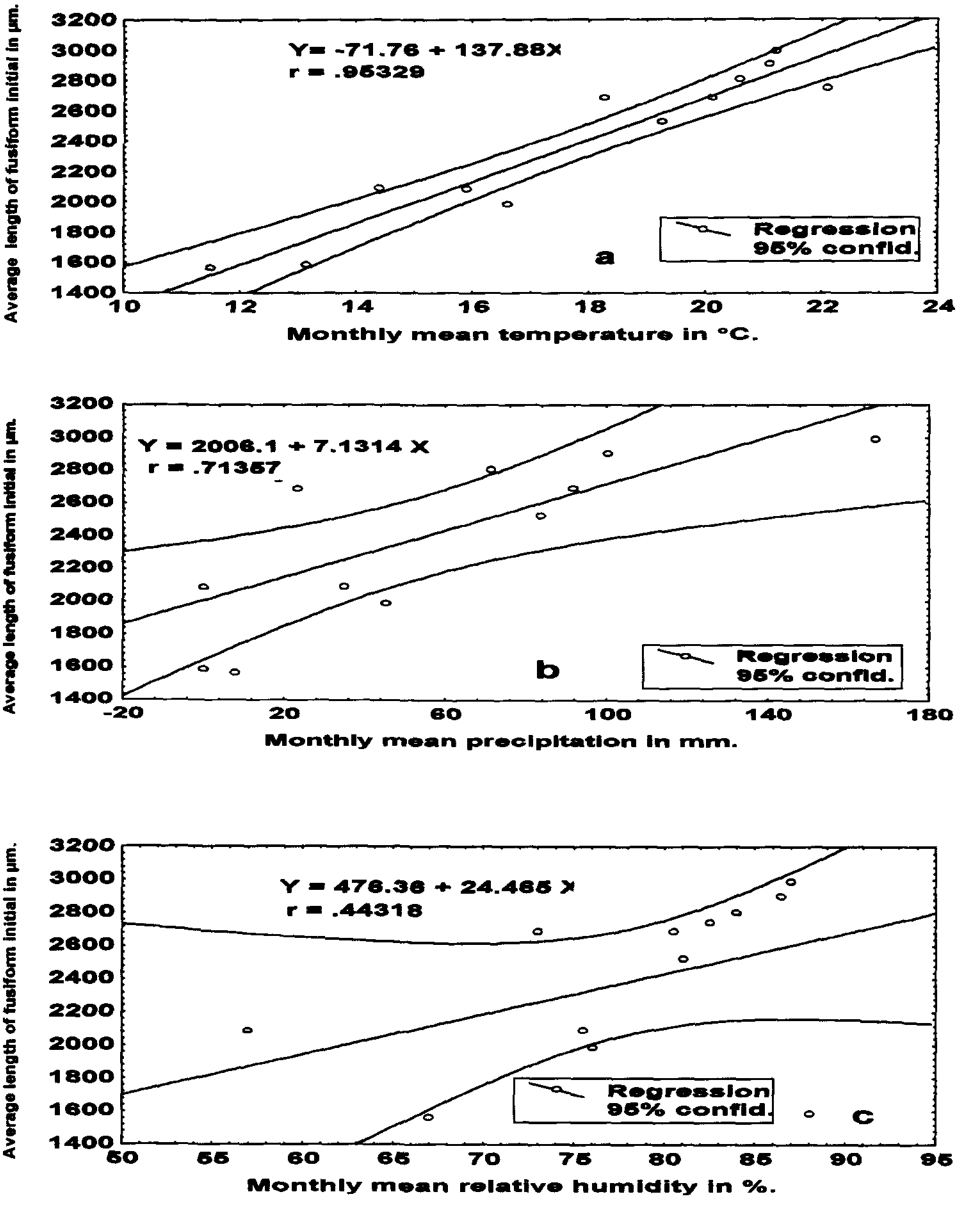


Fig. 4.10 Regression line along with regression equation. r value is significant at $p< 0.005$ in *Pinus kesiya* Royle ex. Gordon.

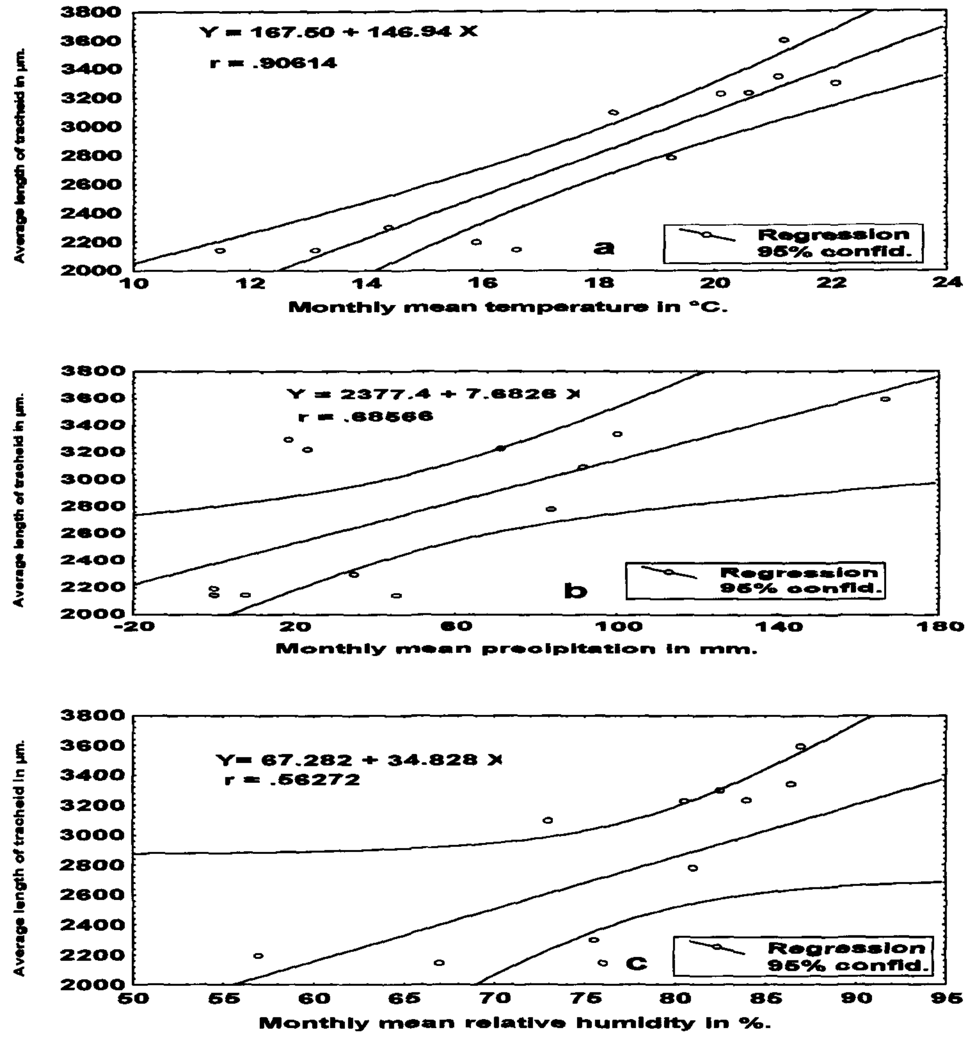
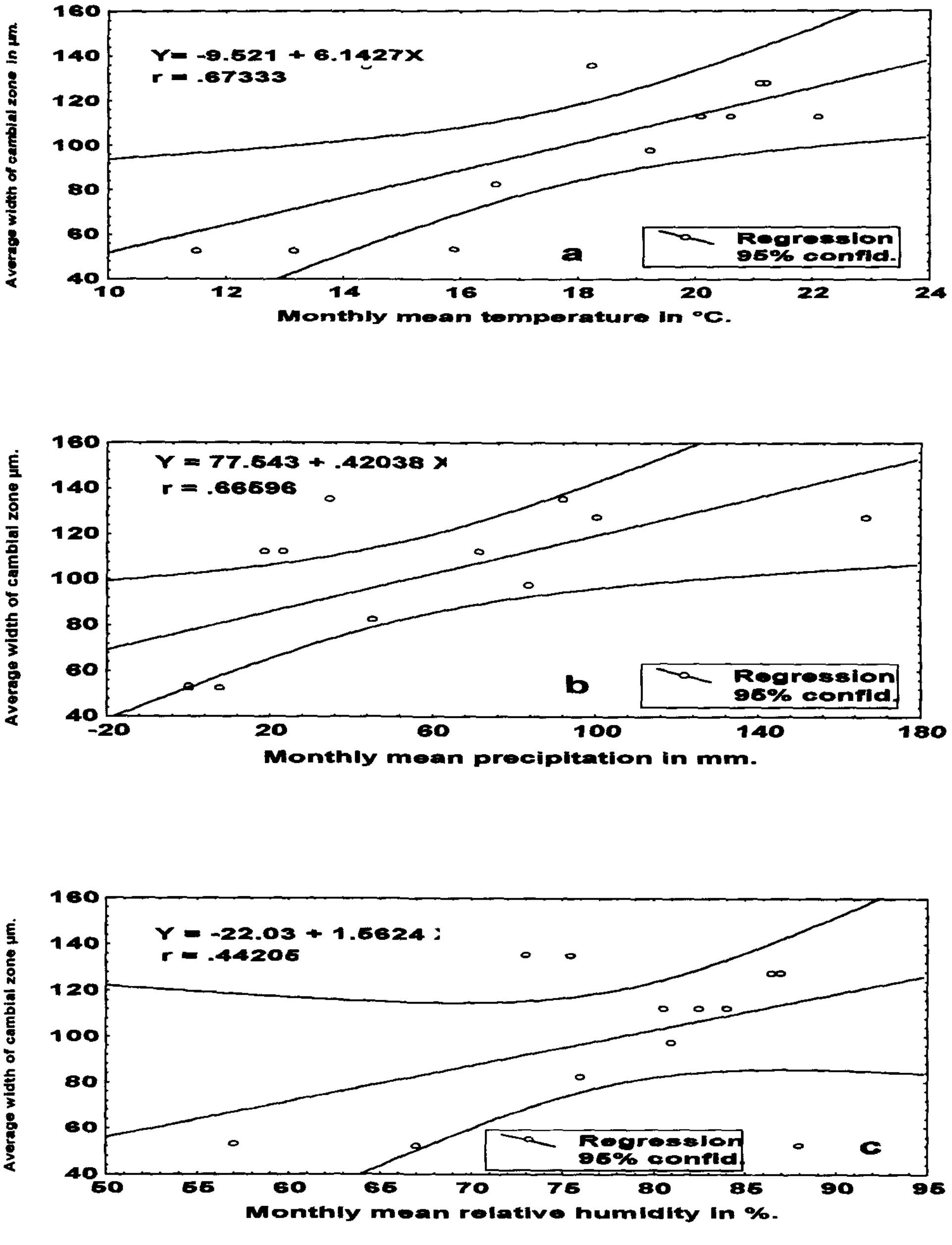


Fig. 4.11 Regression line along with regression equation. r value is significant at $p < 0.005$ in *Pinus kesiya* Royle ex. Gordon.



Discussion

In the present study on *Cedrus deodara, Cryptomeria japonica* and *Pinus kesiya*, the timing of bud breaks, initiation of cambial activity and in turn the production of xylem tissue is shown in Tables 4.1 & 4.2. It is evident from the Tables 4.1 & 4.2 that cambial reactivation and xylem differentiation were seen one week after the onset of bud break in all the gymnospermous trees viz. *C. deodara*, *C. japonica* and *P. kesiya.* The same feature was observed by Fahn (1990), in sub-tropical climate plants like *Quercus boissieri* Reut., *Pistacia atlantica* Desf., *Pinus strobes* (Murmanis 1971), *Pyrus communis* and *Pyrus malus* (Evert 1960 1963) as well as the same phenomenon were observed in tropical species in *Tectona grandis* (Rao and Dave 1981; Venugopal and Krishnamurthy 1987; Rao and Rajput 2001*)*. *P. kesiya* produced new needles thrice in year as shown in the Table 4.2. A similar phenomenon was reported by Das and Ramakrishnan (1986) in the same species. Reactivation of the cambium in different months of the same species growing under the different local climatic conditions is reported in some evergreen species (Zimmerman and Brown 1979), but such comparative studies are lacking in sub-tropical wet forest.

However, Beniwal (1987) recorded the phenology of *P. kesiya* growing in Tawang (Arunachal Pradesh), North East India, showed sprouting of needles once in a year is entirely different from the present study. Probably he observed only the first flush of needles during February. Those *Pinus* species growing in Western Himalaya showed the same phenological character as that of *P. kesiya* as observed by Dogra and Sahai (1984); Sahai (1987). Though there is shedding of needles intermittently, the tree never became barren in any season of a year due to production of new needles in three flushes in *Pinus* and continuous production of new needles in *Cedrus* and *Cryptomeria.* In *P. kesiya* though there are three flushes of new needles in a year, this plant produced distinct ring in a year. A similar phenomenon was observed by Tomlinson and Craighead (1972) in *Swietinia heterophylla.* The cambial activity is continuous throughout the year except during the winter season starting from December end to January end. Wareing et al. (1964) and Roberts (1976) reported that the young leaves and buds are the sites of IAA and GA_3 synthesis and their synergistic effect influences the cambial reactivation during the formation of new leaves and buds. The formation of male cones occurred simultaneously along with the sprouting of needles in *Cryptomeria* and *Pinus* whereas in *Cedrus* the formation of male cones occurred in May and July. It is difficult to find out the role of flowering on the cambial reactivation (Reinders-Gouwentak 1965; Venugopal and Krishnamurthy 1987; Fahn 1990). The dormancy of the vascular cambium is imposed strongly by the climatic conditions. The needle fall was never occurred during winter in contrast to most of the tropical deciduous trees (Dave and Rao 1982; Fahn 1982; Liphschitz and Lev-Yadun 1986; Philipson et al. 1971; Venugopal and Krishnamurthy 1987). All these three Gymnospermous plants growing in sub-tropical wet climate with a limited habitat, the vascular cambium is active throughout the year except during winter as reported by Fahn et al. (1986).

Cedrus, *Cryptomeria* and *Pinus* showed the distinct annual rhythm in cambial activity which resulted in the formation of distinct growth rings annually (Chowdhury 1964; Fahn et al. 1986; Carlquist 1980). Lipschitz et al. (1981) reported two flushes of xylem production in *Cupressus sempervirens* growing in the Mediterranean climate and a similar phenomenon was reported in *Tamarix aphylla* (Fahn, 1958). Amobi (1974) reported a multiple ring formation in correspondence with the number of bud breaks within a growth period in many tropical trees.

. However, in the present study, these three plants showed continuous production of xylem from middle of March to November end even if there were three flushes in *Pinus* and continuous production in both *Cedrus* and *Cryptomeria.* In temperate plants over wintering, partially differentiated xylem elements have been reported in few plants (Timell 1980 in *Picea abies* and *Quercus rubra*; Bannan 1955 in *Thuja occidentalis*; Longman and Coutts 1974 in *Quercus* species; see also Romberger 1963). Over wintering, partially differentiated trachieds and resin canals have been reported for the first time in *P. kesiya*

The present study also indicated the potentiality of using the variation in the length and diameter of different elements of woods for recognition of periodicity in xylem production. Though the character was suggested by Swamy and Govindarajalu (1961), this has not often been used because of the time involved in computing data on length and breadth of fusiform initials and tracheids, whereas the other characters can be used without difficulty since transverse section are sufficient.

Probably starch and crystals of calcium formed the source materials for new cell wall synthesis (e.g. carbohydrates and calcium pectate) when the cambial derivatives are rapidly produced. Davis (1961) also reported the possible usage of calcium oxalate crystals during the development of the embryo in *Podolepis jaceoides*. She reported that their appearance and disappearance from integumentary tapetum is related to the calcium requirement of the growing embryo. Riding and Little (1984) observed maximal and minimal starch content in the xylem of *Abies balsamea* associated respectively with the period of cambial dormancy and reactivation (see also Amobi 1973; Sauter 1966; Parker 1960; Pomeroy and Siminovitch 1971; Tsuda and Shimaji 1971; Essiamah and Eschrich 1985). When there are two flushes of cambial activity and dormancy, the accumulation and depletion of starch and calcium took place twice in a year (Venugopal 1986; Venugopal and Krishnamurthy 1987).

The timing of reactivation, dormancy, peak activity of cambium and xylem production in *C. deodara*, *C. japonica* and *P. kesiya* was studied in relation to variations in climatic factors such as temperature, relative humidity and precipitation. Periodicity of cambium and xylem production is controlled by various environmental and physiological factors (Kramer and Kozlowski 1979; Ajmal and Iqbal 1987; Larson 1994; Rao and Rajput, 1999; Venugopal 1986).

The monthly mean values of the above climatic factors for all the months of the study period in 1998 and 1999 are plotted (Fig.4.1 a, b) and was analyzed. It was observed that both reactivations, peak activity of cambium and xylem production were generally favored by a higher mean temperature in all these three plants. The trees showed a positive correlation between the least cambial activity and xylem production almost negligible with lower temperature range and no production of xylem. Higher temperature was reported to be conducive to cambial reactivation and xylem production in *Picea glauca* (Gregory and Wilson, 1968). A similar view was expressed by Kramer and Kozlowski (1979), that temperature was a significant factor for bud break following cambial reactivation and subsequent shoot growth. On the other hand, a raise and fall in temperature was reported to have no effect on cambial activity in *Cupressus sempervirens* (Lipschitz et al. 1981) and in *Eucalyptus camaldulensis* (Waisel et al. 1966). It appears that temperature factor does not act independently and the law of limiting factor may be in operation (Coile 1936; Keen 1937). The mechanism by which higher temperature promoted cambial reactivation in many tree is not very clear. Wort (1962) on the basis of in vitro experiment, suggested that increase in temperature was responsible for the release of auxin reserves from tissue adjacent to cambium and that in turn activated the cambium. Catesson (1962), on the other hand, had implicated temperature in promoting vacuolation of fusiform initials and may likely to be the effect of increased temperature. Relative humidity doesn't show clear relationship with cambial behaviour. The role of rainfall under drought conditions on cambial behaviour and xylem production was studied much more intensively than other factors in the past. Higher rainfall was reported to be conducive to cambial reactivation in several plants growing especially in tropics and semi-arid climate (Glock 1955; Reinders-Gouwentak 1965; Dave and Rao 1982; Rogers 1981).

The present study also showed the mean rainfall has less correlation than that of temperature in these three plants. Rainfall probably is an important factor only in regions where soil moisture content is dependent on rainfall. This study also have indicated that cambial reactivation/peak activity/xylem production were not mainly limited by rainfall as they grow only in limited habitat of sub-tropical wet forest of North East India with enough soil moisture throughout the year (see Amobi 1974; Fahn 1959; Rolf Borchert 1998, 1999). It was observed that a higher mean temperature generally favoured both cambial reactivation and xylem production in these plants. The other factors such as relative humidity and precipitation add little effect on cambial periodicity and xylem differentiation. A positive correlation also existed between the cambial dormancy and lower mean temperature in *C. deodara*, *C. japonica* and *P. kesiya*.

PLATE - 4.1

a. An enlarged portion of active fusiform (FI) and ray initials (R1). Note the tangential and radial walls are very thin. x 1800.

b. T.L.S. of active vascular cambial zone, the cell walls are very thin. x 100.

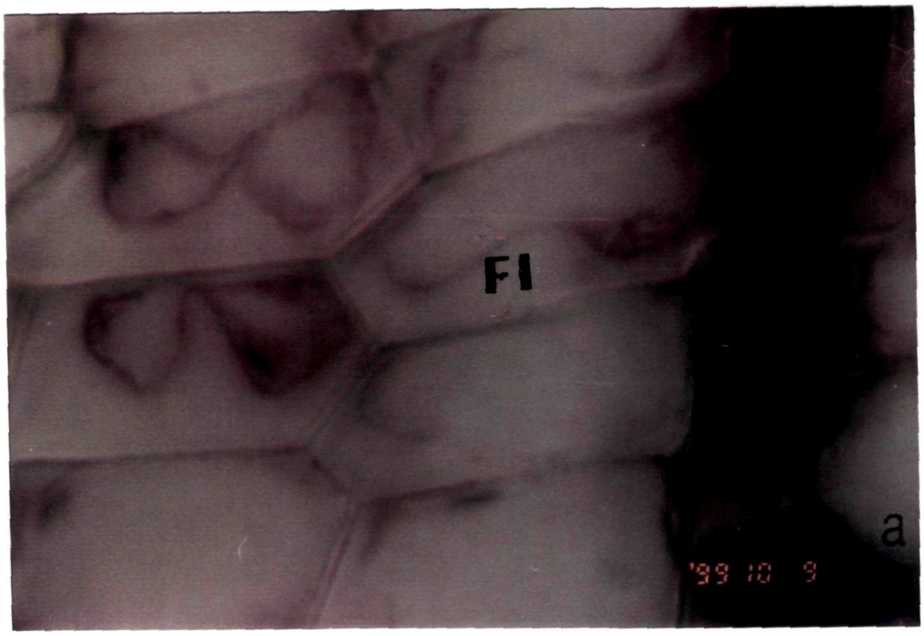
c. T.L.S. of dormant fusiform initials (FI) and ray initials (RI). Note the beaded nature of cell walls. x 250.

d. T.L.S. of xylem with tracheids (T) and xylem (XR). x 125.

PLATE - 4.1

Cedrus deodara Loudon

An Enlarged View of Active Vascular Cambium



Tangential Longitudinal Sections

Active Vascular Cambium

Dormant Vascular Cambium

Xylem

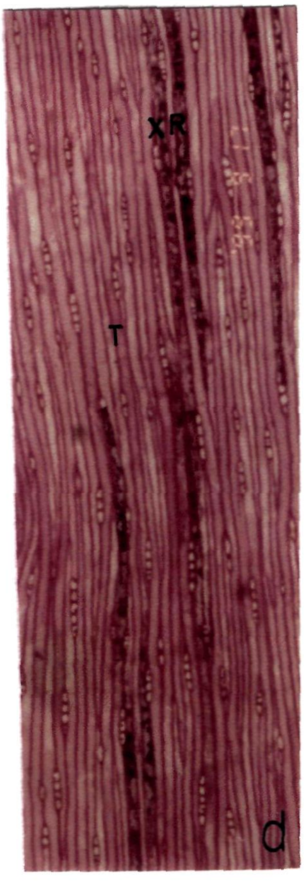


PLATE - 4.2

a. T.S. of dormant vascular cambial zone (CZ) consisting of 3-4 layers. Latewod (LT) and early wood (EW). Note the frequency of Bordered pits (BP) in the early wood. x 250.

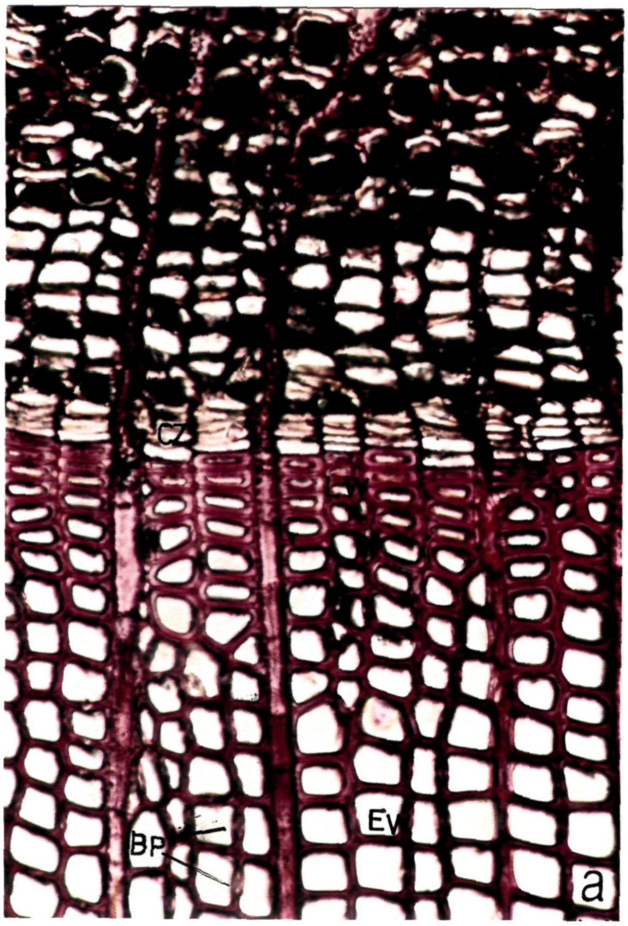
b.T.S. of active cambial zone (CZ) with 8-10 layers and differentiating xylem zone (DX). x.600

c. An enlarged view of dormant cambial zone (CZ) consisting of 3 layers. Note the tangential and radial walls are very much thick. x 850.

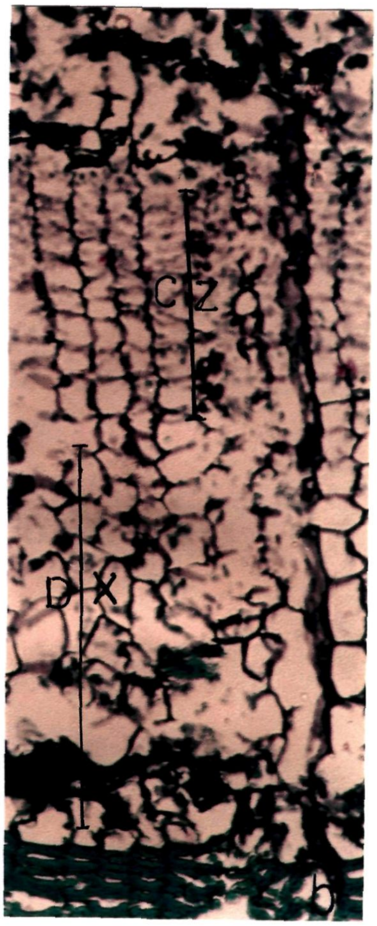
PLATE - 4.2

Cedrus deodara, Loudon

Transverse Section of Dormant Vascular Cambium



Transverse Section of Active Vascular Cambium with Differentiating Xylem



An Enlarged View of Dormant Vascular Cambium

PLATE - 4.3

a. T.S. of reactivated cambial zone (CZ). Note the radial swelling of fusiform initial (SFI). x 800.

b. T.L.S. of active vascular cambial zone consisting of fusiform (FI) and ray initials (RI). Note the walls are very thin and the beads are not distinct. x 200.

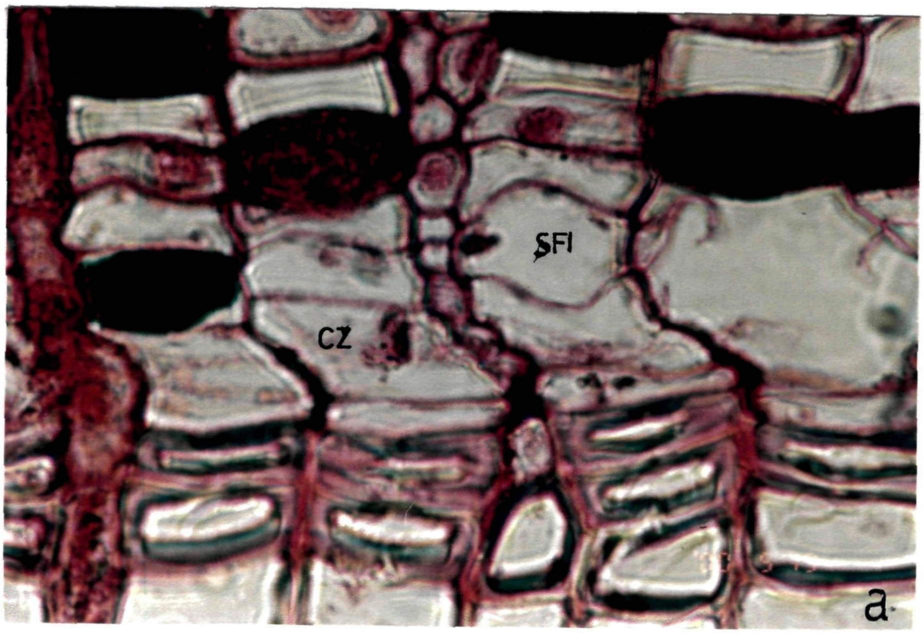
c. T.L.S. of dormant cambium. Note the cell walls with distinct beaded nature and thick. x 200.

PLATE - 4.3

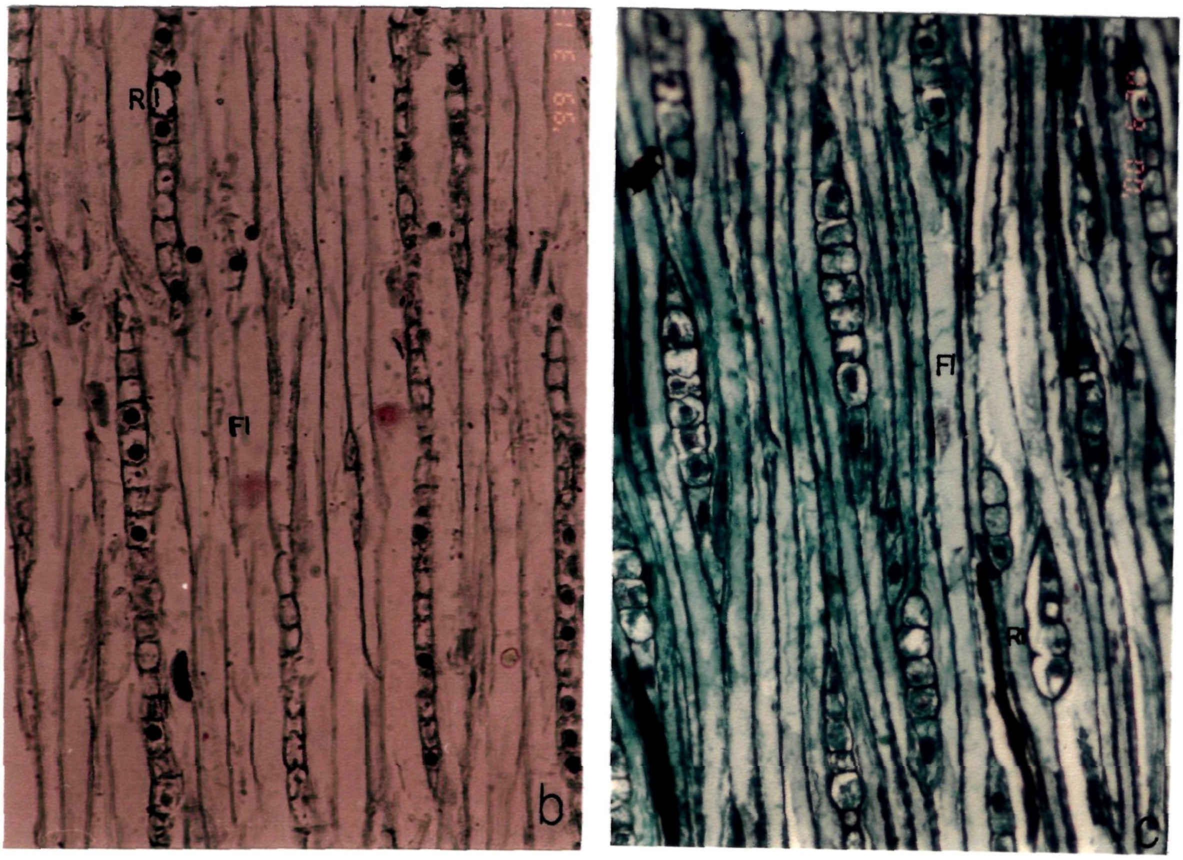
Cryptomeria japonica D. Don

Reactivation of Cambium after Dormancy

Transverse Section



Tangential Longitudinal Section of Cambial Region


Active Vascular Cambium

Dormant Vascular Cambium

PLATE - 4.4.

a. Transverse section of cambial zone showing the accumulation of reserve food material particularly starch grain (stained with IKI) during dormancy. X. 900.

