ANATOMICAL STUDIES ON *HEVEA BRASILIENSIS* MUELL. ARG. WITH SPECIAL REFERENCE TO BARK REGENERATION

Thesis Submitted in Part Fulfilment to the Course Leading to the
Degree of Doctor of Philosophy in Botany
of Birla Institute of Technology and Science
Pilani 333031 India

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August 21, 1974.

CERTIFICATE

The thesis entitled ANATOMICAL STUDIES ON HEVEA BRASILIENSIS MUELL. ARG. WITH SPECIAL REFERENCE TO BARK REGENERATION submitted by Mr. A.O.N. Panikkar for the Degree of Doctor of Philosophy in Science (Botany) embodies the results of investigations carried out under my supervision in this Department and I certify that the work is original.

(B.D. DESHPANDE)

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Words are few to express my gratitude to Dr. B.D. Deshpande for the stimulating guidance and constructive discussions, which enabled me to complete the investigations in the present form.

I am thankful to Prof. S.K. Pillai for many valuable suggestions. I acknowledge with thanks the help I received from Dr. N.V. Gopinath, Dr. M. Ramakrishna, Mr. H.C. Pant, Mr. S.K. Sett and Mr. P.L. Mehta in finalising the work. My thanks are also due to Dr. S.C. Rastogi, Dr. V.N. Sharma, Dr. M.C. Joshi, Dr. S. Bhambie, Dr. D.M. Dholakia, Mr. K.N.S. Nair, Mr. Viney Seth, Mr. M.P.G. Kutty, Mr. T.K. Kaul and Mr. B.L. Soni for their interest in the present studies.

I am thankful to Dr. C.R. Mitra, Director, Prof. A.K. Datta Gupta, Dean of the Faculty of Science, and Dr. H.L. Kundu, Head of the Department of Biological Sciences, for facilities and encouragement and to the Birla Institute of Technology and Science for the award of a UGC Jr. Fellowship.

The materials for the investigations have been procured through the co-operation of Mrs. B. Vasanthakumari (Nagercoil), Mr. C.P. Gopala Pillai (Ezhamkulam), Mr. P.S. Damodaran Pillai (Konni), Dr. A. Bhakthavalsalam (Parakode), Mr. Baby Chacko (Nadumkunnam), Mr. Joe Jacob (Kottayam) and Mr. M. George Abraham (Renny) to whom I extend my thanks. The co-operation received from the Rubber Board and the Rubber Research Institute of India is gratefully acknowledged. I am thankful to the Rubber Research Institute of Malaysia and the Rubber Research Centre of Thailand for valuable literature, which otherwise would have been difficult to consult.

I appreciate the encouragement I received from my wife and children which had been a constant source of inspiration. I express my gratitude to my mother, brothers and sisters who encouraged me to complete this work. The advice and help I received from my father-in-law deserve special acknowledgement.

August 21, 1974.

21.8.1974

(A. Omkaranatha Panikkar)

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CHAPTER 1

INTRODUCTION

1.1 General

1.2 Laticifers

1.3 Latex

1.4 *Hevea brasiliensis* Muell. Arg.

1. INTRODUCTION

1.1 GENERAL

Hevea brasiliensis Muell. Arg. is the most important commercial source of natural rubber - a product of vital importance, recovered from the latex. 12,500 species belonging to 900 genera (Esau 1965a), distributed predominantly to about twenty families (Metcalfe 1966, 1967), are reported to contain latex. Though these plants are mostly dicotyledonous, a few monocotyledons like *Allium cepa* (Hoffman 1933) and members of Alismataceae and Butomaceae (Stant 1964) and one genus of Pteridophytes, *Regnellidium* of the Marsiliaceae (Mahabale 1949), also come under this group. Laticiferous plants range from herbaceous annuals to large trees and occur in all parts of the world.

Although laticiferous plants are of considerable importance only very few of them have received some attention. Even in *Hevea brasiliensis* most of the anatomical studies have been general, being centered around the bark, that too largely on the number of laticiferous rings. Our understanding of the structure and organisation of the tree is still obscure. The present investigation has been taken up as an attempt to bridge some of the lacunae in *Hevea* anatomy.

1.2 LATICIFERS

The term 'laticifer' has been derived from 'latex' (L.)* meaning juice. Laticifers are specialised latex bearing cells or tissues, that are generally tubular in appearance. These may be simple and unbranched or may form very complex tissue systems from initially simple structures. Members within a family normally show only one type of laticifers, although species of certain families, like the Euphorbiaceae, contain different types of laticiferous systems.

Laticifers are grouped into two major classes (DeBary 1884) on the basis of their structure. These are (a) the articulated laticifers** and (b) the non-articulated laticifers**.

(a) The articulated laticifers are compound in origin and consist of longitudinal chains of cells in which the end walls of individual cells either remain intact, or become perforated or are completely dissolved, to develop into long tube-like vessels joined end to end. Depending on the presence or absence of lateral connections they are further grouped into:

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*The term 'lactifer' derived from 'lac' (L.) meaning milky has also been used in the early days, but 'laticifer' and its adjective 'laticiferous' are more correct, since latex need not necessarily be milky in appearance.

**The articulated laticifers and the non-articulated laticifers have been formerly termed as 'laticiferous vessels' and 'laticiferous cells' in the early literature.

(a.1) articulated non-anastomosing laticifers, which are not connected laterally, and

(a.2) articulated anastomosing laticifers, which develop lateral connections with similar cells or tubes to form a reticulum or net like structure.

(b) The non-articulated laticifers show simple origin. From single cells, through continued growth, they develop into tubes like structures without undergoing fusion with other similar cells. Depending on their complexity two sub-groups could be recognised among the non-articulated laticifers:

(b.1) non-articulated unbranched laticifers, wherein the laticifers develop into long more or less straight tubes, and

(b.2) non-articulated branched laticifers, where the laticifers branch repeatedly, each cell forming an immense system of tubes.

1.3 LATEX

The term 'latex' has been first introduced by Lindley (1848) to designate the milky juice of plants. The latex, contained in the laticifers, is a hydrosol consisting of a liquid matrix with organic particles in suspension. The matrix may be regarded as the cell-sap or ground plasm of the laticifer (Frey-Wyssling 1935, 1973). It contains various substances like carbohydrates, organic acids, salts,

alkaloids, sterols, fats, tannine, mucilage, etc., in solution and in suspension. The dispersed particles commonly include essential oils, balsams, resins, camphors, carotenoids, rubber, etc. (Bonner and Galston 1947). In many species rubber is a characteristic component, its amount in latex varying from negligible to as high as 50 per cent. Latex, in addition, may also contain proteins (Ficus callosa), alkaloids (Papaver somniferum), sugars (members of Compositae), tannins (Musa spp.), enzymes (Carica papaya), vitamins (Euphorbia sp.), starch grains and crystals. The colour of latex also shows wide variation from clear (Morus, Nerium) to milky (Asclepiss, Euphorbia, Ficus) or white to yellow (Hevea), or yellowish brown (Cannabis) or golden yellow to orange (Papaveraceae).

The suspended rubber particles vary in size and shape. They are more or less spherical reaching upto 0.75 microns in diameter bounded by a 100 Å lipoprotein layer (Andrews and Dickenson 1961). Southern (1960) considers that smaller rubber particles enclosed within a common membrane also occur in latex. Small rubber particles of 500 Å-1000 Å occur in latex of young Hevea trees and show an apparent composite structure consisting of particulate inclusions of approximately 50 Å-80 Å which are regularly arranged (Dickenson 1968).

1.4 HEVEA BRASILIENSIS MUELL. ARG. (EUPHORBIACEAE)

The genus Hevea comprises nine species, namely H. benthamiana, H. brasiliensis, H. camporum, H. guianensis,

H. microphylla, H. nitida, H. pauciflora, H. rigidifolia and H. spruciana (Schultes 1970). Although all the species contain laticifers of the articulated anastomosing type, only H. brasiliensis is of commercial importance since the latex content of the other species is not economical for exploitation.

The rubber plantation industry is only about a century old and H. brasiliensis is the most recently exploited major crop of the world. The tree is a native of the hot damp forests of Amazon, S. America, and has been introduced to the Eastern hemisphere by Sir Henry Wickham in 1876, with the seeds he brought from Brazil and grown at Kew (Hill 1952).

A sturdy, tall and quick growing tree, H. brasiliensis grows on many types of deep and well-drained soils. It thrives in varying climatic conditions, but a warm, humid, equiable climate (21°C to 35°C) with a well-distributed rainfall (not less than 200 cm) would provide optimum conditions of growth. The leaves are trifoliate with long petioles. Mature trees show annual leaf-fall during December to February in S. India, where it is mostly grown. Refoliation and flowering follow wintering.

The flowers, arranged in panicles, are small, fragrant and unisexual; both male and female flowers occur on the same panicle. The female flowers are borne on the tips of the main and major axes of the inflorescence and are bigger in size compared to the small, numerous male flowers. The fruits

have a period of about five months' maturity, after fertilization, and are usually three-seeded. When mature, they burst, scattering the seeds upto 15-20 metres distance. The seeds are big, about 4-5 gm in weight, have a hard, brown coat with mottlings and possess an oily endosperm.

The rubber tree is propagated by seeds as well as through budgrafting. The tree has an immaturity period of six to seven years, by which time it attains tappability. During the early days of exploitation, wild trees belonging to many species were the only source of natural rubber, which steadily declined with the introduction of Hevea as a plantation crop. During the First World War there had been acute shortage of natural rubber supply, which resulted in active exploitation of wild rubber as well as other rubber yielding plants like Castilla elastica, Funtumia elastica, Taraxacum kok-saghyz, etc., and gave a boost to Hevea plantations. Subsequently there had been such a phenomenal development in Hevea plantation industry that during the Second World War 98 per cent of world's rubber output came from Hevea alone. Careful investigations on planting, propagation, tapping, processing and disease control measures coupled with long term breeding and manurial programmes have resulted in substantial increase in the production potential. Presently Hevea brasiliensis is grown mostly in Malaysia, Indonesia, Sri Lanka, Vietnam, Khmer, India, Brazil and the African countries.

The crop is cultivated over an area of 59,50,000 hectares on the globe. The total production of natural rubber during the year 1972-73 has been 31,25,000 M.tonnes (Rubber Board 1974). India has approximately 3.41% of the total area under natural rubber and contributes about 3.29% of the world production.

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CHAPTER 2

REVIEW OF LITERATURE

2.1 Laticiferous Species - General

2.2 Euphorbiaceae

2.3 *Hevea brasiliensis* Muell. Arg.

2. REVIEW OF LITERATURE

2.1 LATICIFEROUS SPECIES - GENERAL

The earliest reports on laticifers are probably those of Dippel (1865) and Schmalhausen (1877), the former regarding the young tips of laticifers as penetrating in between the cells in the meristematic regions and the latter considering them to arise by cell fusion, followed by those of Scott (1882, 1884a,b, 1886). DeBary (1884) has noted that certain members of Aroideae have long laticifers whereas others lack them. Rendle (1889) and Weiss (1892) have reported laticifers of onion and Eucomia ulmoides respectively. Ross (1908) and Lloyd (1911) have furnished the earliest descriptions of the structure of Parthenium argentatum. Skutch (1927, 1932) has observed the development of laticifers of Musa sapientum. Solereder and Meyer (1928) have found that laticifers are present in certain genera of Araceae. Schaffstein (1932) has observed that in dormant meristematic tissues the laticifers are apparently quiescent and also that parenchyma cells adjacent to the articulated laticifers in certain Asclepiadaceae assume some of the characteristics of laticiferous cells. Hoffman (1933) has noted that the articulated laticifers of Allium consist of rows of cells whose end walls are pitted. Moyer (1937) has reviewed the physiology and

related aspects of latex. Artschwager (1943) has worked out the morphology and anatomy of Parthenium argentatum and Blaser (1945) those of Cryptostegia grandiflora. Milanez (1946) has found that the walls of laticifers are apparently nonlignified and plastic. Bonner and Galston (1947) have summarised the information on rubber synthesis in plants and Vreede (1949) has studied the laticiferous system in Ficus. Mahabale (1949) has noted the presence of laticifers in the inner cortex of stem and petiole of Regnellidium diphyllum (Marsiliaceae). Metcalfe and Chalk (1950) have listed the families in which laticifers are known to occur and given particulars thereof. Labouriau (1952) has also reported latex in Regnellidium. Mahlberg (1959a, 1961, 1963) has studied the development and related aspects of laticifers in Nerium oleander. Milanez (1960-61) has made further contributions to the anatomy of Cryptostegia grandiflora. Hu (1963) notes that the laticifers of Decaisnea fargesii, which are restricted to the fleshy fruit, are different from those of other plants. Kapoor and Sharma (1963) have studied the articulated laticifers of Argemone mexicana. Sarkany (1964) has observed those of Papaver somniferum at submicroscopic level. Sassen (1965) has investigated Achras sapota and Hammond and Polhamus (1965) have summarised researches carried on Parthenium argentatum. Chaudhuri (1966) has made a general comparative study of the bark of Ficus benghalensis and F. racemosa. Mahlberg (1966) notes a successive pattern of nuclear divisions resulting in mitotic waves in the laticifers of Euphorbia marginata. Rao and Malaviya (1966a,b) have

worked out the laticifers of Leptadenia reticulata and Tabernaemontan coronaria. Metcalfe (1966, 1967) has collated the information available on the distribution of latex in the plant kingdom and discussed the important aspects family-wise. Olson et al. (1969) have worked out leaf histogenesis and laticifer ontogeny in Lactuca sativa. Thureson-Klein (1970) notes that in Papaver somniferum laticifers differentiate only after germination of seeds. Alves et al. (1971) have discussed the laticifers in the leaves of Paullinia cupana and Valente (1971) has studied the petiole of Ditaosa edmundi. Seago (1971) has recently studied the primary roots of Ipomoea purpurea and noted immature laticifers in the radicular cortex. Contributions to the ontogeny of laticifers in Cantharanthus have been very recently made by Yoder and Mahlberg (1972).

2.2 EUPHORBIACEAE

Laticiferous members occur widely in the Euphorbiaceae and the laticifers belong to both the articulated (Hevea, Manihot) and non-articulated (Euphorbia, Jatropha) types. The latex of different species exhibit varied chemical composition.

Although Scott (1882, 1884a,b, 1886) has reported the occurrence of articulated laticifers in some genera in the third quarter of the 19th century, only limited work has been done on the laticiferous members of this family. Cameron (1936) opines that the laticifers of Euphorbia marginata are

of the non-articulated type. Vreede (1949) has also reported the non-articulated laticifers in Euphorbia spp. The generally accepted view that the laticifers of species of Euphorbia are non-articulated branched type has not been supported by Milanez (1952a,b) who reports that the tips of the young laticifers occupy cellular spaces and not intercellular spaces. Milanez and Neto (1956) say that in embryos of E. pulcherrima the laticifer system arises at predetermined points in the nodal planes of the cotyledons in the embryos. Moor (1959) has made ultra structural studies on the laticifer walls of E. splendens. Mahlberg (1959b) after studying embryos of E. marginata, in vitro, finds that the laticifers penetrate intrusively and occupy intercellular spaces, thus supporting the earlier view. Rao and Malaviya (1964) have found that the non-articulated laticifer in Jatropha first becomes apparent at the cotyledonary node. Mahlberg (1966) notes a successive pattern of nuclear divisions in the laticifers of Euphorbia marginata. Rao, Menon and Malaviya (1968) have found that laticifers in Euphorbia tirucalli originate at the embryonic stage and develop along with other tissues. Mahlberg and Sabharwal (1968) also note that the initials of the non-articulated laticifers of E. marginata arise in the cotyledonary node. Cass (1968) has initiated electron microscopic observations on the laticifers of Jatropha podagrica. The arrangement of laticifers in E. marginata and in E. supina has been studied by Scott (1968) and Rosowski (1968) respectively. Johnson and Thurston (1972) have made histochemical studies on the unusual epidermal mucilage cells of

Tragia ramosa and suggest that the mucilage is a breakdown product of the cell wall.

2.3 HEVEA BRASILIENSIS MUELL. ARG.

Though Scott (1886) and Calvert (1887) have recorded the presence of articulated laticifers in Hevea, investigations on the anatomy of the Para Rubber Tree began only during 1920s. The pioneering works of Keuchenius (1918, 1920), Bobilioff (1918a,b, 1920, 1923), Teves (1919), Stut (1919), Arisz (1919, 1921), Vischer (1920), La Rue (1921), Heusser (1921), Vischer and Tas (1922), Steinmann (1923), Bryce and Gadd (1924), Bally (1924), Taylor (1926), Quisumbing (1927), Ashplant (1928a,b,c, 1931), Sanderson and Sutcliffe (1929), Hoop (1931), Cramer (1931) and Frey-Wyssling (1931) could provide basic information on the presence of the latex bearing tissue system in the bark. Ashplant (1928b) has suggested that the width of the latex tube is correlated with yield but subsequent investigations (Cramer 1931) questioned its validity. Gunnery (1935) has given a description of the bark and noted that in a mixed population trees with sieve tubes of larger diameter as well as those with smaller bore occur, but that in all parts of the same tree sieve tubes are more or less of the same size. Van Aggelen (1948) and Ruinen (1950) have studied the petiole and Kaimal (1951) has furnished anatomical descriptions of the bark and latex vessels with notes on the exploitation of the trees by tapping. Bouychou (1952) has observed that when excised tissues were grown in vitro, they produced laticifers

capable of producing rubber. Electron microscope observations on the structure of young latex vessel and its contents (Andrews and Dickenson 1961, Dickenson 1965,1968) have also been recently undertaken. Nair and Abraham (1962) have studied the floral morphology of some members of the Euphorbiaceae, of which one is Hevea brasiliensis and Rao (1964) has given a brief account of its embryology. Peries and Satchuthananthvale (1966) have noted nodulation of wood and subsequent cracking of the bark. Gomez and Thai (1967) have showed that the wood and bark elements of the rubber tree have the same angle of deviation, from the vertical, which may vary from clone to clone. George, Panikkar and Nair (1967) have provided data on wintering, refoliation, sex ratio, anthesis, anther dehiscence, fruit set, etc., in several clones, which are useful in breeding procedures. Sulochanamma (1971) has outlined the various anatomical changes which result in the successful establishment of bud union. Panikkar (1971) has made a preliminary study of the tension wood in Hevea. Recently, Rao (1972) has discussed the periodic changes in cambial activity of rubber trees grown in Singapore.

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CHAPTER 3

MATERIALS AND METHODS

3.1 Materials

3.2 Fixatives

3.3 Processing

3.4 Staining

3.5 Maceration

3.6 Clearings

3. MATERIALS AND METHODS

3.1 MATERIALS

Hevea brasiliensis Muell. Arg., Clone Tjir 1 (Tjirandji 1), at appropriate stages for the present investigation, has been collected from different Districts of Kerala and Kanya Kumari District of Tamil Nadu. A primary clone of good vigour, growing well in many types of soils, Tjir 1 is a popular clone cultivated in many Districts. The trees have a heavy crown and the yield is good. Tjir 1 is a good seed parent as well.

3.1.1 Seeds and Seedlings

The seeds collected, after washing well in water, have been sown in trays with sterile river sand. The trays have been covered with coir mat and watered every morning and evening. The seeds which started sprouting from the sixth day onwards, have been raised in pots and fixed at appropriate stages for anatomical studies. Bark and wood of seedlings of one and two years growth have also been collected and fixed.

3.1.2 Mature Trees

Bark, wood and shoot apices, representing active and dormant phases of growth, have been collected from mature

(budgrafted) trees for the studies. Both virgin bark and renewed bark have been collected at appropriate stages as required in the studies. Bark measurements have been recorded using a Schleiper's Gauge.

3.2 FIXATIVES

The fixatives used are formalin-acetic-alcohol, formalin-propionic-alcohol (both with 50% as well as 70% alcohol depending on the nature of material) and 4% formalin. The former two have been used for materials employed for serial sectioning and the latter chiefly for free-hand sectioning. All the fixatives have given satisfactory results.

3.3 PROCESSING

The materials have been dehydrated, infiltrated and blocked in paraffin, through ethyl alcohol-xylene series as well as ethyl alcohol-tertiary butyl alcohol series. Sections have been cut at 8 to 12 micron thickness and serially loaded on slides. Free-hand sections have also been employed for the studies.

3.4 STAINING

For general observations safranin-light green, ferric chloride-tannic acid-safranin and crystal violet-erythrosin have been employed of which the latter has given excellent results especially in studying seedling vasculature.

Laticifers have been stained with Sudan IV and mounted in glycerine jelly after washing with 40% and 70% glycerine.

Congo red has been used for staining tension wood. The sections were mounted in euparal after dehydration.

3.5 MACERATION

Materials macerated with 12% chromic acid and 12% nitric acid, after boiling, have been used to s tudy the bark and wood. The process has been hastened by keeping the materials in the macerating mixture at 60°C.

3.6 CLEARINGS

For the preparation of cleared whole mounts a method employing both concentrated chloral hydrate and sodium hydroxide (20%) has been developed. Sodium hydroxide with basic fuchsin, at 60°C, followed by chloral hydrate at room temperature till the materials become transparent, followed by dehydration and mounting according to usual methods have given good results. Chloral hydrate, alternatively, could be employed first, followed by sodium hydroxide at 60°C, staining in 1% solution of basic fuchsin in 70% alcohol and dehydration and mounting. This method also has provided satisfactory results.

(Note: Specific methods adopted in studying certain aspects are described in the appropriate chapters.)

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CHAPTER 4

SEEDS AND SEEDLINGS

4.1 Seeds

4.2 Germination

4.3 Initial Growth

4.4 Seedling Vasculature

4. SEEDS AND SEEDLINGS

4.1 SEEDS

The mature seeds of Hevea brasiliensis are ovoidally elliptical in shape, being more or less squared at the ends and are dark brown. The seeds sometimes show slight variation in shape. The brown seed coat possesses mottlings, which are black in colour and irregular in shape (Fig. 42A,B). They converge towards the micropyle and the chalazal end are more or less aligned on the lines uniting these two. The adaxial side is more or less flat, with a depression at the distal end and has a prominent ridge extending from the micropyle to the chalazal pole (Fig. 42A). The abaxial side is convex. On an average the seed weigh 5.15 gm and have a length of 28.30 mm and a diameter of 22.25 mm at the broadest point. A summary of observations on seed weight, length, diameter and length/diameter (L/D) ratio is given in Table 1.

TABLE 1: Characteristics of seeds

	Mean	Minimum	Maximum
1. Weight (gm)	5.147	4.12	6.00
2. Length (mm)	28.300	25.50	30.00
3. Diameter (mm)	22.250	20.00	23.50
4. L/D ratio	1.263	1.21	1.31

The mature seed has a fully developed embryo, which measures on the average 3.058 mm in length and 2.094 mm in diameter. The length of the embryo has been found to range from 2.756 mm to 3.498 mm and the diameter from 1.855 mm to 2.332 mm. The cotyledons are large, 24.60 mm long and 16.80 mm broad, on the average, the range being 22.0 mm to 28.0 mm and 14.0 mm to 22.0 mm in length and breadth respectively. They have sheathing stalks, supplied by three traces. The endosperm is very massive and fills in the seed completely. The seed coat is heavily cutinised on the outer surface. The cells of the seed coat are several times longer than broad. The tegmen is a thin layer.

4.2 GERMINATION

The seeds retain viability for a short period only and hence sowing is necessitated within about 10-14 days after picking up from the seed collection areas, under normal conditions. Vivipary has been observed when there are showers during the seedfall season. The seeds start sprouting five to six days after sowing in germination beds. The mode of germination is hypogeal and the cotyledons never come out of the seed coat. The germination percentage is high and 85.0 per cent germination has been noted when the seeds are sown within seven to ten days after collection. The maximum number of seeds sprouted on a day has been the sixth after sowing. After the sixth day, the percentage of germination each day came down sharply and no seed sprouted after the 12th day. The total number of seeds sprouted has accounted to 86.5 per cent of the seeds sown (Fig. 1).

During germination, the radicle comes out first lifting the operculum and when it attains a length of about two mm, a number of primary lateral roots are produced. These

primary lateral roots* are arranged in a whorl, all of them arising from more or less the same level around the radicular axis (Fig. 46). The number of the laterals varies from seven to 18, the average being 12 (Fig. 3). Once the primary lateral roots emerge, the tap root undergoes rapid growth. Initially the primary lateral roots also show very rapid elongation. The lateral roots subsequently produced are irregularly arranged on the tap root.

Rapid elongation of the epicotyl at this stage of growth results in the formation of a hump. Subsequent straightening of the epicotyl effects the emergence of the plumule above the soil surface (Fig. 42C-G). Five to six days after germination promordia of the first and the second leaves are visible externally. A fifteen day old seedling has eight to ten leaves.

The cotyledons are opposite. The sheathing stalks of the cotyledons protect the embryonic as well as the emerging plumule. Although the first two leaves are apparently opposite initially, at right angles to the cotyledons, as the seedlings grow they are found about one cm apart. All the subsequent nodes bear only one leaf.

4.3 INITIAL GROWTH

The seedlings, soon after the emergence of the plumule, show rapid elongation and produce the first flush of leaves

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*The term primary lateral roots is employed to designate the first lateral roots, the primordia of which get differentiated at the embryonic stage.

and subsequently show only very slow growth. This stage is again followed by a rapid growth period, producing the second flush of leaves. The second flush of leaves appears in 20 to 22 days of sprouting.

Observations have been made on the growth of the seedlings during the first five weeks after sprouting. The mean cumulative growth and the growth increment, expressed as percentage of the final length attained by the shoot on the 35th day have been plotted in Fig. 2. The growth of the seedlings is rhythmic and the two peaks in the growth increment graph corresponds to the rapid growth phases, producing the first and the second flushes of leaves respectively.

Generally the seedlings do not show any branching during the first one or two years of growth. However, if the apical bud is damaged or removed, the axillary buds develop into branches. If the damage to the apical bud occurs before any leaves are produced, buds develop from the axil of both the cotyledons (Fig. 43A-D). In such cases only one shoot develops from the axil of each cotyledon and accessory shoots may develop from the first shoot. The shoots arising from the cotyledonary axils initially produce three to five scale leaves before the development of the regular trifoliate leaves. Some of these scale leaves bear axillary shoots also. In several such plants it has been found that the cotyledonary shoots pierce the cotyledonary sheath and emerge.

Scale leaves are generally not present on the healthy and vigorous seedlings. They are characteristically found

on new branches developing on older trees and are produced before the branches develop regular leaves. (Such scale buds from the green stems are used for green-budding on to tender seedlings and the budgrafts raised from them show more vigour compared to those raised from conventionally grafted scions.)

4.4 SEEDLING VASCULATURE

The vascular differentiation in the seedling is acropetal and proceeds towards the shoot and the root from the hypocotyl region. The nature of the seedling vasculature has, therefore, been studied towards the shoot and the root, taking the vascular structure at the cotyledonary node or just below as the base for tracing the relations. Seedlings collected three to five days after sprouting have been found to exhibit clear vasculature for the study.

The cotyledonary node has two sets of traces, one set supplying each cotyledon (Fig. 19). Each set is comprised of a median and two laterals (Fig. 44). The medians are smaller in size compared to the laterals. The cotyledonary traces, as they move out of the procambial cylinder, cause a gap and thus six gaps are formed. The cotyledonary node, thus, is trilacunar. Below and above the cotyledonary node the cylinder becomes continuous.