CZ= cambial zone; R= Reserve materials.

b. Transverse section of active the cambial zone with three growth rings. Note resin cells are mostly restricted towards the latewood. x 140
CZ=Cambial zone; EW= Early wood; LW= Late wood.

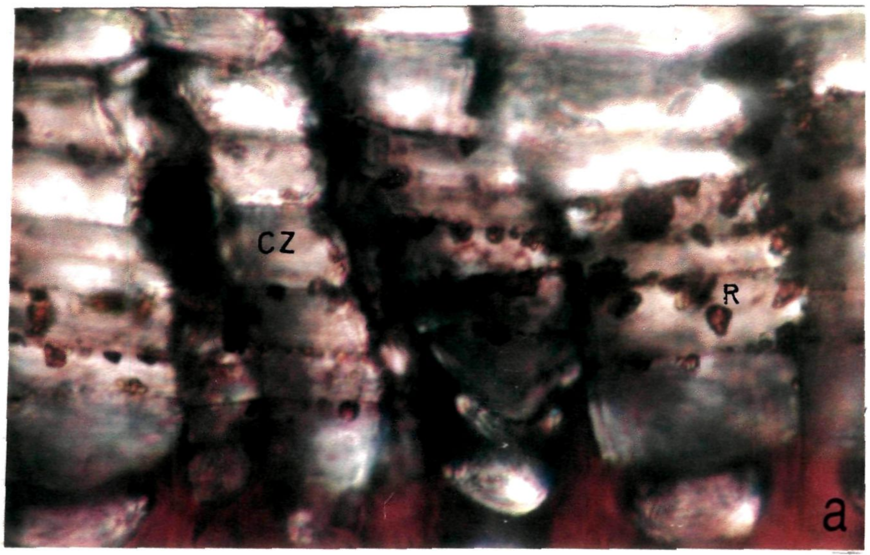
c. Active cambial zone showing the nucleus in the fusiform initials. Note the periclinal division in fusiform initial (arrows). x 1000.
CZ= cambial zone; P=phloem.

PLATE - 4.4

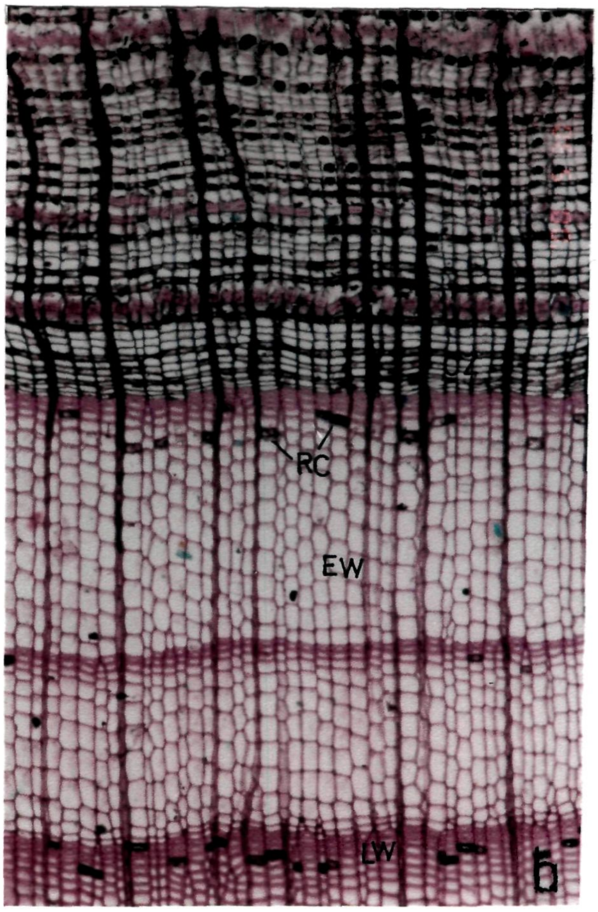
Cryptomeria japonica D. Don

Transverse Sections of wood with Vascular Cambial Region

Dormant Vascular Cambium



Active Vascular Cambium



An Enlarged View of the Active Vascular cambium

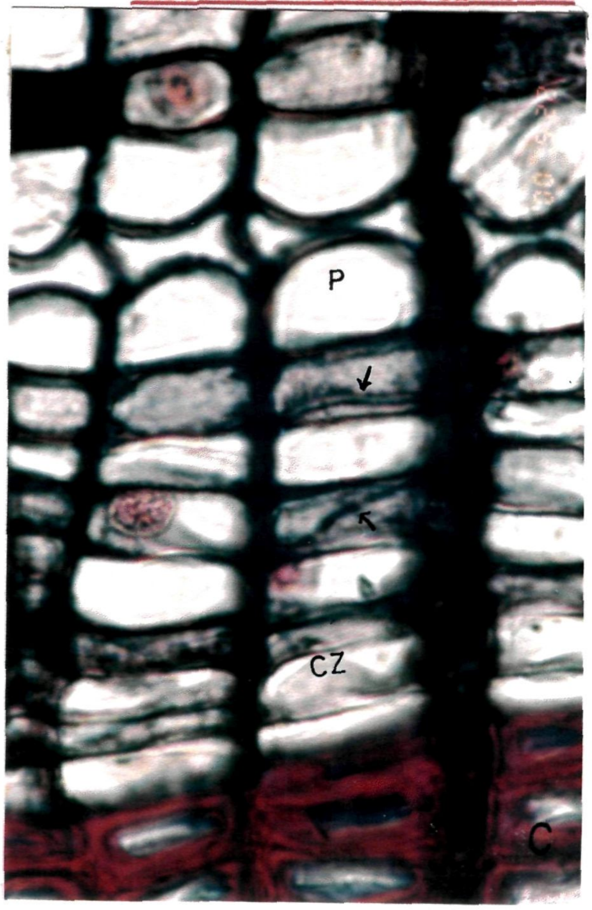


PLATE - 4.5

a. T.L.S. of cambial zone, showing the elongated nucleus (N) with two nucleoli. Note the nuclear shape in ray initials which is always globular . x 1600.

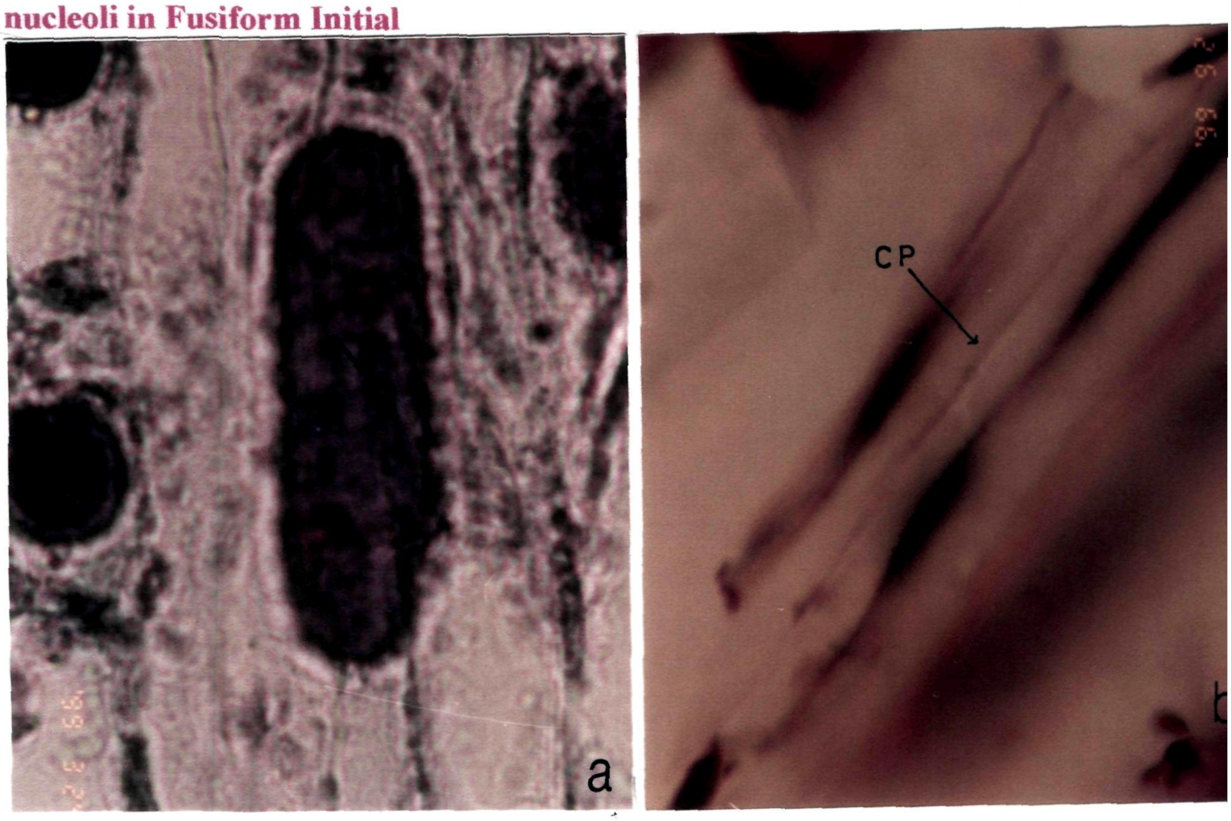
b. Formation of new cell wall plate (CP) during the anticlinal division. x 350.

c. R.L.S. of late wood showing the homogeneous xylem rays (XR), Tracheids (T) with numerous bordered pits (BP) and resin cells (RC). x 280.

PLATE - 4.5

Cryptomeria japonica D. Don

Active Vascular Cambium



A Nucleus Containing two nucleoli in Fusiform Initial

Formation of Cell Plate

Radial Longitudinal Section of Wood

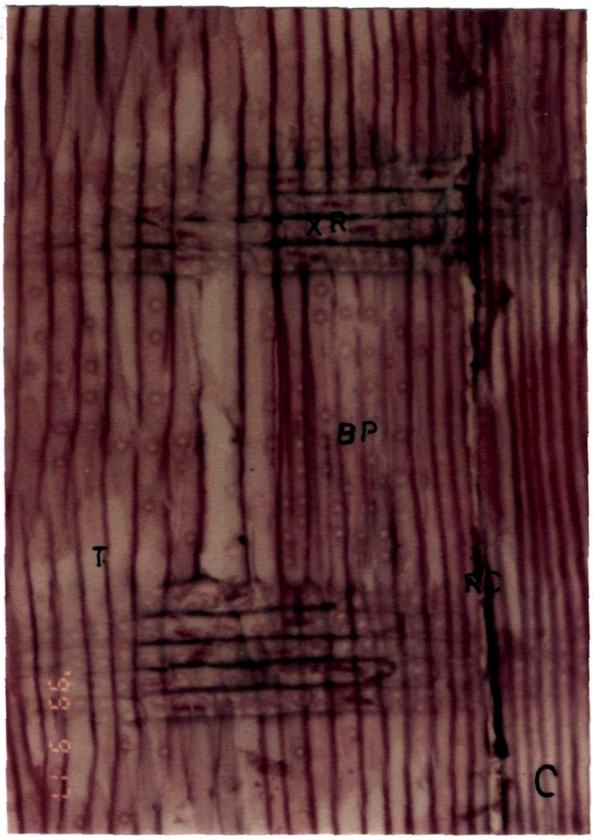


PLATE - 4.6

a. T.S. of Active vascular cambial zone with thin tangential and relatively thick radial walls in the fusiform initial (FI); Ray initial (RI). x 1200.

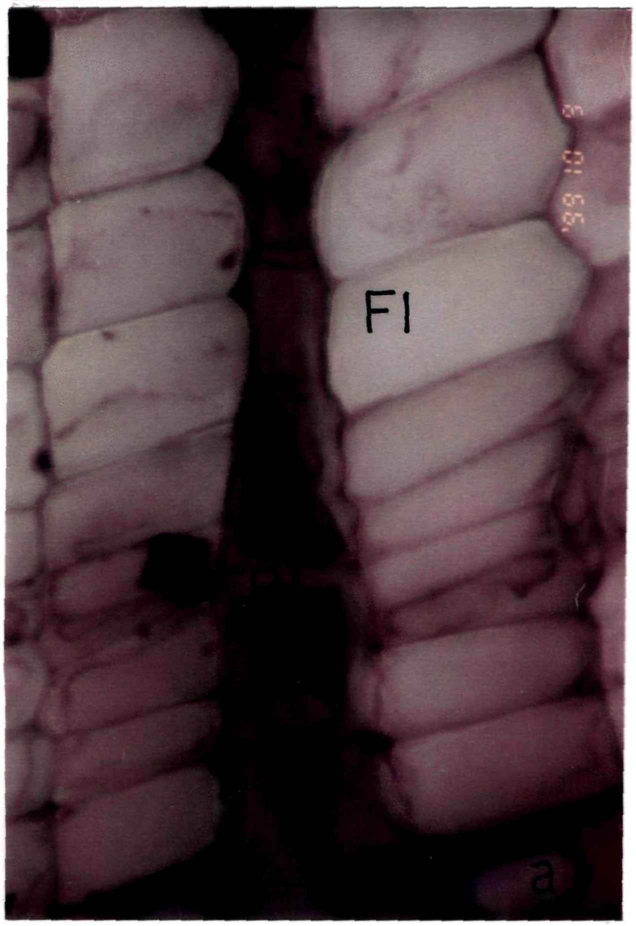
b. T.L.S. of active vascular cambial zone showing the fusiform (FI) and Ray initials (RI). Note the cell walls of fusiform initials are very thin and the beads are indistinct. x 175.

c. R.L.S. of dormant vascular cambium having the fusiform initial (FI) with distinct beads and deposition of crystal (Cr). x 150.

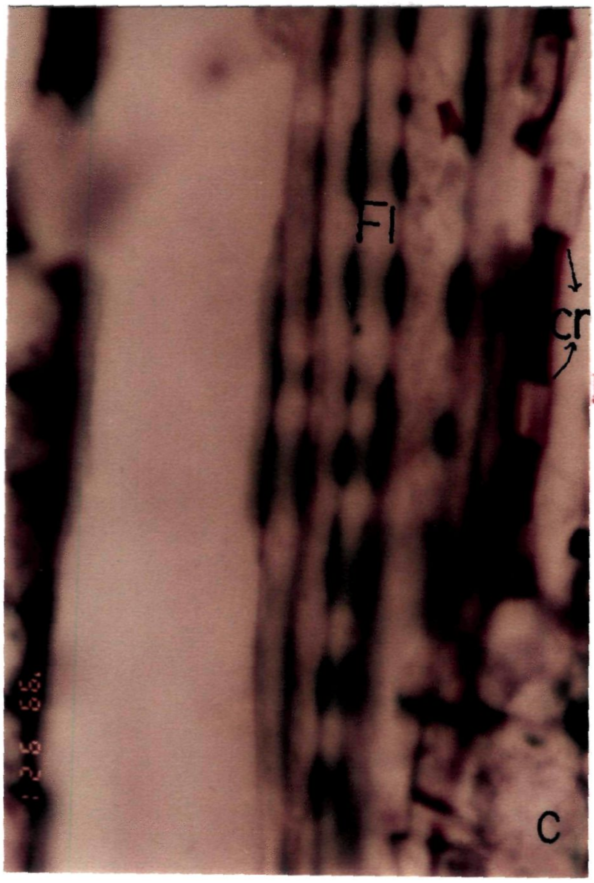
PLATE - 4.6

Pinus kesiya Royle ex. Gordon

Transverse Section of Active Vascular Cambium



Tangential Longitudinal Section of Active Vascular Cambium



Radial Longitudinal Section of Dormant Vascular Cambium

PLATE - 4.7

a. T. L. of dormant vascular cambium. Note the accumulation of starch grains (S) in fusiform initial (FI). Tracheid (T) which abutting the xylem rays having half bordered pits (HBP) x 900.

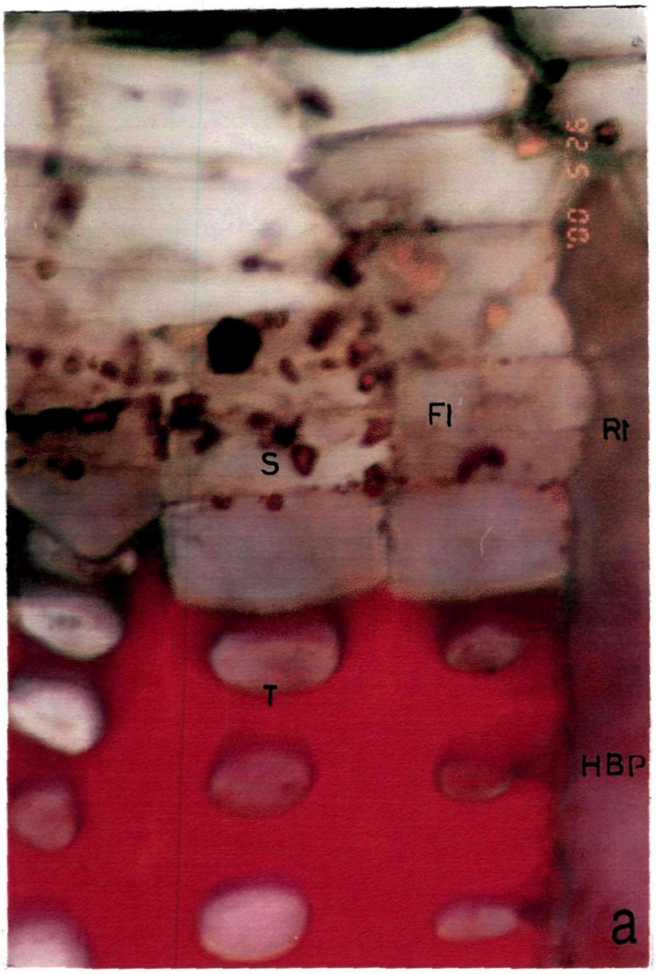
b. T.S. of reactivated cambial zone (CZ) devoid of storage products. Resin canals (RC) in the late wood. x 550.

PLATE - 4.7

Pinus kesiya Royle ex. Gordon.

Dormant Vascular cambium (January).

Tansverse Section



Accumulation of Starch grains

Active Vascular Cambium (March);Devoid of storage products

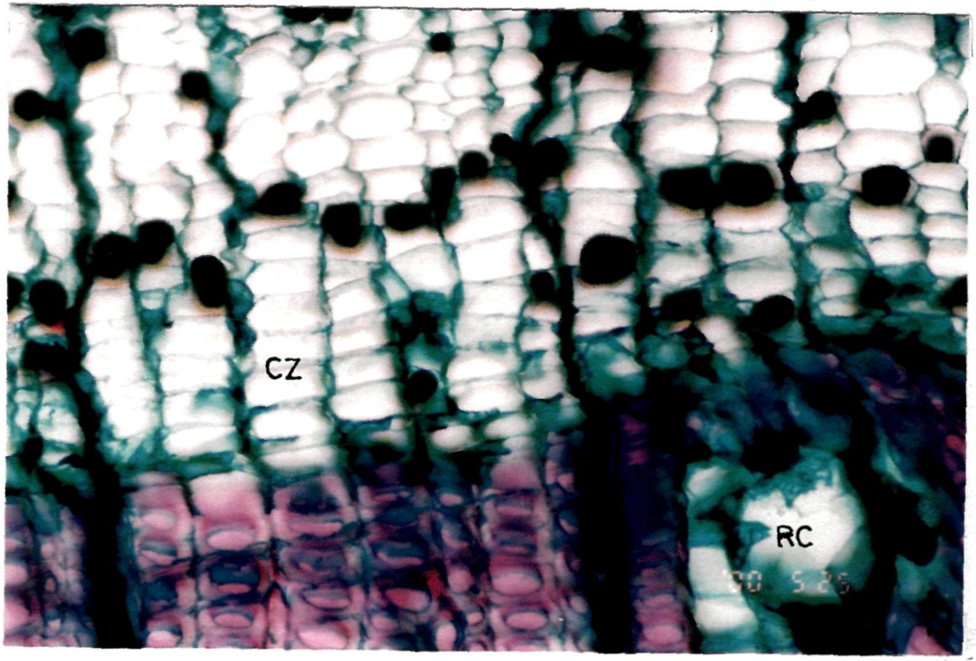


PLATE- 4.8

a. T. S. of cambium, just prior to the reactivation. The fusiform initials undergo radial swelling (SFI). Note the disappearance of reserve food products. Late wood (LW). x 850.

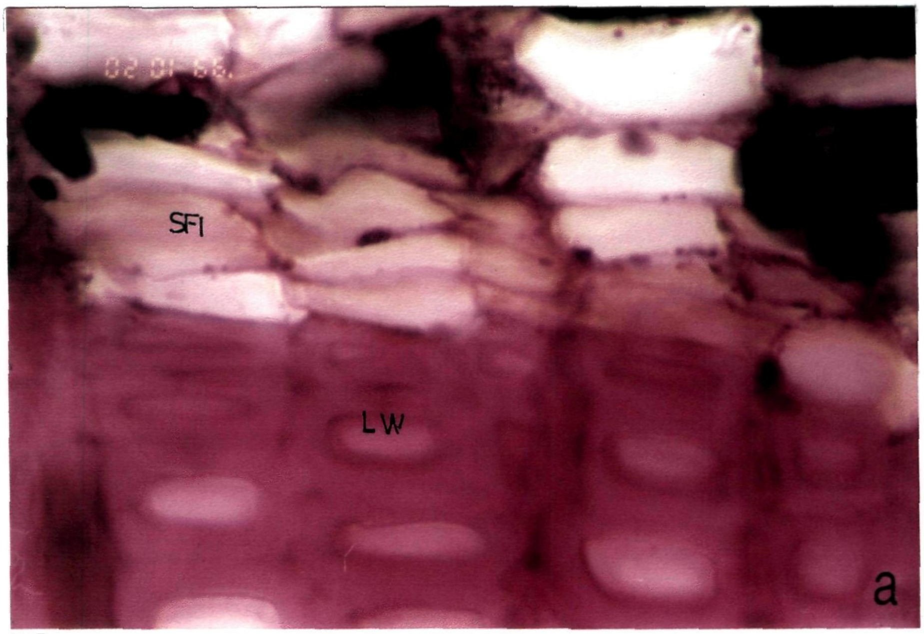
b. T.S. of vascular cambial zone (CZ) x 900.

PLATE - 4.8

Pinus kesiya Royle ex. Gordon.

Transverse Section

Dormant vascular cambium at the time of reactivation (February).



Active Vascular Cambium

PLATE-4.9

a. & b. T.L.S. of fusiform initials showing the multinucleate condition (MN) with many nucleoli (NUI). The shape and size of the nuclei verywith the active and dormant condition. a. x 800; b. x 2000

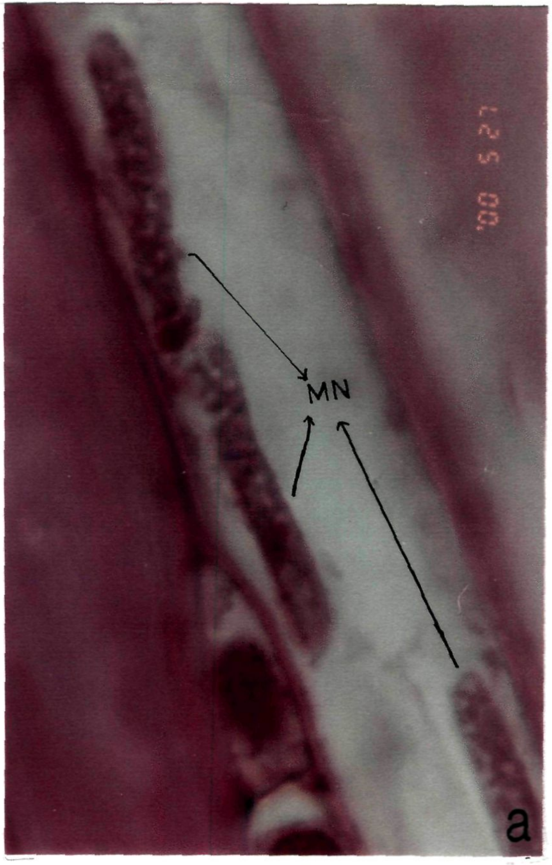
c. T.L.S of fusiform initial showing the cell plate formation (CP) during anticlinal division of fusiform initial. X 1000.

PLATE - 4.9

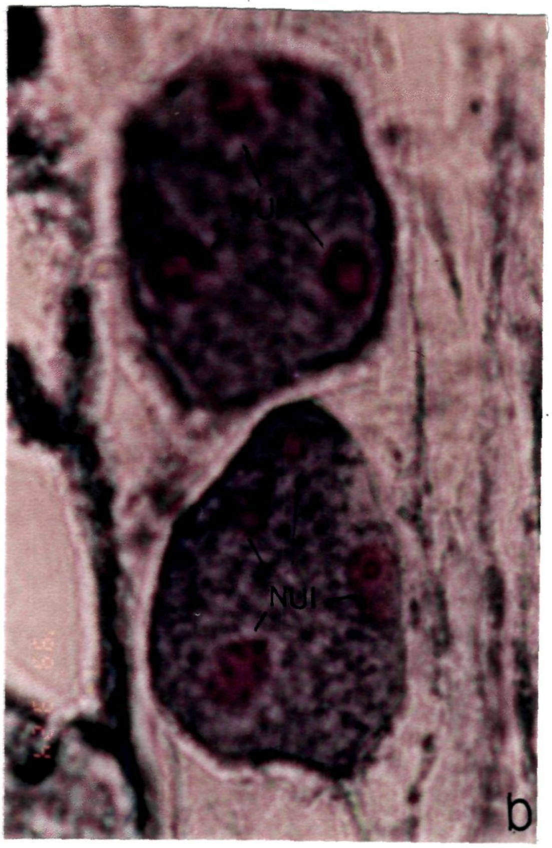
Pinus kesiya Royle ex. Gordon.

(Tangential Longitudinal section)

Elongated nuclei



Globular-ovoid nuclei with nucleoli



Anticlinal Division of Fusiform Initial

PLATE - 4. 10

a. T. S. of early wood (EW) showing the frequency of bordered pits (BP). x 950.

b. An enlarged portion of the T.S. of bordered pit (BP) showing the pit chamber , torus and margo x. 3800.

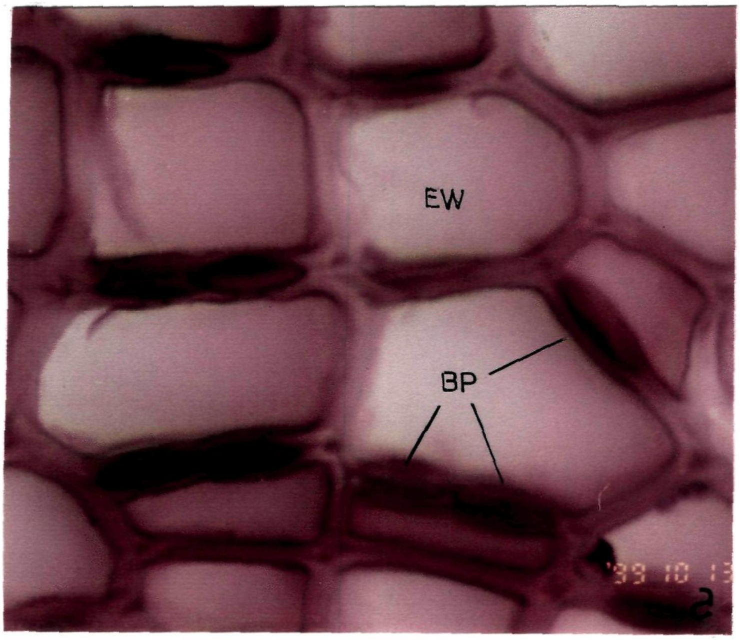
c. R.L.S. of tracheids showing the surface view of the bordered pit (BP) with torus and margo. Bars of Sanio (BS) also distinct inbetween the bordered pits x 400.

PLATE - 4.10

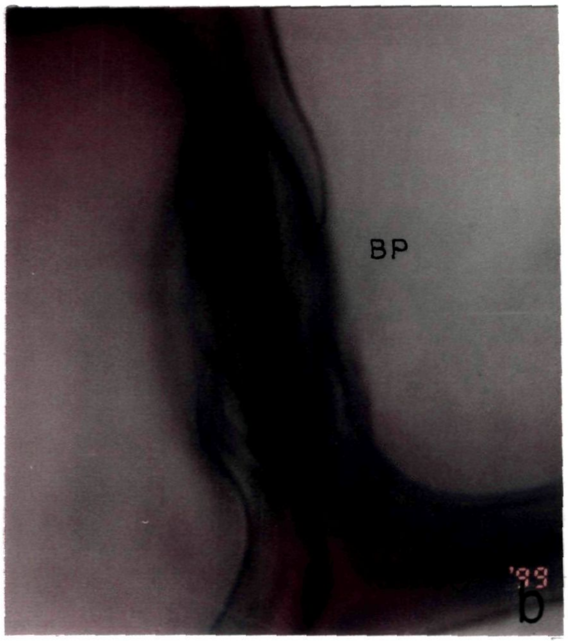
Pinus kesiya Royle ex. Gordon.

Structure of Early wood

Transverse section showing bordered pits



An enlarged view of bordered pit Showing pit chamber and torus.



Radial Longitudinal Section Tracheids showing Bars of Sanio in between Bordered pits

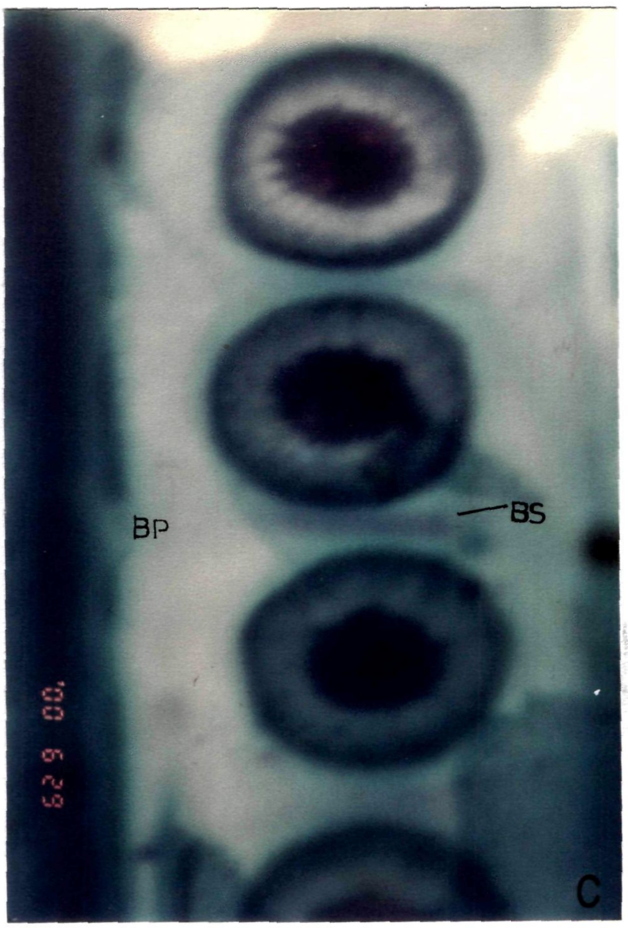


PLATE - 4.11

a. T.S. of wood with cambial zone (CZ). The three annual rings are distinctly marked by late wood elements (LW) and resin canals (RC). The proportion of early wood (EW) is more than the late wood(LW). x 100.

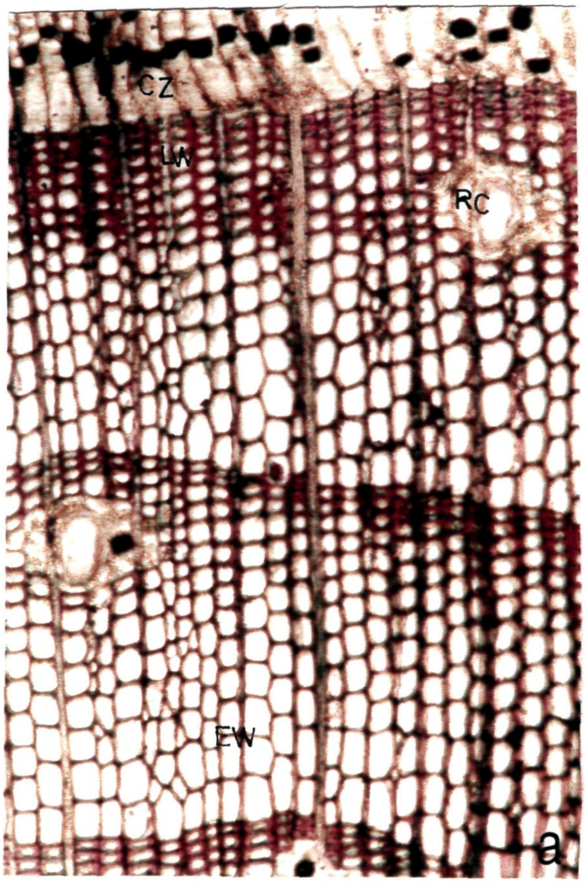
b. T.L.S. of bordered pits(BP). Note the torus closed the pitchamber . x. 1200.

C. R.L.S. of wood showing the distribution and frequency of bordered pits On the radial walls of tracheids (T) and xylem rays are homogenous type (XR), bars of Sanio (BS) are distinct. x 600.

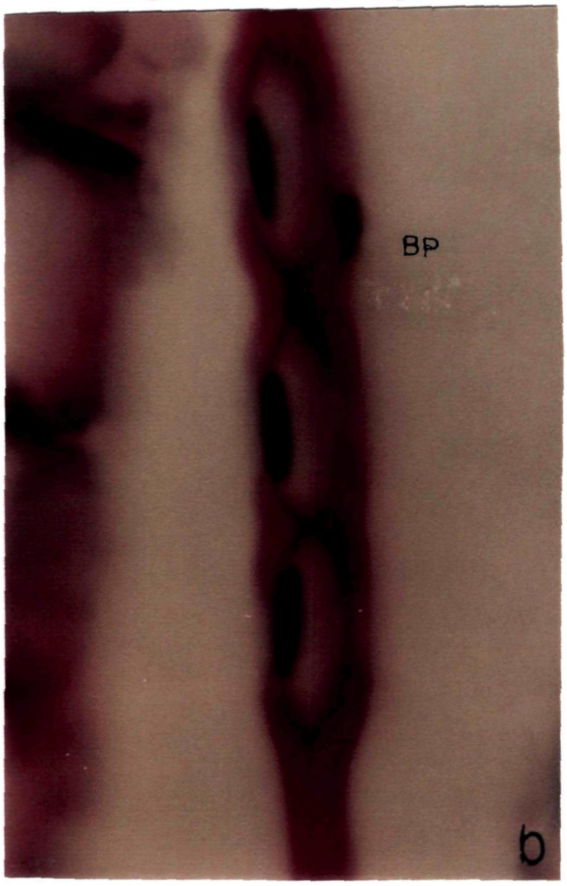
PLATE - 4.11

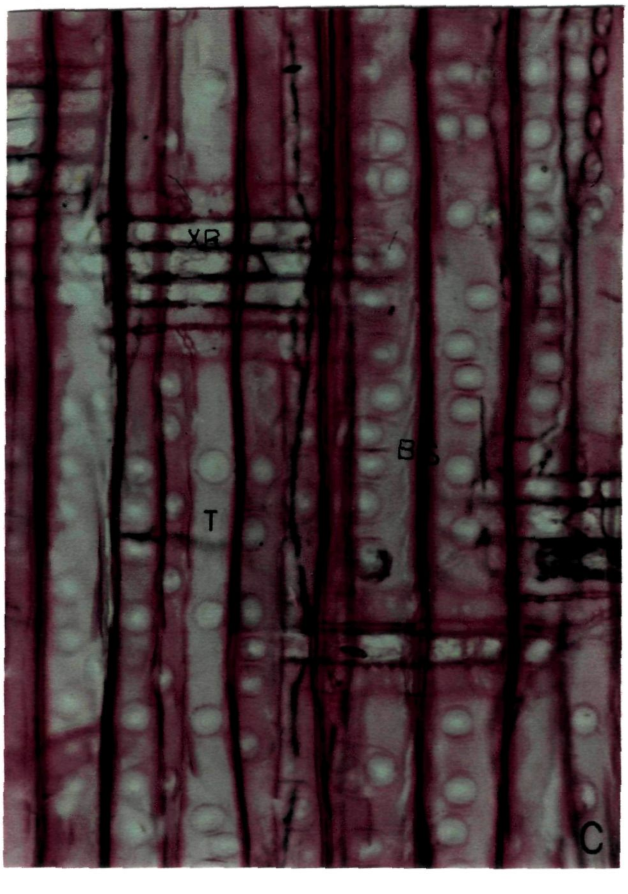
Pinus kesiya Royle ex. Gordon.

Transverse Section of Wood showing Distinct Annual Rings, Resin Canals



Tangential longitudinal section Showing Half Bordered pits and rays





Radial Longitudinal Section Showing bordered pits And Bars of Sanio.

CHAPTER-5

Vascular cambium: organization, activity and xylem production in relation to climatic factors and phenology in two Angiospermous trees viz. *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f.

Introduction

The two dicotyledonous trees *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f. constitute the major dominant species of sub-tropical wet forest regions in North East India (Brandis,1928). These two species also distributed both in the tropical and sub-tropical regions of India, Burma and South Africa, but the cambial activity and dendrochronological work on these two species have not been carried out so far, on those species growing in sub-tropical wet forest. As mentioned in chapter four, there are several investigations on tropical, arid and semi-arid regions. Knowledge of cambial activity and growth ring formation in trees is essential for determining the age and growth rate of trees in the natural forest stands. Relatively little is known about the patterns of growth periodicity and wood formation in sub-tropical wet forest trees. The growth in tropical trees may be annual, semiannual, irregular or continuous (Tomlinson and Longman 1981). According to Aljaro et al. (1972), cambial activity is genetically controlled, and its rhythm is determined by evolution under certain environmental conditions. Local environmental factors can markedly influence the initiation and cessation of cambial activity. As early as 1930, Priestly pointed out that the rhythmic activity of trees was changeable by external circumstances. The rate and duration of cambial activity varied in different forest types in relation to phenology and local environmental conditions (Borchart 1999; Fahn et al. 1981; Liphschitz 1995; Liphschitz and Lev-Yadun 1986; Liphschitz et al. 1985; Wilcox 1962; Zimmermann and Brown 1979).

As already stated, that the cambial activity and duration of xylem has not been investigated thoroughly in the sub-tropical wet forests of India, therefore, in this chapter two evergreen angiospermus trees viz. *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f. has been chosen for this study. It will add further information on the behaviour of cambial activity, structure and xylem production of sub-tropical wet forest type.

Phenology of *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f.

In *Michelia* and *Shorea* the first flush of vegetative bud initiation was seen during the first week of March. It was the most productive one resulting in sprouting of new leaves and young shoots. The process of formation of new foliage continued up to the end of October, of the growing season, in both plants. There was no specific period of leaf fall but a gradual senescence and abscission of older leaves were common during March to the end of May in both the plants. These evergreen trees belong to the vice-deciduous type of deciduous behaviour with minor modifications, where leaf abscission took place over a period of time but the trees begin to leaf out even before this period of abscission is completed (Koriba 1958). According to Longman and Jenik (1974) these two tree species belong to 'D' type of evergreen trees with continuous growth in which there is a continuous production and loss of leaves.

In *Michelia*, flowering was observed from May to June and in *Shorea* during March to April respectively. In *Michelia*, fruits started appearing in August and mature fruits were borne on trees during September to first week of October and seed dispersal took place at the end of October. In

Shorea, the mature fruits were seen in May to June and the winged seeds were dispersed during July to August Table 5.1.

Vascular Cambium: organization, activity and xylem production

In *Michelia*, during the most active period in the months of May, June and July, the cambial zone consisted of 6-10 layers as seen in Transverse section. The fusiform cells were arranged in regular radial files with narrow radial diameter and broader tangential diameter (Plate 5.1 a, b). The radial wall was much thicker than the tangential wall. Interspersed with the files of fusiform initials were files of multiseriate ray initials; uniseriate, biseriate ray initials were absent. An average of 2 oil cells per ray initial were observed in each multiseriate ray cells. For every three to four fusiform initial files, a ray initial file was seen (Plates 5.1 c). Active and dormant cambium of stem was shown in Plates 5.1 a, b, c; 5.2 a, b. During March the new flushes of foliage and buds took place which induced the cambial zone for reactivation. Even if there was no production of xylem in the months of March, the cambium was already undergone radial expansion and cell wall began to become thin.

Data pertaining with the size of fusiform initials and their derivatives are given in the Table 5.2, during different months of the year 1999-2000.

Table 5.1 Different phenophases of *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f. during the years 1999 - 2000.

Different phenophases	***Michelia champaca***	***Shorea robusta***
Formation of new leaves	March first week	March first week
Flowering	May to June	March to April
Fruiting	August to September	May - June
Seed dispersal	October end	July - August

Table 5.2 Average quantitative data of vascular cambial cells and their derivatives in *Michelia champaca* Gaertn.f. in different months of the years 1999 - 2000. (* For plotting the graph during November to January months the length of fusiform initials and tracheids has been used based on the average minimum values of the concerned dormant periods).

Months	Number of cambial layers in μm	Average Cambial zone width in μm	Average length of fusiform initial in μm	Average width of differentiating xylem zone in μm	Average length of xylem fibres in μm	Average length of vessel element in μm	Average radial width of vessel elements in μm
M	3-5	80.3 (5.2)	2540.0 (163.6)	60.5 (3.0)	2794.0 (181.6)	2153.4 (161.50)	385.8 (25.08)
A	3-5	80.2 (5.6)	2540.2 (165.1)	65.5 (3.9)	2794.2 (181.6)	2326.2 (151.20)	398.25 (23.89)
M	6-8	123.7 (6.9)	2960.4 (207.5)	80.1 (4.8)	3404.5 (138.3)	2325.8 (174.43)	430.80 (32.31)
J	6-8	123.7 (6.9)	2980.7 (200.8)	190.1 (7.6)	3404.8 (138.0)	2704.95 (229.92)	445.80 (37.89)
J	6-8	123.7 (6.9)	2962.4 (257.4)	197.5 (5.9)	3554.9 (213.2)	4998.95 (324.98)	484.05 (36.30)
A	5-6	118.2 (9.4)	2950.2 (254.1)	200.7 (11.0)	3392.7 (271.4)	3103.50 (263.79)	470.55 (30.58)
S	5-6	118.2 (9.4)	2950.0 (199.7)	193.2 (11.5)	3245.0 (243.3)	2766.60 (179.82)	453.75 (36.3)
O	3-4	70.5 (4.7)	2648.2 (225.1)	190.5 (5.7)	2913.1 (189.3)	2577.15 (193.28)	432.30 (36.74)
N	2-3	60.5 (4.5)	2487.2* (161.6)	0	2735.9* (316.5)	1947.0* (165.49)	426.0* (23.43)
D	2-3	60.5 (4.5)	2487.2* (161.6)	0	2735.9* (316.5)	1947.0* (165.49)	426.0* (23.43)
J	2-3	60.5 (4.5)	2487.2* (161.6)	0	2735.9* (316.5)	2277.0* (165.49)	426.0* (26.43)
F	3-4	70.75 (5.6)	2487.2 (110.5)	20.2 (0.6)	2686.1 (201.4)	2199.60 (142.97)	382.50 (33.27)

It is evident, that the cambium of *Michelia* is storied type and septate in nature (Plate 5.1 c). Similarly the fibres derived from the fusiform initials also showed the septation. The oils were also observed in the xylem rays (Plate 5.3 a, b).

The dormant period of the cambium of *Michelia* was observed during the months of November to February. During this period the vascular cambium consisted of 4-5 layers, so that the width of cambial zone was also reduced during the dormant period. The walls were highly beaded in nature and the cytoplasm appeared dense. The storage reserved food products appeared towards dormancy and the anticlinal divisions of fusiform initials was more prevalent (Plate 5.2 a, b).

In *Shorea*, the vascular cambium was non-storied and comprised of axially elongated fusiform initials and radially oriented ray initials. The ray initials were uniseriate and multiseriate. The cells of the ray initials were filled with resin and tannin contents. The fusiform initials were multinucleate (Plate5.5 a).

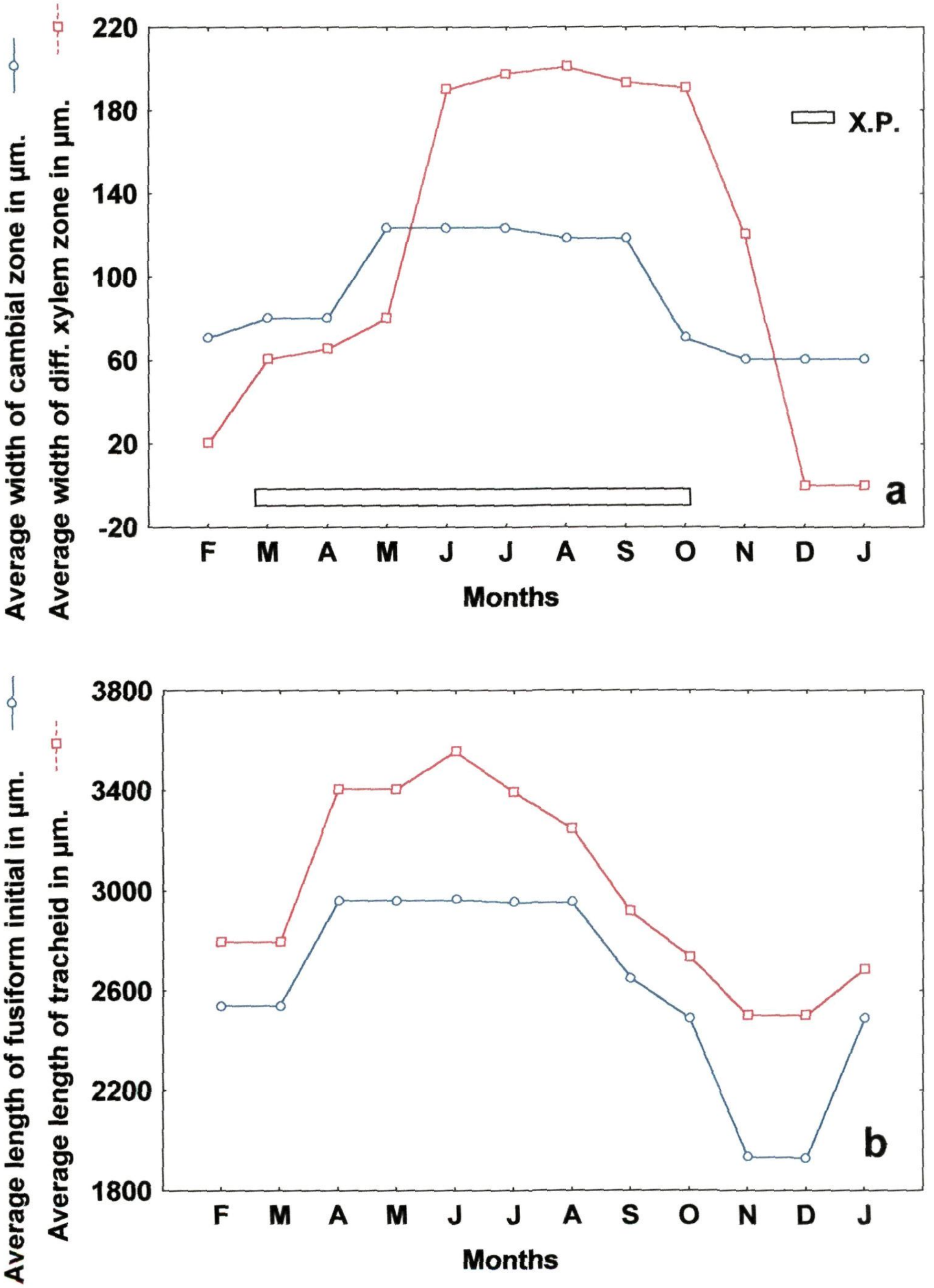
During the active period in March to October the cambial zone comprised of 8-10 layers and its radial width ranged from 150-125µm. The radial walls of fusiform initials were much thicker than the tangential

wall during active period. In active state, the frequency of periclinal division was also more than dormant state of the cambium (Plate 5.6 b, c). In the dormant period from November to February, the cambial zone consisted of only 4-5 layers and its width ranged from 75-80μm. The beads in the walls of fusiform initials were prominent and close with each other than the active cambium (Plate 5.5 a). Towards dormancy the frequency of the anticlinal divisions were more than the periclinal divisions.

Xylem structure and duration of xylem production

In *Michelia*, sap wood white; heartwood light yellowish brown, straight grained and medium textured. Growth rings distinct because of terminal parenchyma 1.5-4mm in width. Vessel elements 600 to 1200μm in length, medium to thin walled, with steeply oblique end walls, perforation plates scalariform, with 7-20 horizontal bars (Plate 5.3 c), 100-50μm in diameter, occasionally occluded with tyloses, thin walled; inter-vessel pits are mostly scalariform and horizontally oriented (Plate 5.4 b); pits adjacent to fibres and rays are half bordered, often confluent, more than 25μm in diameter. Parenchyma cells terminal, paratracheal, in cambiform rows of 7-9 cells in thick, dispersed along the grain, cells

Fig. 5.1 Average data of two years 1999-2000 of *Michelia champaca* Linn. X.P= xylem production, diff. = differentiating



In *Shorea*, growth rings wanting or scarcely distinct and approximately 8-10 per mm^2. Vessels elements large to medium sized (Plate 5.7 c), those of the heart wood occluded with tyloses and appearing light brown, exhibiting no variations in size indicative of seasonal increments, the majority of vessel elements are solitary or paired, occasionally several contiguous, quite evenly distributed, 5-9 per mm.^{2} (Plate 5.6 a, b) ; vessel elements are 400-550μm long, thick-walled, truncate or abruptly short-tailed, the largest 250-350μm wide; simple perforation plates, horizontal or nearly so; inter-vessel pits numerous, small, oval to orbicular, with wide border and linear-lenticular orifice, occasionally confluent, the long diameter 4-7μm (Plate 5.7 a); pits leading to contiguous rays several to each ray cell, rounded and variable in shape, with broad orifice with or without narrow semi border; tyloses very abundant, occluding all vessels in the heartwood, medium thick-walled, with simple pits.

Vesicentric tracheids sparse, paratracheal, intermingled with parenchyma and difficult to distinguish in the transverse section. Xylem parenchyma paratracheal (Plate 5.6 b), paratracheal-zonate, metatracheal, and surrounding all resin canals (Plate 5.6 b), in cambiform rows of usually 4 units along the grain which are sometimes divided further into locules containing solitary crystals.

Fibres libriform, fine, rounded in the transverse section and not aligned in radial rows, forming broad, nearly solid tracts between the vessels and the rays, non-gelatinous, non-septate, 1150-1800µm long, 15-25µm in diameter (Plates 5.6 a, b; 5.7 c); walls 6-10µ thick; inter-fibre pits simple, minute, with slit-like, nearly vertical orifices; lumina frequently plugged with reddish-brown gummy infiltration.

Rays not visible with naked eye, medium fine, medium close (5-7 per mm^2.) separated by 5-15 fibres, of the same colour, nearly homogeneous, the largest 65-80µm wide and up to 660µm height (Plate 5.7 b); pits leading to contiguous vessels several to each cell, rounded and variable in shape, with broad orifice with or without narrow border; reddish-brown gummy infiltration copious in the ray cells; crystals wanting; starch deposits not abundant (Plate 5.7 a, b).

Resin canals present, longitudinal, embedded in parenchyma, solitary or 2-3 contiguous, zonate in uniseriate tangential rows at irregular and often distant intervals, appearing as light lines with the naked eye that extend relatively long distances transversely and for indefinite distances along the grain (Plate 5.6 b).

As in *Michelia*, *Shorea* also produced xylem for a total period of eight months from March to October and during this period eight month; there is a marked increase in the number of cambial layers, cambial zone width, increased in the length of fusiform initials as well as its derivatives, fibres and vessel elements. All the data pertaining to the active period and dormant period are given in Table 5.3 and Figure 5.2 a, b.

Cambial activity and xylem production in relation to climatic factors.

In *Michelia champaca* the average width of cambial zone and monthly mean temperature showed a close relationship (r=+0.84) in the response function analysis (Fig. 5.3 a). The average length of fusiform initials also showed a very close relationship with monthly mean temperature (r=+0.91) (Fig.5.4 a). A similar response was observed in case of mean maximum and minimum temperature (Table 5.4). Whereas, a lesser relationship was observed between precipitation (r=+0.44) and relative humidity (r=+0.51) (see Table 5.4). The relationship between the average width of differentiating xylem zone as well as average length of xylem fibre also showed a very close relationship with monthly mean

Table 5.3 Average Qantitative data of vascular cambial cells and their derivatives in *Shorea robusta* Gaertn.f. in different months of the years 1999 - 2000. (* For plotting the graph during November to January months the length of fusiform initials and tracheids has been used based on the average minimum values of the concerned dormant periods).

Months	Number of cambial layers in µm.	Average Cambial zone width in µm.	Average length of fusiform initial in µm.	Average width of differentiating xylem zone in µm.	Average length of xylem fibres in µm	Average length of vessel element in µm	Average radial width of vessel elements in µm
M	3-5	78.25 (5.8)	1052.9 (89.4)	55.1 (1.7)	1158.2 (69.4)	446.1 (28.9)	290.15 (15.9)
A	3-5	78.20 (4.5)	1465.02 (117.2)	65.2 (1.9)	1507.3 (90.5)	448.5 (31.3)	340.1 (22.1)
M	5-7	119.50 (8.9)	1564.9 (133.02)	110.2 (4.4)	1799.6 (143.9)	510.6 (28.0)	352.5 (24.6)
J	5-7	119.50 (8.9)	1625.2 (130.02)	150.5 (4.5)	1869.1 (168.2)	518.1 (31.0)	419.7 (27.2)
J	6-8	122.3 (7.9)	1782.06 (124.7)	190.2 (6.0)	2138.4 (160.5)	612.6 (41.0)	455.1 (31.8)
A	6-8	122.3 (7.9)	1695.91 (135.6)	200.5 (6.3)	2035.1 (162.8)	562.5 (39.3)	387.9 (21.3)
S	5-6	117.5 (7.9)	1599.51 (135.9)	185.6 (7.4)	1839.4 (156.3)	498.8 (29.8)	267.9 (17.4)
O	5-6	117.5 (9.9)	1414.27 (106.7)	170.5 (5.9)	1555.6 (118.2)	479.4 (33.5)	267.8 (18.7)
N	4-5	82.2 (5.3)	1223.67* (97.89)	0	1346.1* (94.2)	453.3* (33.0)	250.2* (20.0)
D	3-4	73.2 (5.8)	1223.67* (97.89)	0	1346.1* (94.2	453.3* (33.0)	250.2* (33.0
J	3-4	7.2 (5.8)	1223.67* (97.89	0	1346.1* (94.2)	453.3* (33.0)	250.2* (33.0)
F	3-4	75.2 (5.8)	1007.75 (65.5)	20.0 (0.7)	1260.6 (100.8)	441.5 (31.1)	254.2 (17.7)

Fig. 5.2 Average data of two years 1999 - 2000 of *Shorea robusta* Gaertn. f. X.P= xylem production, diff. = differentiating.

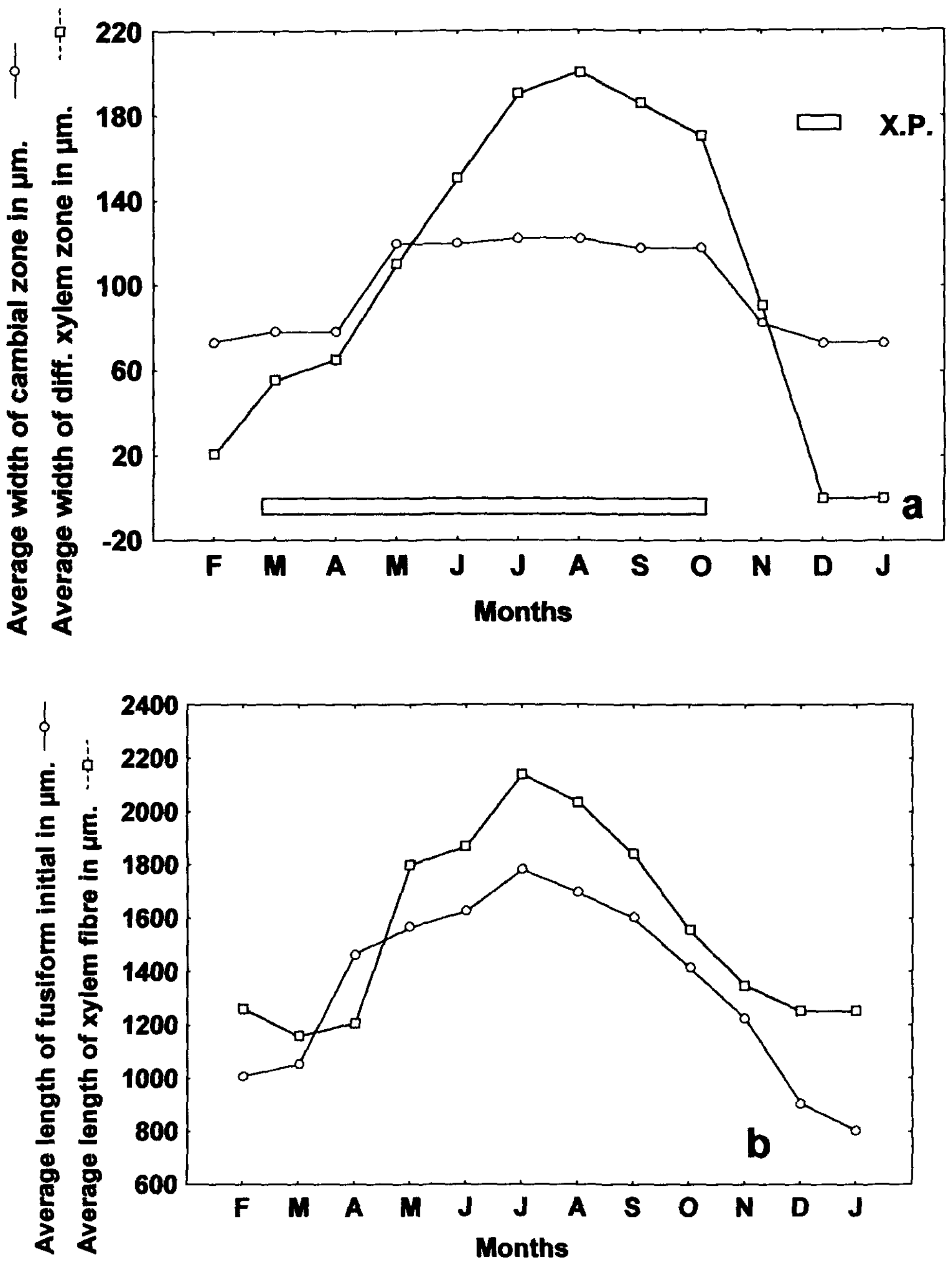
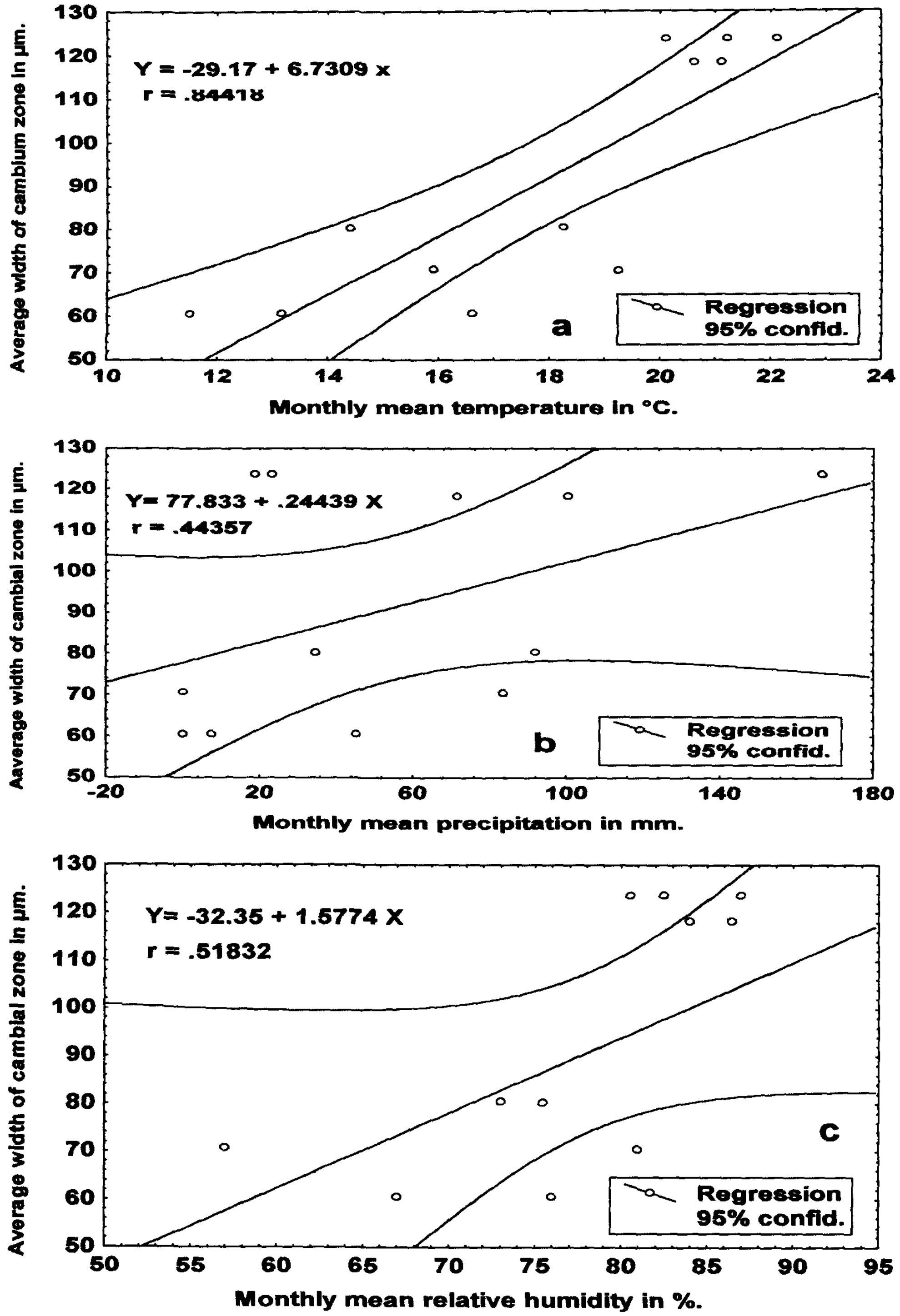


Table 5.4 Correlation coefficient values of cambium and its derivatives versus different climatic factors. All r values are significant at $p<0.05$ level in *Michelia champaca* Linn.