Seedlings of two to three days age are devoid of any traces other than the cotyledonary traces. In the older seedlings, four more strands are found to appear in the

procambial cylinder (Figs. 19,20). These four strands are arranged in two groups and are opposite to each other. They arise at right-angles to the cotyledons and originate at about 335.0 μ below the cotyledonary node. The two strands, in a group on each side, unite and form a single strand higher up in the epicotyl. One of these strands, in the course of development, becomes the median trace of the first leaf and the other that of the second leaf. It may be remembered (vide supra) that the first two leaves develop at the intercotyledonary plane, although they are not initiated simultaneously.

About 100.0 μ below the cotyledonary node the six strands coming from the cotyledons begin to divide, while the other four strands at the intercotyledonary plane do not undergo any change. The new strands formed as a result of the divisions get separated from each other (Fig. 21). Divisions, and the separation of the daughter strands, do not proceed simultaneously in all the six strands. One set of three strands, which deflects as the traces to one of the cotyledons shows division at about 95.0 μ below the cotyledonary node. The three strands of the other set start division only at 165.0 μ approximately. This is an interesting condition and would indicate that, although the cotyledons are opposite and arise from the same node, they are developmentally not identical with each other.

About 400.0 μ below the cotyledonary node the new strands become more apart from each other. They later become arranged

into twelve strands, within the procambial cylinder (Fig. 22). Each of these twelve strands is comprised of a median and two laterals, one on either side of the median.

The whorl of primary lateral roots is situated about 1,350.0 μ below the cotyledonary node. The twelve medians, with their centripetal xylem, depart as the supply to the primary lateral roots (Figs. 23,47). It is significant to recall here that most of the seedlings have twelve primary lateral roots (Fig. 3.). The development of seedling vasculature corroborates that twelve is the basic number of the primary laterals.

The lateral xylem of each group has a straight course to the tap root. Once the medians deviate as the lateral root supply, the lateral xylem of adjoining strands move close. This results in the formation of twelve strands, each being comprised of two lateral xylem (Fig. 24). The primary phloem which flanks the xylem groups centrifugally, as a result, get separated from the latter and lie on different radii in the roots.

As the strands move down through the hypocotyl to the root the centrifugal xylem obliterates and degenerates (Figs. 47,48). Concomitantly centripetal xylem differentiates from the periphery of the procambial cylinder of the root. These indicate a shift in the pole of xylem differentiation.

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CHAPTER 5

APICAL ORGANISATION

5.1 Radicular Apex

5.2 Apex of Seedling Root

5.3 Embryonic Shoot Apex

5.4 Shoot Apex of Seedlings

5.5 Plastochronic Changes

5. APICAL ORGANISATION

The mature embryo (taken out from seeds after the fruit has dehisced) has a pair of well developed cotyledons, an organised shoot apex and a radicular apex. The cotyledons are large and convoluted and have prominent veins. A procambial zone is differentiable in the embryo. This zone is circular in transectional appearance and ovoidal in longitudinal sections (Fig. 49). The cells of the procambium have denser cytoplasmic contents compared to the other cells. The cells are narrow and longitudinally elongated. The procambium forms a continuous hollow cylinder in the embryo as seen in transections, while in longitudinal sections it is continuous but at the plumular and radicular apices. Gaps are present where the cotyledonary traces depart from the procambial cylinder.

5.1 RADICULAR APEX

The radicular apex of the embryo is more or less flat (Fig. 50). The promeristem of the radicle is situated a few cell layers beneath the epidermis of the radicle. The cells of the promeristem have dense cytoplasm and large nuclei. Discrete histogens are not recognisable in the radicular apex and all the tissues appear to develop from a common histogen (Fig. 26). The cells produced by this histogen towards the distal end from four to five tiers of cells which constitute

the columella. Towards the body the histogen gives rise to the periblem and plerome. The cells constituting the plerome first undergo longitudinal divisions soon followed by linear divisions. The cells of the plerome, as a consequence, are arranged in longitudinal seriations. A diagramatic representation of the radicular apex is given in Fig. 25. The expansion of the tissues, in general, is very rapid at the radicular apex of the embryo. As a result, the proximal cells produced by the promeristem follow a semicircular configuration as the tissues converge to the radicular apex (Fig. 26). Initiation of the lateral roots is well pronounced in mature embryos. The promeristems of the lateral roots arise at the same level, arranged in a discrete row, and are thus produced in a whorl. The first lateral roots in Hevea brasiliensis are therefore primary in origin.

5.2 APEX OF SEEDLING ROOT

All the tissues of the mature root at the apex originate from the dermocalyptrogen (which gives rise to the root cap and the epidermis) and from the common group of initials for the cortex and the pith (Fig. 28). The apical organisation of the tap root and that of the lateral roots does not show any difference. A diagramatic representation of the root apical organisation is given in Fig. 27.

5.2.1 Root Cap and Epidermis

A well developed root cap is present in the mature roots (Fig. 51). The cap becomes discrete as the radicle emerges

out of the seed coat in about three to four days after sowing the seeds. The root cap is recognisable into two zones: the columella and the capflanks (Fig. 51). The columella originates, by linear divisions, from the central cells of the common histogen. It does not extend upto the tip of the root cap. The identity of the columella is lost after six to seven rows of cells from the dermocalyptrogen.

The peripheral cells of the common histogen for the epidermis and the root cap predominantly undergo anticlinal divisions in the beginning. While some of the cells produced undergo Kappe divisions subsequently and contribute to the capflanks, a single layer retains anticlinal divisions and differentiates into the epidermis of the root. The epidermis assumes characteristic organisation about 225 μ away from the initiating histogen. The cells of the capflanks are oriented in oblique rows and converge towards the columella.

5.2.2 Periblem

The common histogen for the periblem and the plerome consists of a group of isodiametric cells (Fig. 28), whose number varies from nine to thirteen. The cell lineage in the periblem, when traced forth to the histogen, shows a single cell in longitudinal sections. The daughter cells produced by this cell undergo periclinal divisions till the volume of the stele is made up. Once the cortex has widened sufficiently the cell divisions are mostly in the anticlinal plane only.

Both phloem and xylem differentiate acropetally. The protophloem differentiate earlier than the protoxylem. The first protophloem elements are recognisable 650 to 800 μ away from the histogen and the first protoxylem 1,200 μ to 1,500 μ distal to the histogen.

5.2.3 Plerome

The cells produced by the common histogen proximally differentiate into the plerome by further divisions. The daughter cells produced by the histogen towards the pith divide to a limited extent following the Korper pattern, initially. Subsequently they follow only linear divisions. The cells of the pith, as a result, are arranged in more or less regular longitudinal seriations.

5.3 EMBRYONIC SHOOT APEX

The shoot apex, of the embryo from a mature seed, has a two layered tunica (Fig. 52). Cells of the tunica layers are square in appearance. The cells of the outer tunica layer have prominent nuclei and dense cytoplasm. The outer tunica undergoes only anticlinal divisions of the cells and forms the epidermis of the axis and its appendages. The nuclei of the cells of the inner tunica are also prominent, but the cytoplasm of the cells is comparatively lighter stained. Cells of this layer undergo anticlinal divisions and occasional periclinal divisions. The inner tunica layer looses its identity at the base of the leaf primordia.

Beneath the tunica layers, there is a group of cells with prominent nuclei and light cytoplasm, forming the corpus. These cells are isodiametric and smaller than the cells adjoining. The number of corpus cells varies from thirteen to fifteen and they divide in all planes. The cells situated below the second tunica layer on either side of the corpus gives rise to the cortex. These cells first undergo an anticlinal division and the distal daughter cells further divide periclinally. Cells subsequently produced by these daughter cells also divide first periclinally and later anticlinally, to build up the volume of the cortex. Towards the body of the shoot the cells of the corpus give rise to the pith rib meristem.

The embryonic shoot apex is in the second plastochron (Fig. 52). The shape of the apex at this stage varies from more or less flat to dome shaped, depending on the stage of development. In the latter case, the height of the apical dome measures 15.0 μ and diameter 115.0 μ approximately. The length of the first leaf promordium ranges from 42.0 μ to 63.0 μ and that of the second from 35.0 μ to 45.0 μ.

5.4 SHOOT APEX OF SEEDLINGS

The shoot apex of the seedling is dome shaped (Fig.53) and shows a tunica corpus organisation (Fig. 30). The tunica consists of two layers and cells of both the tunica are square in shape. The cells of the outer tunica layer have dense cytoplasm, with large and prominent nuclei. These cells

undergo anticlinal divisions only, to give rise to the epidermis of the stem and of the foliar appendages. Inner tunica cells have large and distinct nuclei with lighter cytoplasm. At the summit of the shoot apex this layer undergoes only anticlinal divisions, but at the base of the shoot apex they undergo periclinal divisions also. The number of periclinal divisions are more, compared to the number of anticlinal divisions, during the initiation of the leaves. As a result, the outer tunica becomes a continuous structure whereas the inner one is discrete only upto the base of the apical dome. A diagramatic representation of the shoot apex is given in Fig. 29.

The cells of the corpus undergo divisions in all planes, although the divisions in all the cells do not proceed simultaneously. Therefore, the corpus cells are of varying size, but isodiametric with prominent nuclei and dense cytoplasm.

The corpus is differentiable into three zones. The cells just beneath the inner tunica layer are angular and shows divisions in all planes. Their number varies from thirteen to fifteen. This group of cells constitutes the central mother cell zone. The cells beneath this zone functions as the pith rib meristem. These cells first undergo a few anticlinal divisions and become longitudinally elongated. Subsequently, these daughter cells expand radially and undergo linear divisions only. The cells of the pith therefore follow a linear seriation away from the shoot apex. The pith rib meristem is surrounded by the flanking zone, whose cells

undergo periclinal divisions first, followed by anticlinal divisions. Subsequent divisions are both anticlinal and periclinal and the daughter cells produced differentiate into the cortex and the conducting elements. The outermost layer of cells produced by the flanking zone becomes more prominent in the course of development and forms the hypodermis of the axis. Vacuolation commences first in the cells produced by the pith rib meristem and subsequently in the others.

5.5 PLASTOCHRONIC CHANGES

The shape of the shoot apex shows periodic changes during plastochronic cycles. At the minimal phase of the plastochron (Figs. 31,55), the shoot apex is flat and has a width of 95.0 μ. This stage represents the maximum growth of the leaves of the plastochron before the initiation of the next primordium. The rapid growth of the leaves causes a longitudinal stretching of the tissues in general and as a result, one or two rows of cells beneath the second tunica layer also shows square to rectangular shape. The cytohistological zonation is not very distinct at this stage. The extent of the central mother cell zone and the flanking zone becomes reduced and both become situated in close vicinity of the apex. As the apex passes on from the minimal phase, the distal cells of the central mother cell zone becomes more active. The pith rib meristem and the corpus flanks also show divisions more frequently. These divisions contribute more cells in the shoot apex and lead to the elevation of the apical dome. The cytohistological zonations become

apparent as the apex enters the mid plastochron. Radial expansion of the cells in general takes place and the width of the apical dome at this stage measures 142.0 μ to 161.0 μ. The height of the dome varies as the apex enters into the maximal phase. At the maximal phase of the plastochron the shoot apex is a typical dome (Figs. 54,56), which attains a maximum height of 92.0 μ on the average. The zonations of the apex becomes distinct (Fig. 30) and the apex shows tunica corpus organisation (as described under 5.4). Initiation of the leaf primordium takes place at the maximal phase. Cells of the second tunica layer, near the periphery of the dome, undergo periclinal divisions, which are soon followed by anticlinal divisions in the daughter cells producing a group of cells. These cells cause more anticlinal divisions in the first tunica layer just above the leaf primordium. As the initiation of the leaf primordium advances, the cells of the first tunica layer as well as the primordium beneath them are raised above the shoot apex. The width of the dome at this stage of development is sharply reduced. As the leaf primordium continues to develop the apex enters the minimal phase of the plastochron. The initiation of the leaves takes place in quick succession and the plastochronic cycles are of very short duration, a cycle being completed in about 24 hours.

In Hevea brasiliensis the height of the apical dome varies in different plastochronic cycles. The measurement on the maximum height and width, given above, pertain to the fourth plastochronic cycle. In the first few plastochrons, the seedling shoot apex at the maximal phase is typically dome

shaped. In plastochrons related to the later formed leaves, the apical dome at the maximal phase is only slightly raised above the leaf primordia (Fig. 57). From the ninth plastochron onwards, the height of the apical dome does not exceed three to four microns. The width of the dome, however, remains more or less uniform through the different plastochrons of the seedlings.

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CHAPTER 6

PHYLLOTAXIS, NODAL VASCULATURE AND LEAF HISTOLOGY

6.1 Phyllotaxis

6.2 Primary Vasculature of the Axis

6.3 Nodal Vasculature

6.4 Leaf Histology

6.5 Venation Pattern

6. PHYLLOTAXIS, NODAL VASCULATURE AND LEAF HISTOLOGY

6.1 PHYLLOTAXIS

The trifoliate leaves, with entire leaflets, arise in close succession, during the active growth and come out in a flush. Their arrangement has been studied from serial transverse sections passing through several nodes.

The cotyledons are opposite. The first two leaves appear to be more or less opposite at first, arising at right angles to the cotyledons. During development, however, the two are separated. Subsequently, a node bears only a single leaf. The leaves are stipulate (Fig. 58). The arrangement of the leaves on the axis follows a spiral pattern. The spiral winds round the axis in anticlockwise direction towards the shoot apex and takes two complete rounds of the axis to connect two superimposed leaves, the number of intervening leaves being five. The phyllotaxis therefore, can be expressed as 2/5, according to the classical concept. A diagramatic representation of phyllotaxis is given in Fig. 32.

Any two superimposed leaves are five plastochrons apart, the sixth being five plastochrons older than the first, the seventh being five plastochrons older than the second and this sequence is maintained in the definite pattern. Five contact parastichies are observed connecting the leaves 0-5-10, 1-6-11, 2-7-12, 3-8-13 and 4-9-14. The line connecting

each of these parastichies wind around the axis anticlockwise. In addition to this, another set of contact parastichies is present connecting the leaves in the clockwise direction towards the apex. There are three contact parastichies in this set, connecting the leaves 0-3-6-9, 1-4-7-10, 2-5-8-11 respectively. The plastochronic interval between leaves connected by this clockwise contact parastichies is three.

In all thus there are two sets of contact parastichies, one winding around the axis clockwise and the other anti-clockwise. In the former, five contact parastichies are present while the latter has three. These two sets can be represented as 3+5 contact parastichies. The angular divergence between two successive leaves is approximately 136°.

6.2 PRIMARY VASCULATURE OF THE AXIS

The primary vasculature of the axis has been studied, in serial transections of very tender and vigorous shoots of a few days age, with a view to determining the interrelationship of traces. In very tender axis, five distinct sympodia are recognisable at the nodes. They send off vascular traces at the region of the nodes to supply the leaves, both laterals and medians, which leave the sympodia at regular levels. Each leaf is supplied by a median, an aradromic lateral and a katadromic lateral.

Taking any leaf on the axis as the base for understanding the interrelationship of the traces, it is found that its median lies just below or above the median of the sixth leaf.

The medians of the subsequent four leaves in order are related to the next fifth leaf respectively, in a similar manner. Each median is related to the laterals of the two leaves below. Of these two laterals, one is two nodes below and the other three nodes apart; the former being the katadromic and the latter the anadromic. The vertical course of the katadromic and the anadromic lateral is thus different. The katadromic lateral of any leaf is related to the anadromic lateral from the preceding leaf.

The relationship of various traces can be summarised as under:

M_1	M_2	M_3	M_4	M_5
KL_3	KL_4	KL_5	KL_6	KL_7
AL_4	AL_5	AL_6	AL_7	AL_8
M_6	M_7	M_8	M_9	M_{10}
KL_8	KL_9	KL_{10}	KL_{11}	KL_{12}
AL_9	AL_{10}	AL_{11}	AL_{12}	AL_{13}
M_{11}	M_{12}	M_{13}	M_{14}	M_{15}
KL_{13}	KL_{14}	KL_{15}	KL_{16}	KL_{17}
AL_{14}	AL_{15}	AL_{16}	AL_{17}	AL_{18}

In the summary above, the medians are designated M, katadromic lateral KL and anadromic lateral AL. The medians are numbered in their order of development from the youngest M_1 to M_{15} the oldest. KL and AL are also numbered similarly, corresponding to their relation with the median in their order of development.

The relationship of various traces to those above, taking one leaf as base and designated as 1, has been reconstructed from a series of transections and is diagramatically represented in Fig. 33.

6.3 NODAL VASCULATURE

The first strand to become prominent in the internodal region is the median. Its differentiations is followed by the development of two laterals one on each side. These three together diverge to the leaf at each node, leaving gaps in the procambial cylinder. Each lateral leaves a portion in the central cylinder, whereas the median enters the leaf completely. The node as a result becomes trilacunar.

As the traces move out towards the leaf, the two laterals divide and one branch on either side supply the respective stipule. The median strand, defined for the leaf, is composed of three traces (M_1, M_2 and M_3) as may be noted in Fig. 34. Of these the middle one (M_2) divides into three ($M_{2.1}$, $M_{2.2}$ and $M_{2.3}$) and the ones on either side (M_1 and M_3) into two each ($M_{1.1}$ and $M_{1.2}$; $M_{3.1}$ and $M_{3.2}$). The seven strands thus formed deviate towards the leaf base, and maintain the normal arrangement of the primary vascular elements, their protoxylem being adaxial (Figs. 34-37).

The two lateral strands (L_1 and L_2) undergo a series of modifications in their course from the axis to the leaf base (Figs. 34-38). Each divides first into two traces ($L_{1.1}$ and $L_{1.2}$; $L_{2.1}$ and $L_{2.2}$). Those away from the median ($L_{1.1}$ and

$L_{2.2}$) deviate towards the stipule on the respective side, each splitting into four or five traces by the time they become stipular supplies. The remaining two strands ($L_{1.2}$ and $L_{2.1}$) one each on either side move towards the median. During this process, their adaxial protoxylem swings towards the leaf axis. These traces, as they enter the leaf base, swing to such an extent that their protoxylem becomes abaxial with reference to the steam and adaxial with reference to the leaf axis or petriole. These strands undergo further divisions and more of abaxial traces are produced in the leaf base. A procambial crescent develops and amphivasal elements are also produced in between the traces (Figs. 38-40).

The vascular supply at the leaf base is thus semi-circular or crescent shaped. The outer portion is made up of adaxial strands while the inner portion, which bridges the gap between the two ends of the adaxial elements, is constituted by abaxial strands.

Figures 34-40 depict the changes taking place as the traces leave the cylinder and become leaf supplies. A diagramatic representation reconstructed from transections is presented in Figure 41.

6.4 LEAF HISTOLOGY

The vigorous shoot first develops three to five scale leaves before the regular trifoliate leaves are produced. These scale leaves also follow the arrangement typical of the foliage leaves on the axis. Their adaxial surface is glandular,

These cells are long and narrow. Occasionally, the scale leaves bear rudimentary leaflets. The stipules are small, free lateral and glandular. The adaxial surface of the stipules have a row of long and narrow cells, which become shorter towards the two sides and merge into the regular epidermal cells on the convex abaxial surface.

The petiole is long and cylindrical. In a flush of leaves, the oldest leaf has the longest petiole and the youngest the shortest. There is thus a reduction in the length of the petiole as the new leaves develop in a flush. As a result all the leaves in a flush get well exposed to the sun. The petiole has more or less the same structure from base to top. It has a vascular cylinder, which is complete, having both abaxial and adaxial vascular elements. Cambium is present between the xylem and the phloem.

Towards the tip, the petiole flattens and bears three petiolules. The middle petiolule has a straight course along that of the petiole, whereas the two lateral ones are diverged at about 90^{o} to the petiole. The tip of the petiole where the three petiolules are inserted is glandular. Externally these glands are slightly raised on the adaxial side. Usually there are three of them, oval to circular in shape, but may often fuse and form a glandular area of irregular shape. The glandular cells on the adaxial surface are narrow and long. Although they occur mostly in a single row, occasionally two to three rows also could be seen.

The petiolules are short. Their shape varies from circular to semicircular or laterally flat in transectional appearance (Fig. 59). Both adaxial and abaxial vascular elements are present in them which form a complete cylinder in the older petiolules.

The leaflets are entire. A thick cuticle is present on the outer surface of the upper and the lower epidermis. The cuticle of each cell of the lower epidermis has a thick ridge along its long axis in surface view. Several secondary ridges originate from this median ridge and tapers towards their termination in the margins of the individual cells. The cuticle is thus striated, on the abaxial epidermal cells, and forms a reticulate pattern (Fig. 60).

The cells of the upper epidermis are angular and that of the lower are wavy in outline as seen in surface view and in paradermal sections. There is only a single row of palisade layer, on the upper surface. The spongy layer has two to four rows of loosely arranged cells (Fig. 61). Stomata are of the paracytic or rubiaceous type and present on the lower surface. Each has a pair of subsidiary cells flanking the stoma.

The mid-vein is very prominent and abuts the lower surface and is more or less semicircular in transectional view. It has a deeply crescent shaped vascular cylinder (Fig. 62). The margins of this crescent has xylem elements throughout, with phloem occupying the adjoining peripheral area. A cambial layer is present in between the two (Fig. 62). The secondary veins also have a similar organisation (Fig. 63). The

subhypodermal cells undergo sclerification and form a lining layer of hard tissue in the midrib as well as in the major secondaries. This layer is three to five cells thick and is more developed on the adaxial side.

The latifiers of the stem, petiole, petiolules and laminae form a continuous system. In the petiole and the petiolules they are limited to the phloem zone. In the laminae also they occur in close association with the veins.

6.5 VENATION PATTERN

A number of strands are present in each petiolule and all of them enter the leaf base. The outermost ones on either side of the midrib deviate as a secondary in a regular pinnate manner (Fig. 64). Three or four strands in the middle have a straight course and terminate at the tip of the leaf. The secondaries bend acroscopically towards the one above, close to the margin, and form a single row of loops. Branches from the first row of loops form a second row of small loops very close to the margin of the lamina. Tertiaries and quarternaries are produced in order and form a reticulum. Intersecondary veins are also present, but they traverse only upto midway towards the margin, on either side of the mid-vein. The vein islet terminations are simple. The areoles are square to rectangular or nearly so in shape. Their size varies from 6,272 sq.μ to 17,248 sq.μ the average being 11,530 sq.μ.

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CHAPTER 7

BUD DORMANCY

7.1 External Morphology

7.2 Anatomical Features

7.3 Cambium and Cork Cambium

7.4 Cataphylls

7.5 Breakage of Dormancy

7. BUD DORMANCY

Hevea brasiliensis shows episodic growth. The tree is deciduous and normal wintering takes place, in South India, during December-January. During wintering the trees shed off all or almost all the leaves. Prominent scars are left on the axis as the leaves are shed off. In about two to three weeks time new flushes appear. New branches also appear from the axils of leaves already shed off and these also produce a fresh flush of foliage. After the formation of the fresh foliage the buds enter a period of apparent rest till the next refoliation period. The dormant buds are very hard in nature. (Buds have been treated with 50% hydrofluoric acid for two to three weeks before processing them for paraffin infiltration.)

7.1 EXTERNAL MORPHOLOGY

The initiation of growth, after dormancy, results in the production of a fresh flush of leaves. The shoot first develops a few scale leaves and subsequently the regular trifoliate leaves. As the leaves are produced, there is a marked reduction in the internodal length. The internodal length between the leaves produced during the beginning of the growth period is considerable, varying from 50.0 mm to 71.0 mm, while the distance between two successive leaves becomes insignificant from the thirteenth or fourteenth leaf and all the leaves appear to arise in very close proximity to each other on the

axis. The production of leaves during an active growth period is complete within a few weeks time. A tendency, similar to the telescoping of the nodes, is exhibited by the petiolar length and the size of the laminae. The petioles of the first formed leaves are markedly longer, while those of the later formed ones become gradually short. Similarly, the size of the lamina also shows a marked reduction. The last formed leaves have leaflets of the smallest size. After a flush of leaves are developed, the apical buds enter the period of rest.

7.2 ANATOMICAL FEATURES

As the apical buds enter the dormant phases, the size of the cells at the shoot apex showa gradual, but marked reduction. The apex remains almost flat and a number of cataphylls are produced (Fig. 65). The two tunica layers are distinct, but their cells are considerably smaller compared to those of the tunica layers of a vigorous shoot apex. Divisions in the tunica layers are restricted to the flanks. The cells of the central mother cell zone and the flanking zone are closely appressed to each other. All the cells of the apical region possess denser cytoplasmic contents. Linear divisions in the cells produced by the pith rib meristem and divisions of the cells developed by the corpus flanks become less frequent as the buds enter the dormant phase. While there is radical expansion of the cells in general in the subapical region, the apical group of cells does not show a similar tendency. As a result, the cells in

general and those of the cortex in particular, gradually converge towards the shoot apex (Figs. 66,67). The cells of the pith rib meristem, as a result, show a few rows of cambial like cells below the shoot apex. All the cells produced by the apical meristem undergo early vacuolation.

The shoot apex of a dormant bud is situated in a cavity formed by the development of the cataphylls (Fig. 67). The outermost cataphylls are raised up more compared to the level of insertion of the ones close to the apex. Six to seven rows of cells at the apex have a tunica like appearance. However, only the outer two rows are true tunica layers. The cells of these two layers are slightly larger compared to the other cells of the apex. The outer walls of the outer tunica cells have a thick layer of cuticle. The cells of the central mother cell zone are angular and longitudinally compressed. This is a feature common to the cells of the pith rib meristem and of the flanking zones. The cells of the two tunica layers show limited divisions, whereas the frequency of divisions in the central mother cell zone, flanking zone and the pith rib meristem is negligible.

A cork cambium is initiated at the zone of suberisation of petioles. The cork cambium gives rise to three to four layers of rectangular cells which are heavily suberised and form a protective tissue (Fig. 68). The petiolar traces become completely blocked by cell depositions and their identity remains obscure (Fig. 69). Protective tissue of a similar nature is formed in the case of the stipules as well.

7.3 CAMBIUM AND CORK CAMBIUM

The cambium at the shoot tip does not appear to produce any secondary xylem and secondary phloem tissues during the period of dormancy. The tissues which have already been produced by the vascular cambium undergo maturation. The secondary phloem and the secondary xylem which are maturing are thus very close to the cambium, often adjoining the latter on the outer and the inner side respectively (Fig. 70). The structure of the typically dormant bud indicates that at the onset of the rest period the cambium produces sieve elements and xylem vessels. Differentiated xylem vessels and sieve elements are very close to the apex, both being recognisable about 180.0 μ away from the outer surface of the outer tunica layer. The vascular cambium, though it does not produce any new elements radially, to the outer side and the inner side, extends longitudinally and converge to the shoot apex. The fusiform cells of the cambium are traceable to the base of the youngest cataphyll and lie in close proximity to the promeristem of the differentiating cataphyll.