Anatomical variables.	Monthly mean temperature in °C.	Monthly mean maximum temperature in °C.	Monthly mean minimum temperature in °C.	Monthly mean precipitation in mm.	Monthly mean relative humidity in %.
Average width of cambial zone in µm.	0.84	0.83	0.84	0.44	0.51
Average length of fusiform initial in µm.	0.94	0.94	0.93	0.54	0.38
Average width of differentiating xylem zone in µm.	0.87	0.8	0.9	0.68	0.59
Average length of xylem fibres in µm.	0.91	0.83	0.92	0.57	0.53
Average length of vessel elements in µm.	0.59	0.52	0.62	0.82	0.39
Average radial width of vessel elements in µm.	0.91	0.9	0.9	0.65	0.39

Fig. 5.3 Regression line along with regression equation. r value is significant at $p<0.05$ level in *Michelia champaca* Linn.



temperature respectively (r=+0.87; r=+0.91) (see Table 5.4) (Fig 5.6 a & 5.5 a). The monthly mean precipitation and relative humidity responded very less with that of average width of differentiating xylem zone as well as the average length of xylem fibres (Table 5.4) (Figs. 5.5 b; 5.6 b, c). The correlation between the average lengths of vessels elements with monthly mean temperature was not high but the average width of vessel elements showed very good relationship (see Table 5.4). The correspondence was noticed between the precipitation and the average length of vessel element but a decreased relationship was observed regard to average width of vessel elements (Table 5.4). The fusiform initials underwent several transverse divisions to form vessel elements in the longitudinal axis. So that the length of vessel element did not give much significant relationship with mean temperature at the time of xylem differentiation. A very less relationship was observed in the case of monthly mean relative humidity with all the cambial elements and xylem elements in all the cases (see Table 5.4).

In *Shorea robusta* also the mean temperature showed better relationship with the average width of cambial zone than the mean precipitation and mean relative humidity (Fig. 5.7 a, b, & c). The average

Fig. 5.4 Regression line along with regression equation. r value is significant at p<0.05 level in *Michelia champaca* Linn.

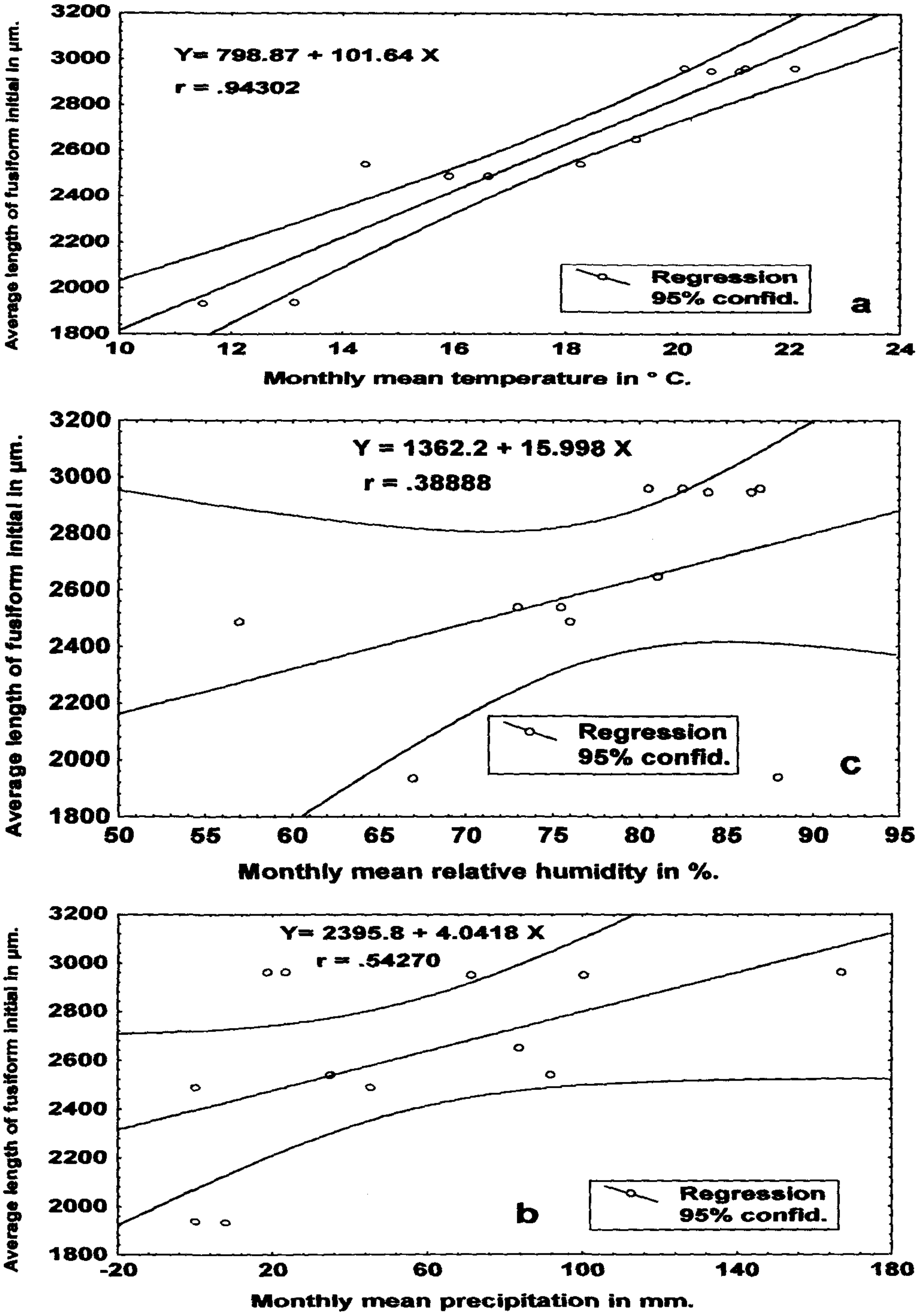


Fig. 5.5 Regression line along with regression equation. r value is significant at $p<0.05$ level in *Michelia champaca* Linn. diff= differentiating

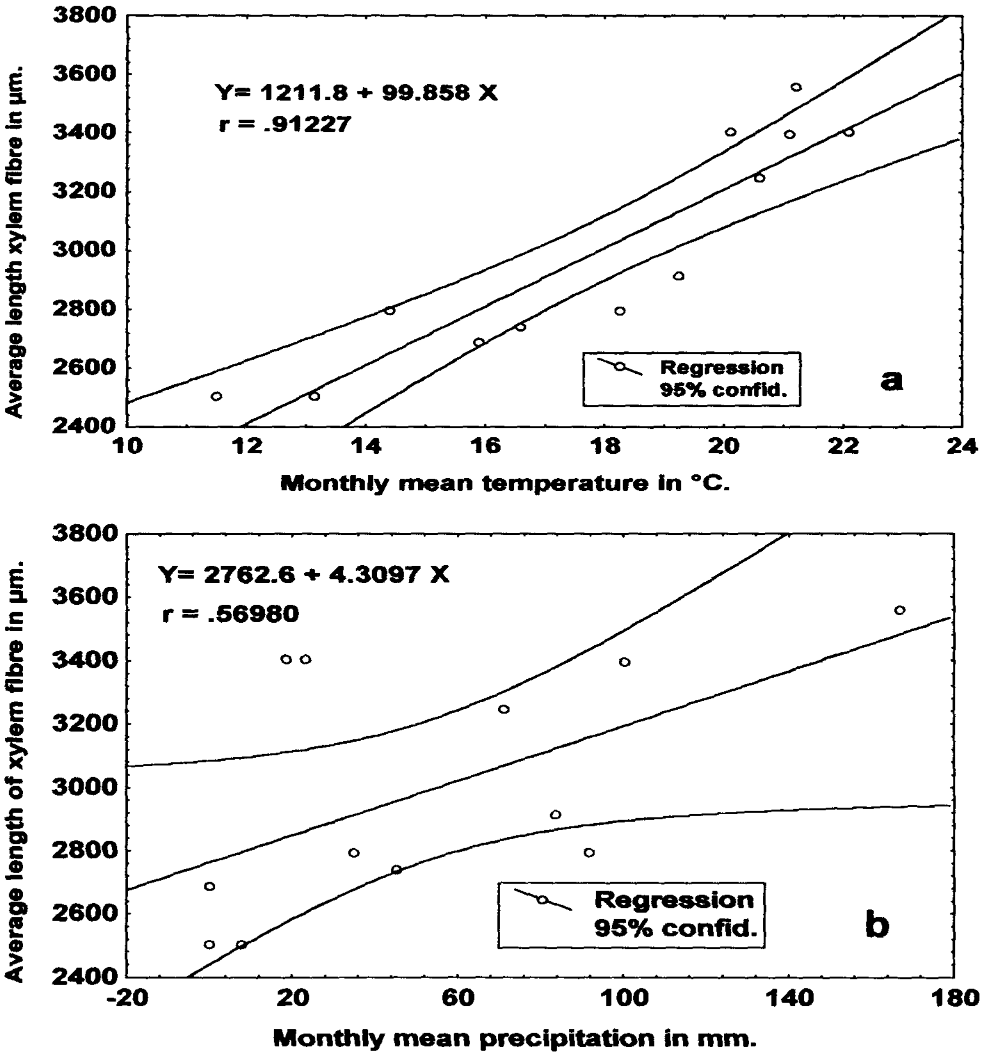


Fig. 5.6 Regression line along with regression equation. r value is significant at $p<0.05$ level in *Michelia champaca* Linn.

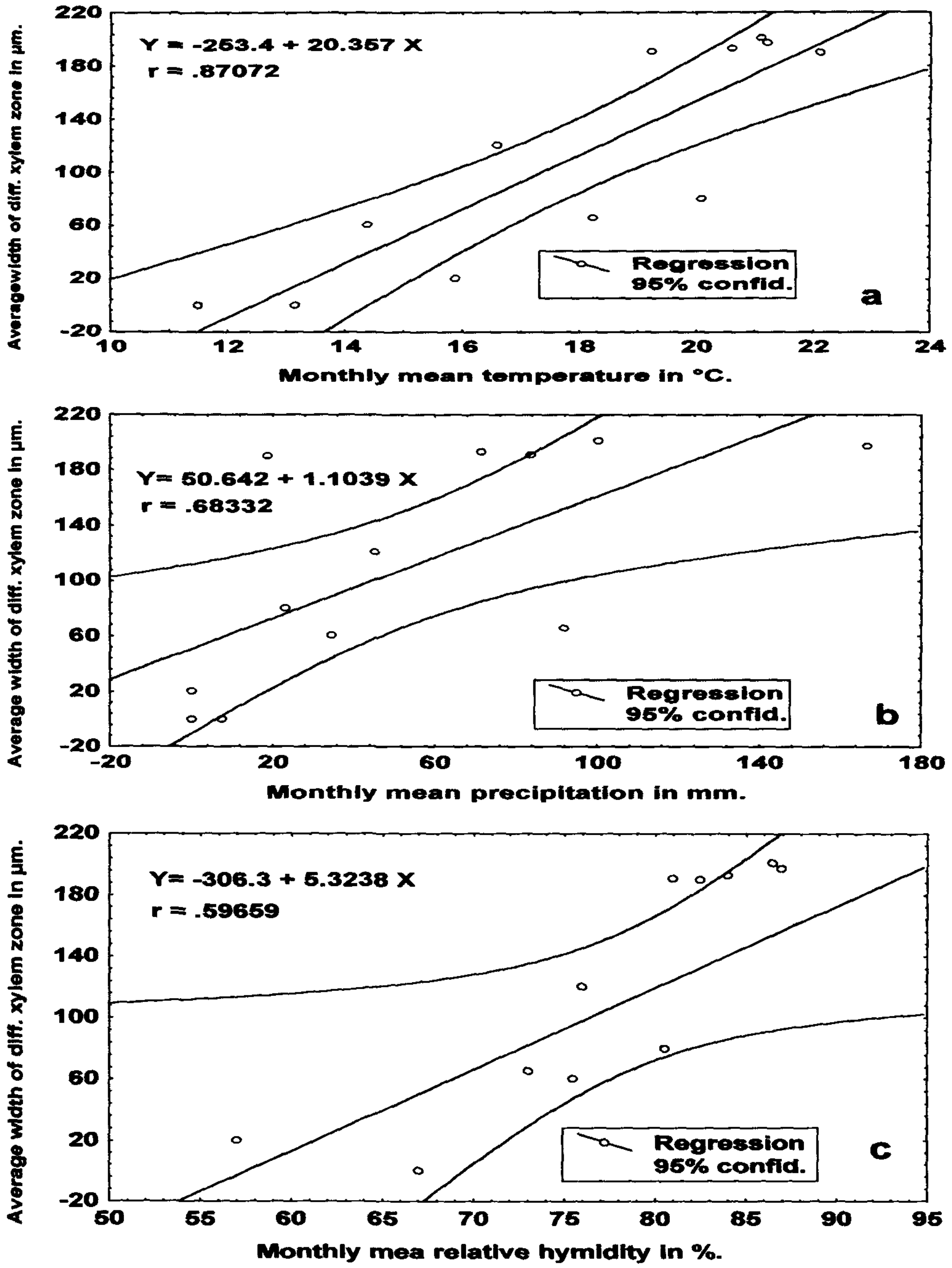
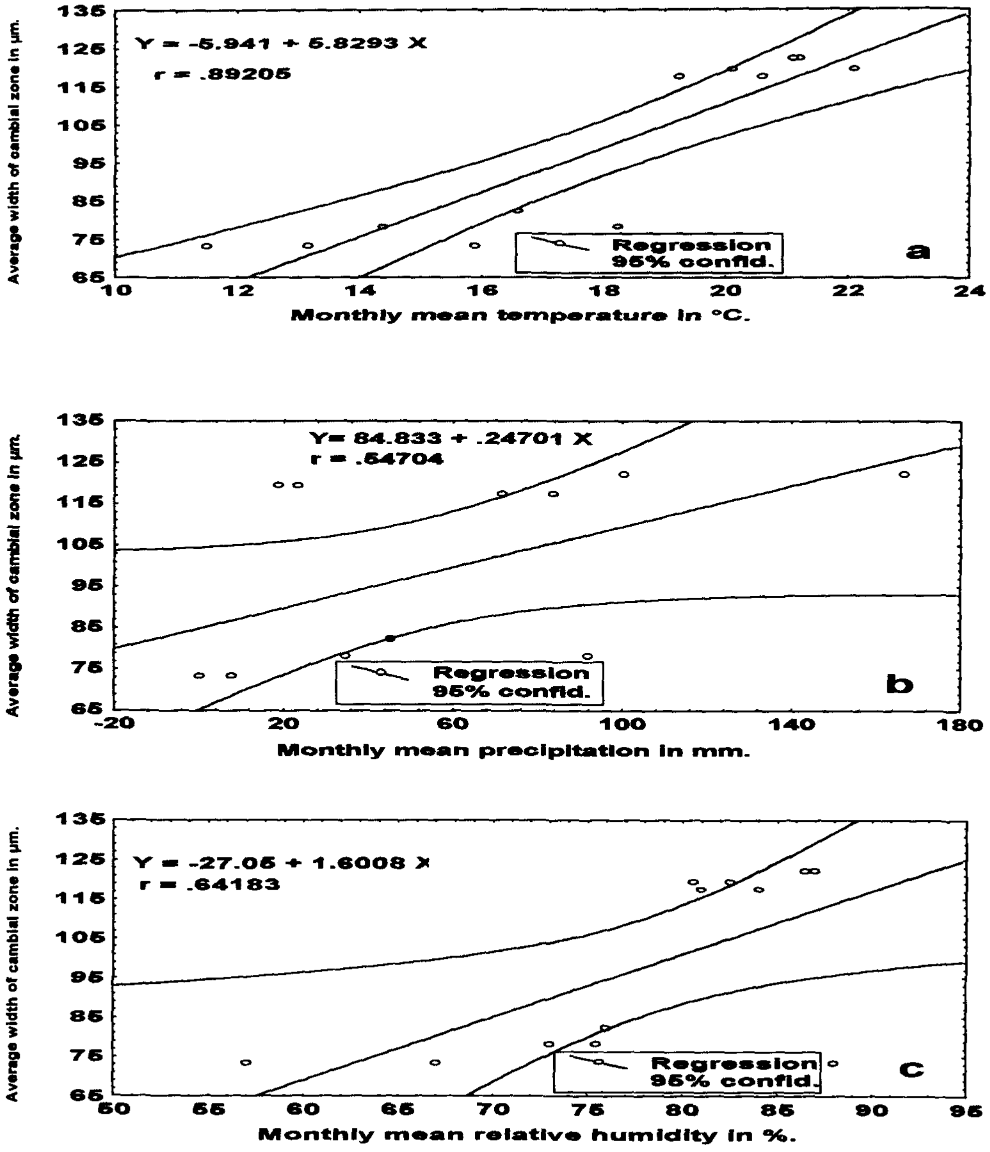


Fig. 5.7 Regression line along with regression equation. r value is significant at $p<0.05$ level in ***Shorea robusta*** Linn.



length of fusiform initials showed a much higher relationship with mean temperature (Fig. 5.8 a) and a similar trend was observed with monthly mean maximum and minimum temperature (Table 5.5). Monthly mean precipitation and mean relative humidity showed a lesser relationship with average length of fusiform initial (Fig. 5.8 b, c). Similarly, the average width of differentiating xylem zone showed a good relationship with monthly mean temperature indicating the influence of temperature in xylem production (Fig. 5.10 a). A similar trend was observed between the wide of differentiating xylem zone as well as length of xylem fibres and the mean maximum and minimum temperature but a lesser relationship was observed in the case of precipitation and relative humidity (Figs. 5.9 a, b, c; 5.10 b and Table 5.5). The monthly mean maximum and minimum temperature revealed more or less similar influence (Table 5.5). Whereas, the average length and width of vessel elements showed a similar correlation value with monthly mean temperature and monthly mean maximum and minimum temperature (see Table 5.5). Whereas, the average length of vessel elements showed a good relationship with monthly mean precipitation but average width of vessel elements showed less relation (Table 5.5) as in the case of *Michelia*.

Table 5.5 Correlation coefficient values of cambium and its derivatives versus different climatic factors. All the r values are significant at p<0.05 level in *Shorea robusta*

Anatomical variables.	Monthly mean temperature in °C	Monthly mean maximum temperature in °C	Monthly mean minimum temperature in °C	Monthly mean precipitation in mm	Monthly mean relative humidity in %
Average width of cambial zone in μm.	0.89	0.83	0.91	0.54	0.64
Average length of fusiform initial in	0.97	0.97	0.93	0.71	0.57
Average width of differentiating xylem zone in μm.	0.9	0.83	0.93	0.72	0.6
Average length of xylem fibres in μm.	0.93	0.78	0.87	0.63	0.39
Average length of vessel elements in μm.	0.77	0.7	0.81	0.73	0.53
Average radial width of vessel elements in μm.	0.72	0.7	0.73	0.53	0.46

Fig. 5.8 **Regression line along with regression equation. r value is significant at $p<0.05$ level in *Shorea robusta* Linn.**

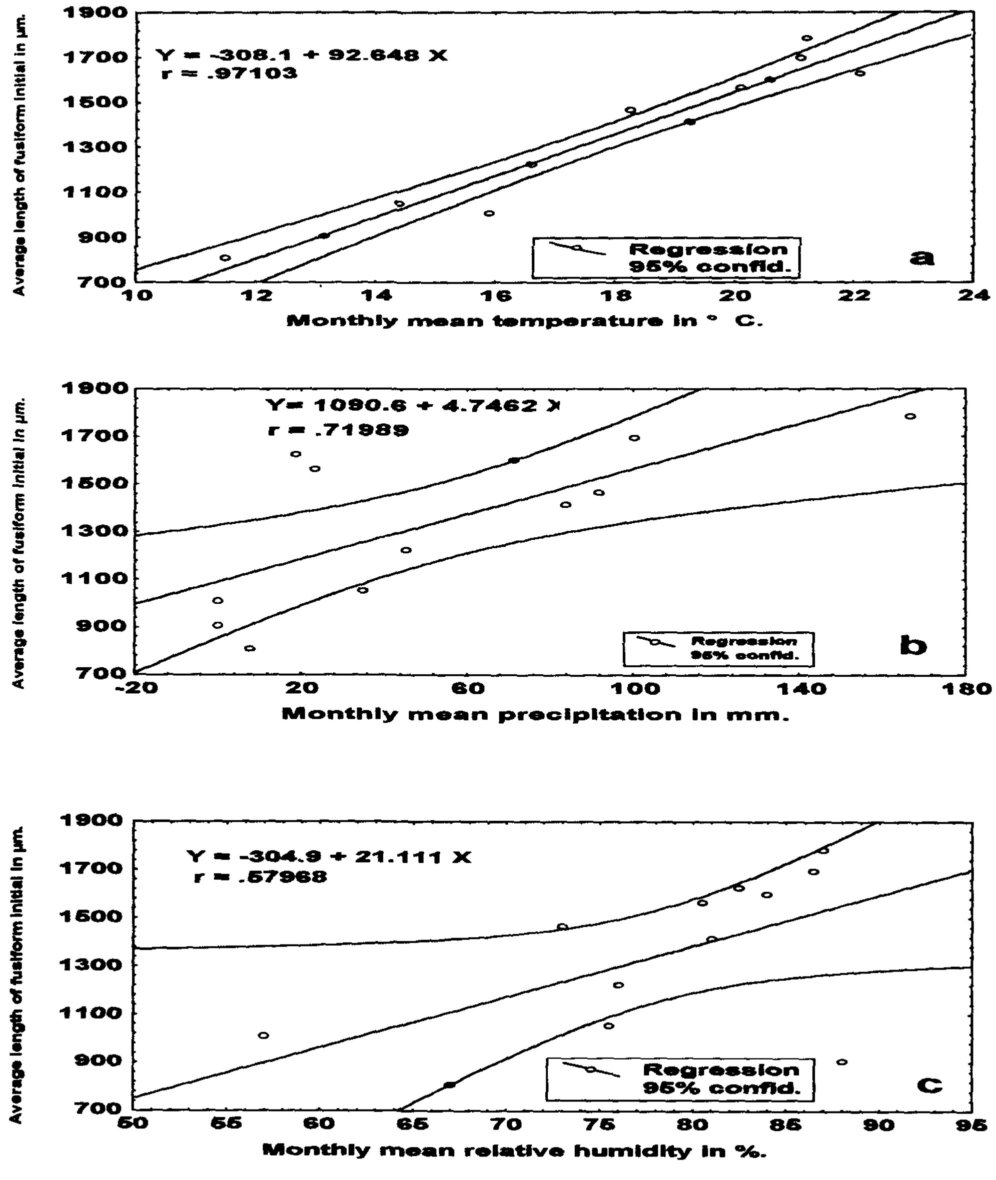


Fig. 5.9 Regression line along with regression equation. r value is significant at $p<0.05$ level in *Shorea robusta* Linn.

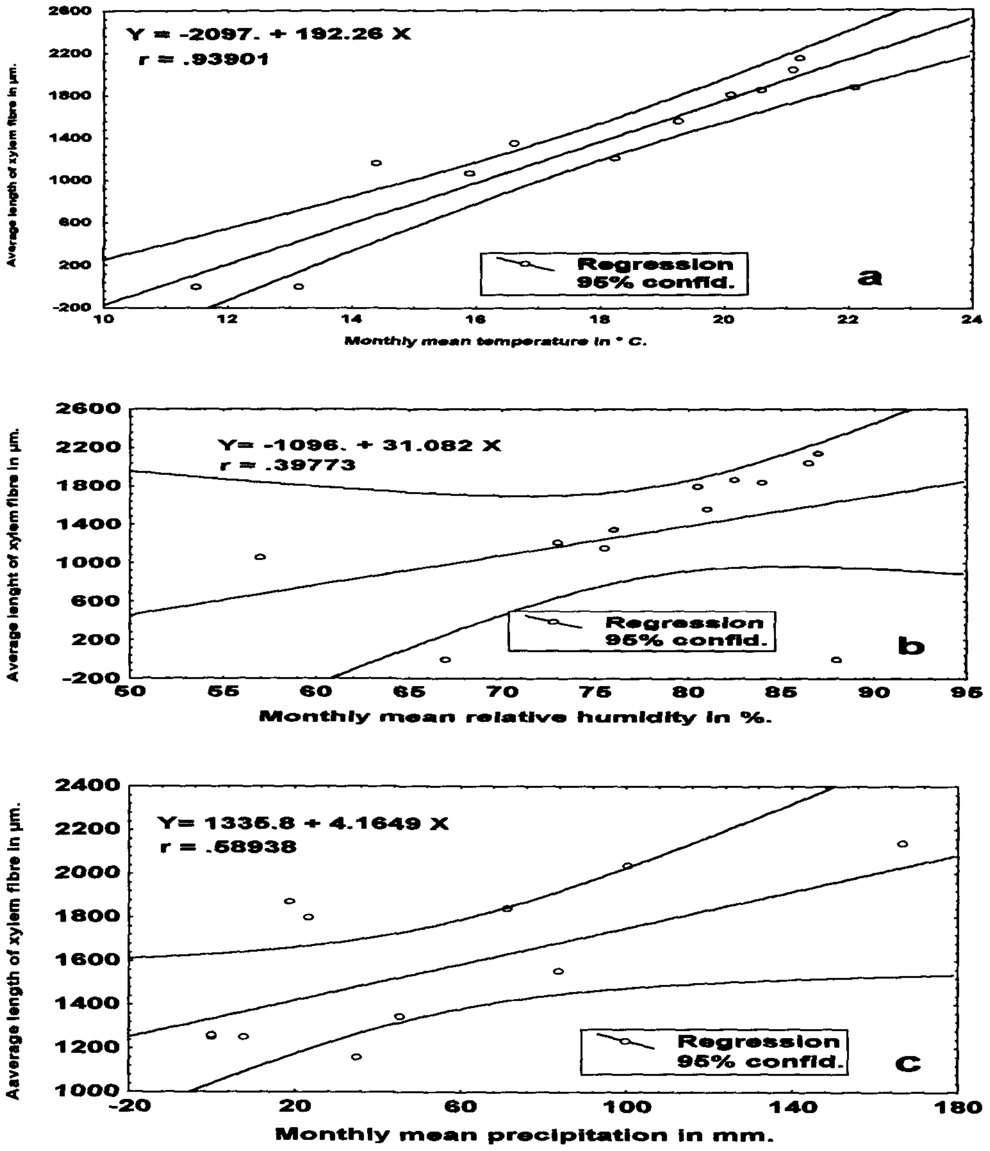
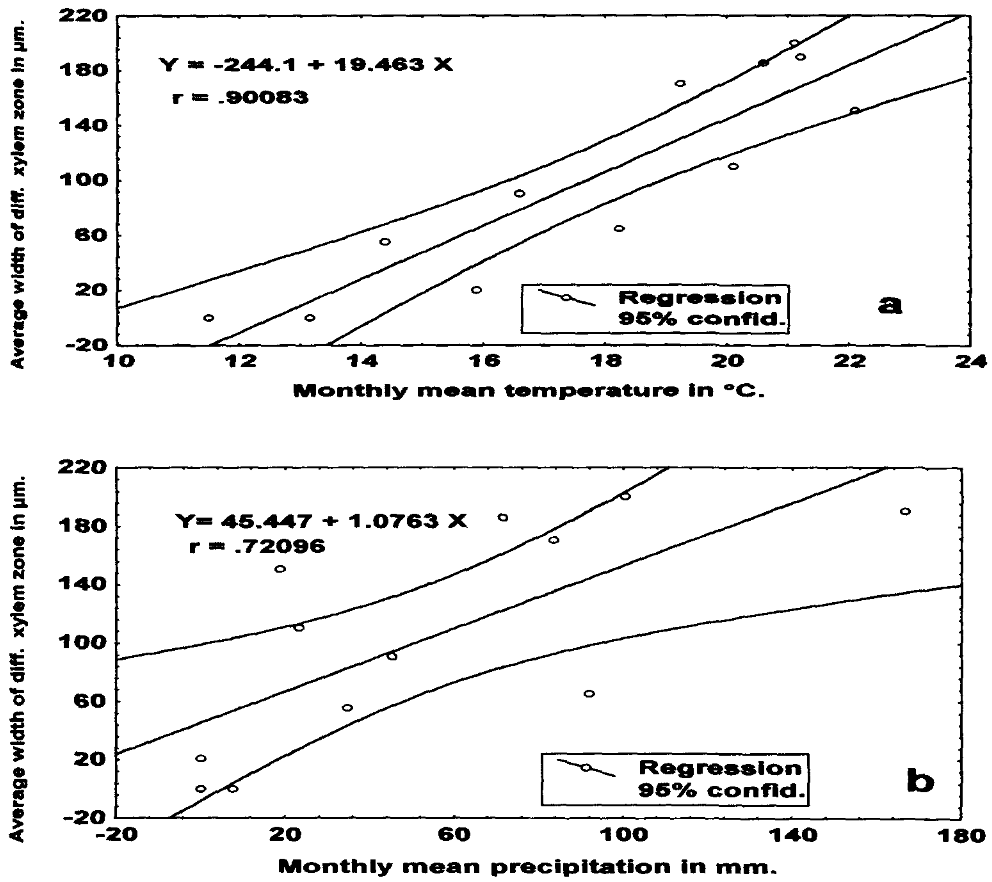


Fig. 5.10 Regression line along with regression equation. r value is significant at $p<0.05$ level in ***Shorea robusta*** Linn. diff= differentiating



Discussion

A survey of literature reveals that the cambial structure has not been described in *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f. growing in sub-tropical wet forest of North east India. That the relationship exists between bud break and cambial activity in conifers and dicotyledons normally starts at the base of the apical bud. A close association between cambial activity and new leaf formation was recorded in many forest trees of the tropical and sub-tropical belts (Iqbal and Ghause 1985a; Iqbal 1990; Paliwal and Paliwal 1990). The present investigation on *Michelia* and *Shorea* revealed that the close relationship existed between the new leaf formation and cambial reactivation during the month of March. The further continued activity of cambium was seen up to October end in both the plants irrespective of the different phenophases of trees. The timing of vegetative bud break, different phonological events, initiation of cambial activity in *Michelia* and *Shorea* are shown in Table 5.1 and Figures 5.1 and 5.2. Amobi (1974), also observed that the cambial cells of the internode nearest to the unfolding bud started expanding after bud break. In these two trees xylem differentiation and formation of new vegetative buds took place simultaneously. The same rhythm of activity was recorded in tropical trees like *Delbergia*, *Terminalia* and *Morinda* (Venugopal and Krishnamurthy 1987).

In *Michelia* and *Shorea* the three events viz. cambial activity, xylem differentiation and formation of vegetative buds took place simultaneously. Ghouse and Hashmi (1979) also reported this type of behaviour in *Polyalthia longifolia.* Amobi (1974) recorded that inflorescence induced wood formation in *Hidelgardia barteri* during leaf flush period. But in the present study on *Michelia* and *Shorea*, these plants are evergreen so that the plant never becomes leafless. The flowering and fruiting were seen at the peak period of cambial activity and xylem production in *Michelia* and *Shorea*, so the effect of flowering on wood formation and intensity of cambial activity was not clear in the present study.

In tropical trees there are conflicting reports on growth periodicity with regard to absence or presence of growth rings (Wilcox 1962; Alvim 1964). Chowdhury (1961) recorded 25% of forest trees in India showed distinct growth ring, where diffuse porous species accounted for over 90% of all woody dicotyledons (Chowdhury 1939). Of the two tree species studied here, *Michelia* and *Shorea* wood are of diffuse porous type. Growth periodicity was observed in both the plants. Production of xylem in *Michelia* and *Shorea* has been recoded once in a year from March to October without any gap. However, Lipschitz et al. (1981) reported two flushes of xylem production in *Cupressus sempervirens* growing in the Mediteranian climate. Fahn (1958) has also reported two installments of xylem production in *Tamaris*. Multiple xylem ring formation in correspondence with the number of bud breaks within a growth period was reported in many tropical plants (Amobi 1972; Tomlinson and Craighead 1972; Venugopal and Krishnamurthy 1987). Rao and Rajput (2001) observed single growth ring formation in *Acacia nilotica* (L.) Del. growing in dry deciduous forest even though these trees produced new leaves twice in a year. Whereas anatomical features such as presence of initial and terminal parenchyma, radially compressed xylem fibres and low frequency of vessel elements in the late wood are used to demarcate growth rings in tropical woods (Chowdhury 1964, Carlquist 1980). According to Chowdhury (1964) all these tropical plants were terminal parenchyma has been reported, though in fact only initial parenchyma. Initial parenchyma and radially compressed late wood xylem fibres/elements characterized growth periodicity (annual ring in *Michelia* and *Shorea*).

The organization of vascular cambium and wood structure in *Michelia champaca* and *Shorea robusta* have been described (Kumar & Dutta (1989); Yadav & Bhattacharya 1989). Fujii (1999) studied the growth periodicity in relation to the xylem development in three *Shorea* species growing in Sarawak, this study showed the similar pattern of growth and xylem production as in *Michelia* and *Shorea* growing in sub-tropical wet forest of North-East India, but there were variations only with reference of dimensions of fusiform and ray initials. In *Michelia* the vascular cambium was storied. It has been an established fact that the storied cambium was gradually derived from non-storied cambial type (Philipson et al. 1971). The difference in range may be due to the age of the material selected for examination. It has been already established that the length of fusiform initial increased with the age of the cambium (Carlquist 1975).

The most characteristic feature of the radial walls of the fusiform initials was their beaded nature. This fact was observed by Bailey (1930). He attributed the beadings was due to the unequal thickening of potions of radial walls, a fact confirmed by the present study in *Michelia* and *Shorea*. A careful review of previous literature and illustrations provided therein revealed that true fusiform initial were, in fact, characterized by beaded radial walls (Evert & kozlowski 1967; Paliwal & Prasad 1970; Ghouse & Yunus 1974; Goosen de Roo & Van Spronsen 1978; Timell 1980, Venugopal & Krishnamurthy 1987). In the present study in *Michelia* the presence of oil cells in vascular cambium especially adjacent to the ray initials was recorded for the first time.

In earlier literature one or more of the following changes have been recorded in the cambium during reactivation from dormancy: 1. Increase in the number of cell layers in the cambial zone. 2. Swelling of cambial cells. 3. Increased vacuolation of the cytoplasm of fusiform initials. 5. Clearing of cytoplasm and decrease in storage substances. 6. Elongation of fusiform initials. 7. Thinning of radial walls. 8. Wider separation of beads on the radial walls of fusiform initials and 9. Onset of periclinal divisions leading to the formation of secondary xylem and phloem. All the above changes were noticed during cambial reactivation in *Michelia champaca* and *Shorea robusta*.

Swelling of fusiform initials and consequently the sudden increase in the width of cambial zone was recognized as the first sign of cambial reactivation in many plants (Catesson 1974; Dave & Rao 1982a, b) and this has been confirmed by the present study. Even in cases where swelling was not apparent, the individual cambial cells underwent expansion before dividing periclinally (Savidge & Wareing 1981).

Many investigators have considered the number of layers in the cambial zone as the most reliable criterion to distinguish cambial dormancy, reactivation and peak activity (see Rao & Dave 1981), a fact also supported by the present study on *Michelia* and *Shorea.* The cambial zone contained fewer layers (2-3) during dormancy than during the active phase (Timell 1980). The dormant cambium of materials investigated here contained invariably 4-5 layers, while at peak activity up to 6 to 8 layers and sometimes 10 layers were noticed as in *Michelia* and *Shorea.* The maximum number of layers recorded elsewhere was 24 in *Tectona grandis* (Rao & Dave 1981). The difference in the number of layers during peak activity appeared to be the age of the material examined, older ones showing greater number of cell layers than young twigs (see also Rao & Dave 1981; Dave & Rao 1982b; Krishnamurthy & Venugopal 1983).

Schacht (1856) was perhaps the first to report multinucleate condition in fusiform initials. This followed by the similar report of Russow (1882) in some pines. Strasburger (1891) and Bailey (1920) questioned this and stated that these two reports were due to erroneous observation. Subsequently Patel (1975) in *Solanum melongena*, Ghause & Khan (1977) in *Psidium guava*, Hashmi & Ghause (1978) in *Polyalthia longifolia* and Dave & Rao (1981) in *Tectona grandis* and in several tropical plants like *Albizzia lebbeck*, *Dalbergia sisoo*, *Tectona grandis*, *Terminalia crenulata*, *Mangifera indica* and *Morinda tinctoria* (Venugopal & Krishnamurthy 1989) conclusively established the occurrence of the multinucleate condition.

In addition to confirming the multinucleate condition of *Tectona grandis*, the present study on *Michelia* and *Shorea* recorded the multinucleate condition in this two species (1-4 nuclei/cell). While details could not be obtained regarding the maximum number of nuclei in a single fusiform initial in plants studied by Schacht (1856) and Russow (1882), recent authors reported the following numbers: *Solanum melongena* 2-5 (Ghouse & Khan 1977), *Polyalthia longifolia* up to 5 (Hashmi & Ghouse 1978) and *Tectona grandis* 1-5 (Dave & Rao 1981).

It is difficult to explain the purpose of multinucleate condition in the fusiform initials. Probably it has no significant in view of the fact that the immediate derivatives formed by both additive and multiplicative divisions of fusiform initials always have a single nucleus. Much more intensive studies are necessary to understand this phenomenon.

There are some data in the literature regarding the duration and rate of xylem production (Artschwager 1950; Bannan 1955; Ghouse and Hashmi 1978; Grillos & Smith 1959; Wilson 1963; Waisel et al. 1966; see also Kozlowski 1971; Rao and Rajput 2001, Pumijumnong 1999; Fujii 1999, Priya & Bhat 1999) both these being subject to variation even within the same plant but depending on environmental conditions (Fahn et al. 1968). Periodicity of cambium and xylem production is controlled by various environmental and physiological factors (Kramer and Kozlowski 1979, Ajmal and Iqbal 1987, Larson 1994 Rao and Rajput 1999). The effect of temperature is considered as a factor of primary importance for reactivation of cambium following its effect on bud break and subsequent shoot growth (Kramer and Kozlowski 1979). All these authors have only commented on the differentiation of wood elements in general. These different elements of xylem are not differentiated simultaneously but at different times within a single flush of cambial activity. There are three types of differentiation of wood elements: 1) production of mainly fibres, 2) of mainly vessel elements, 3) simultaneous productions of fibres and vessel elements. The third type characterizes the wood of *Michelia* and *Shorea*. It was found that the vessel elements in *Michelia* and *Shorea* were shorter than the fusiform initials. The xylem fibres were always longer than the fusiform initials.

The present study also indicated the potentiality of using the variation in the length and diameter of different elements of woods, for recognition of periodicity in xylem production. Though this character was suggested by Swami et al. (1960), this has not often been used because of the time involved in computing length data, whereas the other characters can be used without difficulties since transverse sections are often sufficient. Shorter elements characterize the end of xylem productions while the longer elements marked the peak period of cambial activity and xylem production. Similarly the diameter of wood elements was greater during the periods when their production is at its peak end and was minimum during lest activity of cambium. An analysis of the earlier literature reveals that this is the trend shown by the largest number of plants studied (see also Taylor 1976) although the presence of longer late wood fibres has been recorded in certain temperate trees (Bisset and Dadswell 1950; Panshin and De Zeeuw 1980).

The deposition of and depletion of starch grains and crystals in undifferentiated and partially differentiated xylem tissue adjacent to the cambium during dormancy and cambial reactivation respectively need to be explained. Probably starch and crystals of calcium formed the source materials for new cell wall synthesis (probably carbohydrates and calcium pectate) when the cambial derivatives are rapidly produced. Davis (1961) also reported the possible usage of calcium oxalate crystals during the development of the embryo in *Podolepis jaceoides*; she reported that their appearance and disappearance from integumentary tapetum is related to the calcium requirements of the growing embryo. Riding and Little (1984) observed maximal and minimal starch content in the xylem of *Abies balsamea* associated respectively with the period of cambial dormancy and reactivation (see also Amobi 1973; Sauter 1966; Parker 1960; Pomeroy and Siminovitch 1971; Tsuda and Shimaji 1971; Essiamah and Eschrich, 1985).

In both the *Michelia* and *Shorea* temperature showed much more influence than precipitation and relative humidity when regression analyses was performed taking the anatomical variables as response and climatic variables as predictors. As the temperature rise up from February to March the reactivation of cambium starts and reaching a peak activity during May to August. As the temperature goes down its effect to cambial activity was also reduced and cessation of cambial activity started. Whereas precipitation and relative humidity showed less significant as moisture stress is not observed in this region of sub-tropical wet forest of North-East India.

PLATE-5.1

a. T.S. of active cambial zone (CZ) with differentiating xylem. Cambium consists of 8-10 layers, vessel elements (VE) and xylem rays (R). x 200.

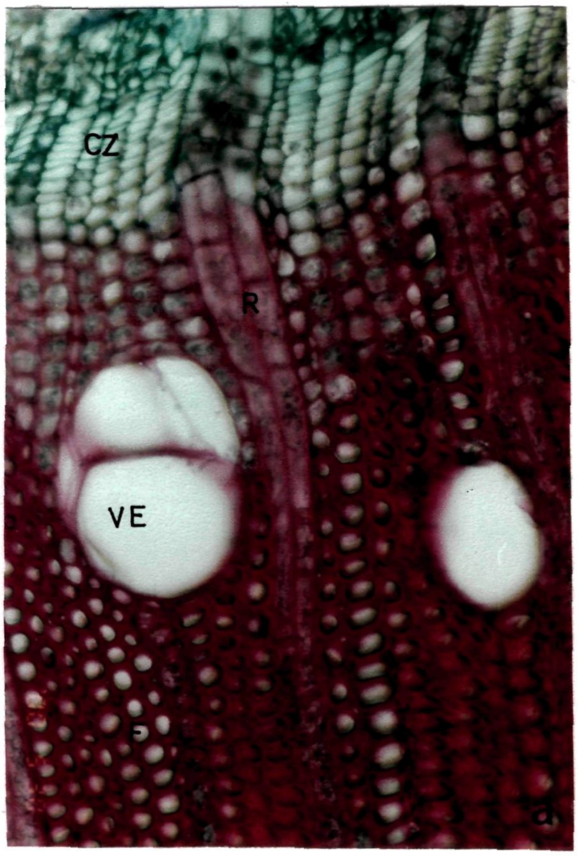
b. An enlarged portion of reactivated cambial zone (CZ) and disappear. differentiating xylem zone (DX). Note the starch grains started to disappear. x 650.

c. T.L.S. of active cambium with multinucleate fusiform initials (FI) and ray initials (RI). The differentiating xylem elements (DX) are at the left hand side. Oil cells are prominent. x 180.

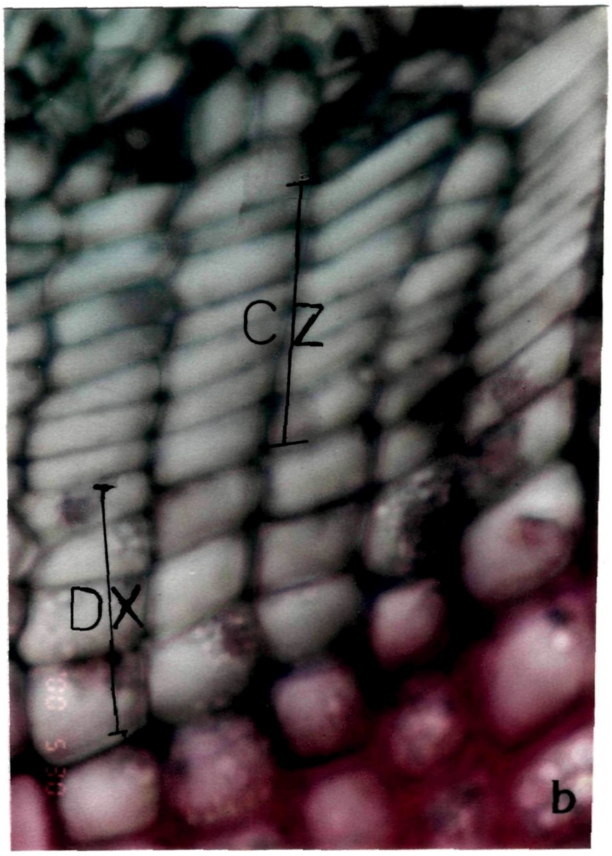
PLATE - 5.1

Michelia champaca Linn.

Active Vascular Cambium with Differentiating Xylem



An Enlarged View of Active Vascular Cambial Zone



Tangential Longitudinal Section of Wood

PLATE - 5.2

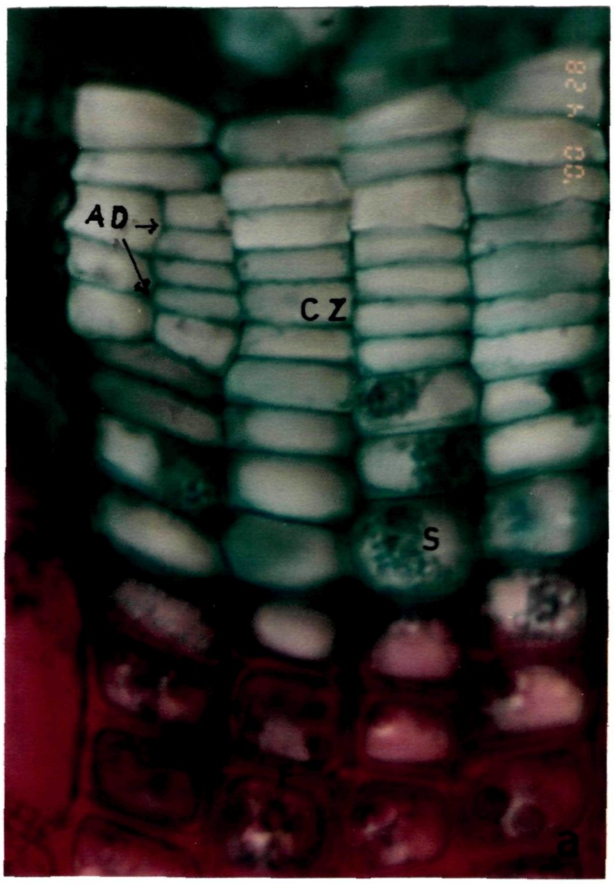
a. T.S. of dormant cambial zone (CZ) consisting of 4 layers with starch grains (S) in the undifferentiated xylem mother cells and late wood elements. Note anticlinal division (AD) in one of the radial files of the cambial zone. x 450

b. T.L.S. of dormant vascular cambium (VC) with oil cells (OC) adjacent to the ray initials. x 150.

PLATE - 5.2

Michelia champaca Linn.

Dormant Vascular Cambium



Tangential Longitudinal section of Dormant Vascular Cambium

PLATE- 5.3

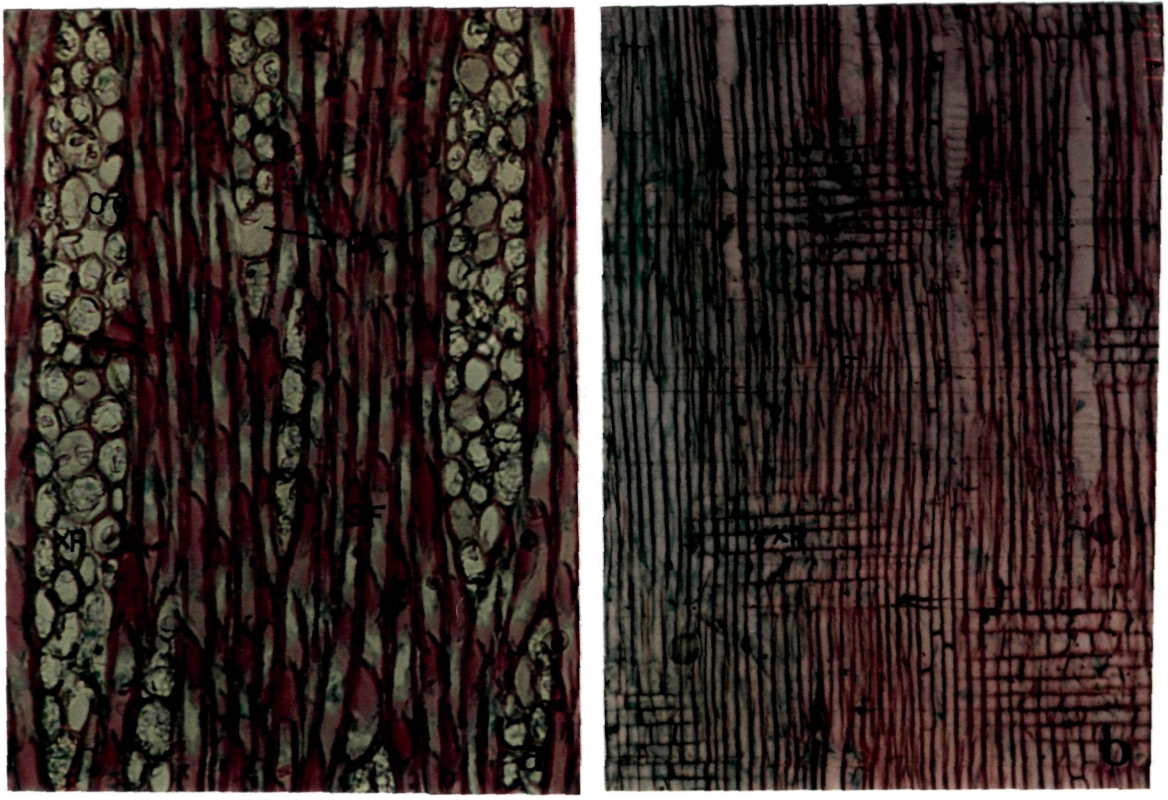
a. T.L.S. of late wood showing the septate libriform fibres (SF) and oil cells in the multiseriate xylem rays. x 250.

b. R.L.S. of early wood showing the heterogeneous xylem rays (XR); xylem fibres (F) and note the differentiating vessel elements with scalariform perforation plate. x 180.

c. An enlarged view of scalariform perforation plate (SP) at the oblique end wall of xylem vessel element having approximately 20 cross bars. x 300.

PLATE - 5.3

Michelia champaca Linn.



Tangential Longitudinal Section of Late Wood

Radial Longitudinal Section of Early Wood

Scalariform Perforation Plate of Vessel Element

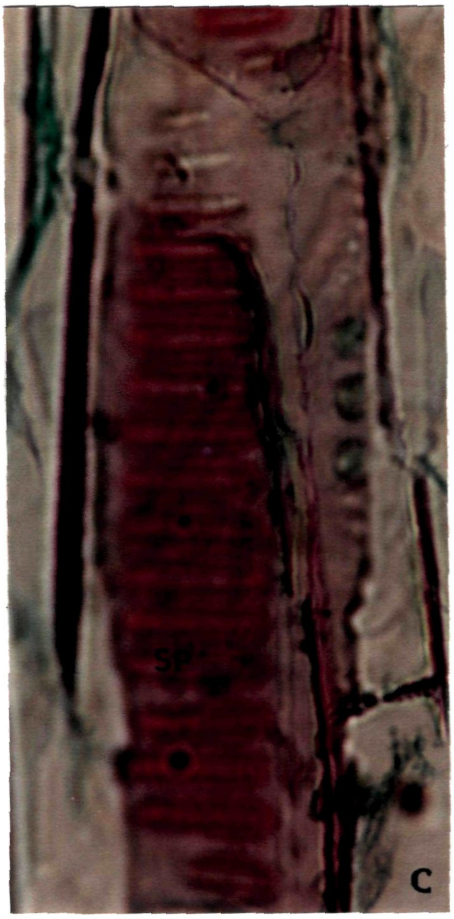


PLATE - 5.4

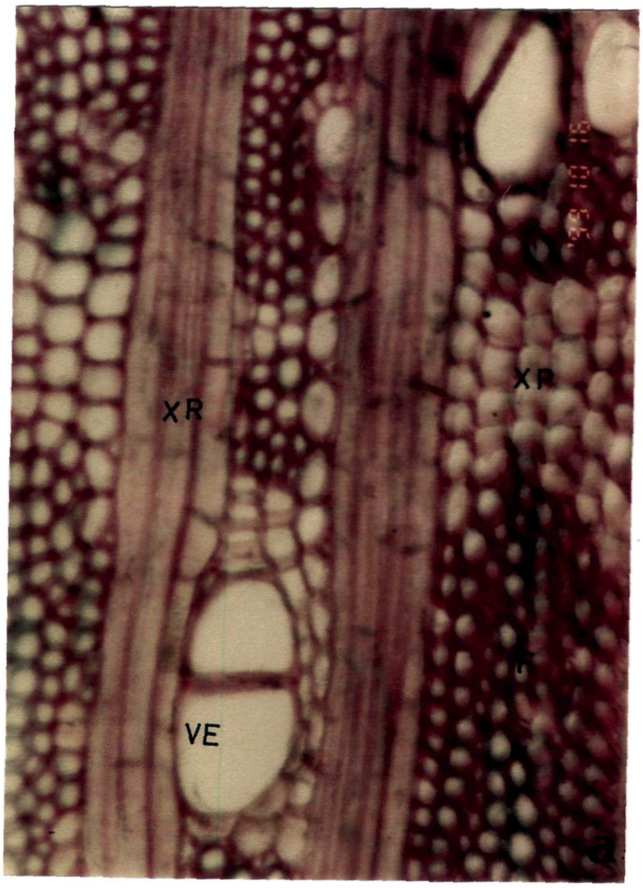
a. T.S. of wood showing the xylem rays (XR), xylem parenchyma (XP), vessel elements in pairs (VE) and xylem fibres (F). x 200.

b. T.L.S. of the wood showing the uni- and biseriate xylem rays, vessel elements with scalariform lateral wall pittings (LP) and fibres(F) x 250.

PLATE - 5.4

Michelia champaca Linn.

Transverse Section wood



Tangential Longitudinal Section of Wood

PLATE - 5.5

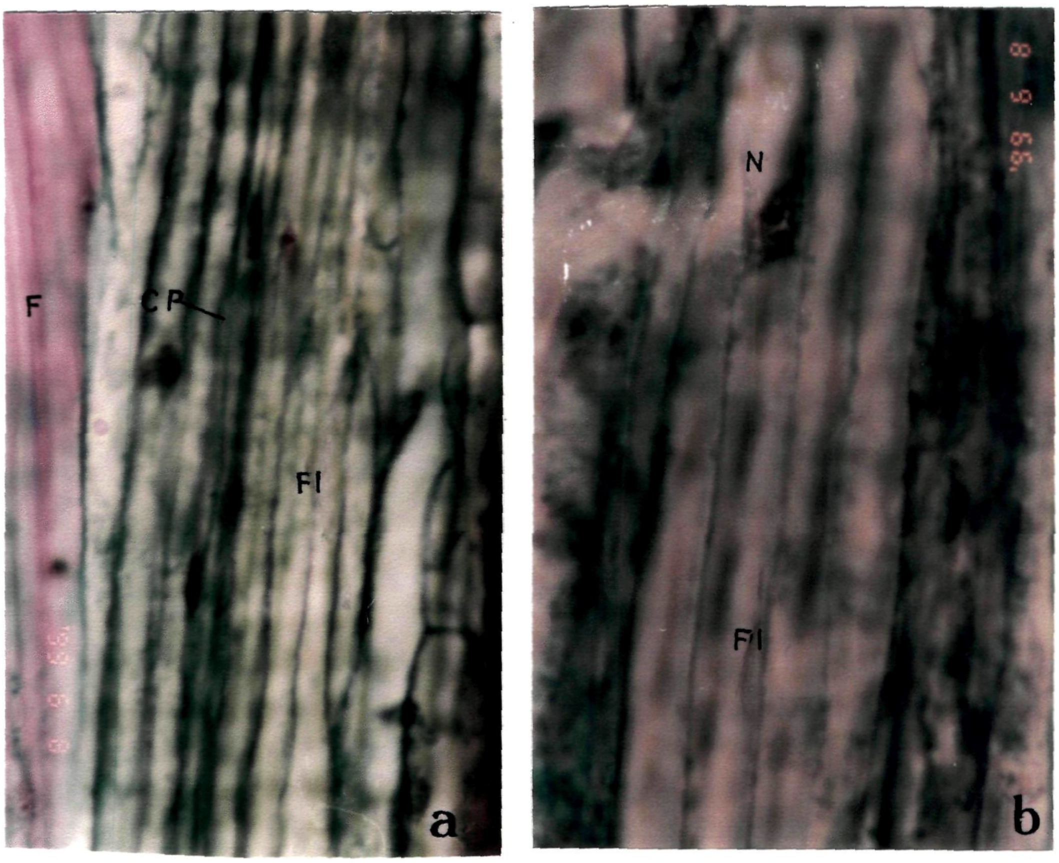
a & b. R.L.S. of active cambial zone. The beading are not distinct in the fusiform initials (FI), the nucleus (N) is oval shaped in figure ‘b’. while the nuclei in the fusiform initials are elongated in ‘a’. Note the cell plate formation (CP) in one of the fusiform initial.
a. = x 150 and b. = x 300.

c. T.L.S. of dormant vascular cambium having many nuclei (N) in initials fusiform initial (F1). Phenolic contents (P) are abundance in the ray initials (RI). x 180.

PLATE - 5.5

Shorea robusta Gaertn. f.