A remarkable feature of the dormant bud is the development of a cork cambium (Figs. 70,71). As the detaching zone of the leaves and the cataphylls are not close to their respective base, the cork cambium appears to arise deep in the cortex of the shoot apex. However, the cork cambium is traceable back to the hypodermis of the axis. Towards the shoot tip it traverses through the base of the leaves and the cataphylls, and bends acroscopically, following a course similar to that

of the vascular cambium, and extends upto the base of the second youngest cataphylls (Fig. 71). At this level the cambium and the cork cambium are very close to each other, the two often being separated only by one or two layers of cells. The cells produced by the cork cambium are narrow and more or less rectangular. The youngest cells of the cork cambium, very close to the summit of the apex, are fusiform in appearance. Cells of the phellem are suberised. There are no indications of a second cork cambium developing at the apical axis during the dormant phase.

7.4 CATAPHYLLS

The cataphylls are initiated by the second tunica layer, by periclinal divisions at the tunica flanks. These periclinal divisions are soon followed by anticlinal divisions in the cells of the outer tunica just above. The daughter cells produced by the outer tunica cells become the epidermis of the cataphylls.

The cataphylls show a relatively simple structure. The epidermal cells on the abaxial side is square to rectangular in the young cataphylls. As the cataphylls grow older, these cells undergo anticlinal divisions and radial elongation of the daughter cells. The outer surface also becomes heavily cutinised. The adaxial epidermis develops simple, glandular trichomes by the periclinal divisions of its cells and the elongation of the outer daughter cell (Figs. 66,74). The glandular trichomes are thin walled and short lived. These

are soon severed off by the suberisation of the cross wall at the base. The adaxial epidermis also thus becomes square to rectangular in shape, subsequently followed by the formation of a heavy cuticle on the outer surface. The hypodermal cells on the adaxial and abaxial surface are square in shape. There is no sharp demarcation among the other cells of the cataphylls. The cells are hexagonal in shape and vary in size. Vascular elements are not well developed; a single trace supply each cataphyll (Fig. 72). Two to three rows of cells, beneath the adaxial epidermis, are narrow and elongated and are continuous with the cambium of the axis. Some of the younger cataphylls, developing towards the latter part of the dormant phase have an adaxial row of glandular cells (Fig. 72). The older cataphylls are sloughed off by the heavy suberisation of the cells beneath the detaching zone. This zone is situated at about two thirds from the base of the cataphyll and is comprised of two to three layers of cells. The cells of this zone are rectangular and they occasionally undergo periclinal divisions, and form a thick protective tissue (Fig. 73).

7.5 BREAKAGE OF DORMANCY

As the dormant phase comes to a close, the shoot tip, instead of producing the cataphylls, gives rise to three or four scale leaves (the origin of the scale leaves being similar to that of the cataphylls) followed by the formation of the regular leaves. The cells at the shoot tip enlarges and their cytoplasm becomes lighter compared to the cells at the dormant period. Anticlinal divisions in both the tunica layers become very frequent. The cells of the central mother

cell zone undergo divisions in all planes and the flanking zone and the pith rib meristem resume their characteristic pattern of cell divisions.

Activity of the central mother cell zone is initiated in the cells which are two layers beneath the second tunica. In buds which are just breaking dormancy, the central mother cell zone appear as a compactly arranged group, the cells of which are smaller than the adjoining cells above and below. Cells of the central mother cell zone and those of the flanking zone are more or less of the same size.

Initiation of the meristematic activity at the apex, culminates in the rapid development of a mass of new cells. Along with the rapid development of these new cells at the shoot apex, the cambium and the cork cambium are pushed back (Fig. 74). The cells of the cambium and the cork cambium become more separated as more and more cells are produced by the flanking zone. The shoot tip, as result of the increased mitotic activity, grows in length and the apex gradually is elevated (Fig. 75). Some of the cataphylls remain at the base of the newly formed shoot, but these are sloughed off soon.

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CHAPTER 8

BARK ANATOMY

8.1 Sampling Specificity

8.2 External Morphology

8.3 Structure

8.4 Expansion Tissues

8.5 Sclerosis

8.6 Lenticels

8.7 Periderm

8. BARK ANATOMY

8.1 SAMPLING SPECIFICITY

Samples for the studies on bark* have been taken representing three stages of development: (a) the very tender bark of four to five days of growth; (b) the young brown bark of about six to seven months of age; (c) the mature bark. Entire twings have been used to study the tender and the brown bark. For studies on mature bark samples of approximately 5×3 cm size have been taken out from the trunk.

A preliminary observation has been carried out, with respect to the mature bark, to assess whether there are any variations in samples collected from different sides of the same tree. Samples for this observation have been taken at 0/360°, 90°, 180° and 270° around the trunk. Thickness of bark, proportion of hard bark and soft, total number of latex vessel rings and their distribution have been found to be the same on all the four samples of the same tree provided the height of sampling is the same. For detailed observations on the mature bark samples have, therefore, been taken out from trees of approximately fourteen years of age and comparable growth, at a height of 125 cm.

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*The term bark is used to designate all the tissues outside the vascular cambium collectively (Esau 1965a, 1967; Fahn 1967). Specific terminology has been employed wherever needed.

8.2 EXTERNAL MORPHOLOGY

The tender bark is green, or green with a brownish tinge. The twig bears a flush of leaves with drooping leaflets. As development and differentiation of tissues proceed, the colour of the bark turns to brown and the leaflets become rigid and well exposed. The leaves are shed when they are about nine to ten months old. The leaf scars remain prominent on the mature bark. Lenticels develop in the brown bark. They are diffuse in arrangement.

Very old trees have rough bark on the trunk, the bark being more rough towards the base. Often shallow fissures are also found on the old trees, especially near the base of the trunk.

The thickness of the bark varies with the age and vigour of the trees. Tender twings of an average diameter of 6.15 mm has bark which is 0.37 mm thick. In one year old stems of average diameter 24.0 mm, the average bark thickness is 0.86 mm. The bark of trees which are six and nine years of age measures, on the average, 7.25 mm and 10.05 mm respectively, at 125 cm height. Bark of even very well developed branches is comparatively less thick than that of the main trunk.

8.3 STRUCTURE

The structure and organisation of the bark differ at different stages of development. These development stages can be grouped into three: (a) the tender, smooth bark which

contains only the primary tissues, (b) the brown bark which cohtains the primary and secondary tissues, and (c) the mature bark which has a well developed periderm and rhytidomes. Anyway, there is no sharp delimitation of these developmental stages andone stage merges into the other as growth and development advance.

8.3.1 Tender Bark

The tender bark of a very active and vigorous shoot, of only a few days of age, contains only the primary tissues. The epidermis is single layered and has a thick cuticle on its outer surface. The cells of the epidermis are rectangular. Stomata are present on the epidermis. The hypodermis has two to three layers of cells. The cells of the hypodermis and those of the primary cortex are photosynthetic. The sieve tubes are pentangular in transectional appearance, accompanied by companion cells which are smaller. A single row of companion cells are associated with a sieve tube and their number ranges from three to five per sieve tube length. There is a row of laticifers occurring beneath the hypodermis. These primary laticifers, arranged in a single row, are separated from each other by intervening cells of the cortex. They are of the anastomosing type and develop lateral connection between them. A pericycle is not well defined in the initial stage, but it becomes discrete as the primary tissues mature. Most of the cells of the pericycle begin sclerification when the bark is still tender (Fig. 76). The adjoining cells of the cortex also become sclerified (Fig. 77). The cells of the

cortex are tangentially elongated and contain rhomboidal crystals.

8.3.2 Brown Bark

The tender bark sooner or later gradually becomes brown in colour. Development of the lenticles could be noted when the bark is about seven to eight weeks of age. The brown bark contains the primary tissues on the outer region and secondary tissues inside the former.

Sieve tubes have dense parietal cytoplasm with oblique sieve plates. Nuclei are absent. Each companion cell has a distinct nucleus and dense cytoplasm. Phloem fibres are rare. The vascular rays of the secondary phloem belong to the uniseriate, biseriate and triseriate categories. Parenchyma is relatively abundant. Secondary laticifers of the anastomosing type also occur in the brown bark. The number of rows of the secondary laticifers varies depending on the extent of secondary growth. Sclerosis, development of lenticels and formation of periderm are phenomena associated with the maturation of the tender bark and are described separately.

8.3.3 Mature Bark

The mature bark has an inner zone which is soft and an outer zone which contains the harder tissues. Most of the functional elements of the secondary phloem occur in the

soft bark region. The hard bark develops well defined periderm and tissues get isolated towards the outermost portion forming thytidomes.

The soft bark contains the sieve tubes, companion cells, secondary laticifers, phloem parenchyma and vascular rays. The characters of these elements could be best studied in the soft bark only, since in the hard bark they become obliterated. On the average the soft bark constitutes 42.6% of the total thickness of the bark as estimated from transverse and longitudinal sections.

8.3.3-1 Sieve tubes

The sieve tubes are about seven to twelve times longer than broad. Sieve plates are compound, with a row of sieve areas (Fig. 78), and are steeply oblique (Fig. 79). The angle of inclination of the sieve plates to the horizontal axis of the sieve tubes varies from 70° to 80°, the average being 75°; or in the other words, they are inclined to the longitudinal axis of the sieve tubes at an angle of 15° on the average, the range being 10° to 20°. The individual sieve areas are elliptical and opposite. The longest one is in the middle and the number per sieve plate varies from seven to eleven (Fig.78). The average length of the sieve tube is 427.0 µ the range being 294.0 µ to 588.0 µ. Maximum number of sieve tubes have a range of 400-500 µ in length. 36% has a length of 300-400 µ and two per cent, between 200-300 µ. The distribution of sieve tubes into different groups on the basis of length is shown in Figure 4. Sieve tube diameter varies from 18.0 µ to 84.0 µ, with the average diameter of 60.66 µ. 38% belong to the

frequency class 25-50 μ in diameter, 36% to the class 50-75 μ and 26% to the class 75-100 μ. A diagramatic representation of their distribution on the basis of diameter is given in Figure 5.

In the hard bark region the sieve tubes and the companion cells loose their identity due to the pressure exerted by the tissues developed by the cambium and the periderm and by the development of the masses of stone cells. They get crushed, tangentially stretched and become nonfunctional.

8.3.3-2 Phloem Parenchyma

The phloem parenchyma occurs in narrow bands. The cells are angular in appearance and are arranged compactly without any intercellular spaces. Many cells contain rhomboidal crystals.

Towards the hard bark region the cells of the parenchyma undergo sclerification. Within the hard bark they occur as masses of stone cells. The masses are very hard and many of the individual stone cells contain rhomboidal crystals. These hard tissues disrupt the regular arrangement of the tissues in the periphery of the soft bark, as the latter develops into the outer bark.

8.3.3-3 Vascular rays

The vascular rays of the mature bark are one, two, three or four cells wide, in the tangential extent (Fig. 80). The multiseriate rays are either triseriate or four-seriate. The

number of rays per mm ranges from nine to thirteen, the average being 10.84. 48% of the rays belong to the triseriate type and 24% are biseriate. The uniseriate and four-seriate rays constitute 14% each. The distribution of the phloem rays into different categories is given in Figure 6.

The ray cells are rectangular to hexagonal in shape and are heterogeneous (Fig. 80). The individual cells of the rays extend longitudinally along the radius of the axis. The height of the rays rangesfrom 196.0 μ to 812.0 μ, the average height being 485.0 μ. Average ray width is 52.15 μ and the and the range 14.0 μ to 84.0 μ. Distribution of rays into different classes of width and height is presented in Figures 7 and 8 respectively.

The uniseriate rays have a large conical or dome-shaped end cell at both the ends. The height of the uniseriate rays ranges from 196.0 μ to 490.0 μ. The average height is 295.4 μ. Width of the uniseriate rays ranges from 14.0 μ to 35.0 μ, the average width being 22.4 μ.

The biseriate and multiseriate rays have one, two or three upright cells at the proximal and distal ends. The body cells are all procumbent and are compactly arranged. The top most cells, on either end of the uniseriate portion are dome shaped or conical and usually large (Fig. 81). The height of the biseriate rays range from 224.0 μ to 574.0 μ and the width from 42.0 μ to 56.0 μ. The mean height and the mean width are 421.4 μ and 49.7 μ respectively. The triseriate rays have an

average height of 611.8 μ and an average width of 60.2 μ, the range being 280.0 μ to 812.0 μ and 49.0 μ to 70.0 μ respectively. The average height and width of the four-seriate rays are 613.2 μ and 76.3 μ respectively. The range in ray height is 336.0 μ to 840.0 μ and that in ray width 70.0 μ to 84.0 μ.

8.3.3-4 Obliteration of tissues

The tissues towards the periphery of the bark are subject to pressure. Continued activity of the cambium and growth in diameter cause considerable pressure from within and the tissues get tangentially stretched. The development of periderm and activity of the phellogen produces more tissues on the periphery. The phelloderm, produced internally by the phellogen, exerts pressure on the tissues from the periphery. This results in a compression of the primary phloem tissues and the secondary phloem tissues situated abaxially. The presence of hard masses of brachysclereids in the hard bark region causes the pressure to affect the soft tissues. As a result the nonlignified tissues of the primary phloem and those of the secondary phloem situated abaxially are crushed. These tissues become obliterated and ultimately loose their identity in the outer bark region.

8.4 EXPANSION TISSUES

Secondary growth and production of phloem tissues externally results in the tangential stretching of the cortical tissues in general. To keep pace with the growth in diameter

more tissues are produced by the pericycle, cortical parenchyma and vascular rays.

The cells of the pericycle which do not undergo early sclerification are the ones which give rise to the expansion tissues of the pericycle. These divide anticlinally and give rise to more cells. These parenchymatous tissues, formed as a result of pericyclic expansion, are however converted into sclereids later. The cells of the cortex also divide anticlinally, once or more than once, and the circumference of the cortex increases to some extent. The divisions and production of more tissues of the cortex increase with the increase in diameter of the axis. Almost all the rays of the phloem undergo expansion. The primary causes of ray expansion is the widening of the axis, in general. This is followed by anticlinal divisions of some of the ray cells. In the outer bark region dissection of the rays become common. The uniseriate, and the multiseriate rays undergo splitting and the two ray groups get separated by intervening parenchyma (Fig. 81).

Due to anticlinal divisions of some of the ray cells, many cells in the body of the phloem rays are smaller (Figs. 80,81). The presence of rays with large and small body cells are more frequent in the outer portions of the inner soft bark. Most of the four seriate phloem rays are also situated near the periphery of the soft bark.

8.5 SCLEROSIS

Development of sclereides takes place when the bark is still young. The first tissue to undergo sclerosis is the

pericycle. Most of the cells of the pericycle start developing lignified walls and this is followed by the conversion of the cells of the adjoining layers of cortical parenchyma into sclereids.

More cells are produced by the cells of the pericycle which retain their primary structure (Fig. 77). Some of the cells of the cortical parenchyma also undergo anticlinal divisions. Most of these cells are also converted into sclereids. The sclereids developed from the pericycle and the adjoining layers of the parenchyma form a discrete and continuous structure in bark which is of few months' growth (Figs. 76,77).

Subsequently sclerification takes place in the parenchyma cells of the cortex. A group of parenchyma cells undergo sclerification and get transformed into a mass of hard sclereids. In the course of development, more parenchyma cells situated deep in the cortex undergo sclerification.

Some of the cells of the vascular rays of the secondary phloem are also converted into sclereids. The stone cells which are found in the cork region originate from the phellogen of the periderm. The stone cells are characterised by a very thick lignified cell wall and narrow lumen (Fig. 82). The deposition of the secondary wall is more or less even and the wall thickness shows uniformity throughout. The pits are simple and rhomboidal crystals are very often found in the lumen.

8.6 LENTICELS

The lenticels are small and plenty. Their number varies from three to six per square mm. The well developed lenticels project out on the surface as small protuberances. They are predominantly found on the mature brown bark. The lenticels first appear before the development of the periderm is initiated (Fig. 83). The first formed lenticels arise beneath the stomata. Subsequent ones develop in between the stomata and are irregularly scattered over the entire surface of the bark.

The first indication of the development of the lenticels is the irregular divisions of the parenchyma cells in the substomatal chamber. These divisions produce a small group of loose tissues (Fig. 83). The cell divisions subsequently become restricted to the subphypodermal layers, and finally are restricted to a single layer and become oriented periclinally. This layer functions as the lenticel phellogen. The loose tissue produced towards outside constitute the complementary tissues. They rupture the epidermis and project out.

Well developed lenticels are more or less circular in surface view. Their size is highly variable depending on the stage of development. The aperture may be as small as 157.0 μ in diameter in the lenticels found on the very young bark. The well developed ones, found on bark, about two years of age, have an average aperture-diameter of 795.0 μ.

8.7 PERIDERM

The first phellogen is superficial (Fig. 84) and, to begin with, arises in localised strips. It is initiated in the subepidermal layer of the hypodermis and soon forms all along the entire circumference. Cells of this layer first divide periclinally forming two daughter layers. The outer layer matures first and forms cork or phellem. The cells of the inner layer undergo one more periclinal division. The adaxial layer gives rise to phelloderm, whereas the abaxial layer functions as the phellogen. The activity of this phellogen layer produces layers of phellem towards the outer side and phellogen. The activity of this phellogen layer produces layers of phellem towards the outer side and phelloderm towards the inner side.

The cells of the phellem, phellogen and the phelloderm are arranged in regular radial seriations, and are rectangular in shape. The cells of the phellem, however, are later compressed and become tangentially flattened. Phelloderm cells are thin walled, and each has dense cytoplasm and a prominent nucleus. The cells of the phellogen are also thin walled and possess well developed nucleus and dense cytoplasm. Additional layers of phellogen develop in the secondary phloem (Fig. 85). These originate as isolated strips in the phloem parenchyma cells. However, they soon unite and replace the first phellogen. The outer tissues, separated by the periderm tissues subsequently formed, constitute the rhytidome layers. The rhytidome layers are ultimately sloughed off.

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CHAPTER 9

BARK REGENERATION

9.1 Significance of Regenerated Bark

9.2 Methods

9.3 Nature of the Tapping Cuts

9.4 Process of Regeneration

9.5 Extent of Regeneration

9. BARK REGENERATION

9.1 SIGNIFICANCE OF REGENERATED BARK

The economic life span of Hevea brasiliensis is about thirty five years and the regenerated (renewed) bark is as valuable as the virgin bark, in the commercial exploitation of the trees.

In the case of seedling trees, the first tapping panel* (Panel A) is opened at 50 cm height and the second (Panel B) on the opposite side at a height of 100 cm. The third panel (Panel C) is opened above the first, at 100 cm height and the fourth (Panel D) on Panel B, at a height of 100 cm. The seedling trees thus provide about 200 cm of virgin bark for the commercial exploitation of the trees. The system adopted for the seedling trees is half spiral, third daily (S/2 d/3; 67% intensity)**, with an annual bark consumption of approximately 15 cm. The virgin bark thus provides enough bark for

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*The part of the tree over which tapping cut is slowly moving down, with every tapping, is called panel.

**Tapping systems are abbreviated according to internationally accepted notations. Length of the cut is expressed as the fraction of the total circumference of the tree: S/1 denotes a full spiral cut; S/2 a half spiral one; S/3 a one-third spiral cut etc. Frequency of tapping is indicated by the symbol 'd' and a figure denoting the number of days in which the cut is opened once: d/1 means tapping every day; d/2 every second day; d/3 every third day etc. The notation also gives the relative intensity, which is calculated taking S/1 d/1 cut as 400 per cent tapping intensity (Guest 1939a,b; RRIM 1940; Paardekooper and Ratana 1969; Panikkar 1969).

exploitation for about thirteen years, after which tapping is resumed on the regenerated bark. In the case of budgrafted trees, both panels A and B are opened at 125 cm height, on the opposite sides of the tree, and the subsequent panels on the regenerated bark also are opened at a height of 125 cm, in the sequence. The tapping system adopted is half spiral alternate daily (S/2 d/2; 100% intensity) with the annual bark consumption being twenty to twenty two cm. The virgin bark is consumed in about twelve years after which exploitation has to be continued on the regenerated bark. Thus part of the third and the whole of the subsequent panels of a seedling tree and the whole of the third and the subsequent panels of budgrafted tree are entirely on the regenerated bark. The yield on tapping the regenerated bark is thus commercially as important as,if not more than, that on the virgin bark.

Two attributes which are very important in tapping are the thickness of the bark and the number of laticiferous rings. The former is important in the efficient exploitation of the trees, a thick bark being easier to be tapped. The number of rows of the laticifers within the bark, on the other hand, is an important factor governing the yield obtained from the trees.

9.2 METHODS

The present study of bark regeneration, includes a detailed observation on the process of regeneration and a

quantitative assessment of renewal over a period of six years. Mostly free hand sections have been employed for the study.

Two characters taken as bases for the quantitative assessment are the thickness of the regenerated bark and the number of rings of the laticifers it contains. A comparison has then been made with reference to the respective character, at a height of 125 cm, of the virgin bark.

Thickness of the bark has been measured at two points near the middle region of the regenerated bark and on two points on the virgin bark of each tree. The number of rows of laticifers has been determined from free hand sections of the respective sample, after staining them with Sudan IV. This assessment has been made on five trees from the first to the sixth year of regeneration.

9.3 NATURE OF THE TAPPING CUTS

Exploitation of the rubber trees for the collection of crop is done through a unique operation, by tapping. The aim of tapping is to cut open the latex vessels, which are filled with latex under hydrostatic pressure. As the laticifers are opened, the pressure within them is released at the point of severing and the latex flows out of them. The initiation of flow concomittantly results in the displacement of more latex, along the length of the laticifers, towards the cut surface due to the high cohesive forces existing in the liquid phase. Eventually the latex in the vessles becomes

diluted due to osmosis from the surrounding tissues of the bark and results in a consequent increase in the rate of flow of latex. The latex flow continues for about three hours, after which it stops. It is explained that the subsequent disturbances in the osmotic concentration in the laticifer would cause damage to the lutoid particles of the latex within the laticifer, culminating in the plugging process of the severed laticifer ends (Rubber Board 1974) and eventual cessation of latex flow. This process is repeated at the time of every tapping.

During tapping a thin shaving of the bark, of approximately 1.25 mm to 1.75 mm in the thickness, is removed to open up the laticifers. This eventually removes the plugs of coagulated latex at the ends of the laticifers previously cut. The tapping cut is obliquely horizontal, being made from high left to low right, along half the circumference of the trees (Fig. 86). In the case of seedling trees, the cut is made at a slope of 25° to the horizontal, while in budgrafted trees the cut is a little more steep being at an angle of 30° to the horizontal as the bark is comparatively thinner compared to that of the seedling trees.

A vertical channel, from the lower end of the tapping panel of approximately 15 cm long is made to direct the latex flowing along the cut surface downwards. A spout is fixed at the lower end of this vertical groove, below which is placed the collection cup supported by a cup hanger. Half split coconut shells are cleaned and used as collection cups in our

Country. The latex which exudes flows along the tapped panel and in turn through the vertical channel and the spout, and drips into the collection cups. This in turn is collected from all the tapped trees in a block, when the flow ceases, for processing.

The same cut is then reopened during the subsequent tappings, at definite intervals depending on the tapping system followed. As the lower end of the cut reaches near the ground level a fresh panel is opened for further exploitation of the trees. The tapping cut is made deep into the bark, reaching very near the cambium. The innermost portion of the soft bark, about two mm in thickness adjoining the cambial layer, is however left uncut (Fig. 87). Hence, the cambium and a small portion of the inner bark usually remain intact after tapping. If the tapping is very deep, it often causes major injury to the cambium, which results in the development of woody burrs, as a response to wounding, and tapping on the regenerated bark becomes very difficult. It is important that the tapping cut is deep and close to the cambium, as far as practicable, in obtaining proper yield from the trees. Occasionally minor ~~changes~~ damages are caused to the cambial layer when the tapping is sufficiently deep and efficient from the exploitation point of view, even when the job is executed by very skilled and experienced tappers.

Tapping is done with a knife especially designed for the purpose. The knife has two sharp cutting surfaces: one which makes the transverse cut of the bark and the other which

makes a vertical cut at right angles to the transverse cut. The latter severes the bark through the inner soft bark, parallel to the periphery of the wood in general. The two cuts together separates the shaving of bark consumed in every tapping operation.

9.4 PROCESS OF REGENERATION

The immediate effect of tapping is a shrinkage in the outermost cells of the bark on the wounded surface which are ruptured due to wounding (Fig. 88). This starts soon after tapping and these cells undergo necrosis (Figs. 88,89). The cells immediately below these enlarge and undergo one or two divisions in irregular planes. Soon, however, the divisions become oriented parallel to the cut surface. The hypodermal or occasionally the subhypodermal layer of the cells assumes rectangular shape and develop prominent nuclei (Fig. 90). Cells of this layer start functioning as the phellogen. The phellogen, thus developing on the cut surface, functions in a manner similar to the normal cork cambium of the untapped bark tissue and gives rise to the phellem towards the periphery and phellogen centripetally.

The parenchyma cells and the cells of the vascular rays of the cortex beneath the cut surface also undergo changes simultaneously with the development of the wound periderm. These cells, which belong to the soft bark region, enlarge in size and divide rapidly. The cells, produced as a result, become lignified and develop into stone cells (Fig. 90).

Sclerification is limited to the derivatives of the cells in the immediate vicinity of the wounded surface of the bark. As such the masses of sclereides are confined to the outermost region of the regenerated bark and are compactly arranged. Development of a periderm and formation of the sclereides take place in about ten to twelve days after tapping injury is caused.

The periderm of the renewed bark and that of the virgin bark meet in the course of development at the point where injury has been caused. This usually takes place only in the upper level of the panel as the tapping panel moves to the base with every tapping.

Subsequently fresh cork cambia differentiate below the first, as the bark undergoes continued regeneration (Fig. 90). As the second and subsequent periderms develop the first wound periderm is thrust to the periphery. Consequently, the first periderm develops shallow fissures and is sloughed off.

There is absolutely no indication of any sieve tube or latex vessel differentiating from the derivatives of the phellogen. The laticifers as well as the sieve tube of the regenerated bark differentiate from the vascular cambium in a manner similar to the situation in the virgin bark. The laticifers keep continuity within the renewed and the virgin bark along its longitudinal course. The tangential anastomoses are also continuous with vessels of the same laticifers ring. The sieve tubes, in a manner similar to the former are also continuous structures. The laticifers and the sieve elements

of the virgin bark which are severed during tapping are pushed to the periphery by the active development of tissues by the vascular cambium and degenerate in course of time.

A remarkable feature of the regenerated bark is the delimitation of the sclereids to the periphery. The thickness of the soft bark in the regenerated bark naturally increases as the period of renewal is more. The hard bark also follows a similar trend; but this, however is predominantly due to the production of tissues by the wound phellogens. The extent of hard bark, therefore, is comparatively much lesser in contrast to the virgin bark. As a result most of the new laticifers produced by the vascular cambium in the regenerated bark remain functional and the extent of their degeneration is very much less in sharp comparison to the situation in the virgin bark.

9.5 EXTENT OF REGENERATION

As all care is taken not cause damage to the cambium (as explained above), the cambium and the adjoining portion of the soft bark are left uncut during tapping (Fig. 87). The bark left uncut also forms a portion of the regenerated bark, and in the quantitative assessment of the extent of regeneration, the values on the thickness of the bark and that on the total number of laticiferous rows include the respective features in the bark left uncut as well. It was therefore desired to observe the thickness of the bark left uncut and the number of laticiferous rows it contains in a few trees. The

thickness of the soft bark left uncut mainly depends on the skill and efficiency of the tapper, although other factors like hardness of the bark, length of the tapping cut and the rate of bark consumption may also influence it. Samples of the bark left uncut with a portion of the untapped virgin bark below attached to it have been taken from ten trees, a few hours after the cessation of the latex flow. The total thickness of the bark, the thickness of the bark left uncut, total number of laticifer rings and the number of rows unsevered have been determined from radial longitudinal sections of the samples.