Radial Longitudinal Sections of Active Vascular Cambium



Tangential Longitudinal Section of Dormant Vascular cambium

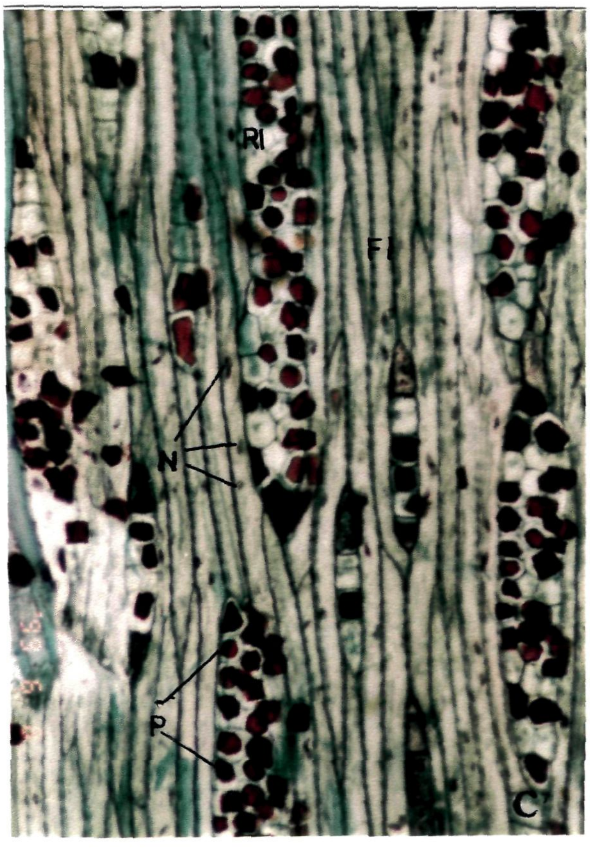


PLATE-5.6

a. T.S. of wood with dormant cambial zone (CZ), consists of 4-5 layers only. x160.

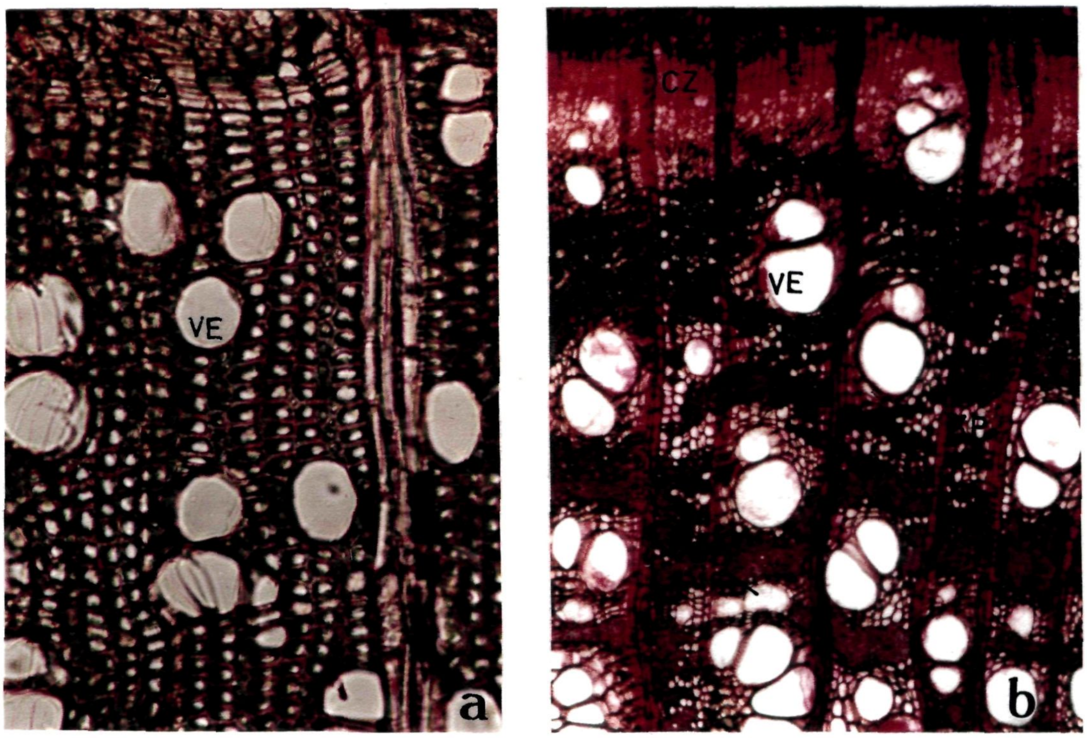
b. T.S. of wood with active cambial zone (CZ), vessel element with paratracheal parenchyma (XP). Parenchyma generally aliform and confluent. Oil canal (OCA) are dispersed within the xylem parenchyma. x 100.

c. An enlarged view of the active cambial zone (CZ) consisting of 8-10 layers. The sieve element (SE) and companion cells (CC) are distinct just above the cambial zone. The periclinal division (PD) marked by arrows. x 900.

PLATE - 5.6

Shorea robusta Gaertn. f.

Transverse Section of Wood



Dormant vascular cambium

Active vascular Cambium

An enlarged portion of Active vascular cambium

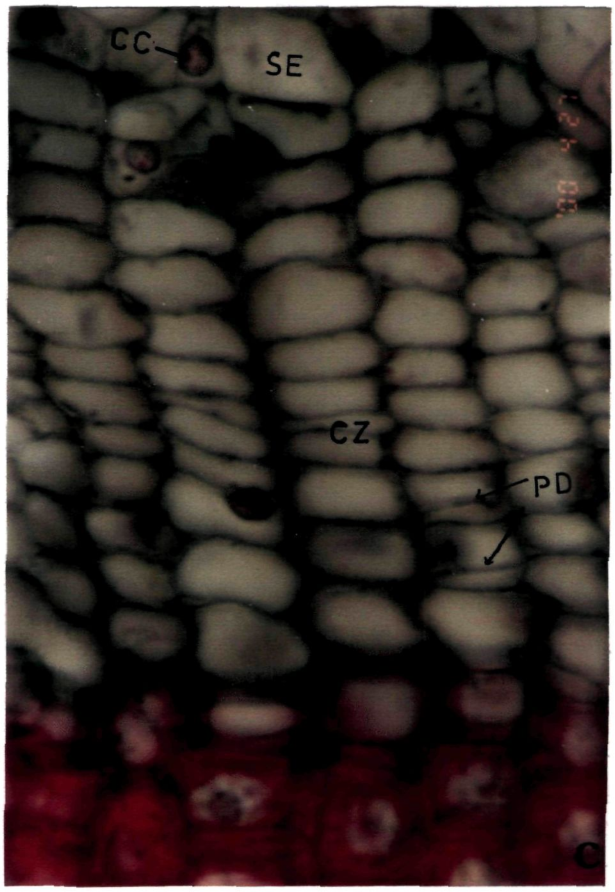


PLATE - 5.7

Shorea robusta Gaertn. f.

Wood

Tangential Longitudinal Section

Radial Longitudinal Section

Macerated Wood Elements

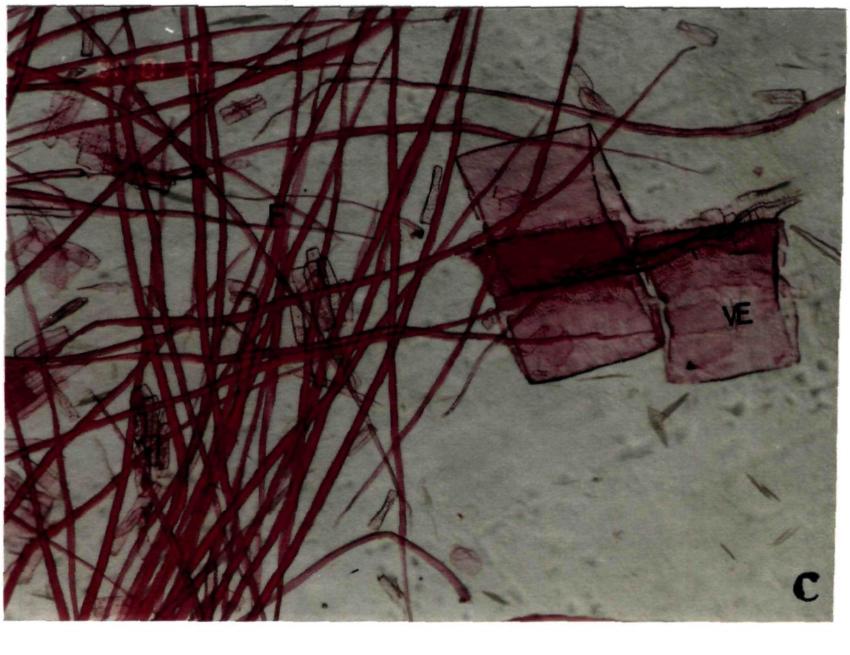


PLATE 5.7

a & b . T.L.S. & R.L.S. of wood showing the different xylem element: libriform fibres (F), lateral wall pitting (LP) on the vessel element; starch grains (S) in the xylem parenchyma and abundant of phenolic (P) and tannin content in the xylem rays both x 250.

c. Macerated wood element showing the libriform fibres (F) and vessel element (VE). Note the xylem parenchyma cells also. x 450.

CHAPTER-6

Dendroclimatic evaluation of climate-growth relationships of *Cedrus deodara* Loudon, *Cryptomeria japonica* D.Don and *Pinus kesiya* Royle ex. Gordon.

Introduction

Studies on the tree ring width sequences in relation to climatic factors have been proven, an effective tool for reconstruction of past climatic situations (Douglass 1914; Schulman 1947, 1951, 1956; Fritts 1976; Fritts and Shashkin 1995; Hughes et al. 1982). It also has been proved to be a very useful technique for analyzing ecological relationships between tree growth and climate (Schweingruber 1996).

Trees growing in the Himalayan zone are well suitable for dendroclimatic works because their well-defined growth rings display a very prominent response to temperature (Pant 1979, 1983). Bilham et al. (1984) have shown that tree ring width series of *Juniperous,* collected from Karakoram had the same climate sensitivity of the ring width pattern with that of the trees growing in the Himalayas. Pant (1983) and Pant & Borgaonkar (1984) found that among the climatic factors, temperature was the main controlling factor in the growth of Chirpines (*Pinus roxhburghii*) at Kumaon region Uttar Pradesh. Likewise ring width sequence of *Cedrus deodara* and *Pinus gerardiana* at lower altitudes of Pirpanjal Range, south of Kashmir, exhibits a high mean sensitivity, good intra and inter species correlation among the chronologies (Bhattacharyya et al. 1988). A climatic reconstruction of August to September mean temperature in Kashmir way back to the late 18th century was carried out by Hughes and Davies (1986) by using the tree ring width sequence of *Abies pindora.* Similarly, a reconstruction work of summer precipitation, way back to 17th A.D, was presented by Borgaonkar et al. (1994) based upon the tree ring width sequences of *Cedrus deodara* for Kashmir. Borgaonkar et al. (1996) also reported a significant relationship between pre-monsoon summer (March-April-May) climate (temperature and precipitation) and *Cedrus deodara* chronology from the Western Himalayan region. Further they discussed the potential of the species for reliable reconstruction of pre-monsoon temperature for that region. Thus, the possibility of using tree-ring chronologies from sub-alpine sites to reconstruct spring and early summer temperature, or even whole summer temperature and precipitation, demonstrate that the dendroclimatology is a tool to study the effect of climate variability on systems such as crops, rivers and glaciers in the Western Himalaya. Whereas tree ring chronologies from Eastern Himalayas shown little response to climate and growth relationship (Vandana et al. 1999). They also have suggested that further addition of more samples and extensive collection from undisturbed forest sites may solve the problem of low signal to noise ratio.

Therefore, the present investigation deals with the analyses of the response of growth to the climatic factors on *Cedrus deodara* Loudon, *Cryptomeria japonica* D.Don, *Pinus kesiya* Royle ex. Gordon growing in the sub-tropical wet forest of Shillong, India.

Materials and method

A total of 37 cores were extracted from 23 trees at breast height (DBH) from two directions per tree but some trees were taken only 1 core in *Cedrus deodara* (on September, 2000), 15 cores from 8 trees of *Cryptomeria japonica* (on July, 1997) and 15 from 8 trees of *Pinus kesiya* (collected on September, 2000). All cores were mounted, and sanded, and visually cross-dated (Eckstein et al. 1984; Pilcher 1990) by counting the number of ring. No rings were observed to be missing in any of the cores.

Ring width was measured to the nearest 0.01mm using a lens with 20x30 standard magnifications with a fitted increment scale. Absolute dating of the cores was verified statistically by using the COFECHA program (Holmes 1983).

Standardization of measurement series was done using the program ARSTAN (Cook 1985). The measured series of *Cedrus deodara* were individually detrended by applying line through mean to remove age related decline in growth rate and low frequency variance due to natural disturbance (Cook 1985), thus enabling the mean value to 1 or less than 1. The tree-ring widths of *Cryptomeria japonica* were detrended by applying negative exponential curve plus 60 years cubic spline. Whereas tree-ring widths of *Pinus kesiya* were detrended by applying negative exponential plus 50 years cubic spline. After synchronizing the individual series, a standardized chronology was constructed by averaging all the cores (Table 6.1).

Result

The growth rings are markedly distinct by the radially compressed late wood xylem element (tracheids) in *Cedrus deodara*, *Cryptomeria japonica* and *Pinus kesiya.* As mentioned in Chapter - 4 it is evident that the growth rings are annual.

In *Cedrus deodara* a 71 years standardized chronology (Fig.6.1 a) ranging from 1927 to 1997 was developed (Plate 6.1 a). The strength of cross-dating among these trees was high as reflected by an inter series correlation of 0.23, and the mean correlation between trees of approximately 0.22 and within trees of approximately 0.53 (Table 6.1). Mean sensitivity of the standardized chronology was 0.12. Common interval analysis for the standardized chronology showed a signal to noise ratio 6.579, agreement with population chronology 0.868 and a variance due to first eigenvector 27.79%.

Whereas in *Cryptomeria*, after standardization of all the cores, a 131 year long chronology was developed (Plate 6.1 b) (Fig. 6.1 b). The strength of cross-dating among these trees was reflected by an inter series correlation of 0.186, and the mean correlation between trees of approximately 0.182 and within trees of approximately 0.269 (Table 6.1).

Fig. 6.1 Standardized chronologies of ***Cedrus*, *Cryptomeria*** and ***Pinus***.

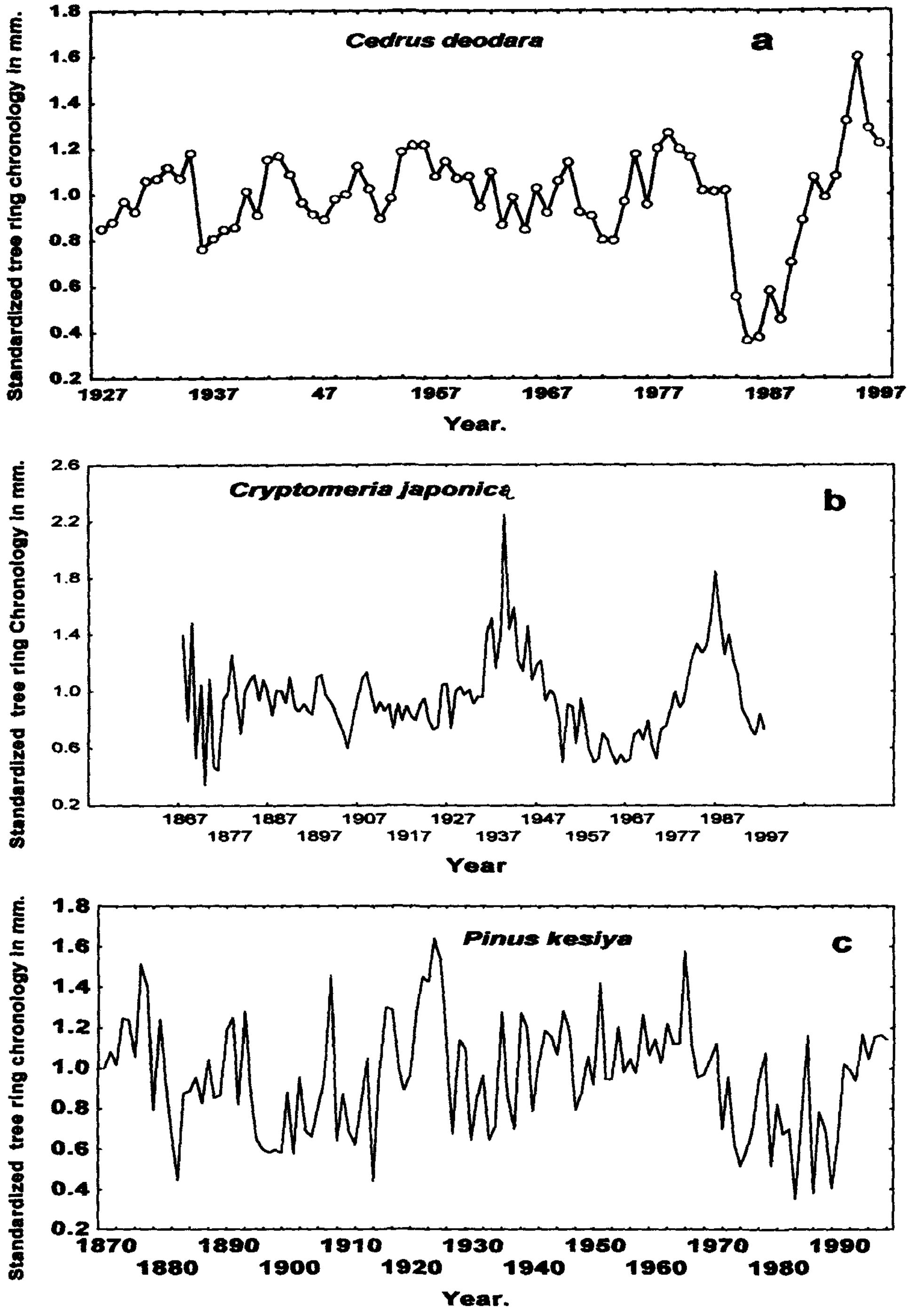


Table 6.1 Descriptive statistics of tree-ring widths of ***Cedrus deodara***, ***Cryptomeria japonica*** and ***Pinus kesiya***.

Statistics	***Cedrus deodara***	***Cryptomeria japonica***	***Pinus kesiya***
Mean sensitivity	0.12	0.19	0.25
Autocorrelation	0.72	0.61	0.22
Correlation among all radii	0.13	0.18	0.32
Between trees	0.53	0.18	0.31
Signal to noise ratio	6.57	2.0	4.20
Agreement to population chronology	0.86	0.66	0.80
Variance due to first eigenvector	27.79%	26.64%	39.24%

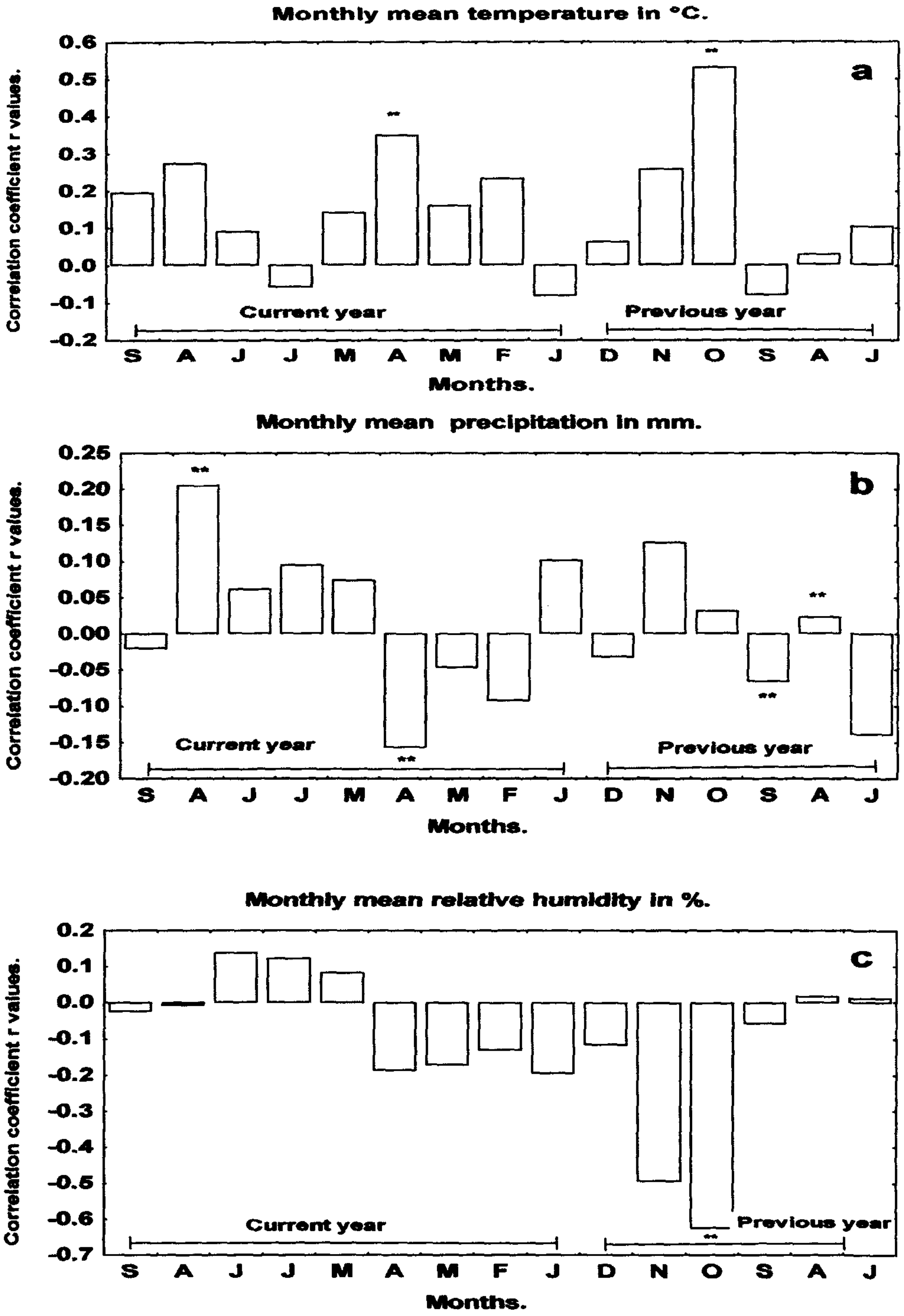
Mean sensitivity of the standardized chronology was 0.19. Common interval analysis for the standardized chronology showed a signal to noise ratio 2.09 with agreement to population chronology of 0.668 and a variance due to first eigenvector 26.64%.

In *Pinus* a chronology time span of 1870 to 1999 for 130 year from 15 radii was developed (Plate 6.2) (Fig 6.1 c). The strength of cross dating among the trees was high as reflected by interseries correlation of 0.326 and mean correlation between trees of approximately 0.318 and within the trees of approximately 0.464. The signal to noise ratio was 4.206 and variance due to first eigenvector was 39.24. The mean sensivity of the standardized chronology (0.25) indicates its suitability to obtain accurate results with correlation function methods (Rolland 1993).

Response function analysis

Response function analysis showed positive correlation with monthly mean temperature of February to May and subsequent August to September with the current year growth. Positive correlations are evident between *Cedrus* growth and temperature in July through November of the previous year, particularly the temperature in the previous October (Fig. 6.2 a). The precipitation in the month of January was positively correlated

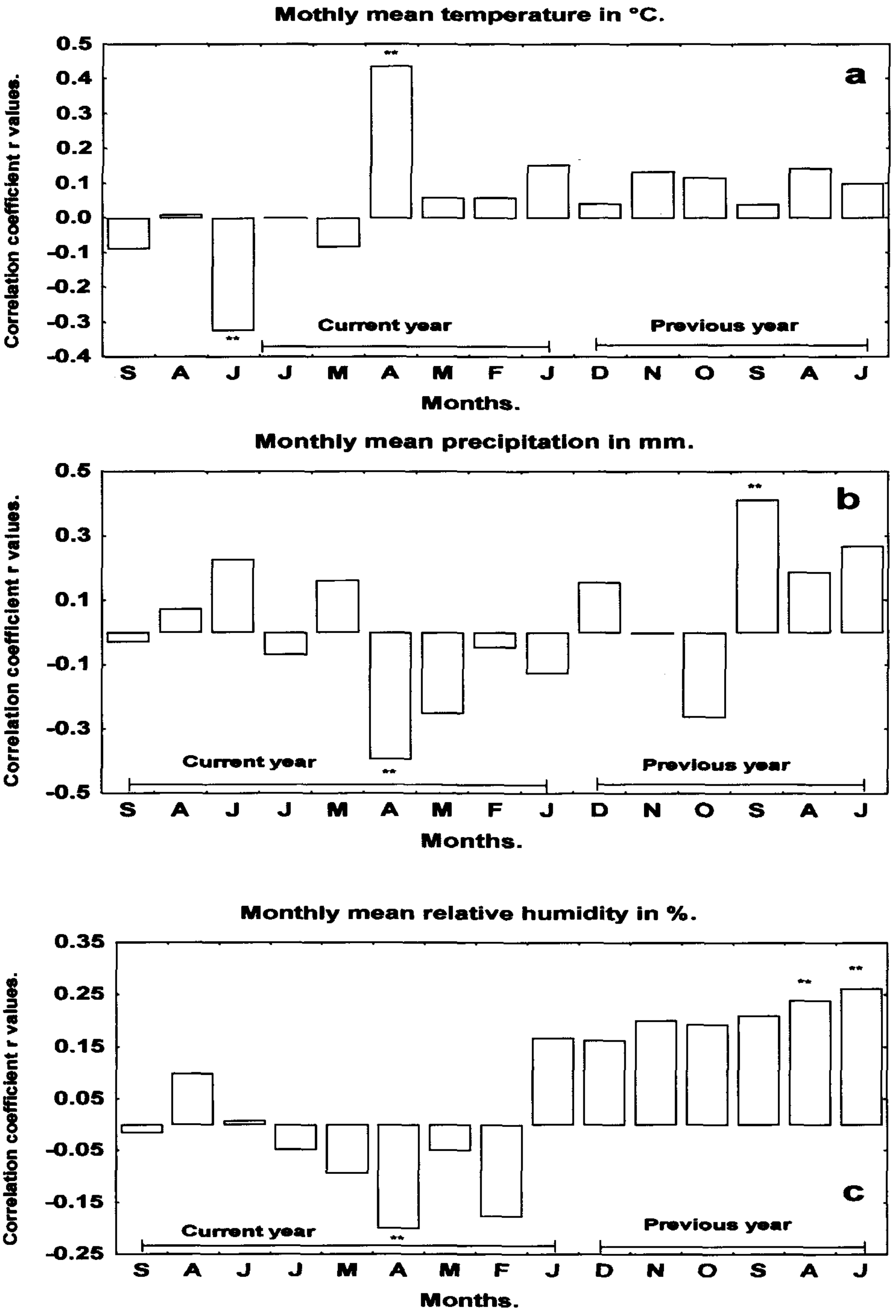
Fig. 6.2 Correlation values represented by bar plot of ***Cedrus deodara***. ** indicates r value is significant at $p < 0.05$ level.



with current year's growth even though there was less rainfall. Current year's August precipitation showed good correlation with *Cedrus* growth (Fig. 6.2 b). In case of relative humidity, current year's March, June and July showed positive correlation even though it is not significant. However, the previous year's relative humidity showed negative correlation in all the months except during the month of July and August (Fig. 6.2 c).

The response function analyses of *Cryptomeria* growth showed positive correlation with temperature during the months of January, February, March and April of the current year growth (Fig. 6.3 a). However, the previous year's growth responded positively with temperature during the month of July through November but not significant (Fig. 6.3 a). Whereas the growth of *Cryptomeria* showed a negative correlation during the months of February, March and April with monthly mean precipitation of the current year growth (Fig. 6.3 b). But, very low positive correlation was observed during the months of May, July and August precipitation with the current year growth (Fig. 6.3 b). While, a positive correlation was observed from July through September precipitation of the previous year with the growth of *Cryptomeria*

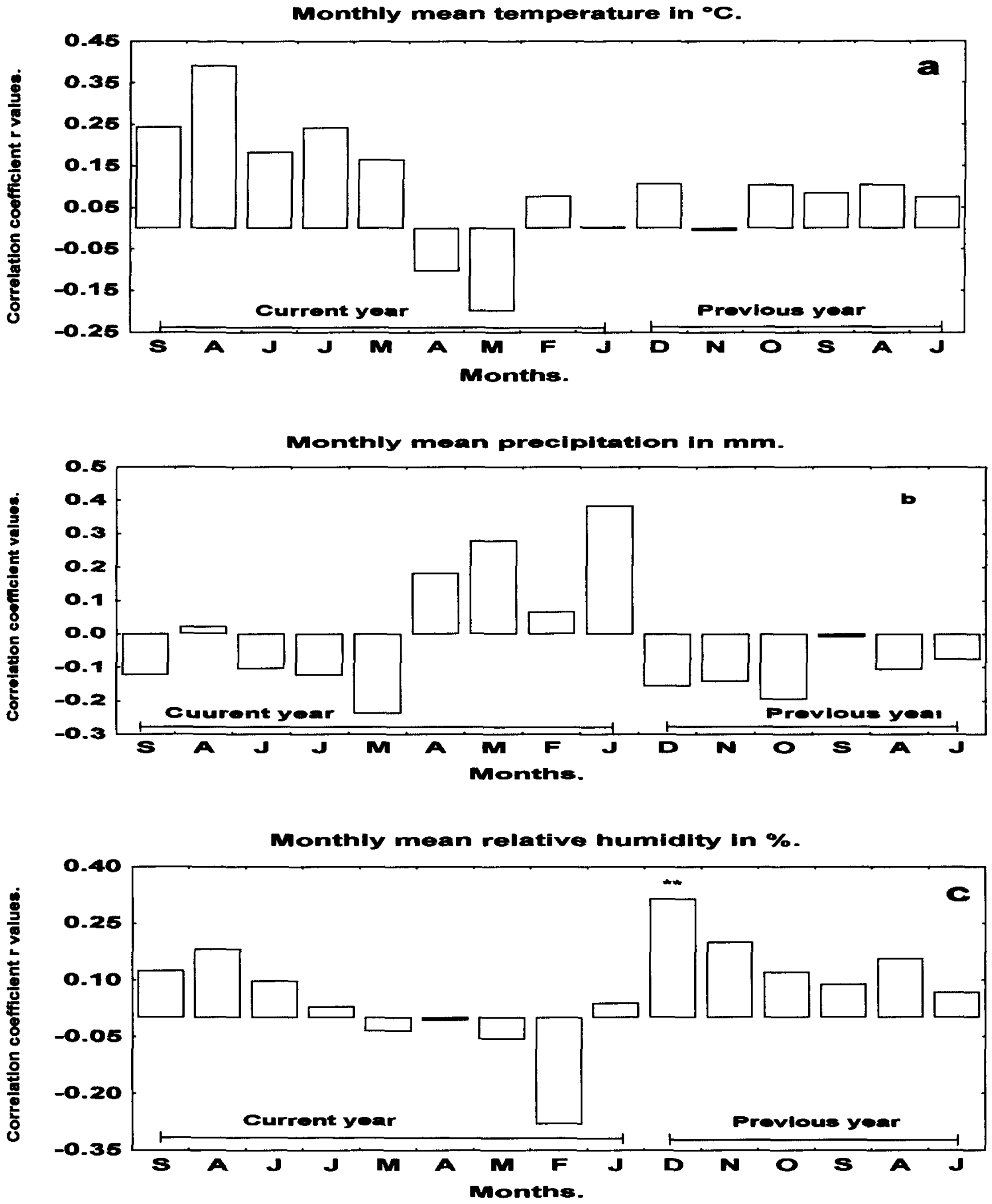
Fig. 6.3 Correlation values represented by bar plot of ***Cryptomeria japonica***. ** indicates r value is significant at $p < 0.05$ level.



(Fig. 6.3 b). As the relative humidity is concerned there was negative correlation with the current growth except during the month of August (Fig. 6.3 c). A positive correlation was observed in June through the month of December of the previous year.

Pinus kesiya growth responded positively with monthly mean temperature of September through May of the current year growth (Fig. 6.4 a). Among these months, the less correlated month was May temperature (Fig. 6.4 a). Whereas precipitation during the months of September through May of the current year growth responded negatively but a positive correlation was observed during the months of April through January of the current growth season with precipitation (Fig. 6.4 b). A very less correlation in the month of July through November of the previous growth was observed with mean temperature (Fig. 6.4 a). A negative response was observed with rainfall in these months of previous growth (Fig. 6.4 b). *Pinus* growth responded to relative humidity in the months of February and August of the current growth year (Fig. 6.4 c). Other months responded negatively. A good response was observed during the months of July through December previous year.

Fig. 6.4 Correlation values represented by bar plot of ***Pinus kesiya***.
** indicates r value is significant at $p < 0.05$ level.



Discussion

The significant correlation among individual standardized chronologies showed the synchronicity in inter-annual variation in ring-width patterns. The high signal to noise ratio and the expressed population signal, as well as the percentage of variance accounted for by the first eigenvector, and variance due to auto regression of the tree ring indices, indicated that all trees share a strong regional common signal (Table 6.1). The mean sensitivity of the standardized chronology was high enough to obtain accurate result with correlation function methods (Rolland 1993). Statistical characteristic of the chronology indicated that *Cedrus deodara* in this region might be a promising species for dendroclimatic studies.

The growth of *Cedrus deodara* responded positively to temperature in all the months except in the months of January, June, and August of the current year. Other dendroclimatic studies in Northern India also displayed a similar response to climate during March-May i.e., temperature and rainfall (Borgaonkar et al. 1996). Whereas Borgaonkar et al. (1999), reported a negative response to the mean monthly temperatures during the months of February, March, April, May and June, while precipitation showed positive correlation during these months when temperature was negatively responded. The negative response showed by *Cedrus deodara* in the case of precipitation might be due to the optimum availability of soil moisture in the present study. In other words, the temperature and precipitation were inversely correlated during this period. As the temperature rises up slowly, from February onwards, it might be an important factor to initiate reactivation of cambium after the dormant period during December and January. Moreover, during February the sprouting of new buds, needles and branches occurred which might initiate the cambial reactivation. Akarheilm (1940) noted that a small increase of temperature brought about a remarkable increase of radial growth of old *Pines* in the North of Europe. In Norway, Eidem (1943a) held the view that the temperature of the growing season to be a leading factor in determining ring thickness in fir. During the month of April, the response of growth is well explained as temperature favoured in radial growth. The negative correlation in the month of June might be responsible due to the high temperature and high rainfall (Hustich 1948a). In Northern Indiana, Diller (1935) studied on beech growth from 1913-1933 and he got correlation value of -0.785 between radial growth and temperature especially in the month of June. The much reduced response observed in the present study on *C. deodara* during the month of July during current year growth may be due to heavy male cone formation. Eis et al. (1951) and Tappeiner (1969) also observed the same phenomena of male cone formation which reduced the radial growth in *Pseudotsuga menziesii*, *Abies grandis*, and *Pinus monticola.* Eis et al. 1965 attributed that most of the photosynthate might be utilized for the reproductive growth. The radial growth initiation takes place within a few days after the establishment of mean daily temperature above 10°C which follows closely the beginning of swelling of terminal buds in white pine (Friesner and Walder 1946). The growing season of *Cedrus deodara* lengthened due to the earlier initiations of cambial activity. Fraser (1956) found that the average radial growth of yellow birch was greatest in years with warmer temperature and attributed the increase to a lengthened growing season due to the earlier initiations of cambial activity.

The growth of *Cedrus* showed a very high correlation to the previous year's October through November temperature (Fig. 6.2 a). Though it is not possible to give concise idea, it may be stated that during these months particularly in October the tree approaches dormancy as well as the accumulation of photosynthate might took place for the use of next growth towards the end of the growth ring formation. The accumulation of abscissic acid in the vascular cambium leads to the termination of cambial activity so that the growth ring formation is completed for that particular year (Wodzicki and Wodzicki 1980). In *C. deodara* also, the accumulation of reserved materials was observed at the end of the growing season (See Chapter-4). This assimilate may help for the next year growth, provided if there is any physical and physiological stress of that particular year. Larson (1967) reported that the early wood development depends on stored reserves of the previous years; while the late wood is dependent on current year assimilate that available an extended growing season. The positive correlation between August precipitation and the current year growth period in *Cedrus deodara* may be interpreted as it helps in the increased availability of soil moisture during the month of August. Till now the report on the response behaviour of the growth to relative humidity have not been reported. But in this study on growth response to the mean monthly relative humidity did not showed much correlation. Thus the tree ring indices of *Cedrus deodara* will be useful for dendroclimatic studies.

Whereas, in *Cryptomeria* growth responded positively to temperature in the months January, February, March and April of the current year. From the month of May onwards the growth of *Cryptomeria* showed negative response to the mean temperature of the current year growth. Kleine, Potzger and Friesner (1936) studied 4 species of oak in Indiana and they observed negative correlation between temperatures of June-August with growth. Whereas Borgaonkar et al. (1999) reported a negative response to the mean monthly temperatures of February, March, April, May, June, but in the same month precipitation showed positive correlation with the current year growth. As the temperature rises up slowly, temperature of February might be an important factor to initiate reactivation of cambium in this plant after the dormant period during December and January. Moreover during February the sprouting of new buds, needles and branches occurred. During the month of April, the response of growth is well explained as temperature favoured in radial growth. The negative correlation in the month of June onwards might be responsible due to the high temperature and high rainfall (Hustich 1948a). Even if there was positive correlation with January temperature, the reason of this might be due to the warming of the air temperature by the end of this month with 11-12°C as a critical threshold value where the cambial reactivation could be initiated. The radial growth initiation takes place within a few days after the establishment of mean daily temperature above 10°, and follows closely the beginning of swelling of terminal buds in white pine (Friesner and Walder 1946). The positive correlation to May, July and August rainfall with the current growth with low correlation value may not have a sound influence as did by temperature. Kleine, Potzgar and Friesner (1936) reported a good correspondence with the growth of oak trees with precipitation of June-August.

Pinus kesiya growth responded negatively to the mean temperature of February-April, whereas a positive correlation was observed with monthly mean temperature of September through May of the current year growth. Erlandsson (1936) worked in Northern Sweden and Finland; found that the direct influence July temperature in particular and subsequent month's temperature positively correlated with growth of trees. Among these months, the less correlated month was May temperature. Whereas precipitation during the months of September through May of the current year growth responded negatively but a positive correlation was observed during the months of April through January of the current year growth.

Coile (1936) found a significant correlation mean with precipitation of January to April with the growth of pine in southern United States. A very less correlation in the month of July through November of the previous growth was observed with mean temperature. A negative response was observed with rainfall in these months of previous growth. *Pinus* growth responded to relative humidity in the months of February and August of the current growth year. Other months responded negatively. A good response was observed during the months of July through November previous year. Thus the tree-ring width pattern of *Cedrus deodara* and *Pinus kesiya* proves to be a useful tool for the dendroclimatic studies. Whereas, *Cryptomeria japonica* may not be that much promising species for dendroclimatic studies as its growth response to climate was not so significant and the problem of low signal to noise ratio is to be considered. Further addition of tree-ring chronologies may improved problem of low signal to noise ratio.

PLATE-6.1

a. A wood disc of 71 years old (1927 to 1997) ***Cedrus deodara*** Loudon (reduced into 6 times from the original size) collected from Shillong

b. A wood disc of ***Cryptomeria japonica*** D. Don of 131 years old (1892 to 1997), (reduced into 7 times from the original size) collected from Shillong.

PLATE - 6.1

a

b

PLATE-6.2

C. *Pinus kesiya* Royle ex. Gordon. wood disc showing the distinct annual rings. The age of the plant is 130 years (1870-1999). (Reduced into 5.12 times from the original size) collected from Shillong.

PLATE - 6.2

c

CHAPTER-7

Dendroclimatic evaluation of climate-growth relationships of *Michelia champaca* Linn. and *Shorea robusta* Gaertn.f.

Introduction

Tree-ring width is traditionally used to established relationships between tree growth and climate (Fritts 1976). In the early 1970s, it has been shown that maximum latewood density of sub-alpine conifer species is more sensitive to temperature than tree-ring width (Schweingruber 1982).

Anatomical variables have been exploited for dendroecology and dendroclimatology quite early (Eckstein et al. 1977). Eckstein and Frisse (1982) found that the vessel area of oak, a ring-porous species, has a stronger relationship with climate particularly with rainfall, than tree-ring width. Sass and Eckstein (1992, 1995) showed the same for the diffuse porous *Fagus sylvatica* L. Woodcock (1989) studied the ring-porous species, *Quercus macrocarpa* Michx., *Q. rubra* L. and *Fraxinus pennsylvanica* L. for various variables such as diameter of the largest vessels, total conductive area, and vessel density. She concluded that the vessel density in the late wood is appropriate for precipitation reconstruction. Tree-ring width of teak (*Tectona grandis* L.) has already been tested for its dendroclimatic potential: Thailand (Pumijumnong 1995), Indonesia (Murphy and Whetton 1989; Jacoby and D'arrigo 1990; Palmer and Murphy 1993) and India (Pant and Borgaonkar 1983; Bhattacharyya et al. 1992; Wood, 1996). In Thailand the precipitation from April to July were reconstructed way back to 1870 (Pumijumnong et al. 1995a, b) using tree-ring width of Teak. Limin Xiong et al. (2000) evaluated the Dendroclimatic potential of *Cathya argyrophylla*, *Cinnamomum camphora*, *Gordania acuminate* and *Schefflera delavayi* from three gorges reservoir region of China. They observed the response to temperature, precipitation and river flow with the tree-ring widths of these tree species.

Materials and method

A total of 10 cores were extracted from 10 trees at breast height (DBH) from one direction per tree, 1 core on 30th March, 1996 for *Michelia champaca* from Tura (Meghalaya), 15 cores from 8 trees of *Michelia champaca* from Bhalukpong (Arunachal Pradesh) and 15 from 8 trees of *Shorea robusta* (Assam). All cores were mounted, and sanded, and visually cross-dated (Eckstein et al. 1984; Pilcher 1990). No rings were observed to be missing in any of the cores. Ring width was measured to the nearest 0.01mm using a lens with 20x30 standard magnifications with a fitted increment scale. Absolute dating of the cores was verified statistically by using the COFECHA program (Holmes 1983).

Standardization of measurement series was done using the program ARSTAN (Cook 1985). The measured series were individually detrended by applying selected detrending method to remove age related decline in growth rate and low frequency variance due to natural disturbance (Cook 1985), thus enabling the mean value to 1or less than 1. The ring width measurements of each core were divided by the fitted spline values to produce a standardized tree ring series for each core. Thus tree-ring widths of *Michelia champaca* from Garo was detrended by applying negative exponential curve plus 50 year cubic spline, whereas *Michelia* from Bhalukpong was detrended by applying negative exponential curve plus 60 year cubic spline. The tree-ring widths of *Shorea robusta* was detrended by applying line through mean plus 50 year cubic spline. After synchronizing the individual series, a standardized chronology was constructed by averaging all the cores.

Results

A standardized chronology of all the tree-ring measurement series of chronology time span from 1855 to 1994 was developed for *Michelia champaca* from Tura (Fig. 7.1 a). Mean sensitivity was good enough for obtaining a good correlation (Rolland 1993) (Table 7.1). The signal to noise ratio was 15.71 suggesting the climatic signal than other factors in the growth of this plant. The mean correlation among the series was 0.61 indicating the synchronicity in interannual variation in ring-width patterns (Table 7.1).

Whereas, the *Michelia champaca* from Bhalukong showed a time span of 1829 to 1994 with a total of 166 year after standardization method (Fig. 7.1 b) (Plate-7.1 a). The mean sensitivity was observed with 0.14, correlation between the radii was 0.41 and signal to noise ratio of 5.77. The variance accounted for by the first eigenvector was 49.71 indicating the absence of zero correlation among the measured ring widths (Table 7.1).

On the other hand the standardized chronology of *Shorea robusta* showed a time span of 1908 to 1999 for a total of 92 years (Fig. 7.1 c) (Plate-7.1 b). The mean sensitivity was low (0.11) in comparison to other plants. The

Fig. 7.1 Standardized chronologies of *Michelia* and *Shorea.*

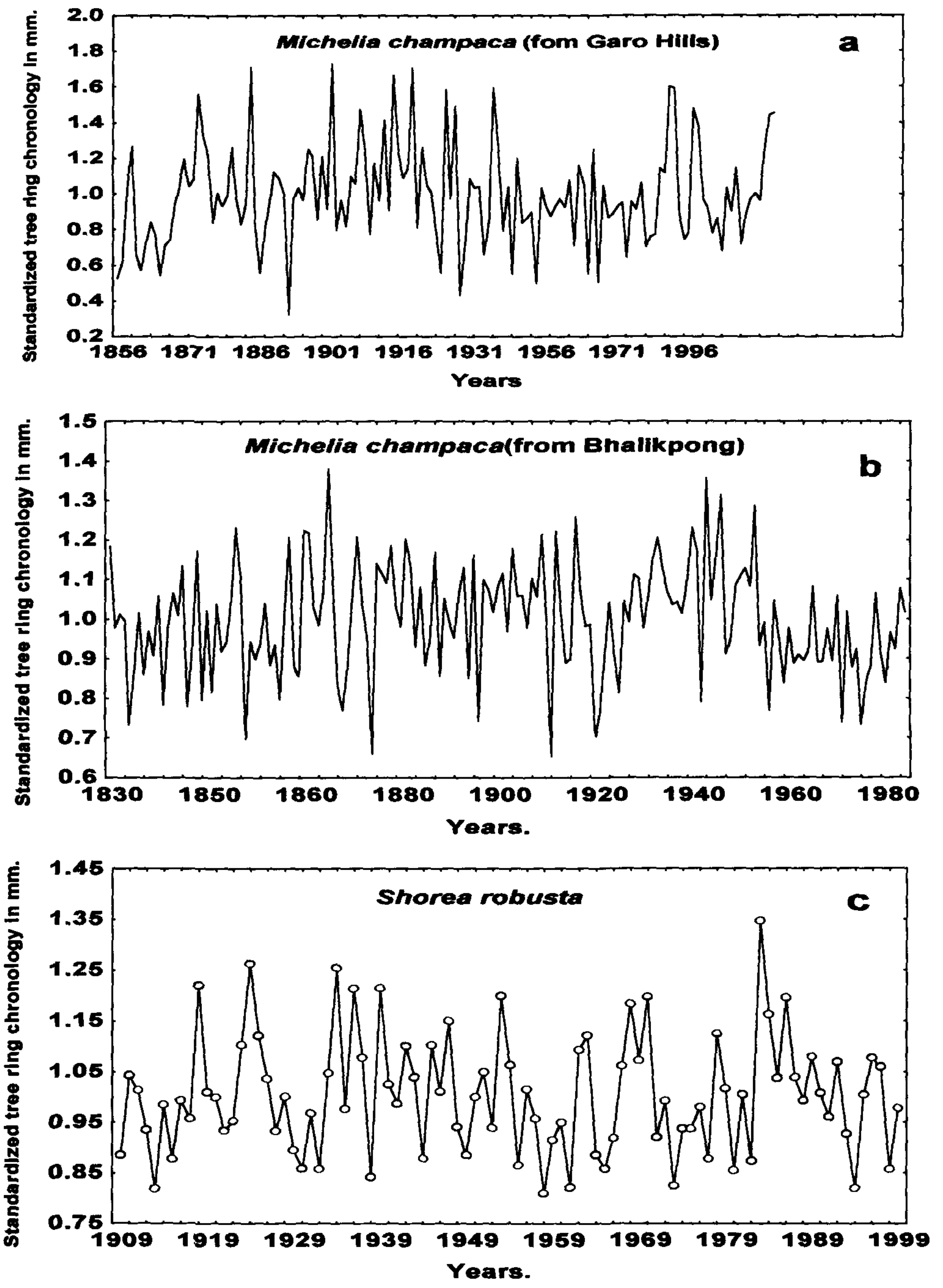


Table 7.1 Descriptive statistics of ***Michelia champaca*** (from Tura), ***Michelia champaca*** (from Bhalukpong) and ***Shorea robusta***.

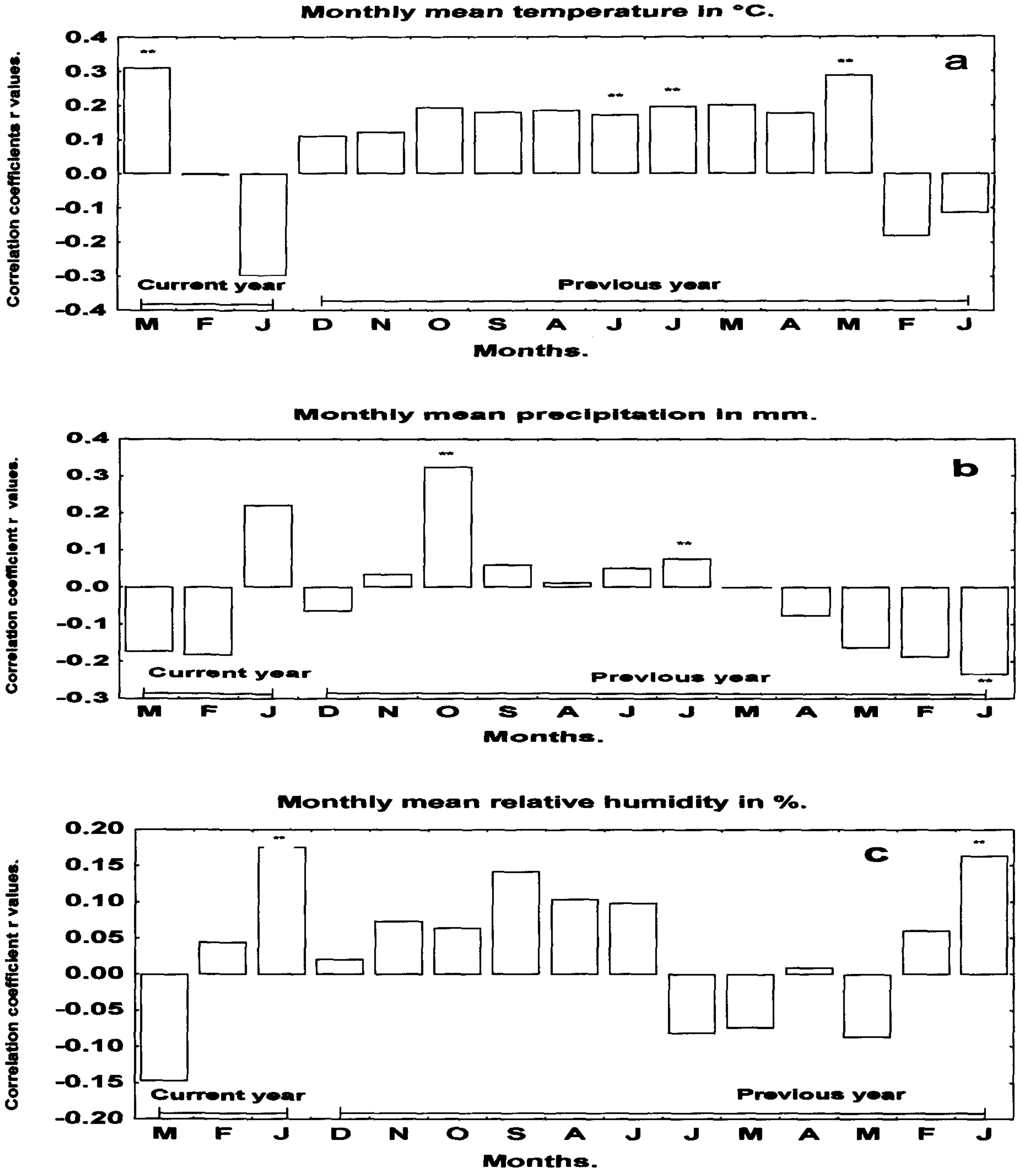
	Michelia (Tura)	*Michelia* (Bhalukpong)	*Shorea*
Mean sensitivity	0.12	0.14	0.11
Autocorrelation	63	0.45	0.47
Correlation among all radii	0.61	0.41	0.40
Between trees	0.6	0.41	0.40
Signal to noise ratio	15.71	5.77	6.81
Agreement with population chronology	66.12	0.852	0.87
Variance due to first eigenvector	66.12%	49.7%	47.87

correlation among the radii was 0.405 and a signal to noise ratio of 6.81. The variance due to the first eigenvector was 47.87% (Table 7.1).

Response function analysis

As the tree-ring samples were collected during the month of March, the growth response analysis was done in *Michelia champaca* collected from Tura (Meghalaya) going back to previous months of January. Growth of *Michelia* responded positively to the mean monthly temperature during the months of March of the current growth season and January and February responded negatively (Fig. 7.2 a). Whereas, the response to precipitation was negative during the month of March with current year growth (Fig. 7.2 b). Growth of this tree responded well to the mean temperature of the previous growth period from March to November and January and February responded negatively (Fig. 7.2 a). But a positive response was observed in growth of this plant with previous years temperature form July through November (Fig. 7.2 a). The positive response observed in the case of relative humidity with growth of this plant in most of the growing period are insignificant (Fig. 7.2 c). Precipitation did not played a significant role in the growth of this plant as revealed in the figure 7.2 b.

Fig. 7.2 Correlation values represented by bar plot of ***Michelia*** from Tura. ** indicates r value significant at $p < 0.05$ level.



Michelia champaca from Bhalukpong showed a positive response during the months of September through March with monthly mean temperature of the current year growth (Fig. 7.3 a). A positive correlation was also observed between the growth of *Michelia* with temperature of the previous year from July to November temperature (Fig. 7.3 a). Precipitation did not much influence as evident from the figure 7.3 b with the growth of this plant. But relative humidity was not useful for the growth of this plant as revealed by the value of correlation(r) in the response function analysis in every month (Fig. 7.3 c).

The growth of *Shorea* responded positively to the monthly mean temperature of February, March and May (Fig. 7.4 a). Whereas growth of *Shorea* responded positively with mean temperature from July through October during the previous year growth (Fig. 7.4 a). A negative response was observed by the growth of *Shorea* with precipitation except in the month of April and September of the current year (Fig. 7.4 b). A positive response was also shown during the months of September through July precipitation in previous year but not significant (Fig. 7.4 b). Response to relative humidity was almost nil with the growth of *Shorea* except during the month of July and September current year growth (Fig. 7.4 c).

Fig.7.3 Correlation values represented by bar plot of ***Michelia*** from Bhalukpong. ** indicates r value is significant at p< 0.05 level.

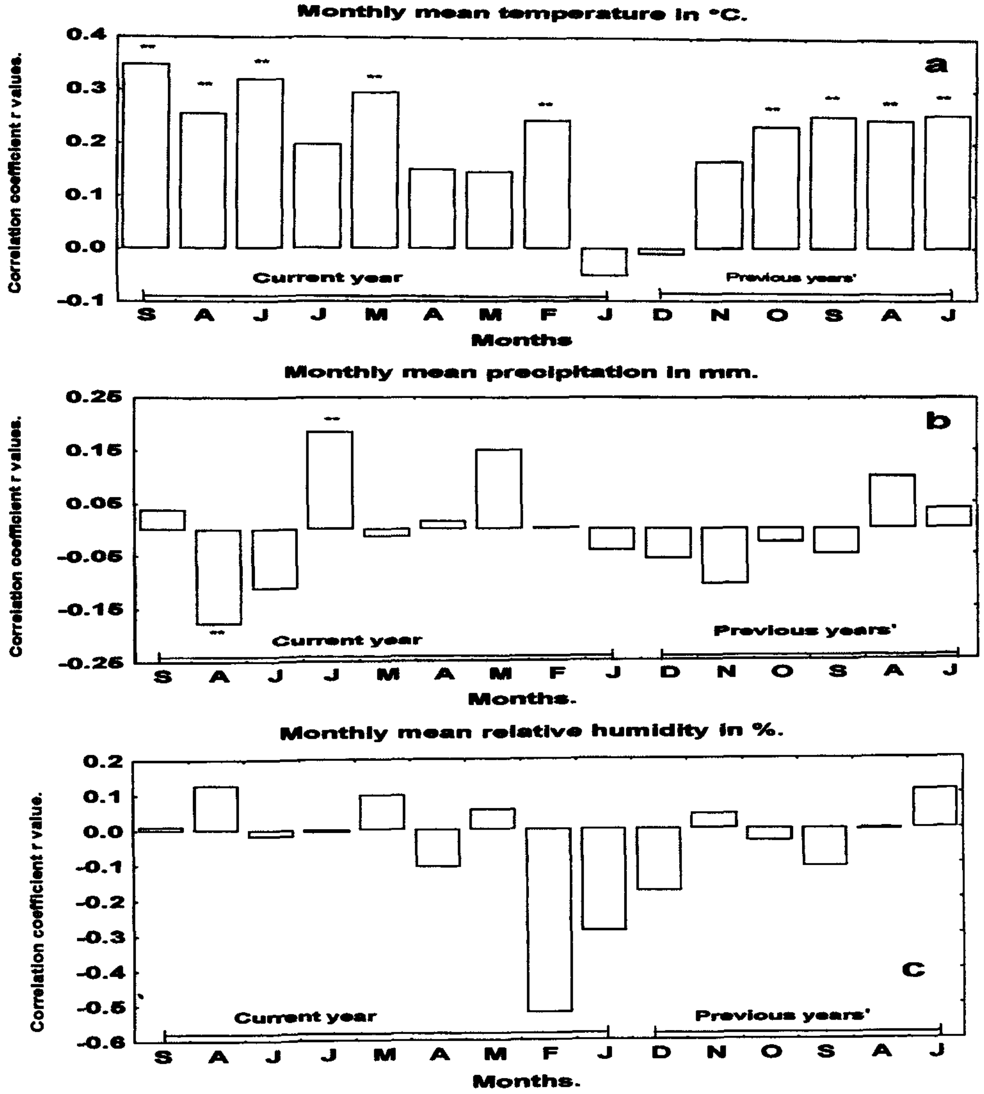
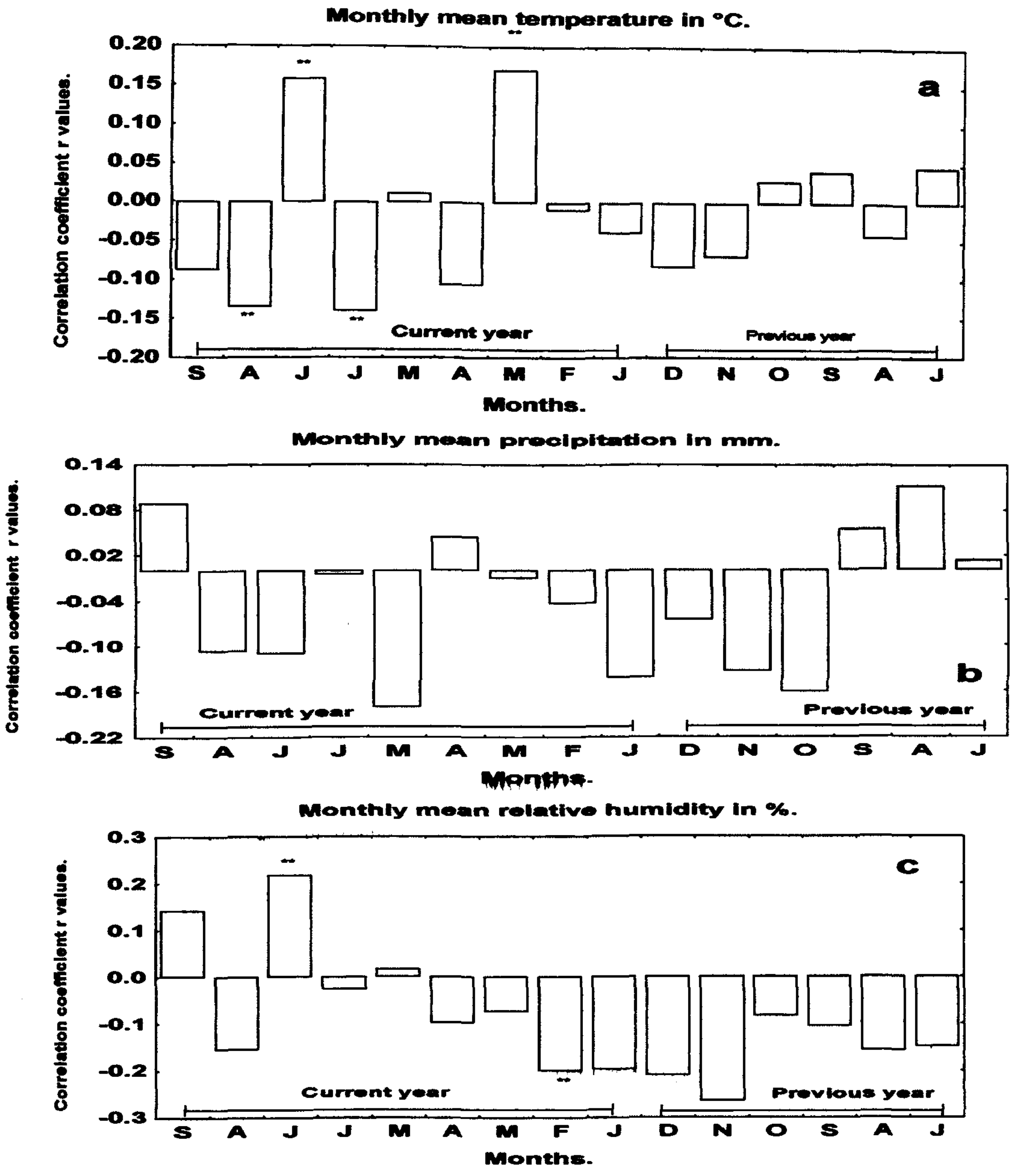


Fig. 7.4 Correlation values are represented by bar plot of ***Shorea***. ** indicates r value is significant at $p < 0.05$ level.