The thickness of the bark left uncut varies from 1.25 mm to 2.23 mm, the average for the trees observed being 1.72 mm. Considering in terms of the total thickness of the bark, whose average has been 9.67 mm (ranging from 7.48 to 10.25 mm), 17.79% of the bark remains uncut after tapping. The total number of laticiferous rings in the whole bark varies from sixteen to twenty two (average 17.79) and the number of unsevered laticiferous rows it contains has been 6.50 (average), the number varying from four to nine. In terms of the average number of laticifer rings in the whole bark, that in the bark left uncut on tapping accounts for 35.33%. In other words, only about 65% of the laticifer rows are opened on tapping, the remaining 35%, which are close to the cambium, being left unexploited. Considering the longitivity of the trees and the question of continued exploitation throughout the economic life span, total extraction of the crop through tapping is an impracticable event.

9.5.1 Bark Thickness

The mean thickness of the regenerated bark varies considerably, depending on the period of regeneration. Regenerated bark of one year's renewal has an average thickness of 4.98 mm and that regenerated over a period of six years 8.75 mm. The virgin bark, at 125 cm height, of the trees observed has a mean thickness of 9.35 mm. A summary of observations is presented in Table below.

TABLE 2: Thickness of regenerated bark

S.No.	Description	Mean	Range
1.	Girth (cm)	71.90	62.00-82.50
2.	Virgin bark: thickness (mm)	9.35	7.38-10.25
3.	Regenerated bark: thickness (mm)		
3.1	Regenerated over 1 year	4.98	3.00-5.88
3.2	Regenerated over 2 years	5.88	3.50-7.50
3.3	Regenerated over 3 years	6.48	3.88-8.00
3.4	Regenerated over 4 years	7.16	4.63-8.25
3.5	Regenerated over 5 years	7.91	5.88-8.75
3.6	Regenerated over 6 years	8.75	6.75-9.50

The thickness of regenerated bark increases gradually as the period of renewal increases. Bark regeneraed over several years is found to be thicker than the virgin bark of the same tree at a height of 125 cm.

The thickness of the virgin bark also has a definite influence on the extent of regeneration as assessed from bark

thickness. Those with a thick virgin bark show rapid regeneration after tapping compared to the trees with thinner virgin bark, as may be seen from the following table.

TABLE 3: Thickness of virgin bark and regenerated bark

S. No.	Thickness of virgin bark (mm)	Thickness (mm) of bark regenerated over					
		1 year	2 years	3 years	4 years	5 years	6 years
1.	10.38	5.50	7.50	8.00	8.25	8.75	9.50
2.	10.25	5.75	6.25	7.25	8.13	8.75	9.25
3.	9.75	5.50	7.50	8.00	8.25	8.75	9.50
4.	9.00	4.75	5.75	6.25	7.00	7.78	8.25
5.	7.38	3.00	3.50	3.88	4.63	5.88	6.75

The observation on the thickness of the regenerated bark (Table 2) can be expressed in terms of the virgin bark thickness at 125 cm height (Table 4). Taking the latter as 100.00%, the total thickness of regenerated bark during the first year after tapping is approximately 53%. The total thickness of the renewed bark regenerated over a duration of two, three, four, five and six years represents 62.89, 69.30, 76.58, 84.60 and 93.58 per cent respectively of the virgin bark thickness. The results are summarized in Table 4.

TABLE 4: Extent of regeneration in terms of bark thickness

S.No.	Nature of bark	Period of renewal (years)	Extent of renewal in terms of the thickness of virgin bark (per cent)	Actual renewal pertaining to each year (per cent)
1.	VB	-	(100.00)	-
2.	RB	One	53.26	35.47
3.	RB	Two	62.89	9.63
4.	RB	Three	69.30	6.41
5.	RB	Four	76.58	7.28
6.	RB	Five	84.60	8.02
7.	RB	Six	93.58	8.98

VB - Virgin bark RB - Regenerated bark

Though the extent of regeneration, in terms of the total bark thickness, during the first twelve months period is 53.26% of the virgin bark, it does not exclusively represent the bark of an year's regeneration; but represents the residual bark as well as the regenerated bark. About 18% of the bark is left uncut (vide supra) and making allowance for this, the actual thickness of the first year regenerated bark is about 35% in terms of the virgin bark thickness. This indicates that the initial response to wounding caused by tapping is very high. Subsequently, this response is not that pronounced. The thickness of bark regenerated from the second to sixth year represents, on the average, 8.06% increase annually in terms of the thickness of the virgin bark (Table 4).

9.5.2 Laticifers

The renewal in terms of the regeneration of laticifers also follow a similar trend. Compared to the total number of productive laticiferous rows of the virgin bark (average 17.00) that in the regenerated bark is 8.40, 11.40, 13.80, 15.80, 16.60 and 17.20 in the bark renewed over 12, 24, 36, 48, 60 and 72 months respectively. The mean number of laticiferous rows and the range have been given in Table 5.

TABLE 5: Number of laticifer rings in the regenerated bark

S.No.	Descriptive	Mean	Range
1.	Girth (cm)	71.90	62.00-82.50
2.	No. of laticifer rings in virgin bark	17.00	14-21
3.	No. of laticifer rings in regenerated bark:		
	3.1 One year	8.40	7-10
	3.2 Two years	11.40	8-12
	3.3 Three years	13.80	10-16
	3.4 Four years	15.80	12-18
	3.5 Five years	16.60	14-20
	3.6 Six years	17.20	15-20

Considering the number of rows of laticifers in the virgin bark, at 125 cm height, as base (100.00%) the number of rows of productive laticifers in the regenerated bark of one, two, three, four, five and six years represents 49.41, 67.06, 81.18, 92.94, 97.65 and 101.18 per cent respectively.

The number of rows of laticifers in the residual bark accounts for 35.33% of the total number of productive ones and the renewal in terms of the number of laticifer rows regenerated during the first year represents only 14.08%. The results are summarised in Table 6.

TABLE 6: Extent of regeneration as assessed from the number of laticifer rings

S. No.	Nature of bark	Period of renewal (years)	Extent of renewal in terms of the laticifer rows in the virgin bark (per cent)	Actual renewal pertaining to each year (per cent)
1.	VB	-	(100.00)	-
2.	RB	One	49.41	14.08
3.	RB	Two	67.06	17.65
4.	RB	Three	81.18	14.12
5.	RB	Four	92.94	11.76
6.	RB	Five	97.65	4.71
7.	RB	Six	101.18	3.53

The regeneration of laticifers in response to wounding is high in the initial three to four years during which period the number of laticifer rows in the regenerated bark tends to be closer to that in the virgin bark. Thereafter there is a gradual decline in the number of laticifer rows produced, in the regenerated bark, per annum. It is significant to recall from Tables 5 and 6 that the total rows of productive laticifers

in the regenerated bark exceed their number in the virgin bark by the end of six years. In bark regenerated over several years this tendency continues and the number of laticifer rings outnumber that in the virgin bark. As sclerification, by which the outer laticifers are degenerated, is restricted to the periphery alone in the regenerated bark, the number of new laticifers differentiating from the derivatives of the vascular cambium is much more than that rendered unproductive.

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CHAPTER 10

LATICIFERS

10.1 Origin and Development

10.2 Distribution

10.3 Degeneration and Regeneration

10. LATICIFERS

The laticiferous system of Hevea brasiliensis comprises of primary and secondary laticifers. The primary laticifers have an embryonic origin, while the secondary laticifers develop along with the secondary phloem. The laticifers permeate the organs of the plant body in close association with the phloem elements. In the axis they are restricted to the bark. Very rarely isolated laticifers occur in the pith. Such laticifers are branched and occur singly. In contrast to those in the bark, there laticiferous cells do not form a continuous system nor do they develop anastomoses. From the commercial point of view only the laticifers of the bark are important.

10.1 ORIGIN AND DEVELOPMENT

The primary laticifers originate from the procambium of the mature embryo and their initials occur at the hypocotyl region. The initials are situated at about the periphery of the procambial cylinder and their number is variable. They occur in a single row and are separated from each other by the other cells of the procambium. The laticifer initials are angular in transectional appearance and contain dense cytoplasm and well developed nuclei.

As the embryo enlarges the primary laticifer initials become conspicuous by their larger cell size. Their angular

appearance in transverse view is also lost and they become more or less round. Compared to the adjacent cells, there is an increase in the wall thickness of the laticifers. Soon, longitudinal and tangential extension of the laticifers takes place. The longitudinal extension results by the differentiation of the procambial cells adjoining above and below the developing laticifer into laticifer initials and the subsequent dissolution of the cross wall separating the former with the latter (Fig. 91). The tangential extension is brought about by the intrusive growth of the laticifers and subsequent dissolution of the cross wall, as they come in contact with parenchyma cells of the procambium. The intrusive growth is preceded by the development of small lateral protuberances on the laticifer, which find their way through the procambial cylinder (Fig. 92). The laticifers at this stage of development are not of uniform diameter through their length (Figs. 91,92).

The secondary laticifers originate from the cells produced by the vascular cambium externally (Figs. 93,94). Some of the cells developing from the fusiform initials differentiate into laticifers. Initially it is difficult to distinguish between the cells differentiating into the laticifers and those developing into sieve elements. The laticifer initials, however, show slow dissolution of their end walls, in their longitudinal course. They are not of uniform diameter, often being wider at places where they enlarge prior to intrusive growth. The sieve tubes, on the contrary, do

not exhibit wide variation in the diameter. Development of the sieve plates, which are steeply oblique, also marks the identity of the sieve tube in contrast to the more or less transverse end walls of the developing laticifers.

The extension of the laticifers of the bark longitudinally and tangentially follow a pattern similar to those of the primary laticifers. During the tangential extent, the laticifer initials first develop branches which arise as small protuberances. These protuberances develop at right-angle to the differentiating laticifer, but soon become oblique. As they come into contact with the intervening parenchyma cells of the cortex, the cross walls separating the two get dissolved and the parenchyma cells also get transformed into a part of the laticiferous system. As a result, the laticifers form interwoven connection in between them (Fig. 95). The laticifers thus form long and continuous structures throughout the length of the tree, as growth and development proceed.

The wall of the laticifer is composed predominantly of cellulose as revealed by staining reactions and is plastic. The cytoplasm is parietal and the nuclei prominent in young laticifers. As the cells unite in the tangential and longitudinal directions with the subsequent dissolution of their end walls, they are coenocytic in nature.

10.2 DISTRIBUTION

The element of the bark and wood do not have a straight vertical course, even in the trunk of perfectly straight trees.

They show an angle of inclination from the vertical, which varies near vertical (negligible angle of inclination to the vertical) to 14.0°, in the anticlockwise direction, from base upwards.

The number of laticiferous rows in the bark is variable depending on the conditions of growth. Trees with comparatively large diameter and thicker bark have more number of laticiferous rows. The total number of rows varies from elevel to twenty one in the bark of 13-14 year old trees. In transverse sections of the bark, the laticifers appear in discrete rows which are concentric. In radial longitudinal view they appear as straight tubes, more or less parallel to each other as well as to the wood and bark surface (Fig. 87). The tangential longitudinal sections of the bark, the anastomoses of the laticifers look like an expanded mesh being composed of the vascular rays and parenchyma of the bark (Fig. 95).

The number of anastomoses of the laticifers belonging to a ring, as observed from tangential longitudinal sections of the bark, varies from 98 to 124 per square mm (average 114.8) at the inner part of the soft bark. Towards the outer zone of the soft bark their number is less, ranging from 82 to 98 (average 89.4) per square mm. This reduction in number is an expression of the expansion of the tissues of the bark, including that of the phloem rays, which effects a tangential stretching of the laticiferous vessels as well.

Laticifers of different trees show variation in diameter from 36.0 μ to 56.0 μ, the average being 48.6 μ. The laticifers

of a single tree do not, however, exhibit marked variation in diameter. Of the total number of laticifer rows, approximately 73.0% occur in the soft bark region and remaining in the hard bark zone. The laticifers of the soft bark are continuous and productive.

10.3 DEGENERATION AND REGENERATION

In the hard bark region, the thin walled laticifers are crushed by the pressure exerted by the stone cells and the tissues developed by the cambium and the cork cambium. In the periphery of the bark the latex vessels become shrivelled up and discontinuous. These degenerated laticifers, occurring in the hard zone, are not productive. The first laticifers to get obliterated are the primary ones which occur near the periphery of the bark. As sclerification proceeds deep into the bark, the course of the secondary laticifers nearby is disrupted and they also loose the longitudinal and tangential continuity.

As the cambium continues to produce the secondary tissues, more laticifers are developed in the secondary phloem. Their initiation and development follow the pattern described already (vide supra). The rate of regeneration is more than the rate of degeneration. Hence, as the trees grow more, the number of laticifers in the bark also increases.

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CHAPTER 11

WOOD ANATOMY

11.1 Sampling Specificity

11.2 General Features

11.3 Wood Fibres

11.4 Vessel Elements

11.5 Xylem Parenchyma

11.6 Vascular Rays

11.7 Variations along the Radius

11. WOOD ANATOMY

11.1 SAMPLING SPECIFICITY

Samples for the studies on wood anatomy have been taken from mature healthy trees of about fourteen years of age. A preliminary observation has been carried out to avoid errors due to sampling. For this purpose wood samples of approximately 2×2×2 cm size have been taken at 0/360°, 90°, 180° and 270° around the trunk after debarking. The observations have shown that fibre length, fibre diameter, vessel distribution, vessel length and vessel diameter are comparable in all the four samples of the same tree, provided the height of sampling as well as the relative position of the sample (distance from the pith or the periphery) are the same. For detailed observations samples have been collected at a height of 125 cm from trees of the same age. They have been collected after debarking, at a depth of one cm from the periphery of the wood. In addition, variation of wood characteristics at different relative positions has also been studied. Five samples each, at different relative positions on the same radius and level have been taken from four mature straight growing branches for the observation.

11.2 GENERAL FEATURE

Secondary thickening in Hevea brasiliensis starts when the seedlings are only a few days of age (Figs. 76,93). Although

the pith is massive and well defined composed of thin walled hexagonal cells (Fig. 93) in the tender branches, it becomes crushed when growth in diameter takes place. As a result the massive wood completely obliterates the pith and the latter looses its identity.

The wood is diffuse porous (Fig. 96). The vessels are solitary or occur in radial multiples or radial-tangential aggregates (Figs. 96,101). They have long tails mostly on both the proximal and distal ends. The perforation plates are simple and vascular pitting alternate. Apertures are oblong and borders angular (Fig. 97). Tyloses are commonly present, especially in the older vessels, and seen throughout its length in such vessels prepared by maceration (Figs. 100, 101). Tracheids are very rare and those present have simple pits which are oblique. Fibres are nonseptate, with tapering ends (Fig. 98). One or two layers of fibre cells are sometimes smaller in their radial extent and appears like growth rings, in transections of samples of older wood. Vascular rays are mostly biseriate, their proximal and distal ends being uniseriate and elongated. Parenchyma is sparse. Those present are apotracheal extending in between vascular rays in uniseriate, biseriate or triseriate bands.

11.3 WOOD FIBRES

The wood fibres are long, several time longer than broad (Fig. 98). They are arranged in regular radial seriations. The pits to fibres are few, minute and simple. The

fibres appear square to rectangular in transverse sections, are nonseptate and appear clean. The wall is of almost uniform thickness throughout. In mature fibres of the fibre walls measure 3.7 μ in thickness and lumen 26.8 μ in diameter. on the average. Those fibres which occur in the tension wood, however, have a massive tertiary wall which almost completely fills the lumen.

The length of the fibre varies from 901 μ to 1325 μ, the average being 1127 μ and diameter ranges from 21 μ to 42 μ, the mean diameter being 32 μ. The length/diameter ratio also show a similar range, the mean, minimum and maximum being 35.1, 25.0 and 58.0 respectively. 85 per cent of the fibres measure 1001 μ to 1300 μ, the percentage of fibres falling into each frequency class of 100 μ within this range being almost the same (Fig. 9). About 90 per cent of the fibres have a range of 20 μ to 40 μ in diameter (Fig. 10) and maximum percentage of fibres (47%) fall under the frequency class 31-40 as regards the length/diameter ratio (Fig. 11). The average length/diameter ratio is 35.10.

11.4 VESSEL ELEMENTS

The vessel elements, which have simple perforation plates and alternate pitting, show a good range of variations with regard to the size and the presence of the tails and its extent when present. Apertures of the alternate pittings are oblong and they are arranged more or less transversely (Fig. 97). They measure 1.7 μ in diameter and 10.8 μ in length, on the average; the range being 1 μ to 2 μ and

8 μ to 14 μ respectively.

The perforation plates are transverse to steeply oblique and consequently show a wide range as regards their angle of inclination, with respect to the horizontal axis of the vessels (Figs. 98, 99, 100). In those with transverse perforation plates, the perforation plate is more or less along the horizontal axis, i.e. the angle being zero (Fig. 98). The angle of the steeply oblique ones (Fig. 99) measures upto 78^{o} to the horizontal axis. Many vessels have their perforation plates showing the intermediates between these extremes.

The distribution of vessels per unit area, observed from transverse sections, shows an average of ten vessels to a square mm, the minimum number being $7/mm^2$ and the maximum $24/mm^2$. They occur mostly in radial multiples and solitary and a few in radial-tangential aggregates. The vessel arrangement into solitary, radial multiples and aggregates occur in the proportion 36.0:48.6:15.4. The number of vessels in a radial multiple ranges from two to five and that in an aggregate three to nine.

Average length of the vessel is 716 μ, the range being 518 μ to 994 μ. 30% of them are less than 600 μ long and 54% more than 700 μ. The distribution of vessels in different frequency classes of length is shown in Fig. 12. The vessel diameter ranges from 70 μ to 196 μ, the mean being 123 μ. Their distribution in different frequency classes is shown in Fig. 13. Concomitantly there is a fair range in the length/diamter ratio of the vessels as well (Fig. 14).

The tails form a conspicuous part of the vessels. 85% of the vessels have tails at both the ends whereas 15% have a tail only at one end. Records on the length of the body and the tails show that the body constitutes approximately 83 per cent of the vessel and the remaining portion the tail.

Based on the diameter and total length, the vessels can be grouped into four types: (1) short and narrow, (2) short and broad, (3) long and narrow, and (4) long and broad (Fig. 15). The vessels belong to the medium* category with regard to diameter as well as length. The long and narrow vessels are more abundant (34.0%). The results are summarized in Table 7.

TABLE 7: Vessels of Hevea brasiliensis

S.No.	Length	Diameter	Relative abundance (%)
1.	Medium short (less than 716 µ)	Medium narrow (less than 123 µ)	22
2.	Medium short (less than 716 µ)	Medium broad (more than 123 µ)	24
3.	Medium long (more than 716 µ)	Medium narrow (less than 123 µ)	34
4.	Medium long (more than 716 µ)	Medium broad (more than 123 µ)	20

*Vessel length medium: 350 to 800 µ according to Metcalf and Chalk (1950) and 400 to 800 µ according to Rodriguez (1957)

Vessel diameter medium: 100 to 200 µ according to Dadswell and Eckersley (1935) and Chalk (1938)

Tyloses are commonly present and in many cases they are found all along the length of the vessel elements (Figs. 100,101). Vessels with tyloses are comparatively older than those without them.

11.5 WOOD PARENCHYMA

The wood parenchyma are apotracheal and banded. Many extent tangentially in between vascular rays (Fig. 96). They are mostly uniseriate, being biseriate or triseriate at portions in contact with the rays, often being so only along one or two cells in length. Parenchyma are also seen close to the vessels but all vessels do not have any parenchyma associated with them. Some occur as scattered uniseriate lines. Strands contain four to six or seven cells.

11.6 VASCULAR RAYS

Rays are heterogeneous (Fig. 102); mostly biseriate with marginal rows composed of a single row of upright cell at the distal and the proximal ends. Triseriate rays with uniseriate margins and uniseriate rays are also present. Number of rays per mm ranges from six to nine, the average being 8.16/mm. Length of the rays ranges from 532 µ to 896 µ and width at the broadest point 56 µ to 168 µ, the average length and width being 772.80 µ and 34.24 µ respectively. Occurrence of rays in different classes of height and width is shown in figures 17 and 18 respectively. The marginal row in the case of the biseriate and triseriate rays is composed of four to six

upright cells, each about two to three times longer than the diameter. The number of cell layers in the biseriate or triseriate portion ranges from six to ten. The individual cells of the vascular rays extend longitudinally along the radius of the stem.

Maximum number of rays belong to the biseriate type (57%) whereas the uniseriate and triseriate ones constitute 25% and 18% respectively of the total number of rays (Fig.16). Very rarely, four seriate rays are present but these are negligible in number.

Dissection of the rays is occasionally found in the wood (Fig. 103). When a ray splits into two, fibre cells inside intrude in between the two split ends. The identity of the ray from single to two could be traced in transverse sections, while in tangential longitudinal sections they appear as independent.

11.7 VARIATION IN WOOD CHARACTERISTICS ALONG THE SAME RADIUS

Variations in the characteristics of wood due to different relative positions along the same radius have been studied with respect to (i) porosity, (ii) length of wood fibres, (iii) diameter of wood fibre, (iv) length of vessels, (v) diameter of vessels, and (vi) the number of rays per mm length.

The observations recorded have shown that properties of the wood elements differ when sampled from periphery towards

the pith. The differences are gradual but they are pronounced the farther any two samples are apart on the same radius. Number of vessels per unit area and the number of rays per mm length show a progressive increase when the samples approach the pith from the periphery of the wood core. Vessel length and diameter and fibre length and diameter are also affected. These show a correspondingly progressive decrease in their respective values. A summary of observations is presented in Table 8.

The vessels and fibres formed early are thus narrower and shorter compared to the ones formed later. The number of vessels and ray groups are more compact in the wood relatively older though it occupies different positions along the same radius as that of the relatively young wood.

TABLE 8: Variation in the characteristics of wood elements from different positions across the stem (mean values)

	Position on the radial axis	Distance from periphery (mm)	No. of vessels per sq. mm	Vessel length (μ)	Vessel diameter (μ)	Fibre length (μ)	Fibre diameter (μ)	No. of rays per mm
1.	Periphery	0.75	11.38	722.7	128.4	1252.2	33.7	8.5
2.	Intermediates in order	3.63	12.68	714.3	129.5	1256.5	33.6	8.9
3.		6.00	14.76	648.9	124.9	1160.7	30.3	10.3
4.		8.63	18.74	606.9	107.8	1034.8	27.3	12.4
5.	Near pith	10.63	19.32	521.2	88.6	924.9	25.7	12.8

CHAPTER 12

TENSION WOOD

12.1 Sampling Specificity

12.2 Occurrence

12.3 Development

12.4 Relative Abundance

12.5 Vessel Distribution and Arrangement

12.6 Vessel Characteristics

12.7 Fibre Characteristics

12.8 Parenchyma and Vascular Rays

12. TENSION WOOD

12.1 SAMPLING SPECIFICITY

Materials for the present study of tension wood represent stem and root of one and two year old seedlings and mature branches of budgrafted trees. For comparing characteristics of tension wood with those of normal wood, leaning branches of comparable diameter have been chosen. From each branch, samples have been taken from the tension wood portion and the normal wood of comparable relative position on the opposite side, free from tension wood. This has been strictly adhered to, as properties of wood fibres, vessel elements and rays show variations in samples collected at the same level but occupying different relative positions on the same radial axis (vide supra).

12.2 OCCURRENCE

Macroscopically the tension wood in Hevea brasiliensis is not very conspicuous. However, in well sawn logs their presence is indicated by crescent shaped bands which are slightly lighter in colour compared to the other portions of the transverse cut surface. In some cases there is slight eccentricity of growth in diameter, more woody elements being present on the tension wood side. This however is found only occasionally, in branches which are of larger diameter.

The presence of cells with a massive cell wall, arranged into compact groups is characteristic of the tension wood in mature branches. The presence of an additional inner layer is restricted to the xylem fibres alone. These fibres provide a sharp contrast to areas which possess the normal wood fibres. The inner wall of the tension wood fibres is deeply stained with cellulose stains like fast green, light green, bismark brown and congo red. Very often, the inner wall becomes so massive that it delimits the lumen into a narrow slit as seen in transverse sections of well developed tension wood.

The tension wood belongs to the compact type, the fibres being arranged into well defined bands which are conspicuous on appropriate staining. In straight and upright stems they are found to be more or less concentric, with the width of the individual bands not showing any uniformity. The number of such bands also show wide variation, in different upright branches of comparable age and diameter.

In mature branches, which are horizontal or leaning, the tension wood occurs in crescent shaped, well defined bands (Figs. 104,105). These bands are wide and are found predominantly on the upper side (Fig. 104). The number of such bands and their width show variations. The two ends of a crescent shaped tension wood band sometimes spread over to the lateral sides and even extend to part of the lower side (Fig. 104). A few bands of tension wood fibres are occasionally found on the lower side of some of the leaning branches (Fig. 105).

Seedling stems also show the presence of tension wood. It is first recognisable about 20 cm away from the stem tip. The fibre cells with the gelatinous inner wall are arranged in concentric rings. The number of these rings is more towards the base, upto nine or ten in one year old seedlings, though it varies in different seedlings of the same age and diameter. Tension wood is not restricted to the stem alone. It is as well found in roots. Tap roots of seedlings of one and two years of age, sampled at 2.5 cm and 5.0 cm below the ground level, showed the presence of well developed tension wood fibres. Their arrangement is similar to that in seedling stems.

12.3 DEVELOPMENT

The first indication of the development of tension wood, is the presence of an ill-defined gelatinous layer of the inner wall close to the secondary wall of the wood fibres. Such fibres are scattered in the case of young seedling stems, but belong to a discrete layer or layers as revealed by close examination. All other wood fibres of such layer or layers, subsequently undergo the process of addition of an inner layer and thus become a concentric ring (or rings. In leaning branches all the fibres of a layer on the side under tension have the development of the inner wall more or less at the same time. The process of gelatinisation of the wall then extends laterally to both the sides. Further extension in the longitudinal direction is both basipetal and acropetal in leaning or horizontal branches, but acropetal in the case

of seedlings. The initiating layer may or may not be close to the cambium in either case. The radial expansion in the area occupied tension wood is brought about by the gelatinisation of fibres of the adjacent layers both centripetally and centrifugally when the initiating layer is not close to the cambium. When it is close to the cambium, the new fibres after differentiation develop the inner layer, characteristic of the tension wood fibres.

12.4 RELATIVE ABUNDANCE

The relative area occupied by tension wood has been estimated from transverse sections. The extent of tension wood present is highly variable. Quantity of tension wood is much more in leaning and horizontal branches compared to stems which are straight growing. It is predominantly seen on the upper side in the case of the former, arranged in wide crescent shaped bands. However, a few tension wood fibres have been noted on the lower side also of such branches. In stems which are more or less straight the characteristic arrangement is concentric, the bands being narrow.

An assessment of the area occupied by tension wood in transverse sections of a number of leaning branches has given the following information.

TABLE 9: Distribution of tension wood in leaning branches

Position	Area occupied by tension wood as percentage of the total area	
Upper half:	Average	46.36
	Range	39.60-56.20
Lower half:	Average	13.97
	Range	7.00-23.80
Whole:	Average	30.17
	Range	23.95-37.85

12.5 VESSEL DISTRIBUTION AND ARRANGEMENT

Distribution of vessels and the vessel arrangement have been studied in tension wood and normal wood of comparable relative position in the same sample. The former has been assessed as the number of vessels per square mm and the latter as proportion of their occurrence as solitary, radial multiples and radial tangential aggregates. The summary of these observations is tabulated in Table 10.

The number of vessels per unit area of tension wood does not show marked difference compared to that in normal wood. However, there is a slight tendency for reduction in the number of vessels in areas occupied by tension wood, but this is not at all pronounced. In the tension wood there is a slight increase in the percentage of vessels arranged in radial multiples and radial tangential aggregate with a

reduction in the number of vessels occurring solitary, but here too these difference are not marked.

TABLE 10: Vessel distribution and arrangement in tension wood and normal wood

	Tension wood	Normal wood
1. Number of vessels per mm		
Average:	9.22	9.30
Range:	5.00-13.00	5.00-14.00
2. Vessel arrangement %		
Single:	32.47	34.48
Radial multiples:	51.07	49.75
Aggregates:	16.30	15.75

12.6 VESSEL CHARACTERISTICS

No differences could be noticed in the morphology of vessels of the tension wood and those of the normal wood.

Records have been taken with regard to the length, diameter and the length/diameter ratio of the vessels of the tension wood and of the normal wood. The mean length of the vessels in the tension wood has been found to be 691.60 µ compared to 715.96 µ of those in the normal wood. The vessels of the former has an average diameter of 130.48 µ, while the average diameter of the vessels of the normal wood has been found to be 132.72 µ. The observations have provided the following summary with regard to this comparative assessment

TABLE 11: Length and diameter of the vessels of tension wood and normal wood

	Tension wood	Normal wood
1. Length of vessels (μ)		
1.1 Average:	691.60	715.96
1.2 Maximum:	966.00	1064.00
1.3 Minimum:	448.00	462.00
2. Diameter of vessels (μ)		
2.1 Average:	130.48	132.72
2.2 Maximum:	182.00	182.00
2.3 Minimum:	70.00	70.00
3. Ratio Length/Diameter	5.29	5.38

12.7 FIBRE CHARACTERISTICS

Except for the presence of the massive tertiary wall (Figs. 106,107), no other difference could be seen in the morphology of tension wood fibres compared to those of the normal wood.

Records of the length, diameter and the length/diameter ratio of the fibres of tension wood and the normal wood have been taken. The mean length of the fibres from tension wood has been found to be 1140.56 μ, while the fibres of the normal wood have an average length of 1152.22 μ. The former has an average diameter of 29.82 μ compared to 30.52 μ of the latter. A summary of observations is furnished in table below.

TABLE 12: Length and diameter of fibres of tension wood and normal wood

	Tension wood	Normal wood
1. Length (μ)		
1.1 Average:	1140.56	1152.22
1.2 Maximum:	1537.00	1537.00
1.3 Minimum:	952.00	954.00
2. Diameter (μ)		
2.1 Average:	29.82	30.52
2.2 Maximum:	42.00	42.00
2.3 Minimum	21.00	21.00
3. Length/Diameter Ratio (Mean)	37.80	38.21

The observation show that the tension wood fibres tend to be shorter and narrower, compared to the fibres of the normal wood. This tendency, however, is not pronounced to any appreciable extent.

12.8 PARENCHYMA AND VASCULAR RAYS

While no distinction could be noted in the characteristices of parenchyma occurring in the tension wood and the normal wood, the vascular rays exhibit interesting variation. The rays of both type of wood belong to the uniseriate, biseriate and triseriate groups, and the proportion of their occurrence into these groups also does not show any appreciable

variation. The number of rays per unit area of length (of tangential longitudinal sections) is also comparable in the two types of wood.

Measurements on the length and the diameter of the rays show that as far as the former is considered no marked difference exists. On the contrary, there is a tangential compression of the rays in the tension wood. The observations are summarised in the Table 13.

TABLE 13: Vascular rays in tension wood and normal wood

	Tension wood	Normal wood
1. Number of rays per mm length (mean)	9.48	9.39
2. Mean diameter (μ)	24.00	33.12
3. Mean height (μ)	693.88	692.02

The compression of the vascular rays in the tension wood is a remarkable feature. Compared to the average diameter of the rays in the normal wood, that of the rays in the tension wood is 27.5% lesser. The thin walled cells of the vascular rays are subjected to the pressure exerted by the comparatively harder fibre cells of the tension wood, as a result of which their diameter becomes appreciably lesser in contrast to the diameter of the vascular rays of the normal wood.

CHAPTER 13

DISCUSSION

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13. DISCUSSION

Hevea brasiliensis Muell. Arg., the commercial source of natural rubber, has been studied with reference to the anatomy of the vegetative organs. The observations have brought to light many interesting features of the plant hitherto unknown.

13.1 SEED GERMINATION

The seeds of *H. brasiliensis* remain viable only for a short period and have high percentage of germination if sown on time. The occasional occurrence of viviparous germination makes one wonder whether it is indicative of a relatively brief viability. Hartmann and Kester (1968) consider that wet weather during harvest season may induce premature sprouting of seeds while attached to the plants in some grain crops. Van der Pijl (1969) has termed this type of germination, which occur due to excessive humidity, as 'incidental vivipary'.

Germination is hypogeal and the cotyledons remain within the seed coat. The plumule and the radicle emerge by lifting the operculum. The latter remains attached to the seed coat on one side even after the radicle and the plumule have emerged. While the radicle has a straight course through the operculum soon followed by a downward deflection

due to geotropism, the emergence of the plumule is effected by the rapid growth of the epicotyl resulting in the formation of a hump and its subsequnet straightening. Work done on the germination of seeds in members of Euphorbiaceae as a whole is scanty. Troll (1948), however, has reported typical epigeal pattern of germination in Ricinus communis.

A noteworthy feature in Hevea is the development of the first lateral roots, which have their differentiation in the embryo itself. These roots, which have been termed in the present study as the primary lateral roots considering their time of origin and differentiation in the development of the plant, are arranged in a single whorl around the radicular axis while the lateral roots produced subsequently are irregularly arranged. The initial growth of the seedling is very rapid and the average height attained during the first five weeks after sprouting is 42.0 cm, by which time the seedlings have passed through two phases of active growth each of which culminates in the production of a flush of leaves. In terms of the total height attained on the 35th day, the growth during the first five days represents 12.14%. The increment in plant height during the fifth to the tenth day represents 47.1% and that during the 21st to 25th day 27.86% of the total growth in height. The growth of the seedlings indicates that there is a rhythm. One flush about 10-14 leaves arises, after which it appears as though the shoot apex organises the generative centres for some time to produce the next flush of about 12-17 leaves. It is

worthwhile to recall that during the short duration of apparent rest, the seedling does not generally initiate any lateral appendages like scale leaves and bud scales.

13.2 SEEDLING VASCULATURE

Transition, the main theme of seedling vasculature studies, has been conceived as a rearrangement of vascular strands by splitting, rotation and fusion (Van Teighem 1891) and Eames and MacDaniels (1947) have recognised four different types under transition phenomenon. Bonnier (1900) believes that a shift in the pole of xylem differentiation and of the primary phloem effect the transition, while Sterckx (1900) considers that stem, leaf and root are fundamental morphological entities and that the traces of cotyledons, leaves and roots are put into contact by mere juxtaposition in the hypocotyl. Chauveaud (1911,1923) details that in the seedling root and the lower hypocotyl an alternate arrangement of xylem and phloem is characteristic, while above this level there is an addition of xylem elements to the flanks with an ultimate extrusion of root xylem with split halves of phloem abaxially superimposed at the upper hypocotyl region. Chauveaud's view also takes into consideration a shift in the pole of xylem differentiation, though he considers the differences in arrangement to represent successive stages of vascular evolution in the axis. A shift in the pole of xylem differentiation has been recorded in Tridax procumbens (Padmanabhan 1968) and other members of the Compositae (Misra Raj 1970). Recently, in Amaranthes leucocarpus

Sebastian (1971) finds a shift in the pole of differentiation of xylem and obliteration of centripetal xylem. The latest contribution to our understanding of seedling anatomy (Pillai *et al.* 1974) also records degeneration of centripetal xylem in *Albizzia lebbeck* while the authors consider that the development of lateral and centrifugal xylem is independent of the centripetal xylem in this woody species.

The primary vasculature of the seedling and confluence of root and shoot vasculature of *Hevea brasiliensis* bring to light a very interesting pattern. The vascular differentiation proceeds towards the shoot and root apices, in contrast to Chauveaud's (1911) concept of acropetal development from the radicle to the plumule. Of the six strands present in the upper hypocotyl, a set of three departs as the cotyledonary traces to the respective side while the two strands present at each pole of the intercotyledonary plane unite and later depart as the respective median of the first and the second leaves. As the six cotyledonary strands move towards the root apex, they divide and the daughter strands separate to form twelve strands at the lower hypocotyl. Each of these twelve strands is composed of a median flanked on either side by a lateral. The medians move to the primary lateral roots, while the lateral xylem of the adjoining strands move closer to each other and move straight to the tap root. Concomitant with these changes, the centrifugal xylem characteristic of the primary shoot undergoes gradual degeneration and obliteration as the strands approach the region of departure of the primary

lateral roots.

The situation observed in the present study does not seem to have a parallel in the literature available on seedling vasculature. It does indicate a continuous vascular system through the root-hypocotyl-shoot axis, in contrast to Stercks' view. The gradual shift in the pole of differentiation supports the views of Bonner (1900) and Cheauvaud (1911,1923). The degeneration of the centrifugal xylem is unique, although the reverse (namely the degeneration of centripetal xylem) has been reported in Amaranthes and Albizzia. The first-formed lateral roots, which have an embryonic origin and which are arranged in single whorl of twelve, do influence the nature of the transition and suggest a strong and continuous vasculature, which could be recognised into a hypocotyledon-shoot axis system above and a hypocotyl-primary lateral root-tap root system below.

13.3 ROOT APICAL ORGANISATION

Most of the works on root apices have been oriented in classifying the configuration of the promeristems and have been influenced by the histogen theory of Hanstein (1868) and its elaboration (Janczewski 1874; Popham 1952). The literature on root apical organisation (Guttenberg 1960; Clowes 1961; Esau 1965a; Fahn 1968; Wardlaw 1968, Pillai 1972) bring forth the fact that no systematic attempts have been made to study the structure in species within a family or belonging to closely related groups.

The configuration of the structural net of the seedling root apices of Hevea brasiliensis shows two discrete promeristems, one giving rise to the dermatogen and the root cap and the other to the cortex, stele and pith. The central region of the root cap is composed of a few vertical files of cells which constitute the columella. This region is surrounded by oblique rows of cells which widen from the cap flanks towards the columella following Kappe divisions (Schuepp 1917). Korper type of divisions as described by Schuepp, occur in the periblem which on the other hand, bring about the increase in cell number in the radial tangential extent of the root body and ultimately effect an increase in the diameter of the roots. Such a configuration belongs to type B of Eames and Mc Daniels (1947) and type 14 of Pillai (1972). A common group of initials which ultimately gives rise to all the tissues of the root cap and root body is characteristic of Manihot utilissima (Pillai et al. 1965) while Raju et al. (1964) have recognised three meristematic layers, in the long and short roots of Euphorbia esula, the first representing the stelar initials, the second the initials for the cortex and the third for the root cap - epidermis complex.

13.4 SHOOT APICAL ORGANISATION

The shoot apical organisation in Hevea brasiliensis shows a uniform pattern from the embryonic stage to the mature, save for the structural changes associated with bud dormancy.

The recent review of Gifford and Corson (1971) shows that almost all plants, which have been worked out, possess cytohistological zonations. It also reveals that the tunica-corpus theory of Schmidt (1924) can be used with advantage to explain the apical configuration and that it has become so popular as to provide the basis for subsequent classifications of shoot apices (Foster 1939; Popham 1951). Johnson and Tolbert (1960) introduced the concept of 'metrameristem' to designate the central part of the shoot apex, which include the tunica and the corpus initials. Buvat's (1950, 1951, 1952a,b, 1953, 1955) concept of shoot apical organisation, on the contrary, is based on the theory of multiple helices (Plantefol 1947) which considers that the leaves are disposed on the stem along the foliar helices and are in continuity along the length of each helix. The theory of the French School, however, can be explained as conceiving the apical zone including the tunica and corpus together as 'meristeme d'attente', the flank meristem as the 'anneau initial' and the pith rib meristem as the 'meristeme medullaire'. Newman (1961, 1965) on the other hand recognised the 'monoplex' (wherein there is a single apical cell at the shoot apex), the 'simplex' (those with a single zone of initials which is superficial at the shoot apex) and the 'duplex' (having two discrete zones of initials, one zone being superimposed on the other) types of shoot apical organisations on the basis of a 'continuing meristematic residue'.

The shoot apex of Hevea brasiliensis shows typical zonations and belongs to the normal angiosperm type (Popham 1951). The apex is characterised by a two layered tunica, a zone of central mother cells, a pith rib meristem and the flank meristem. While the outer tunica cells undergo only anticlinal divisions, the inner ones divide periclinally also during the initiation of leaves. A tunica corpus organisation of the shoot apex has been reported for certain members of the Euphorbiaceae. Soma (1958) finds a two layered tunica in Euphorbia lathyris. Shah and Jani (1964) have recorded a single tunica layer in Euphorbia nerifolia. Raju (1968), however, has preferred to use the terms mantle and core of Popham and Chan (1950) in his studies on Euphorbia esula and noted a variation in the number of mantle layers at different stages of development (Ho and Raju 1972).

13.5 PLASTOCHRONIC CHANGES

The generalised use of the term plastochron to designate the time interval between two successive events in a series of similar nature as formulated by Askenasy (1880) has been confined by Schmidt (1924) to designate the period between the initiation of two successive leaf primordia, or pairs of leaf primordia in plants with opposite leaf arrangement or whorls of leaf primordia in those with a whorled leaf arrangement. Schmidt has broadly recognised two phases of plastochron, on the basis of the size of the shoot apex; the maximal (stage of maximum apical area with the beginning of leaf initiation) and the minimal (stage of reduced apical

area after the appearance of the leaf primordium). One stage of the plastochron gradually merges into the other and, obviously, more subdivisions have been adopted by various researchers in describing the shoot apex on the basis of size. Such a sub-division is more easy wherein the time interval between two successive stages in the leaf initiation is greater.

The shoot apex of the embryo of Heavea brasiliensis is in the second plastochron. Sanghas (1956), from a study of 85 species belonging to 26 dicotyledonous families, has found two types of embryos: one type having no primordia except the cotyledons and the other showing plastochronic changes and the embryonic shoot tip having varying number of leaf primordia. The shoot apex of H. brasiliensis at the maximal stage of the fourth plastochron is typically dome shaped with an average height of 92.0 μ and an average width of 151.5 μ. The apex is more or less flat during the minimal phase of the plastochron with an average width of 95.0 μ. Soma (1958) has also recognised maximal and minimal phases of plastochron in Euphorbia lathyris and Shah and Jani (1964) have observed fluctuations in the width of apical meristems in all the phases of plastochron in Euphorbia nerifolia.

The development of a leaf primordium, which takes place during the maximal phase, is initiated in the second tunica layer soon followed by divisions in the daughter cells as well as anticlinal divisions in the outer tunica layer. An interesting feature in Hevea brasiliensis is the reduction in the height of the apical dome during successive maximal

phases within the production of a flush of leaves. In plastochrons related to the late formed leaves of a flush, the height of the apical dome at the maximal stage does not exceed three to four microns. External morphology also reveals this structural peculiarity. There is a telescoping of the internode from the first to the last, between the leaves belonging to any flush, and the latter ones are borne in very close proximity with each other on the shoot axis.

13.6 PHYLLOTAXIS AND TRACE RELATIONS

The attachment of leaves on the axis in Hevea brasiliensis follow a 2/5 phyllotactic arrangement according to the concept of genetic spiral and the angular divergence of the leaves. Two sets of contact parastichies, which wind around in opposite directions, could be recognised. Any two leaves which are superimposed are five plastochrons apart. While the spiral arrangement is characteristic since the third leaf onwards, the cotyledons and the first two leaves appear to be opposite. The number of parastichies increases as growth advances. Esau (1965a) also opines that the production of leaves initiates along two parastichies, beginning with the cotyledons, after which the number increases. Enlargement of the apical meristem tends to increase the number of parastichies and a rapid opening out of the genetic spiral (Richards 1951; Esau 1965a). The sequence in leaf arrangement from the third leaf onwards shows remarkable regularity in H. brasiliensis and the pattern is maintained in the flushes of old trees as well.

This indicates that an increase in the diameter of the vascular cylinder is brought about by a tangential spread of leaf traces at higher levels of the shoot, as has been observed by O'Neill (1961) in Lupinus.

Dormer (1945, 1954) has distinguished two types of primary vascular systems in shoots: the open type where the leaf traces diverge to one side only in any sympodium and the sympodia not interconnected to a reticulum; and the closed type where the sympodia re interconnected into a reticulum by the leaf traces. The open system noted in H. brasiliensis, which has an early development of secondary growth, supports the view of Dormer (1945) that the tangential continuity in open systems is accomplished only with the establishment of the secondary growth and occur in species with early activity of vascular cambium.

In H. brasiliensis the median trace of any leaf is related to two lateral traces, an anadromic lateral which is three plastochrons apart and a katadromic lateral which is two plastochrons separate from the median in question. This appears to be of general occurrence in species with a 2/5 phyllotaxis and has been recorded in Prosopis juliflora (Trivedi 1969), a woody species of Leguminoseae having a 2/5 leaf arrangement.

13.7 NODAL VASCULATURE

The nodes are trilacunar in H. brasiliensis. The stipules are supplied by a branch of the lateral trace.

Unilacunar one traced and trilacunar three traced conditions are recorded in the family Euphorbiaceae. Sharma (1972) has found five trace trilacunar condition in Euphorbia nerifolia and five trace pentalacunar nodes in Euphorbia grandifolia. Singh (1972) has noted that in species with three traced nodes, the lateral traces may supply the stipules before entering the leaf base or are entirely consumed in supplying to the stipules or may disappear soon after differentiation, in some of the non-cyatheous members of the family and considers the trilacunar three traced conditions as the basic type. Trilacunar nodal pattern has been considered to be basic by Sinnott (1914) and Benzing (1967), while Marsden and Bailey (1955), Bailey (1956) and Esau (1960) consider the unilacunar double traced one as the basic pattern.

In H. brasiliensis the median trace consists of seven strands and the laterals of two each as they deflect to the leaf base. The strands undergo a series of modifications in their course from the axis to the base of the leaf, finally forming crescent shaped or semicircular vascular cylinder, being made up of adaxial and abaxial strands. Esau (1960, 1965a) has illustrated that the median trace in Brassica, which also has a trilacunar nodal pattern, consists of several bundles. Philipson and Philipson (1968) have recognised a complex trilacunar node, in certain species of Rhododendron, where several bundles leave the stele by independent gaps and join the central complex in the base of the petiole. It appears that a single trace composed of

several strands, which together cause a lacuna in the procambial cylinder, is of rare occurrence.

13.8 LEAF HISTOLOGY AND VENATION

The cuticle on the abaxial epidermis in H. brasiliensis shows a reticulate surface pattern. Priestly (1943) is of the opinion that the cuticle may develop folds, which change progressively during cell growth and extension and may show a reticulate pattern. The present observations, however, do not indicate any change concomitant with growth, for the reticulate pattern is noted on very tender leaves and the old ones. While lamellata cuticle is the most common type, striated cuticle is occasionally met with. Reticulate cuticle, however, is of very rare occurrence. Striated cuticle which generally occur on the abaxial side, has been recorded in species of Cestrum (Ahmed 1962, 1964), some members of Asclepiadaceae (Krishnamurthy and Sundaram 1967) and Flavaria contrayerba of Compositae (Banerjee 1972). The striations are present as continuous or broken lines radiating from the outer surface of the guard cells or the base of glandular trichomes. While the striated cuticle apparently does not have any bearing on any environmental factor, it would be of some taxonomic significance (Ahmed 1962, 1964; Krishnamurthy and Sundaram 1967). This could hold true with regard to the reticulate cuticle of Hevea as well.

The venation of H. brasiliensis belongs to the 'Camptodromous type' of Ettinghaunsen (1861), wherein the

secondary veins curve acroscopically to form series of loops with adjacent secondaries and their branches. This represents a closed type of venation, in contrast to the open or 'Craspedodermous type' in which the secondaries follow a direct course to the leaf margin wherein they terminate. The primary, secondary and tertiary veins of H. brasiliensis constitute the major venation and the quarternaries and branches thereof the minor venation. Two types of secondary veins are observed: those which form loops at the margin; and those coming out in between two secondary veins and ending up blindly in the intercoastal panel delimited by the former. Foster (1950) has termed these as 'intermediate veins'.

13.9 BUD DORMANCY

Precise rhythmic growth is characteristic of H. brasiliensis, right from the seedling stage. A period of vigorous growth alternates with one of apparent rest though there is little change in environment. These processes are controlled by an endogenous rhythm, which Bunning (1956) explains as 'the term used in describing biological processes which alter periodically although external conditions remain constant'. While there occurs three to five periods of active growth and rest of the buds per year in seedlings, the number reduces as the plants become more mature. Four to five years of age onwards, the trees show only one active period of short duration, during which a flush of leaves is produced, after which they exhibit bud dormancy. Dormancy

of buds sets in much ahead of the beginning of an unfavourable season and the buds develop a high degree of resistance. Vegis (1964) finds that this highly useful adaptation which sets in well before the unfavourable season ensures successful survival. Wareing and Phillips (1970) have termed the type of dormancy, as noted in H. brasiliensis, as 'innate' or 'spontaneous' dormancy. The prolonged period of bud dormancy exhibited by H. brasiliensis could be comprised of three intermerging phases: the first phase or predormancy where the maturing leaves check bud growth (summer dormancy, correlative inhibition); rest, when the buds are innately dormant (true dormancy, winter dormancy) and the post dormancy when the buds become capable of resuming growth (Doorenboos 1953; Samish 1954; Romberger 1963; Wareing and phillips 1970).

Though the cells have a dense cytoplasm, no contraction of the cytoplasm away from the cell walls could be noticed. Swarbrick (1927) and Priestly (1930) report an actual shrinking of protoplast during dormancy, but this has not been supported by many workers. Genkal and Okina (1948) could not find a contraction of protoplast in Juglans regia, while Betula, Pinus and Taxus behave differently. Romberger (1963) feels that some of the observations on shrinkage of cytoplasm relate to frost hardiness rather than to bud dormancy.

Telescoping of internodes, production of cataphylls and the presence of denser cytoplasm in cells of the shoot apex, observed in H. brasiliensis, are features commonly

associated with bud dormancy in general. The present observations reveal that during the dormant stage little growth in length takes place whereas cells of the different tissues already produced during the active phase undergo maturation fast. Concomitantly, there is the development of the cork cambium, suberisation of abscission zones of cataphylls, foliage leaves and stipules, development of secondary cork cambia beneath the abscission layers, sclerification of cells and obliteration of petiolar traces, which are all adaptations aimed at the conserving water and ensuring mechanical protection.

The cataphylls in H. brasiliensis are supplied with a single vascular trace, and the presence of reduced vascular system and lack of tissue differentiation are characteristics of cataphyll of seed plants (Foster 1931, Sacher 1955, Sterling 1958, Singh 1961). Production of the bud scales at a faster rate than that in the case of foliage leaves of the same species (Foster 1931) coupled with negligible apical growth (Stone and Stone 1943) result in crowding of cataphylls forming a resette around the dormant bud.

Though the physiology of bud dormancy has been extensively worked out and reviewed from time to time (Samish 1954, Romberger 1963, Vegis 1964, Wareing 1969, etc.) anatomical studies are limited and mostly confined to coniferous species. The features of the dormant buds of H. brasiliensis are different from those of the vigorous ones (vide supra). It is very interesting to note the case of

Acer platanoides in this context, wherein Steward (1968) finds 'astonishing similarity' of the apices in actively growing and dormant buds. Apical abortion and development of the uppermost axillary buds after the dormant period are characteristic of plants like Ailanthes, Robinia, Tilia, Ulmus (Wareing and Phillips 1970), Betula pubescens and Catalpa bignoides (Romberger 1963), while the lower axiliary buds continue growth in Gymnocladus and Viburnum opulus (Romberger 1963). No instances of apical abortion have been noted in H. brasiliensis.

13.10 MORPHOLOGY OF BARK

Early initiation of cambial activity in Hevea brasiliensis results in the formation of fair amount of secondary phloem tissues, as in the case of woody dicotyledons in general. The bark of the very tender twigs contains, however, only the primary phloem tissues, while it is composed of both primary and secondary tissues once the activity of cambium begins. In mature trees, on the other hand, the primary tissues are separated and sloughed off and the bark exclusively contains secondary phloem tissues.

The bark when tender is smooth, but becomes slightly rough due to the development of lenticels, growth of the peridem and separation of tissues. As the subsequent peridems develop faster near the base, the trunk near the ground level has scaly bark which is more rough, containing pockets of dead tissues of the cortex and the phloem towards the periphery.

Stratification of the bark into an inner portion of soft tissue and an outer hard bark is characteristic of Hevea brasiliensis. The outer bark consists of the superficial layers of the periderm and the sclerified portions of the cortex whereas the soft bark denotes the living phloem tissues next to the vascular cambium. While the former affords high protection, the latter contains the functional elements. Phloem fibres are of rare occurrence in Hevea brasiliensis. Esau (1964) finds that the secondary phloem may lack fibres in some species, in others it is present and distributed irregularly or in regular tangential bands, while some have sclereids alone or fibres and sclereids. Absence of fibres in the bark has been noted in Caesalpinia pulcherrima and Delonix regia (Ashok Kumar 1969). Presence or absence of fibres and the pattern of distribution when it is present, however, impart special characteristic to the secondary phloem (Zahur 1959) which could be of diagnostic significance (Ashok Kumar 1969).

13.11 SIEVE TUBES

Cheadle and Whitford (1941) and Cheadle (1948) believe that transverse or slightly oblique end walls of sieve tubes are highly specialised while very oblique end walls are primitive. They also consider that the former is associated with regular stratified arrangement of sieve elements. While the sieve tubes in H. brasiliensis have deeply oblique end walls, there is a tendency for a regular arrangement of the

sieve tubes belonging to any group. Localisation of the sieve areas on the end walls (and not on the longitudinal walls), noted in H. brasiliensis is also considered an indication of structural specialisation (Cheadle and Whitford 1941, Cheadle 1948, Cheadle and Uhl 1948, Esau 1965b) while the presence of compound sieve plates represents a primitive feature (Hemenway 1913, Eames and McDaniels 1947).