Discussion

The significant correlation with temperature of the current year growth of *Michelia* from Tura (Meghalaya) revealed that as the temperature increase slowly, the activity of cambium started and its activity in the production of wood also initiated as well as this result was observed in chapter-5. This idea is further proved by the negative correlation showed by the temperature of January and February (Fig. 7.2 a) with the current year growth. Also a similar positive correlation is also evident between *Michelia* growth and temperature in March through October of the previous year. As discussed in chapter-5, the activity of cambium of this plant observed from the month of March and continued its activity to October end. Whereas precipitation and relative humidity showed less correlation with the growth of *Michelia* in the current year as well as previous year suggesting a strong influence of temperature in the growth of this tree. But, Bhattacharyya et al. (1992) reported that *Michelia champaca* growing in tropical regions (Western Ghats) of India is not favourable for dendroclimatic studies. Whereas the present study showed a high positive correlation with the monthly mean temperature with the growth of *Michelia*. As well as the high interseries correlation and high signal to noise ratio suggested that this species will be a promising species for dendroclimatic studies in sub-tropical wet forest of North-East India. In most of the dendroclimatic studies conducted at Western Himalayas, rainfall of the pre-monsoon was the sole factor for the growth of trees in this region (Borgankar et al. 1999). There are other reports of temperature influence in the growth of trees in Western Himalayas in *Chirepines* (Pant and Borgaonkar 1984).

A similar positive correlation was observed in the response function analysis of the growth of *Michelia* with temperature of the current year growth in Bhalukpong (Arunachal Pradesh). The growth of this plant in this region responded to the temperature changes from the February to September during the current year growth. The significant correlation observed between the growth of *Michelia* and temperature of July through September in the current year indicates the peak period of xylem production favoured by temperature. Mikola (1955) reported the radial growth of Norway spruce and Scots pines were affected by temperatures of the growing season (especially July temperature). Also a positive correlation is evident between the growth of *Michelia* and temperature in July through October of the previous year. The response to precipitation by the growth of this plant is very less during the current year growth as well as during the previous year. Relative humidity did not play any significant role in the growth of this plant.

Whereas, the growth response of *Shorea robusta* was not significant to any climatic factor. The growth of *Shorea* responded positively to the monthly mean temperature of February, March and May but not significantly as revealed by the low correlation values (Fig. 7.4 a, b &c). Lyon (1936, 1940, and 1940) could not find out the relationships between tree growth and temperature of the growing season but a positive relation between March-April temperatures was observed. The growth of *Shorea* responded positively with mean temperature from July through October in the previous year. A negative response was observed by the growth of *Shorea* with precipitation except in the month of April and September of the current year that is also negligible. A positive response was also shown during the months of September through July previous year but not significant. Response to relative humidity was almost nil with the growth of *Shorea*. Therefore this plant may not be suitable for dendroclimatic studies since any environmental factor did not play a significant role. Since the growth of *Michelia* from both the regions (Tura and

Bhalukpong) showed a good correlation with mean temperature, it will be a promising tool for studying the past climatic changes as well as ecological disturbances in this North-East region of India.

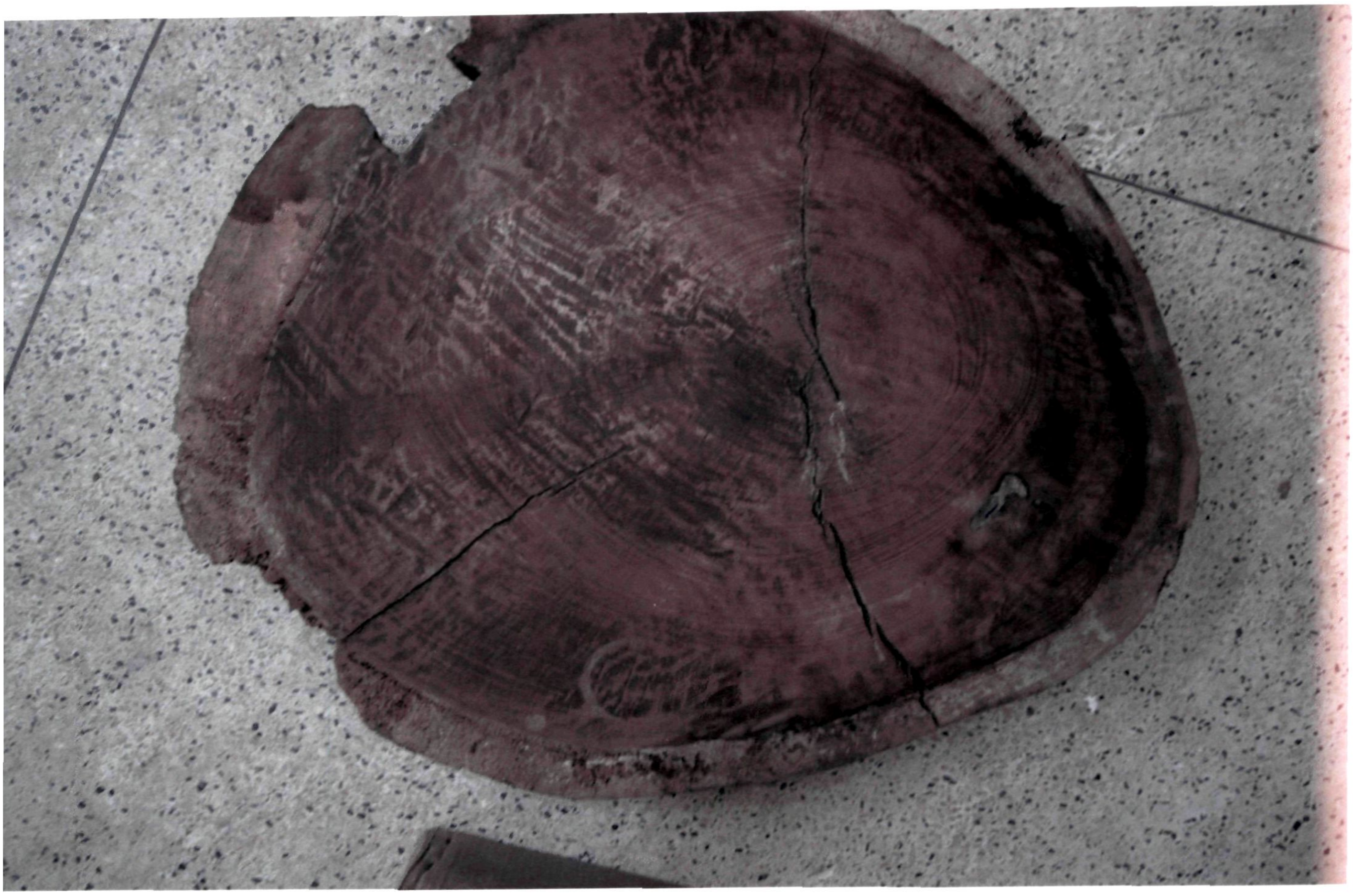
PLATE-7.1

a. ***Michelia champaca*** Linn. wood disc, having distinct annual rings. The age of the plant is 166 year (1829 to 1994), collected from Bhalukpong (Arunachal Pradesh). (Reduced into 10 times from the original size)

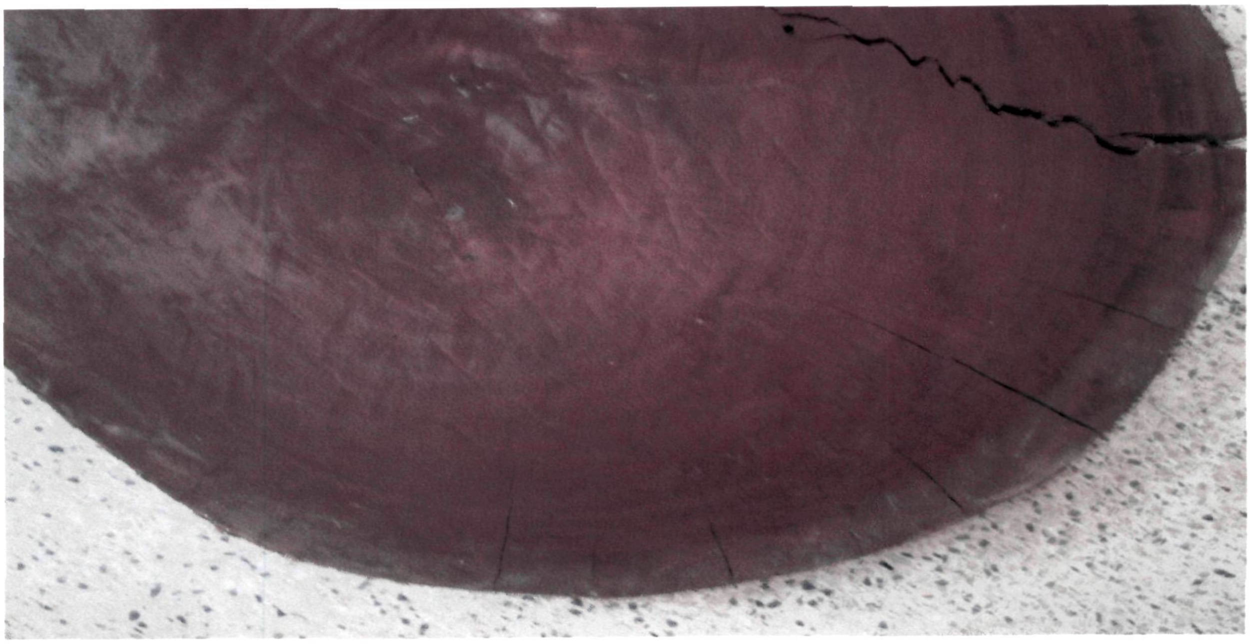
b. ***Shorea robusta*** Gaertn.f., a portion of wood disc, showing indistinct growth rings. The age of the disc is 92 years (1908 to 1999), collected from Nameri (Assam). (Reduced into 5.79 times from the original size).

PLATE - 7.1

a



b



CHAPTER-8

General Discussion

In *Cedrus deodara, Cryptomeria japonica and Pinus kesiya,* a correlation existed between the timing of new bud formation, cambial reactivation and in turn the production of xylem tissue. The same feature was observed in plants growing in the sub-tropical and tropical climates (Fahn 1990, Murmanis 1971, Evert 1963, Rajput 2001). Though, the tree *P. kesiya* produced thrice in year but the activity of the cambium and xylem production did not correlate with the intermittent flushes of needle formation. The same phenomena were observed in pine species growing in Western Himalaya (Dorga and Sahai, 1984). Tomlinson and Craighead (1972) observed the multiple flushes of leaves in *Sweitenia heteophylla.* Wareing et al. (1964) and Roberts (1976) reported that the young leaves and bud is the site of IAA and GA3 synthesis and their synergistic effect influence the cambial reactivation during the formation of new leaves and buds. Auxin (IAA) is a key regulator of cambial growth. Polarly transported auxin maintains the cambial meristem stimulates the cambial cell division and expansion of derivatives (Aloni 1987, 1988; Roberts 1988). Uggla et al. (1998) measured the concentration of IAA by using mass spectrometry in combination with cryosectioned. Cambial zone with its derivatives and they formed that IAA was distributed in a steep radial concentration gradient across the developing xylem and phloem elements. In general, all these three gymnosperm trees the reproductive phase occurred simultaneously along with the sprouting of needles, it is difficult find out the role of male and female cone formation on the cambial reactivation (Fahn 1990; Reinders-Gouwentak 1965; Venugopal and Krishnamurthy 1987). The dormancy of the vascular cambium is imposed by mainly by the climatic factors. *Cedrus, Cryptomeria and Pinus* showed the distinct annual rhythm of cambium which resulted into the formation of distinct growth rings (Chowdury 1964; Fahn et al 1986; Carlquist 1980) multiple ring formation in correspondence with the number of both the gymnospermous and angiospermous plants (Amobi 1974; Fahn 1958 and Lipschitz et al. 1981). However, such multiple ring formation did not encounter in *Pinus,* though this plant produced new bud and needle thrice in a year (Das and Ramakrishna 1986)

In temperate plants over wintering partially differentiated xylem element have been reported in several plants. (Bannan 1955; Longman and Coutts 1974; Romberger 1963; Timell 1980). Over wintering, partially differentiated tracheids and resin canal observed for the first time in *Pinus kesiya.*

The storage products such as starch and crystal of calcium stored in the cambial zone and its derivative during the dormant period of the current year, probably served as the source for the new cell wall synthesis for the next year growth. (Davis 1961; Little 1984; Essiamah & Eschrich 1985; Sauter 1966; Parker 1960; Pomeroy & Sminovitah 1971; Tsuda & Shimaji 1971). *Pinus kesiya* growth responded negatively to the mean temperature of February-April, whereas a positive correlation was observed with monthly mean temperature of September through May of the current year growth. Erlandsson (1936) worked in Northern Sweden and Finland and he found that the direct influence July temperature in particular and subsequent month's temperature positively correlated with growth of trees. Among these months, the less correlated month was the May temperature. Whereas precipitation during the months of May through September of the current year growth responded negatively but a positive correlation was observed during the months of April through January of the current year growth. Coile (1936) found a significant correlation mean with precipitation of January to April with the growth of pine in southern United States. A very less correlation in the month of July through November of the previous growth was observed with mean temperature. A negative response was observed with rainfall in these months of previous growth. *Pinus* growth responded to relative humidity in the months of February and August of the current growth year while the months responded negatively. A good response was observed during the months of July through November previous year. Thus the tree-ring width pattern of *Cedrus deodara* and *Pinus kesiya* proves to be a useful tool for the dendroclimatic studies. Whereas, *Cryptomeria japonica* may not be that much promising species for dendroclimatic studies as its growth response to climate was not so significant and the problem of low signal to noise ratio is to be considered. Further addition of tree-ring chronologies may improved problem of low signal to noise ratio.

The significant correlation among individual standardized chronologies showed the synchronicity in inter-annual variation in ring-width patterns. The high signal to noise ratio and the expressed population signal, as well as the percentage of variance accounted for by the first eigenvector, and variance due to auto regression of the tree ring indices, indicated that all trees share a strong regional common signal. The mean sensitivity of the standardized chronology was high enough to obtain accurate result with correlation function methods (Rolland 1993). Statistical characteristic of the chronology indicated that *Cedrus deodara*, *Pinus kesiya* except *Cryptomeria japonica*, growing in this region might be a promising species for dendroclimatic studies.

The growth of *Cedrus deodara* responded positively to temperature in all the months except in the months of January, June, and August of the current year, while, in *Cryptomeria* growth responded positively to temperature in the months January, February, March and April of the current year. From the month of May onwards the growth of *Cryptomeria* showed negative response to the mean temperature of the current year growth. Other dendroclimatic studies in Northern India also displayed a similar response to climate during March-May i.e., temperature and rainfall (Borgaonkar et al. 1996). Whereas Borgaonkar et al. (1999), reported a negative response to the mean monthly temperatures during the months of February, March, April, May and June, while precipitation showed positive correlation during these months when temperature was negatively responded. The negative response showed by *Cedrus deodara* in the case of precipitation might be due to the optimum availability of soil moisture in the present study. In other words, the temperature and precipitation were inversely correlated during this period. As the temperature rises up slowly, from February end onwards, it might be an important factor to initiate reactivation of cambium after the dormant period during December and January. Moreover, during February the sprouting of new buds, needles and branches occurred which might initiate the cambial reactivation. Akarheilm (1940) noted that a small increase of temperature brought about a remarkable increase of radial growth of old *Pines* in the North of Europe. In Norway, Eidem (1943a) held the view that the temperature of the growing season to be a leading factor in determining ring thickness in fir. During the month of April, the response of growth is well explained as temperature favoured in radial growth. The negative correlation in the month of June might be responsible due to the high temperature and high rainfall (Hustich 1948). In Northern Indiana, Diller (1935) studied on beech growth from 1913-1933 and he got correlation value of -0.785 between radial growth and temperature especially in the month of June. The much reduced response observed in the present study on *C. deodara* during the month of July during current year growth may be due to heavy male cone formation. Eis et al. (1951)

and Tappeiner (1969) also observed the same phenomena of male cone formation which reduced the radial growth in *Pseudotsuga menziesii*, *Abies grandis*, and *Pinus monticola*. Eis et al. (1965) attributed that most of the photosynthate might be utilized for the reproductive growth. The radial growth initiation takes place within a few days after the establishment of mean daily temperature above 10°C which follows closely the beginning of swelling of terminal buds in white pine (Friesner and Walder 1946). Fraser (1956) found that the average radial growth of yellow birch was greatest in years with warmer temperature and attributed the increase to a lengthened growing season due to the earlier initiations of cambial activity.

The growth of *Cedrus* showed a very high correlation to the previous year's October through November temperature see (Fig. 6.2 a). Though it is not possible to give concise idea, it may be stated that during these months particularly in October the tree approaches dormancy as well as the accumulation of photosynthate might took place for the use of next growth towards the end of the growth ring formation in both the trees The accumulation of abscissic acid in the vascular cambium leads to the termination of cambial activity so that the growth ring formation is completed for that particular year (Wodzicki and Wodzicki 1980). In *C. deodara and Cryptomeria*also, the accumulation of reserved materials was observed at the end of the growing season (See Chapter-4). This assimilate may help for the next year growth, provided if there is any physical and physiological stress of that particular year. Larson (1967) reported that the early wood development depends on stored reserves of the previous years; while the late wood is dependent on current year assimilate that available an extended growing season. The positive correlation between August precipitation and the current year growth period in *Cedrus deodara* may be interpreted as it helps in the increased availability of soil moisture. The positive correlation to May, July and August rainfall with the current growth with low correlation value may not have a sound influence as when compare to the temperature in *Cryptomeria.* In this study on growth response to the mean monthly relative humidity did not showed much correlation. Thus the tree ring indices of *Cedrus deodara* will be useful for dendroclimatic studies.

The significant correlation with temperature of the current year growth of *Michelia* from Tura (Meghalaya) revealed that as the temperature increase slowly, the activity of cambium started and its activity in the production of wood also initiated (see chapter-5). This idea is further proved by the negative correlation showed by the temperature of January and February (Fig. 7.2 a) with the current year growth. Also, a similar positive correlation is also evident between *Michelia* growth and temperature in March through October of the previous year. As discussed in chapter-5, the activity of cambium of this plant observed from the month of March and continued its activity to October end. Whereas precipitation and relative humidity showed less correlation with the growth of *Michelia* in the current year as well as previous year suggesting a strong influence of temperature in the growth of this tree. But, Bhattacharyya et al. (1992) reported that *Michelia champaca* growing in tropical regions (Western Ghats) of India is not favourable for dendroclimatic studies. Whereas the present study showed a high positive correlation with the monthly mean temperature with the growth of *Michelia.* The high interseries correlation and high signal to noise ratio suggested that this species will be a promising species for dendroclimatic studies in sub-tropical wet forest of North-East India. In most of the dendroclimatic studies conducted at Western Himalayas, rainfall of the pre-monsoon was the sole factor for the growth of trees in this region (Borgankar et al. 1999). There are other reports of temperature influence in the growth of trees in Western Himalayas in *Chirepines* (Pant and Borgaonkar 1984).

A similar positive correlation was observed in the response function analysis of the growth of *Michelia* with temperature of the current year growth in Bhalukpong (Arunachal Pradesh). The growth of this plant in this region responded to the temperature changes from the February to September during the current year growth. The significant correlation observed between the growth of *Michelia* and temperature of July through September in the current year indicates the peak period of xylem production favoured by temperature. Mikola (1955) reported the radial growth of Norway spruce and Scots pines were affected by temperatures of the growing season (especially July temperature). A positive correlation is evident between the growth of *Michelia* and temperature in July through October of the previous year. The response to precipitation by the growth of this plant was very less during the current year growth as well as during the previous year. Relative humidity did not play any significant role in the growth of this plant.

Whereas, the growth response of *Shorea robusta* was not significant to any climatic factor. The growth of *Shorea* responded positively to the monthly mean temperature of February, March and May but not significantly as revealed by the low correlation values see (Fig. 7.4 a, b & c). Lyon (1936, 1940 & 1940) could not find out the relationships between tree growth and temperature of the growing season but a positive relation between March-April temperatures was observed. The growth of *Shorea* responded positively with mean temperature from July through October in the previous year. A negative response was observed by the growth of *Shorea* with precipitation except in the month of April and September of the current year that is also negligible. A positive response was also shown during the months of September through July previous year but not significant. Response to relative humidity was almost absent with the growth of *Shorea*. Therefore, this plant may not be suitable for dendroclimatic studies since any environmental factor did not play a significant role. Since the growth of *Michelia* from both the regions (Tura and Bhalukpong) showed a good correlation with mean temperature, it will be a promising tool for studying the past climatic changes as well as ecological disturbances in this North-East region of India.

CHAPTER-9

Summary and Conclusion

Trees are stationary living organisms, responding to environmental factors during their life span. The ever-changing environmental stimuli are transformed in permanent tree structures and as such recorded over periods as along as the life time of trees (Schweingruber 1983). The ability to incorporate external stimuli is reflected in different characteristics. The most interesting are the growth rings. A pattern of tree rings contains environmental information, generally because through conducive environmental conditions broad rings are being formed and years with stressful conditions provide smaller rings.

The characteristic feature of growth ring is affected by the activity of the vascular cambium and this activity is controlled by many factors, both endogenous and exogenous. Climatic factors play a significant role in the activity of cambium. It is only lately that the dendroclimatology received a lot of public attention; such studies will be beneficial to scientific community (climatologist, ecologist, policy makers of both national and international level as well as public will be informed by vulgarization effects of deforestation etc.). In India only a few investigations have been published (Pant 1978; Hughes 1993; Bhattacharyya et al. 1988). Therefore, in this thesis, three Gymnospermus trees viz. ***Cedrus deodara*** Loudon, ***Cryptomeria japonica*** D.Don. and ***Pinus kesiya*** Royle ex. Gordon. and two angiospermous tree species ***Michelia champaca*** Linn. and ***Shorea robusta*** Gaertn.f. were studied with reference to the following aspects:

1. To study the response behaviors of the above mentioned tree species in relation to climatic factors.
2. To study the relationship between previous years' ecological conditions and growth ring formation.

The interrelationship between the timing of different phenological events such as vegetative bud break, needle formation, needle fall, male and female cone formation, pollen dispersal, seed dispersal in gymnospermous and emergence of new buds and foliage, leaf fall, flowering and fruiting in the case angiospermous with environmental factors such as water stress, temperature, rainfall, relative humidity and periodicity in cambial activity was examined for all the five plants. It was observed that there was a clear cut correspondence between timing of bud break and cambial reactive in both the gymnospermous and angiospermous plants and increased intensity of cambial activity was noticed immediately after bud break. Since the timing of cone formation in gymnosperms and flowering in angiospermous trees overlapped with that of vegetative bud break, it could not be categorically proved that reproductive phase was really responsible for enhanced activity of the cambium in the three gymnosperms and two angiospermous trees.

It was observed that both cambial reactivation and peak activity were generally favoured by a higher mean temperature in all the investigated plants; a positive correlation also existed between the least cambial activity/dormancy and lower mean temperature. Relative humidity had no effect on cambial periodicity. Wind velocity had little effect on cambial periodicity in the three Gymnosperm plants. The selected plants did not have any water stress because they are growing the subtropical wet forests of North east India, where water was not all a limiting factor. Moreover, the study area situated near the world's highest rainfall station the Cherapunjee.

The cambium of ***Michelia champaca*** Linn. is storied with characteristic feature of oil cells in the ray initials, while that of other plants viz. ***Shorea robusta*, *Cedrus deodara*, *Cryptomeria japonica*** and ***Pinus kesiya*** is non-storied. The fusiform initial of the ***Michelia*** had the least length range. The radial and tangential walls of fusiform initials were primary in nature; however, the radial wall was not only thicker than the tangential wall but also was always beaded. The beading was more prominent and closer to one another during dormancy than during the active period of the cambium. During the active state, the fusiform initials of all plants showed multinucleate condition (2-5) and the nuclei were multinucleolate of varied shapes and sizes. Cambial reactivation was marked by increase in width of cambial zone due to swelling of the cambial cells followed by an increase in the number of layers in the cambial zone due to the onset of periclinal division. There was also an increase in length of fusiform initials which consequently brought about the wide separation of the beads in the radial walls. The frequency of periclinal divisions was more during the active state of the vascular cambium, while towards dormancy the cambial zone exhibited predominantly anticlinal divisions in all the plants.

The structure of the secondary xylem of all plants has been briefly described. The angiospermous trees ***Michelia champaca*** and ***Shorea robusta*** were diffuse porous wood. In ***Michelia*** the perforation plates scalariform with 10 to 20 bars, which are oblique in various degrees; while in ***Shorea*** the perforation plates simple, almost transverse. Parenchyma vasicentric in both the angiospermous plants. Presence of initial parenchyma marked the growth rings in ***Michelia*** and ***shorea***. Oil cells are present in the xylem rays of ***Michelia***. Fibres libriform septate in ***Michelia*** and non-septate in ***Shorea***. In the three gymnosperms, ***Cedrus***, ***Cryptomeria***, and ***Pinus*** the wood is pycnoxylic; tracheids with bordered pits dispersed on radial walls, bars of Sanio (crassulae) distinct; xylem rays varied including unicellular, uniseriate, biseriate and multiseriate types; Resin canals and resin cells characterized the wood of ***Pinus*** and ***Cryptomeria*** respectively. Occasional traumatic resin canals were seen in ***Cedrus***.

The Duration of xylem production in ***Cedrus***, ***Cryptomeria*** and ***Pinus*** was about nine months while in the angiosperms ***Michelia*** and ***Shorea*** was about eight months. The length of fusiform initials and their derivatives like tracheids (in gymnosperms), the vessel elements, xylem fibres was the least during cambial dormancy and the length was maximum during the high intense activity of the vascular cambium. Similarly, in all the plants studied the radial width of fusiform initials was the least during dormancy and increased during cambial reactivation. The trend in variation in the length of different vascular elements followed closely the trend in variation in length of fusiform initials from which they were derived.

Conspicuous changes could be found in the content of secondary metabolites (ergastic substances) of xylem cells, adjacent to the cambial zone during the approach of dormancy as well as during cambial reactivation. In all the plants studied starch grains and crystals appeared in large quantity with the approach of dormancy but disappeared slowly with the onset of cambial reactivation. Probably, these substances form the source of new wall materials of the new cambial derivatives.

The significant correlation among individual standardized chronologies showed the synchronicity in inter-annual variation in ring-width patterns. The high signal to noise ratio and the expressed population signal, as well as the percentage of variance accounted for by the first eigenvector, and variance due to autoregression of the tree ring indices, indicated that all trees share a strong regional common signal. The mean sensitivity of the standardized chronology was high enough to obtain accurate result with correlation function methods (Rolland 1993). Statistical characteristic of the chronology indicated that *Cedrus deodara, Pinus kesiya* except *Cryptomeria japonica,* growing in this region might be a promising species for dendroclimatic studies.

A positive correlation is also evident between the growth of *Michelia champaca* and temperature in July through October of the previous year. The response to precipitation by the growth of this plant was very less during the current year growth as well as during the previous years'. Relative humidity did not play any significant role in the growth of this plant. Whereas, the growth response of *Shorea robusta* was not significant to any climatic factor. The growth of *Shorea* responded positively to the monthly mean temperature of February, March and May but not significant as revealed by the low correlation values. Therefore, this plant may not be suitable for dendroclimatic studies since any environmental factor did not play a significant role. Since the growth of *Michelia* from both the regions (Tura and Bhalukpong) showed a good correlation with mean temperature, it will be a promising species for studying the past climatic changes as well as ecological disturbances in this North-East region of India.

Conclusion

- It was observed that the ph~~o~~enological event specially sprouting of vegetative leaves, buds had a direct relationship with cambial reactivations.
- It was also observed that both the cambial reactivations after dormancy and peak activity were generally favoured by higher mean temperature. Further activity of vascular cambium and differentiation of xylem occurred due to the synergistic effect of both temperature and precipitation. Relative humidity had little/no effect on xylem formation. Cambial dormancy was imposed by the fall in temperature and short day duration of sunlight.
- The winter precipitation does not have effect on the xylem production.
- Conspicuous changes could found in the content of storage materials of vascular cambium and xylem tissues towards the approach of dormancy.

- The formation of resin canals in *Pinus kesiya* and resin cells in *Cryptomeria japonica* took place towards the onset of dormancy i.e. towards the time of late woof formation.
- The frequency of bordered pits in gymnosperms and different type of pits in angiosperms are more in the early the wood than the late wood formation.
- The reduction in the size of vascular cambial cells and xylem elements with the approach of dormancy may be gradual or abrupt depending upon the plant.
- Multinucleate condition in fusiform initial was reported in many angiosperms. This is the first record of multinucleate condition in the fusiform initials of gymnosperms.
- The significant relationship of pre-monsoon temperature with the tree indicated that in these sub-tropical moist forests of North-East India, the monthly mean temperature plays an important role in the tree-growth ring formation than other climatic conditions.
- Response function analyses showed a similar pattern across different regions and the relationship between tree growth and

- climate suggested that the climate condition particularly temperature from February month to April plays a critical role in the initiation of tree growth process and it continue to the month of September.
- In this Study, a tree ring network was established for some part of North-East India and the result confirm its Dendroclimatic potentials as revealed by mean sensitivity, signal to noise ratio and variance due to first eigenvector.

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