Ashok Kumar (1969) in his studies on the bark anatomy of leguminous species has categorised sieve tubes on the basis of diameter following criteria laid down by Dadswell and Eckersely (1935) and Chalk (1938) for vessels. The one proposed by Chalk (1938) is more precise and classifies vessel diameter as under:

1 Small	1.1 Extremely small	upto 25 µ
	1.2 Very small	25-50 µ
	1.3 Moderately small	50-100 µ
2 Medium		100-200 µ
3.Large	3.1 Moderately large	200-300 µ
	3.2 Very large	300-400 µ
	3.3 Extremely large	over 400 µ

Adopting this grouping, the sieve tubes of H. brasiliensis are small; either very small (38%) or moderately small (62%). Following Metcalfe and Chalk (1950) who classify vessel length into (1) Short: upto 350 µ, (2) Medium: 350-800 µ, and (3) Long: above 800 µ, the sieve tubes are either short (16%) or medium (84%). Adopting the classification of

Rodriguez (1957), however, 40% are small (upto 400 μ long) while 60% belong to the medium category (400-800 μ). In either case, the medium type is the dominant one.

13.12 PHLOEM RAYS

The vascular rays in the secondary phloem follow a pattern similar to that of the wood. The wood rays have been classified into (Kribs 1935; Metcalfe and Chalk 1950; Committee on Nomenclature 1957):

1. Homogenous (Composed of procumbent cells only)

   Type I: Entirely uniseriate.

   Type II: Rays all not uniseriate.

2. Heterogenous (Composed of procumbent and upright cells)

   Type I: Rays entirely uniseriate; procumbent and upright cells which are taller than broad more or less alternating with each other by irregularly arranged.

   Type IIA: Upright cells taller than broad, confined to the margins and the uniseriate portions.

   Type IIB: Uniseriate rays composed of alternating upright and procumbent cells; multiseriate rays with upright cells confined to the terminal uniseriate portions.

   Type III: Uniseriate rays of two sorts; composed of either upright or procumbent cells. Multiseriate rays composed of square upright cells.

The phloem rays of H. brasiliensis belong to Type IIA and triseriate rays are the dominant ones. Chalk (1938) has suggested a classification of rays on the basis of ray width which has been accepted by the International Association of Wood Anatomists (1939). According to this, the different categories are:

1.	Extremely fine	upto 15 μ
2.	Very fine	15-25 μ
3.	Moderately fine	25-50 μ
4.	Medium	50-100 μ
5.	Moderately broad	100-200 μ
6.	Very broad	200-400 μ
7.	Extremely broad	above 400 μ

While this classification holds good in general, as different types of rays which show fair variation in the width depending on the number of cell rows exist together it would be appropriate to categorise each type of ray separately. Considering this aspect, the uniseriate rays of H. brasiliensis are very fine or moderately fine. The biseriate rays belong to the groups moderately fine or medium, the triseriate rays are mostly medium while all the four-seriate rays belong to the medium group.

13.13 EXPANSION TISSUES

The stress and strain subjected to the bark as a result of secondary growth, is partly accommodated by the development of phellogen. And noncambial secondary growth by tissues

outside the vascular cambium, which is termed as 'diffuse secondary growth' by Tomlinson (1961) and as 'dilation growth' by Schneider (1955), Chattaway (1955) and Esau (1964, 1965b), keep pace with growth in diameter on the other hand. Whitmore (1962) has noted phloem proliferation and phloem expansion under dilation growth in Dipterocarpaceae, whereas Ashok Kumar (1969) differentiates cortical expansion, pericyclic expansion, ray expansion and phloem proliferation in Leguminoaseae. Dilation growth in H. brasiliensis is effected by cortical expansion, pericyclic expansion and ray expansion. Tangential stretching and anticlinal divisions take place in most of the cells of the cortex. In the pericycle, the cells which do not undergo early sclerification divide and constitute the expansion tissues. Expansion of rays is brought about by division of the body cells and dissection of rays followed by interpolation of parenchyma.

Sclerosis of cells is very common in the bark of H. brasiliensis and begins when the axis is relatively very young. The first cells to undergo sclerification are those of the pericycle, which when completed forms a continuous ring of perivascular sclereids. Sclerification also takes place in the cells of the cortex and of the vascular rays. These groups of sclereids are arranged in irregular discontinuous rings and affords the delimitation of the bark into the hard and the soft zones. It is worthwhile to recall here that the absence of pholic fibres is probably compensated effectively by early sclerosis and production of masses of stone cells which afford enough mechanical

strength. A similar feature is found in Caesalpinia pulcherrima and in Delonix regia (Ashok Kumar 1969), the former having irregularly distributed patches of sclereids and the latter lignified parenchyma in the nonfunctional phloem.

13.14 PERIDERM

Periderm consists typically of three parts: the phellogen which is the initiating layer, the tissues produced centrifugally called the phellem and the phelloderm which is produced centripetally. Fahn (1967) defines phellogen as a secondary meristematic tissue in all respects, lateral in position and histologically simpler than the vascular cambium as it consists of only one type of initials. Considering the origin, the first phellogen may be initiated at different depths outside the vascular cambium: in the epidermis (Nerium oleander, Quercus suber, Solanum dulcemara); in the subepidermal layer (Populus, Juglans, Ulmus); partly from the epidermis and partly from the subepidermal cells (Pyrus); in the second or third cortical layer (Aristolochia, Robinia) and near the phloem or from within the phloem parenchyma itself (Arbutus, Camellia, Punica) and development from the subepidermal layer is most common (Eames and McDaniels 1947, Esau 1965a, Fahn 1967). In H. brasiliensis the first phellogen arises in the subepidermal layer, when the stem is only about a few months old and usually persists for about an year. The subsequent periderms develop within, to begin with as isolated strips but soon becoming more or less complete cylinders.

These in course of time separate the cork tissues formed earlier, which become variably cracked and are sloughed off.

Kaimal (1951) in his general description of Hevea bark mentions that the cork cambium is situated along the outer boundary of the hard bark, but does not specify whether it is the first phellogen or the subsequent ones nor does he remark about the place of its origin.

The phellogen does not give rise to any tissues other than the phellem and phelloderm in the usual manner. As such the present studies do not support the observations of Metcalfe (1966, 1967) who believes that some of the laticifers in the outer bark arise from the phellogen.

13.15 NATURE OF BARK REGENERATION

Bloch (1941) recognises three major categories of tissue regeneration as a consequence of wounding in higher plants. These are (1) in roots and shoot apices the undifferentiated parts of intermediate meristems reproduce the parts lost completely, more or less directly from the cells abutting the cut surface, (2) away from the apex repairs are effected by secondary meristems like phellogen or cambia, and (3) in mature zones redifferentiation is induced in the differentiated tissues and the tissue pattern near the injury becomes partly restored. Bloch (1952) further states 'strictly speaking the concept of wound healing would not seem to imply much more than closing and

scarification of a wound by means of strictly local cellular changes involving cell division, cell growth and differentiation or, as in the majority of cases, a combination of these'.

Bark regeneration in Hevea brasiliensis typically signifies the process of wound healing and takes into consideration the subsequent production of normal tissues in the bark beneath the healed surface, and the pace at which the process takes place is important from the commercial view of exploitation of the trees. The tissues which are severed due to tapping differ considerably in the stage of development and maturity. The transverse cut passes through the hard bark region and part of the soft bark, whereas the vertical cut passes through the soft bark parallel to the wood core. Nevertheless, the nature of reaction to wounding is remarkably the same all along the cut surface. This signifies that neither the stage of maturity nor the plane of severing affect the essential features of the healing process in general in H. brasiliensis . While the cells which are ruptured and exposed due to tapping undergo necrosis, the row of cells immediately beneath enlarge and divide forming a thin layer of callus. A wound phellogen differentiates from this callus tissue by the orientation of cell divisions parallel to the cut surface and functions in the normal way. Sinnott (1960) also mentions that when a wound is caused in an already differentiated tissue hyperplasia and hypertrophy of cells and a differentiation of a wound

phellogen are all what happens. The cells at the cut surface thus undergo a process of dedifferentiation and redifferentiation, to some extent. These processes, however, occur only to a very limited extent and the cells are not completely totipotent as Wareing and Phillips (1970) consider. No evidence of any tissue differentiation, other than the wound phellogen, could be noticed in H. brasiliensis as a response to wounding. Redifferentiation, however, occurs to the extent of establishing vascular connections in some herbaceous plants (Simon 1908, Kaan Albest 1934, Sinnot and Bloch 1945, Jacobs 1952) where the severed strands successfully establish interconnections in the course of wound healing and regeneration.

13.16 LATICIFERS

Both articulated and non-articulated laticifers occur in members of the family Euphorbiaceae. However, most of the species which are laticiferous possess the non-articulated ones.

The non-articulated laticifers have a simple origin. Their initials are recognisable at the cotyledonary node of the embryo, as in Euphorbia sp. (Cummings 1941), Jatropha gossypifolia, J. pandurifolia var. rosea and J. podogarica (Rao and Malaviya 1964). Extensive development of the laticifers takes place by intrusive growth which has been worked out in Euphorbia marginata (Mahlberg 1959b) and in E. splendens (Moor 1959). The specialised initials ultimately develop into a much organised tissue system.

The articulated laticifers are characteristic of members like Hevea and Manihot of the family. However, the origin and development of the articulated laticifers do not appear to have been traced in any member of this family. Information available on these aspects are limited to some members of the Compositae only (Esau 1965a; Metcalfe 1966, 1967; Fahn 1967). The laticifer initials, in this case also, appear very early in the ontogeny and become discernible at the hypocotyl of the embryo, on the periphery of the procambium (Baranova 1935; Sperlich 1939). The initials differentiating from the procambium develop into the primary laticifers. Later, the secondary laticifers develop from the initials produced by the vascular cambium (Scott 1882).

The laticifers of Hevea brasiliensis represent a tissue system closely associated with the phloem elements. As in the phloem, depending on the time of appearance and the tissue from which they originate, the laticifers belong to two categories: the primary and the secondary. Both are confined to the bark in the axial organs of the tree. The initials of the primary laticifers occur at the periphery of the procambial cylinder, along with the initials for the sieve elements at the hypocotyl region of the mature embryo.

The procambium of the embryo in H. brasiliensis is a hollow cylinder. The procambium in mature embryos is often regarded as a Y-shaped structure, having a solid core at the radicular end and continuing as two flanges into the cotyledons (Misra Raj 1970). Mahlberg (1960) and Hayat and

Canright (1965) consider the lower part of the procambium to be a cylinder in Nerium oleander and some species belonging to Annonaceae respectively, while Padmanabhan (1968) finds a solid core in the radicle which forms a hollow cylinder at the hypocotyl in Tridax procumbens. Hayat and Carnright (1965) further consider that, in general, herbaceous species have a solid core while a hollow cylinder is prevalent in woody plants. The shape of the procambium in H. brasiliensis agrees with the observations of Mahlberg (1960) and Hayat and Canright (1965).

The secondary laticifers, on the other hand, develop from the cells cut off by the fusiform initials of the vascular cambium centrifugally. Differentiation of both the primary and the secondary laticifers of H. brasiliensis is acropetal and takes place by successive conversion of adjoining cells into laticiferous cells to form continuous vessels. Dissolution of cross walls is more or less complete and the laticifers are coenocytic. The tangential connections begin with the development of protuberances, but some of the parenchyma cells along their path are redifferentiated into laticifers. A similar course of development of laticifers has been reported in certain members of Cichoreae like Tragopogon (Scott 1882), Scorzonera (Baranova 1935) and Taraxacum (Artschwager and McGuire 1943; Krotokov 1945). From the commercial point of view, only the secondary laticifers are important in H. brasiliensis. The primary laticifers become non-productive and are degenerated when the formation of periderm and sclerification of tissues in the outer bark take place.

The latex vessels of the leaf occur in close proximity with the vascular elements, lying more or less parallel to each other. Branching of a vein in the leaflet is accompanied by forking of the laticifer, associated with it, in a similar manner. The leaves of Jatropha gossypifolia (Kakkar and Paliwal 1972) and Euphorbia thymifolia (Paliwal and Kakkar 1972) are also reported to contain branched laticifers associated with the vascular tissues in a similar way.

A brief summary of the different types of laticifers occurring in plants is given in the following page.

13.17 WOOD POROSITY

The wood of the members belonging to Euphorbiaceae may vary from diffuse porous to semi-ring porous and ring porous (Metcalfe and Chalk 1950) and that of Hevea brasiliensis belongs to the diffuse porous type. The number of vessels per unit area, which is 10/mm^2 on the average, shows that they are moderately few according to the classification suggested by Chattaway (1932). He considers the vessel distribution per mm^2 as very few (upto 2), few (2-5), moderately few (5-10), moderately numerous (10-20), numerous (20-40) and very numerous (over 40). Occurrence of vessels as solitary or in multiples of 2-3 and aggregates and with simple perforation plates the Hevea also follows the pattern of Euphorbiaceae-Crotonoideae (Metcalfe and Chalk 1950). Although Coster (1927) records the presence of growth rings in Hevea, the presence of one or two layers of cells which

LATICIFERS

Specialised cells or tissues which contain latex

- **NON-ARTICULATED**

  Develop from single cells, which elongate and their tips keep pace in growth of the cells of the surrounding meristem penetrating among the new cells

  - **UNBRANCHED**

    More or less straight tubes developing into long structure .. Cannabis, Utrica, Catharanthus

  - **BRANCHED**

    Each laticifer cell branches repeatedly forming an immense system of tubes .. Asclepias, Cryptostegia, Euphorbia, Ficus, Nerium

- **ARTICULATED**

  Originate from rows of cells by the partial or complete absorption of the separating walls in early ontogeny

  - **NON-ANASTOMOSING**

    Long, compound tubes, not connected with each other laterally .. Achras, Chelidonium, Convolvulus, Ipomoea

  - **ANASTOMOSING**

    Forms anastomoses laterally with cells or tubes of similar nature, all combined forming a reticulum .. Argemone, Carica, Cichorium, Hevea, Manihot, Taraxacum

Classification of laticifers: A schematic representation

are narrow in their radial extent, noted in the present study, indicate only false growth rings and their nature does not reveal any growth zonations. False growth rings occur in many woods (Esau 1965; Fahn 1955, 1958) and it is difficult to distinguish growth rings microscopically although macroscopically presence of rings may be apparent (Fahn 1958). It is also worth mentioning here that tension wood, which occurs as concentric bands in straight ~~items~~ stems, stands out in sharp contrast when viewed in transverse sections and these concentric bands may often give a false impression of growth rings.

13.18 WOOD FIBRES

Fibre length is of some practical interest (Metcalfe and Chalk 1950) and an important feature in comparative studies (Carlquist 1961). Metcalfe and Chalk (1950) suggested grouping of dicotyledonous wood fibres into short (mean length less than 900 µ), medium (900-1600 µ) and long (above 1600 µ). According to this, the fibres of Hevea brasiliensis belong to the medium category, having an average length of 1127 µ, 85% of them measuring 1001-1300 µ. They are of uniform thickness and the wall thickness does not show a wide range being only 3.0 µ to 4.0 µ, although the picture with regard to the tension wood fibres is different. To this may be added the observations on fibre diameter, the average being 32 µ, and the length/diameter ratio (average 35.10). The variation in fibre length and diameter (Fahn 1955, 1958, 1959a,b; Carlquist 1961, 1970; Hans, Burley and Williamson 1972)

is a limiting factor in their use as a diagnostic feature, while no attempt has been made to assess the L/D ratio which would be a more useful tool, provided the length and diameter recorded belong to the same fibres.

13.19 VESSELS

Dadswell and Eckersley (1935) classify the vessel diameter into minute (less than 100 μ), small (100-200 μ), medium (200-300 μ) and large (over 300 μ), while the International Association of Wood Anatomists (1939) has adopted the one suggested by Chalk (1938). According to this, vessels whose diameter is upto 100 μ are small, 100-200 μ medium and above 200 μ large. The former is further classified into extremely small (upto 25 μ), very small (25-50 μ) and moderately small (50-100 μ) and the large vessels into moderately large (200-300 μ), very large (300-400 μ) and extremely large (over 400 μ) while the medium group (100-200 μ) is not subcategorised. Metcalfe and Chalk (1950) have accepted the major groups and recognise small (upto 100 μ), medium (100-200 μ) and large (above 200 μ) for vessel diameter. The mean diameter of vessels in Hevea brasiliensis is 123 μ and thus belong to the medium group according to both the groupings. Vessel length has been classified into short (upto 350 μ), medium (350-800 μ) and long (above 800 μ) by Metcalfe and Chalk (1950), while Rodriguez (1957) considers upto 400 μ length as small, 400-800 μ as medium and above 800 μ as long. The average total length (Chalk and Chattaway

1934) of vessels in the present study being 716 μ qualifies the vessel to belong to the medium group. While length and diameter of vessel elements have been considered separately by workers in wood anatomy no place has been accorded to the ratio total length/diameter of the vessel which takes both the characters into account. Since both length and diameter shows a wide range of variation it is essential that length and diameter of the same vessel be measured for this purpose. The average L/D ratio of vessels has been found to be 6.54. Only a thorough investigation on a large number of species can judge the merits and demerits of L/D ratio as a tool in classifying vessels and fibres.

As the vessels show a range of 518-994 μ in length and 70-196 μ in diameter a further grouping of them has been attempted taking into consideration both length and diameter of the same individual vessels. The average values have been taken as a basis for this subgrouping and the vessels have been classified into (1) medium short (less than 716 μ long) and medium narrow (less than 123 μ diameter), (2) medium short and medium broad (more than 123 μ), (3) medium long (more than 710 μ) and medium narrow, and (4) medium long and medium broad. The results indicate that within the medium group, with regard to length and diameter, there occurs short and narrow, short and broad, long and narrow and long and broad vessels, their proportion being 11:12:17:10. This type of grouping has not hitherto been attempted, although wood anatomical studies have established

that vessel length and diameter show a fair range in the same sample (Carpenter and Leney 1952; Fahn 1955, 1958, 1959a,b; Venkateswaralu and Rao 1964; Carlquist 1970; Hans *et al*. 1972). The observed variations stress the scope of subgrouping when critically viewed and a grouping or subgrouping of the vessels taking into account both length and diameter would certainly be more useful in wood anatomical studies.

13.20 WOOD PARENCHYMA

Arrangement of parenchyma in different members of Euphorbiaceae-Crotonoideae varies from predominantly paratracheal in *Celaendendron* and *Pogonophora* to apotracheal in many other genera worked out (Metcalfe and Chalk 1950). Carlquist (1961) has adopted the types of axial parenchyma suggested by Kribs (1937) and recognises (1) diffuse, (2) diffuse in aggregates, (3) paratracheal scanty, (4) apotracheal banded narrow, (5) apotracheal banded wide, (6) vasicentric, (7) absent, and (8) terminal. Jane (1956) has recognised three major groups following Kribs (1950) and classified parenchyma into A. Apotracheal (1. diffuse 2. diffuse aggregate 3. concentric), B. Paratracheal (1. paratracheal scanty 2. unilaterally paratracheal 3. vasicentric 4. aliform 5. confluent) and C. Boundary (1. initial 2. terminal). The situation in *Hevea brasiliensis* is apotracheal banded narrow according to the former or apotracheal concentric according to the latter classification. Banded parenchyma is considered the most advanced type of

apotracheal parenchyma (Carlquist 1961).

Though Metcalfe and Chalk (1950) consider that parenchyma in Crotonoid wood is 'abundant', the situation in Hevea does not show that they are abundant. It is worth remembering that apparently no standards are available to judge the degree of their abundance. The only mention is that of Ricinodendron rautanenii in which parenchyma is very abundant, occupying more space than the space occupied by the fibres. Considering this as an indication of 'very abundance' the condition in Hevea is 'not abundant'.

13.21 XYLEM RAYS

The vascular rays of the secondary xylem of Hevea are few and heterogeneous composed of procumbent and upright cells, the latter being confined to the tails on both the sides. Kribs (1935, 1950), has recognised different types of ray organisation under the heterogeneous and the homogenous types. In the former three types are described. Type I - composed of procumbent and upright cells more or less alternating with each other or irregularly arranged; II(A) - upright cells confined to the margin and the uniseriate portions, II(B) - uniseriate rays composed of alternating upright and procumbent cells and multiseriate rays with upright cells confined to the terminal uniseriate portions (Kribs 1935, 1950; Metcalfe and Chalk 1950; Committee on Nomenclature 1957). In Hevea in both uniseriate and multiseriate rays the procumbent cells are in the middle

or the body of the vascular rays. Accordingly they belong to heterogeneous type II(A) of the above classification, at large. Strictly speaking the situation is slightly different in that the terminal portions are composed of four to six upright cells and in that the body or the middle is comprised entirely of procumbent cells. Their length falls within the range of less than one mm exhibited by many Crotonoid woods and are fine (Metcalfe and Chalk 1950). The marked nature of the ray cells to extend radially, when viewed in transverse sections, is a feature Hevea shares with woods of Euphorbia spp. (Carlquist 1970).

Dissection of biseriate and triseriate rays, occasionally noted in the present study, is a peculiar feature and is associated with increase in diameter. Splitting of the xylem rays into two does not appear to have been recorded in wood anatomy. It appears that this feature may be present in many woods, but is apparently overlooked.

13.22 VARIATIONS ACROSS THE STEM

The observations on the variations across the stem along the same radius show that the features of the wood elements are markedly affected, there existing a gradient from the periphery of the wood to the pith or vice versa. It is found that vessel length, vessel diameter, fibre length and fibre diameter progressively increase from the pith towards the periphery, while the number of vessels per unit area and the number of rays per unit length increase progressively from

the periphery towards the pith. No morphological differences or variations in the general features of the wood elements could be found along with the changes in the quantitative values. Kribs (1928) has found that the length of tracheids in Jack Pine is affected by their relative position across the tree and Bisset, Dadswell and Amos (1950) note that within one growth ring there exists a variation of fibre length in the wood formed at the beginning and that formed later. Stern-Cohen and Fahn (1964) record that in Eucalyptus gomphocephela there is a general trend for fibre length to increase towards the periphery. Recently, Goo (1971) and Hans et al. (1972) have studied this problem. Goo finds that in Acacia mollisima the fibre length increased from the pith towards the bark upto eight growth rings after which the tendency slowed down or stopped, and a similar tendency in the specific gravity of the wood. Hans, Burley and Williamson also report large variation of 12.4% and 16.1% respectively in the specific gravity of wood and in the fibre length, exhibiting a gradient from pith outwards in Eucalyptus grandis. The available information on the variation of wood characteristics across the stem is thus restricted to fibre length and specific gravity alone. It may be recalled from Table 8, that the variations between positions one and two (near the periphery) are markedly less, compared to the variations between the other samples not only in fibre length, but in other characters as well. The present observations in Hevea signify that quantitative values of wood elements follow a gradient from periphery to pith, the characters being length and diameter

of vessels and fibres, porosity and number of rays per unit length in the tangential plane. It also indicates that this variation is more pronounced during the early phases of growth in diameter, after which it is likely to narrow down.

13.23 WOOD SAMPLING

Samples to assess the properties of xylem elements of tension wood and normal wood have been taken at the same level of the respective branch. This would avoid inherent differences due to age and growth. Area of the normal wood has been marked out at the same relative position as that occupied by tension wood on the opposite side at 180° and observations taken from both. Taking samples of normal wood from the same side for comparison would be misleading as their age will not be identical with that of the tension wood sampled. Sampling of normal wood at 90° may not often be possible as the large bands of tension wood usually extend to the lateral sides. It may be pointed out here that even with all the care it is really problematical to obtain samples of tension wood and normal wood which are strictly comparable. Within the same growth ring (Bisset et al. 1950) and between different growth rings (Stern-Cohen and Fahn 1964) fibre length or diameter has been found to show marked variation and the same could hold true in the case of vessel elements as well. The difficulty in choosing strictly comparable samples are more in case where growth is eccentric, a feature often associated with reaction wood formation in many species.

13.24 OCCURRENCE AND DISTRIBUTION OF TENSION WOOD

Reaction wood is the type of wood produced on the lower sides of leaning and crooked stems of gymnosperms, termed compression wood, and on the upper sides of axial parts of similar nature in dicotyledons, called tension wood (Dadswell and Wardrop 1949; Jane 1956; Esau 1965a; Fahn 1967). Tension wood is of general occurrence and found, in a survey, in 50% of the species in their stems and in roots of 25% (Hoster and Liese 1966; Tsoumis 1968). Though mostly found in leaning and crooked stems its presence in perfectly straight stems, however, cannot be ruled out (Tsoumis 1968).

Tension wood has been found to occur in a large number of species belonging to unrelated families (Jane 1956; Ghosh and Rao 1958). It has become conventional to pinpoint tension wood to the upper side of leaning or horizontal branches. In Hevea it has been found to be present in straight and leaning stems as well as in roots, right from seedlings about two-three months old (Panikkar 1971). As a rule it cannot be conceived to delimit its presence on the upper side of leaning branches, although it is predominantly so, and has been found to extend to the lateral sides and present on the lower side as well. The quantity of tension wood present depends on several factors and is as such a feature of high variability, and the present observations support the earlier report on the occurrence of tension wood in Hevea (Panikkar 1971). On the average tension wood occupies 46.36% area of the upper half of leaning branches and 13.97% of the lower, as measured

from transverse sections of wood. Considering the whole area, tension wood occupies 30.17%.

Wardrop (1961) has recognised two types of tension wood, the compact and diffuse. In the former, the xylem fibres with unlignified inner layer, termed the gelatinous layer, occur in a particular region of the stem whereas in the latter they are scattered singly and in groups among normal cells. Eccentricity of growth and wider growth rings need not necessarily indicate the presence of tension wood (Dadswell et al. 1958). The diagnostic feature is the xylem fibres which have a conspicuously thickened cell wall, part or all of which is unlignified (Munch 1938; Wardrop and Dadswell 1948, 1955; Jutte 1956; Wardrop 1961; Panikkar 1971).

While Hevea brasiliensis has tension wood of the compact type, assymetry of growth is not often associated with its presence. Onaka (1949) in his elaborate survey on reaction wood also finds that in many species no eccentric growth occurred and that when it is present such growth is confined to the upper side. Jane (1956) also does not assume that an eccentric pith be necessarily associated with tension wood, although it may be generally present.

13.25 FEATURES OF TENSION WOOD ELEMENTS

Literature available on tension wood advocates contradictory views on the properties of wood elements compared to the normal wood. Although Esau (1965a) says that in reaction wood the tracheids and fibres have a rounded

appearance and include intercellular spaces among them, Chow (1946) finds that they are radially compressed. The present observations fail to note any such difference in shape of fibres or vessels and presence of intercellular spaces, compared to those in the normal wood. The fibres are square to rectangular in transectional view arranged in radial seriations in both tension and normal wood and there are no intercellular spaces in either. The vessels may show slight variations in shape depending on whether they occur solitary or in groups and this trend is common to both tension wood and normal wood and cannot hence be ascribed to a particular type of wood.

The characteristic feature of tension wood fibre is the presence of an additional inner layer which is very thick and often more or less completely filling the lumen, reducing it to a narrow slit in cross sectional appearances. That this additional layer, which is the innermost, is composed of cellulose or hemicellulose, as observed in the present study by staining reactions, has also been found by Wardrop and Dadswell (1948) in Eucalyptus regnans and by Jayme and Harders Steinhauser (1950) in poplar (cf. Jane 1956; Dadswell et al. 1958). From the present studies, it becomes evident that the additional inner layer is apposed to the secondary wall of fibres. Onaka (1949) finds that it may sometimes consist of a special inner layer or the whole or part of the secondary layer.

In Hevea the properties of vessel elements do not show variations in tension wood and normal wood. Their number per unit area, arrangement, length, diameter and length/diameter ratio are comparable in both. This is in contrast to what is reported in Fagus sylvistris (Chow 1946) that vessels are fewer and radially compressed. Scurfield and Wardrop (1962) and Wardrop (1964) also note that there is a reduction in the number of vessels. Chow (1946) reports that fibres tend to be smaller in sectional area and longer. Clarke (1937) and Dadswell and Wardrop (1949) do not find any difference in wood fibre characteristics in tension and normal wood as has been seen in the present study. A marked feature of the reaction wood in Hevea is the tangential compression of the vascular rays. The number of rays per unit length however remains unaffected whereas the diameter of rays has been found to be, on the average lesser by 27.5% compared to those of the normal wood. This is in contrast to the report of Scurfield and Wardrop (1962) who find a reduction in the number of vascular rays but apparently do not note any reduction in their tangential extent. The contradictory reports on the quantitative characters of tension wood elements compared to those of the normal wood, however, indicate that the reaction responses vary widely in different species.

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SUMMARY

SUMMARY

The seeds of Hevea brasiliensis Muell. Arg. keep viability only for short period and record high percentage of germination if sown on time. The germination is hypogeal and the growth of the seedlings is rhythmic. The two cotyledons are supplied with three traces each. As the six traces which supply the cotyledons move down through the hypocotyl, they divide and organise into twelve strands, each comprised of a median flanked by laterals. The medians move to the primary lateral roots, whereas the laterals of the adjoining strands move closer and pass straight into the tap root.

The root apex of seedlings shows two promeristems: one giving rise to the dermatogen and root cap and the other to the cortex, stele and pith. The shoot apex has a two layered tunica, a central mother cell zone, pith rib meristem and flank meristem. The shoot apex at the maximal stage of the plastochron is dome shaped. The apex is almost flat at the minimal stage.

The leaf arrangement follows a 2/5 pattern. Two contact parastichies are discernible: one set of five winding around the axis anticlockwise and the other of three winding in the opposite direction. The median trace of a leaf is related to an anadromic lateral three plastochrons apart and

a katadromic lateral two plastochrons behind. The node is trilacunar. The median trace, however, is composed of seven strands and the laterals of two each. The strands undergo a series of changes in their course to the leaf base and form a crescent shaped vascular cylinder composed of adaxial and abaxial elements. Stomata are restricted to the abaxial surface of the leaves. The abaxial cuticle has reticulate surface pattern. The leaf venation is camptodermous.

Rhythmic growth is characteristic of the mature trees. Period of vigorous activity, which culminates in growth in length and production of a flush of leaves, is limited to a short period. The annual rhythm of wintering, refoliation and dormancy is more or less precise. On the onset of dormancy the nodes become telescoped lamina are reduced in size and petiole gets shortened progressively. A reduction in the size of apical dome at successive maximal stages of the plastochron is also noticed. Little growth in length takes place during dormancy. Cataphylls are produced which cover the dormant apex. Suberisation of abscission zones of appendages and development of periderm are also associated with dormancy. Further, the tissues at the shoot apex in general are more mature and differentiated compared to those in the vigorous apices.

The young bark is smooth. As growth advances lenticels, which are small and plenty, develop, Leaf scars are prominent. Very old bark is rough due to shallow fissures. The bark has an outer zone of hard tissues and

an inner one which is soft that contains functional elements of the secondary phloem. The sieve tubes have oblique end walls and compound sieve plates. Their diameter is very small or moderately small. They are of short or medium length. Triseriate phloic rays are dominant. Uniseriate, biseriate and four seriate rays also occur. They belong to heterogenous type IIA and range from very fine to medium on the basis of ray width.

Dilation growth is effected by cortical expansion, pericyclic expansion and ray expansion. Ray splitting is noticed in the outer portions of the bark. Sclerosis begins when the axis is relatively young and involves the pericycle, cortex and phloic rays. Periderm is superficial. The first phellogen is initiated in the subepidermal layers. Subsequent periderms differentiate within, separating the cork tissues formed earlier.

Tapping causes wounding of the outer hard bark and major part of the soft bark. The cells beneath the cut surface undergo hyperplasia and to a limited extent hypertrophy and a wound phellogen differentiates parallel to the severed surface. The layers of cells immediately beneath undergo sclerosis.

Both primary and secondary laticifers occur in the bark. The initials of the primary laticifers arise at the hypocotyl of the embryo, from the procambial cylinder. The secondary laticifers develop from the derivatives of the

fusiform initials of the vascular cambium. The laticifers belong to the articulated anastomosing type. In the bark they occur in concentric rings. The anastomoses are restricted to the laticifers belonging to a ring and those belonging to adjacent rings do not develop radial anastomoses. Intrusive growth is very limited. Dissolution of parenchyma cells as the laticifer protuberances come across parenchyma cells and conversion of the latter into part of the laticiferous system establish the tangential connections. Differentiation of more initials adjoining above and below the first initials brings about longitudinal extension. In both the cases, there is more or less complete dissolution of cross walls. The laticifers are coenocytic and their walls are plastic and non-lignified.

The number of vessels per unit area of the wood is moderately few. Wood parenchyma is apotracheal, banded narrow. Considering the length and diameter, the vessels belong to four categories: (1) medium short and medium narrow, (2) medium short and medium broad, (3) medium long and medium narrow and (4) medium long and medium broad. Xylem rays belong to heterogenous type IIA. Both uniseriate and multiseriate rays are present. Dissection of rays is rarely observed. Fibres of the secondary xylem are medium long and their wall thickness is uniform. The wood elements show marked variation across the stem along the same radius. Vessel length, vessel diameter, fibre length and fibre diameter progressively increase from the pith towards the

periphery, whereas the number of vessels and rays per unit area decreases.

Tension wood of the compact type occur in seedlings as well as in mature stems. It is also observed in roots. The properties of tension wood elements do not show appreciable variation compared to those of the normal wood, in general. However, the vascular rays in the tension wood show marked tangential compression.

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PLATES 1 to 27:

HEVEA BRASILIENSIS MUELL. ARG.

PLATE-1

Fig. 1. Germination of seeds. The seeds start sprouting from the fifth day onwards.

Fig. 2. Growth behaviour of the seedlings during the first five weeks after sprouting. Growth is rhythmic.

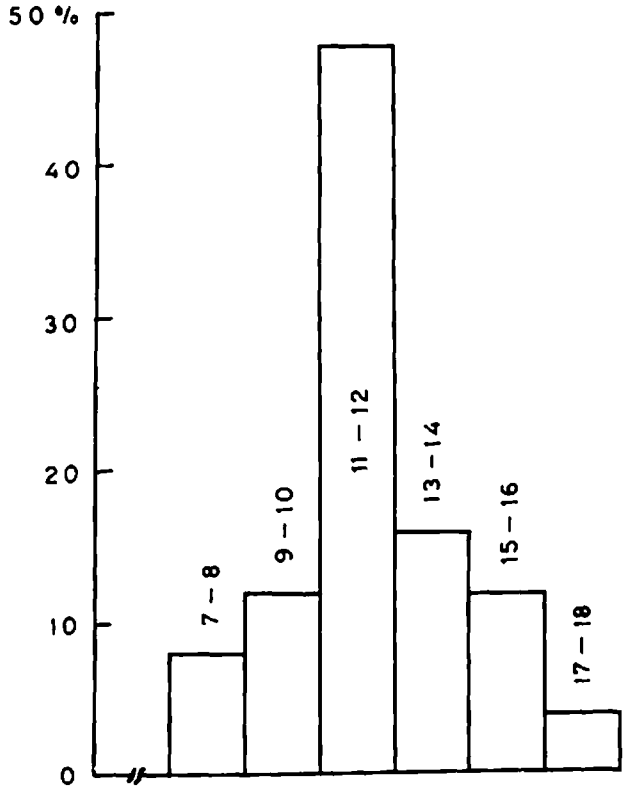
PLATE-2

Fig. 3. Percentage of seedlings belonging to different classes of primary lateral roots number.

Fig. 4. Percentage of sieve tubes belonging to different classes of length.

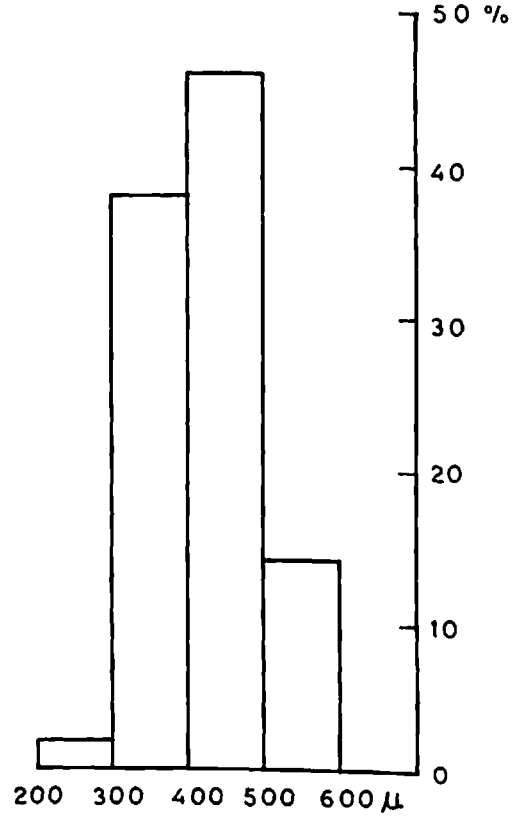
Fig. 5. Percentage of sieve tubes of different classes of diameter.

Fig. 6. Percentage of phloic rays belonging to different types.



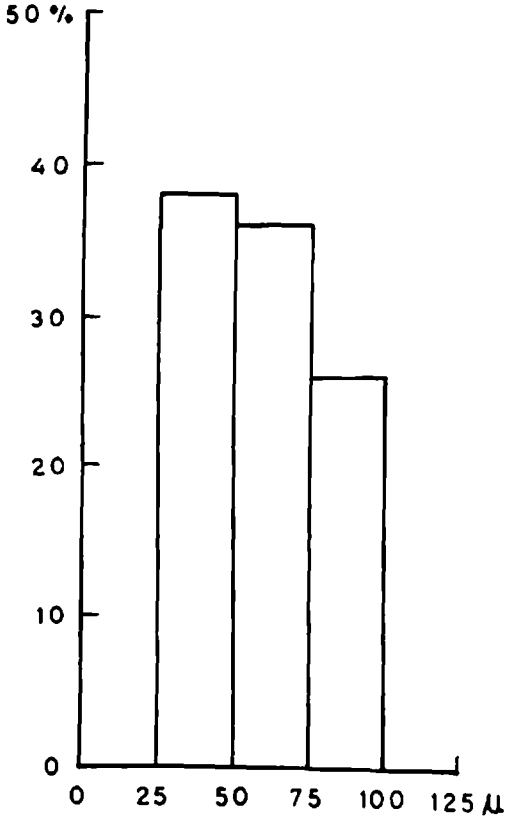
No. OF PRIMARY LATERAL ROOTS

FIG. 3



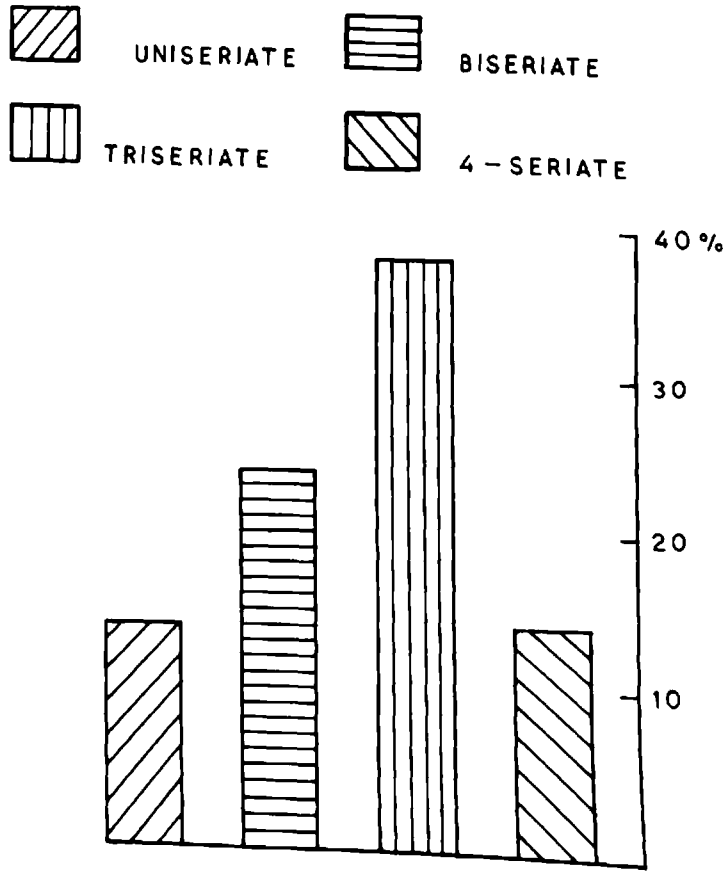
SIEVE TUBE LENGTH

FIG. 4



SIEVE TUBE DIAMETER

FIG. 5



PHLOIC RAY TYPES

FIG. 6

PLATE-3

Fig. 7. Percentage of phloic rays belonging to different classes of width.

Fig. 8. Percentage of phloic rays belonging to different classes of height.

Fig. 9. Percentage of fibres belonging to different classes of length.

Fig.10. Percentage of fibres belonging to different classes of diameter.

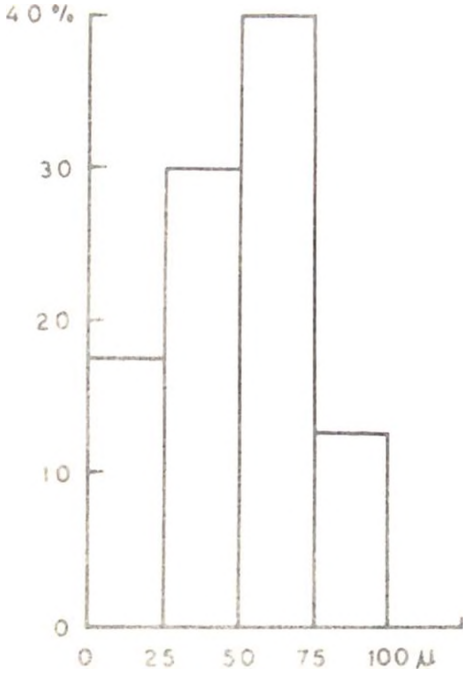
PLATE-4

Fig. 11. Distribution of fibres into different classes of length/ diameter ratio.

Fig. 12. Percentage of vessels belonging to different classes of length.

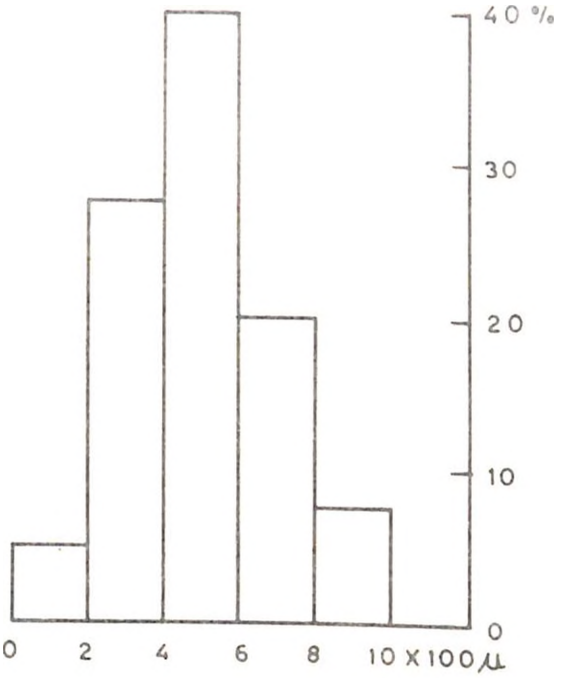
Fig. 13. Percentage of vessels belonging to different classes of diameter.

Fig. 14. Distribution of vessels into different classes of length/ diameter ratio.



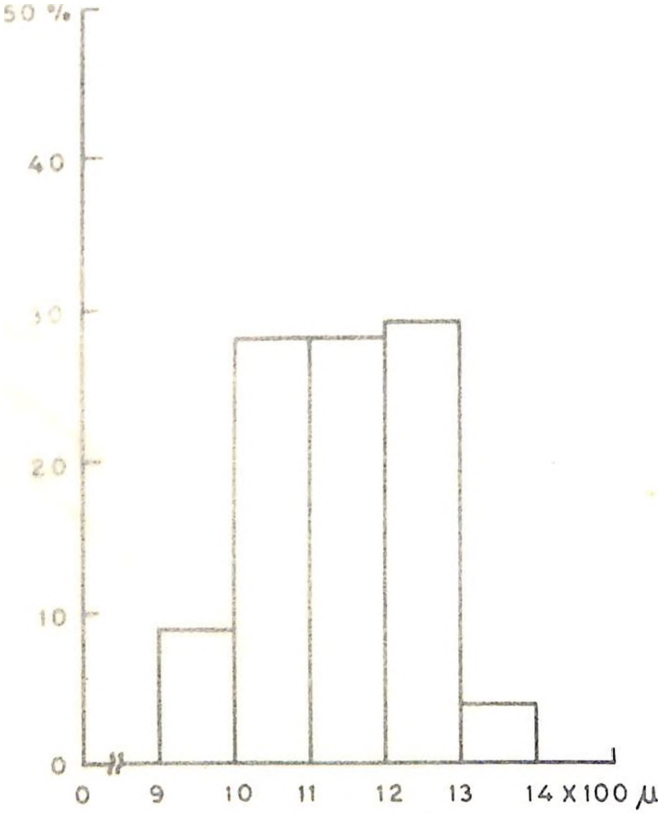
PHLOIC RAY WIDTH

FIG. 7



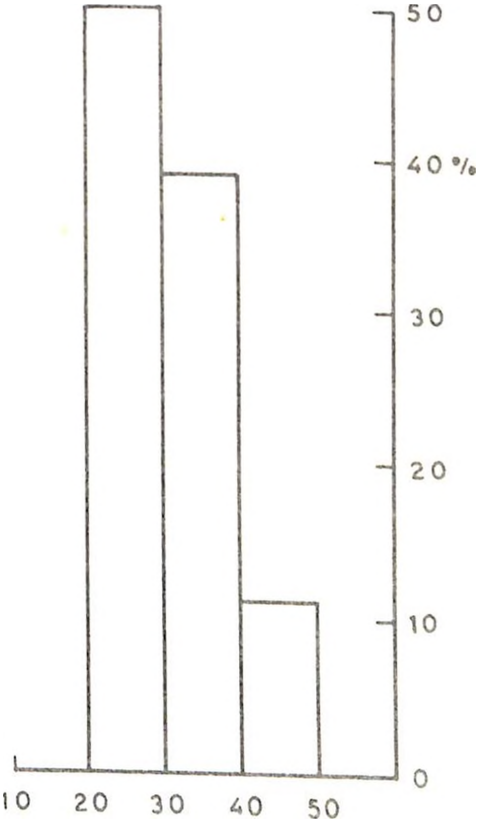
PHLOIC RAY HEIGHT

FIG. 8



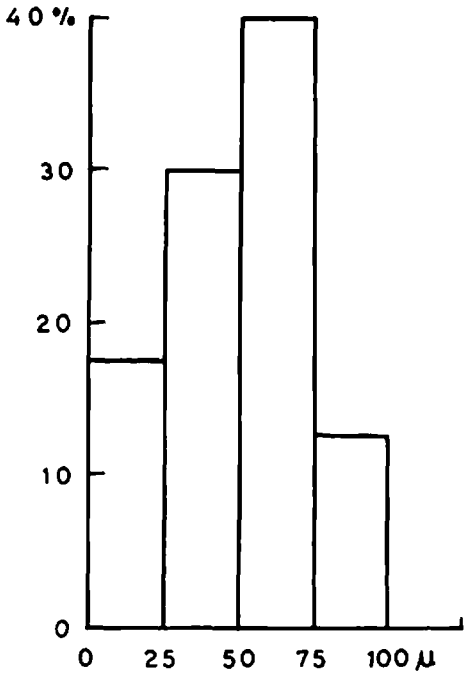
FIBRE LENGTH

FIG. 9



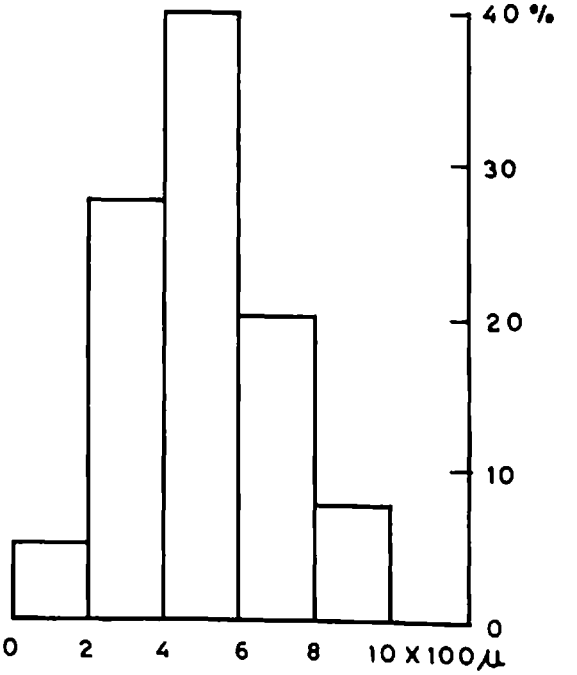
FIBRE DIAMETER

FIG. 10



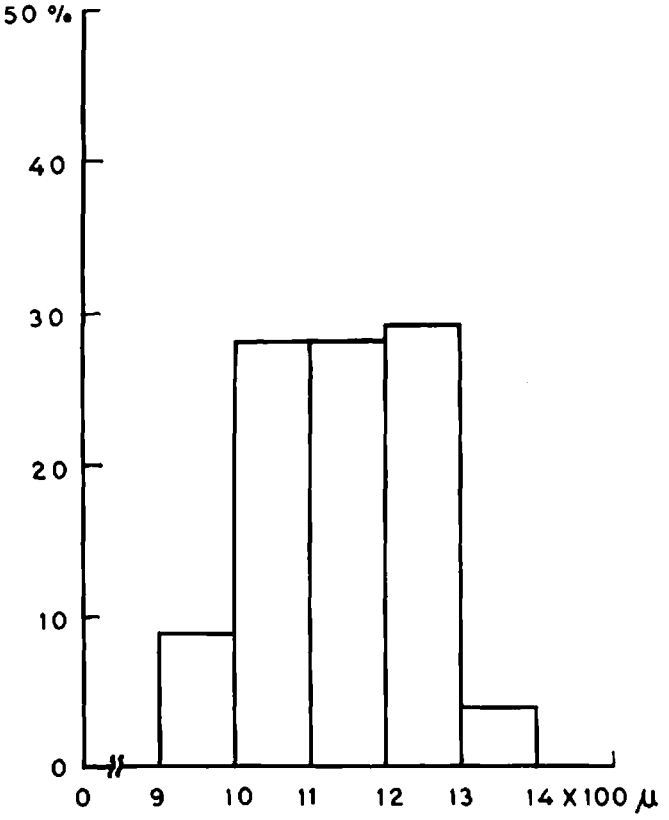
PHLOIC RAY WIDTH

FIG. 7



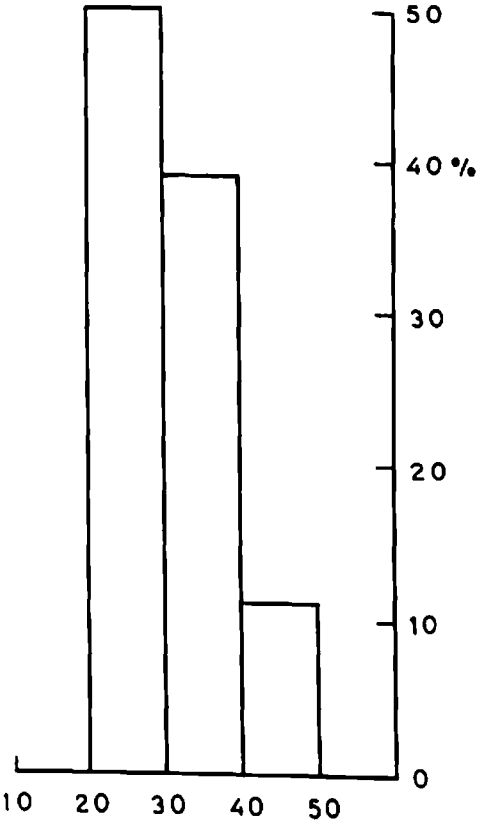
PHLOIC RAY HEIGHT

FIG. 8



FIBRE LENGTH

FIG. 9



FIBRE DIAMETER

FIG. 10

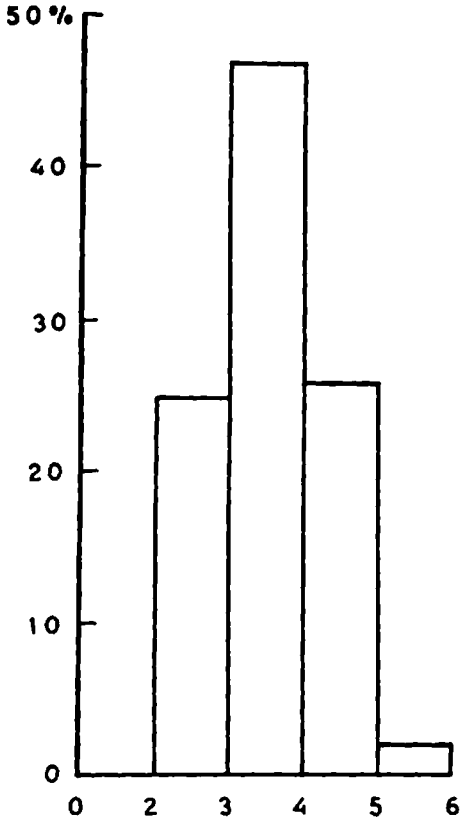


FIG. 11

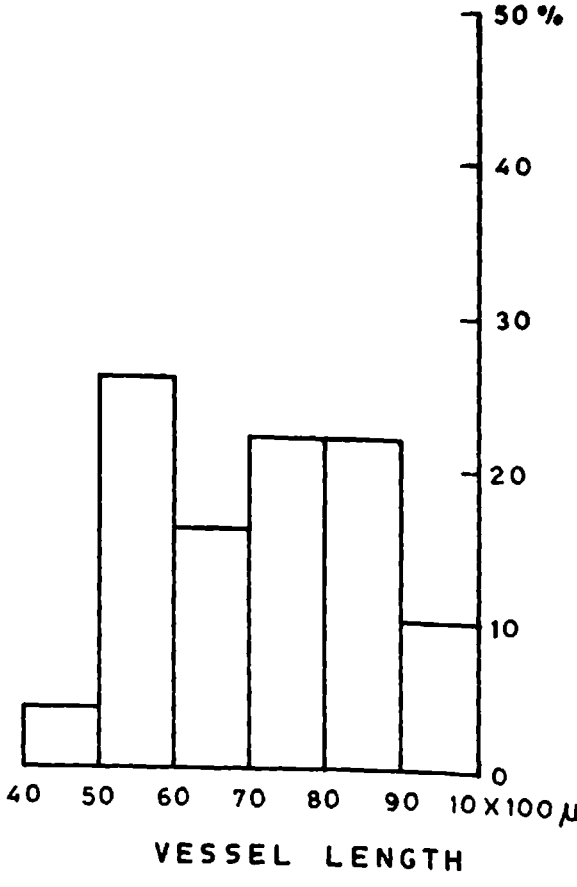


FIG. 12

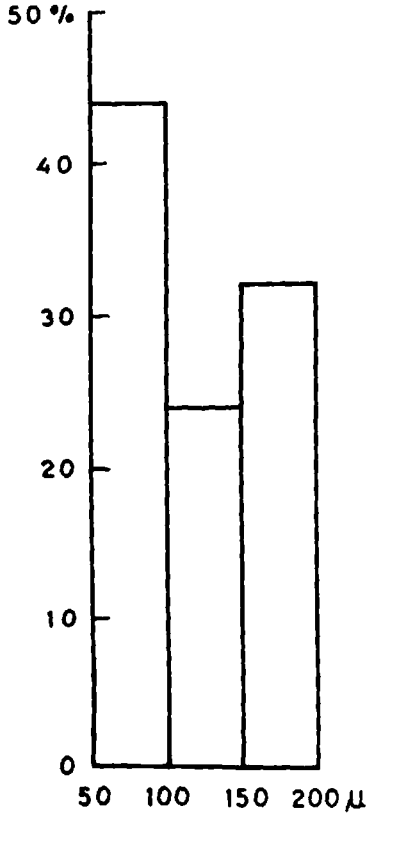


FIG. 13

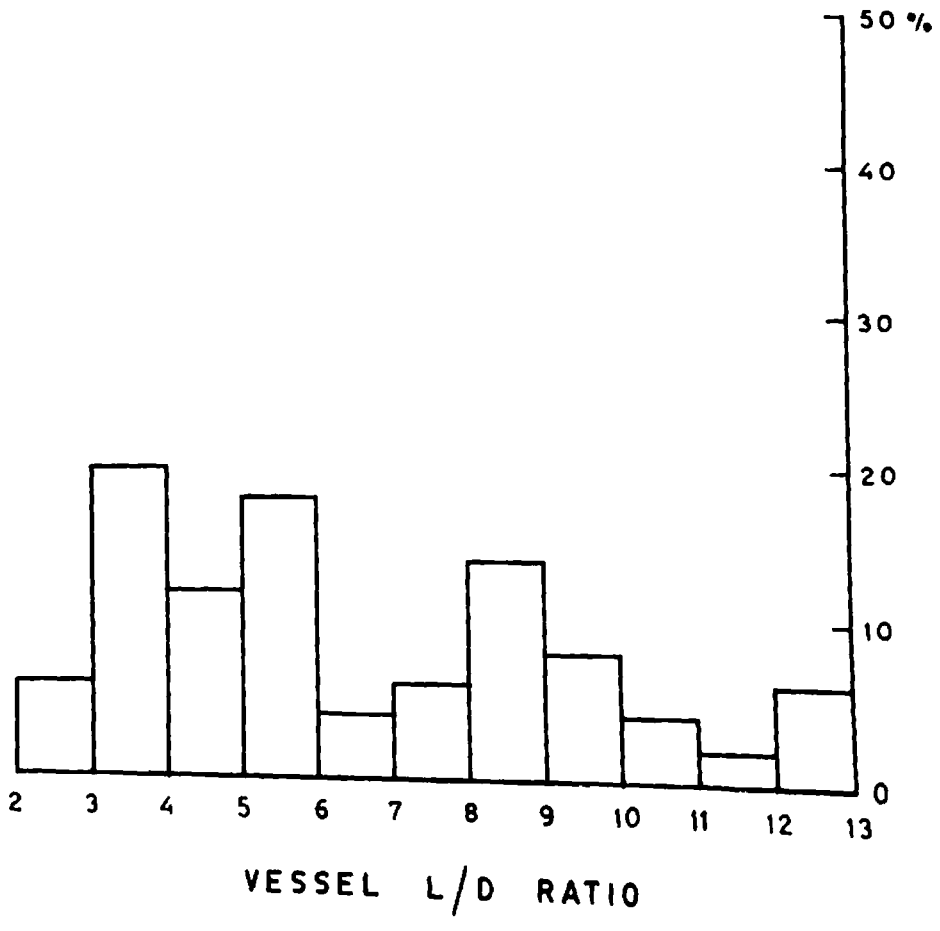


FIG. 14

PLATE-5

Fig. 15. Distribution of vessels into different types on the basis of length and diameter.

Fig. 16. Percentage of xylic rays belonging to different types.

Fig. 17. Percentage of xylic rays belonging to different classes of height.

Fig. 18. Percentage of xylic rays belonging to different classes of width.

PLATE-6

Figs. 19-24. Transections showing the different stages of transition. 19 - Above the cotyledonary node. 20 - Just below the cotyledonary node showing the six cotyledonary strands and four strands in two groups at the intercotyledonary plane. 21 - The six cotyledonary strands begin to divide and separate. 22 - Twelve strand stage. 23 - Departure of the medians to the primary lateral roots. 24 - Just below the level of primary lateral roots. The lateral xylem of adjoining strands move closer and pass straight to the tap root.

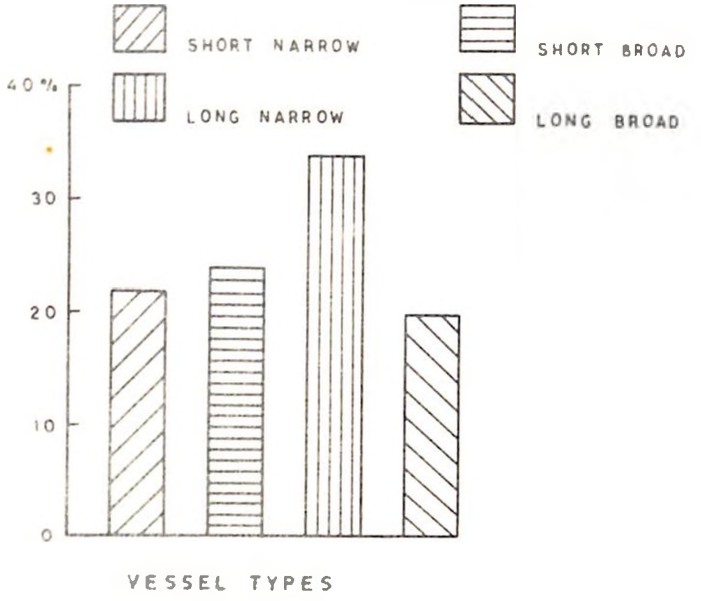


FIG. 15

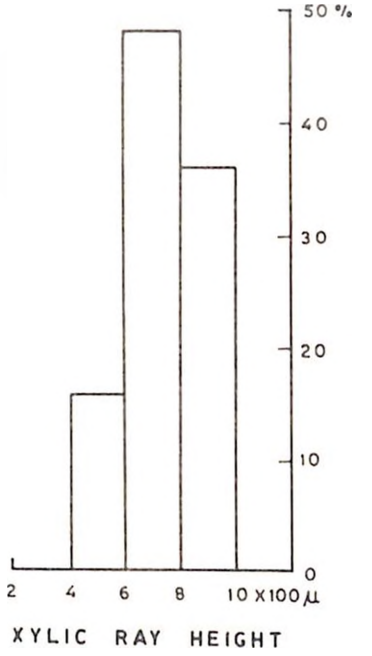


FIG. 17

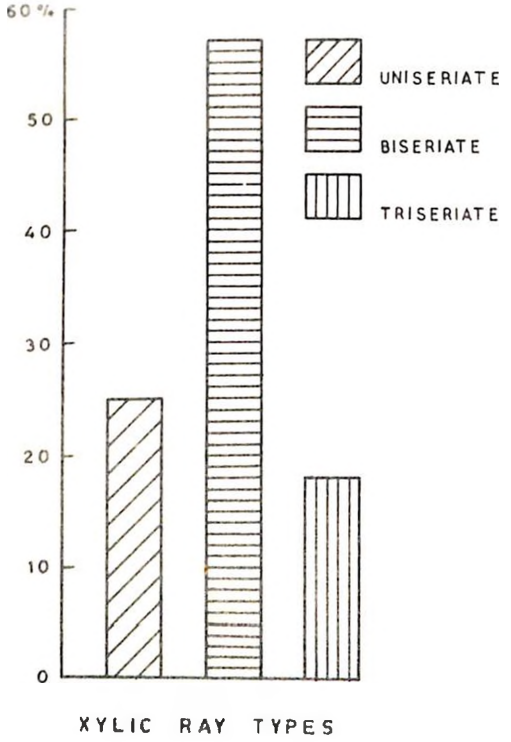


FIG. 16

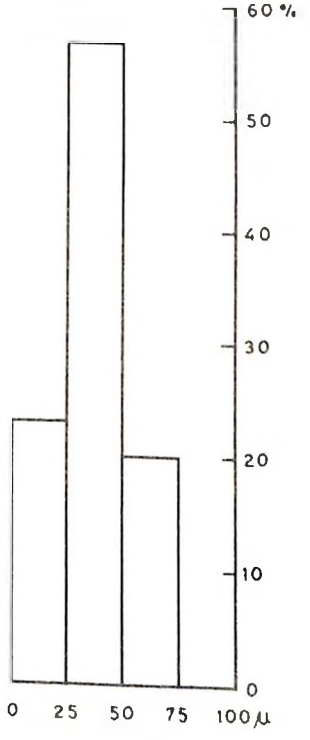


FIG. 18

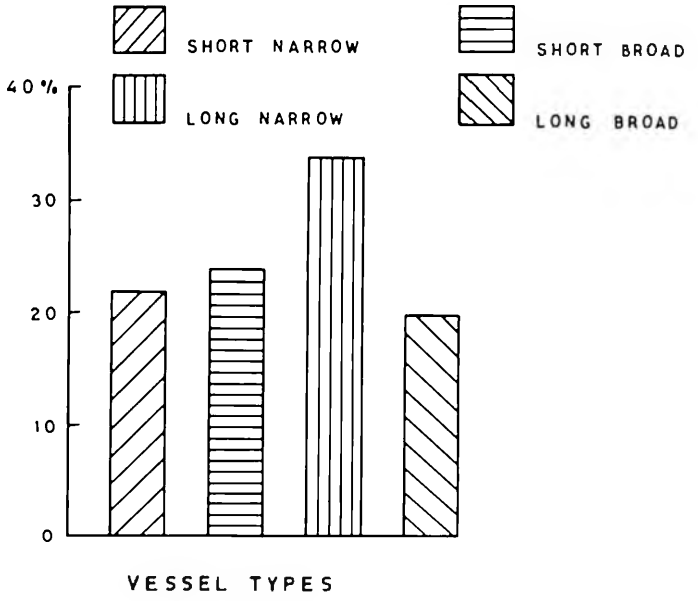


FIG. 15

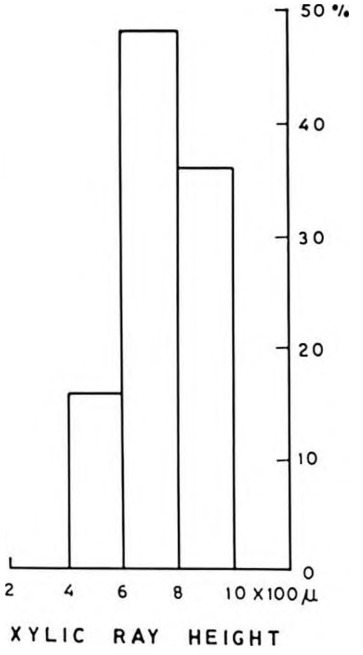


FIG. 17

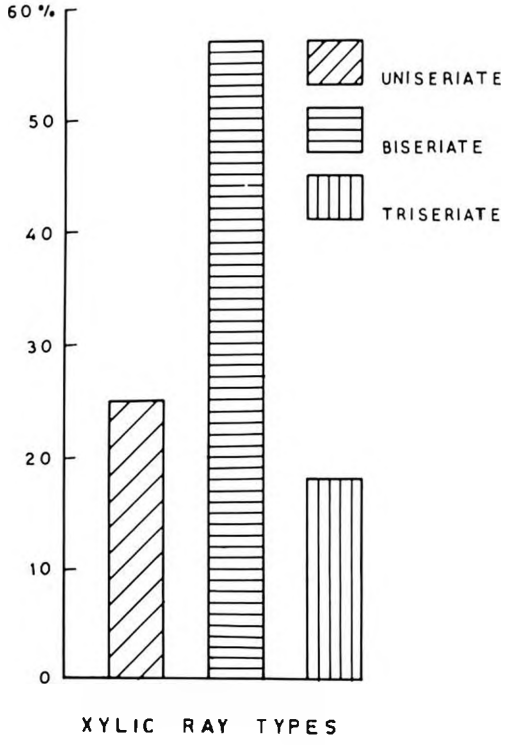


FIG. 16

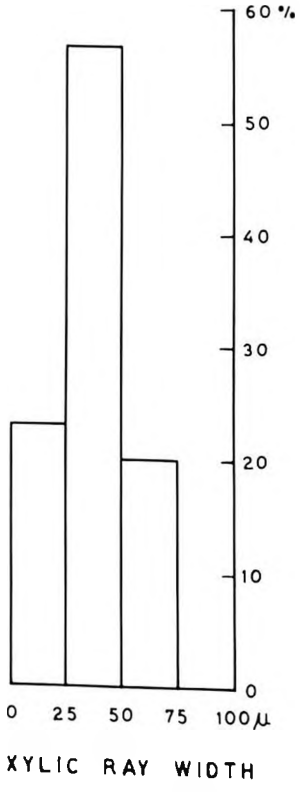
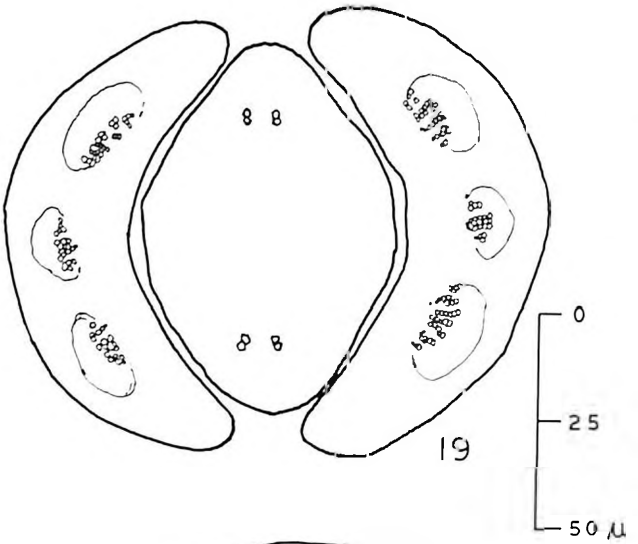


FIG. 18



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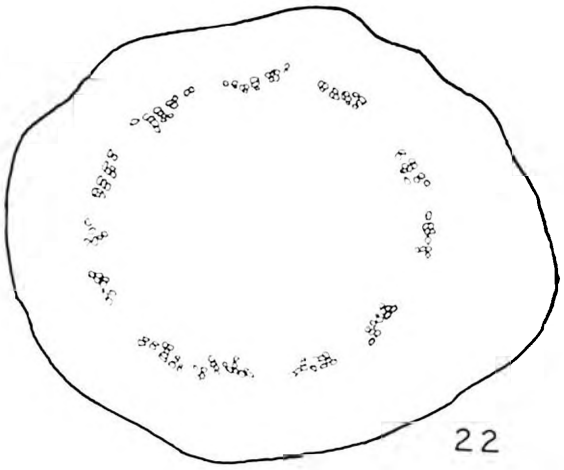

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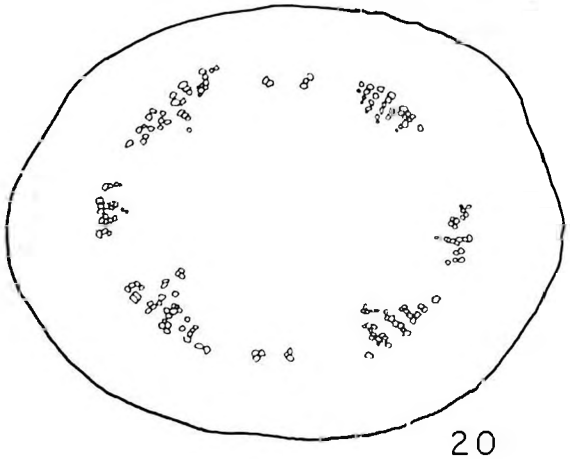

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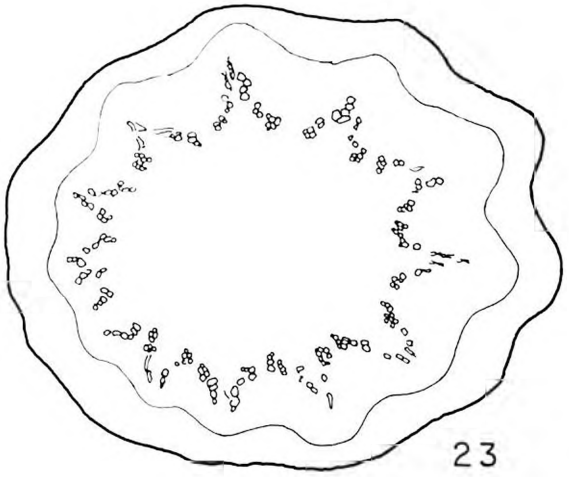

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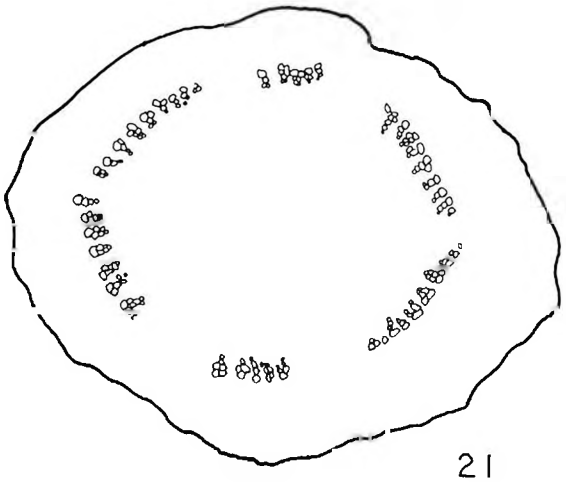

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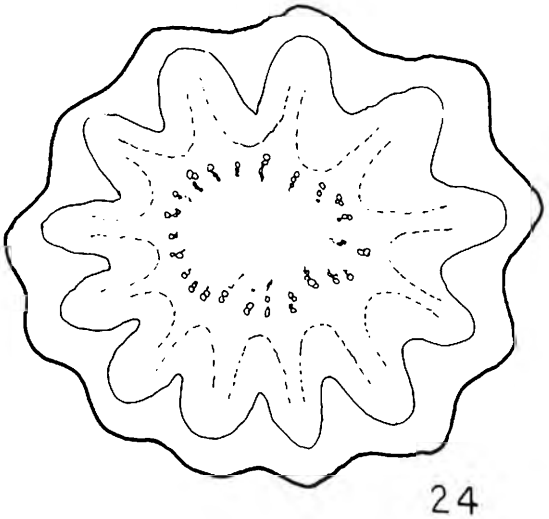


24

PLATE-7

Fig. 25. Diagramatic representation of radicular apex.

Fig. 26. Radicular apex in longisection.

Fig. 27. Diagramatic representation of root apex of seedlings.

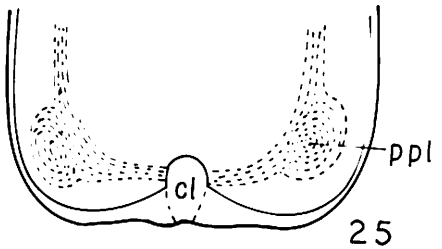
Fig. 28. Longisection of the root apex of seedling.

Fig. 29. Diagramatic representation of shoot apex.

Fig. 30. Longisection of shoot apex at maximal phase of plastochron.

Fig. 31. Longisection of shoot apex at minimal phase of plastochron.

(ch - common histogen for periblem and plerome. cl - columella. cmc - central mother cell zone. dc - dermocalyptrogen. fz - flanking zone. ppl - promeristem of primary lateral root. prm - pith rib meristem. t_1, t_2 - first and second tunica)



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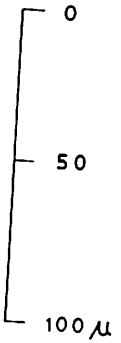

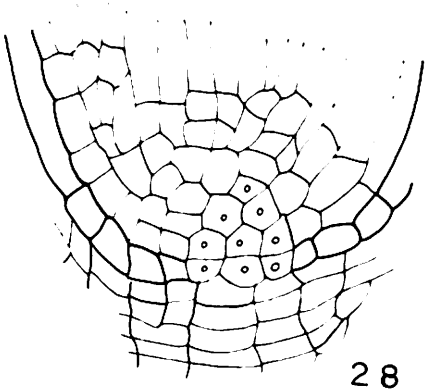

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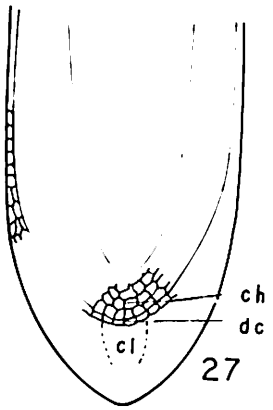

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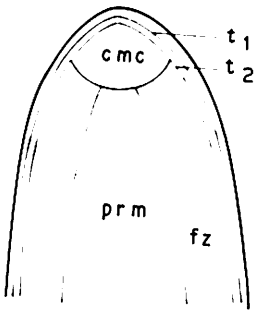

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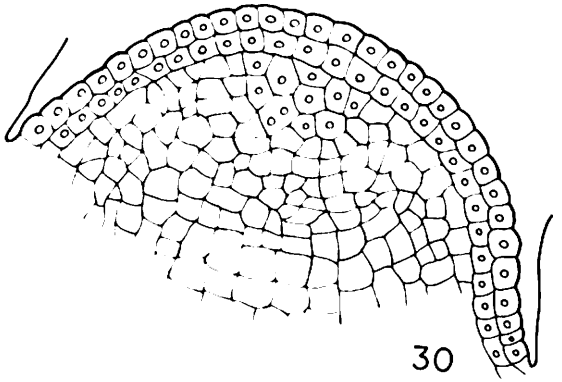

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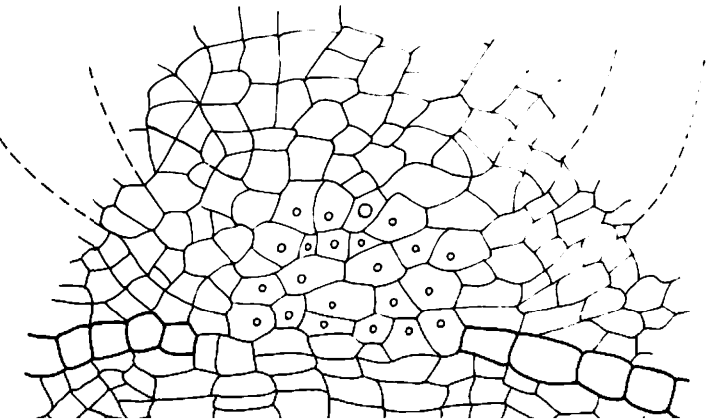


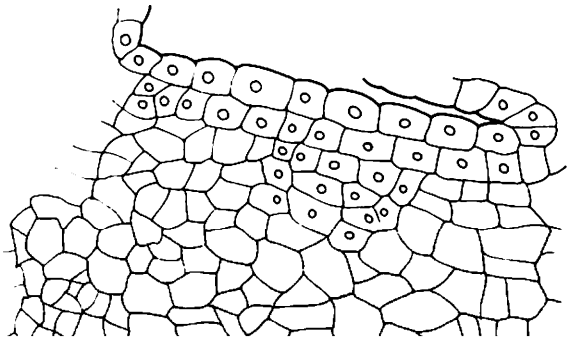
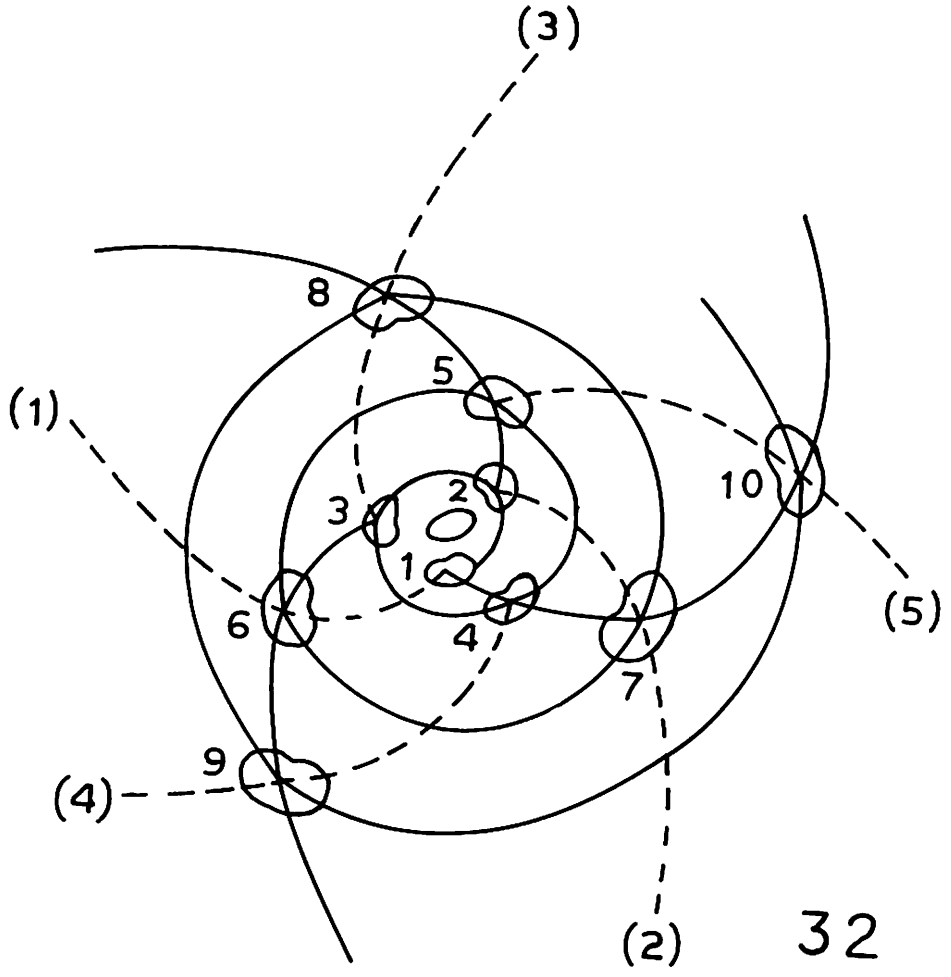


PLATE-8

Fig. 32. Diagramatic representation of phyllotaxis.

Fig. 33. Diagramatic representation of trace relationships.



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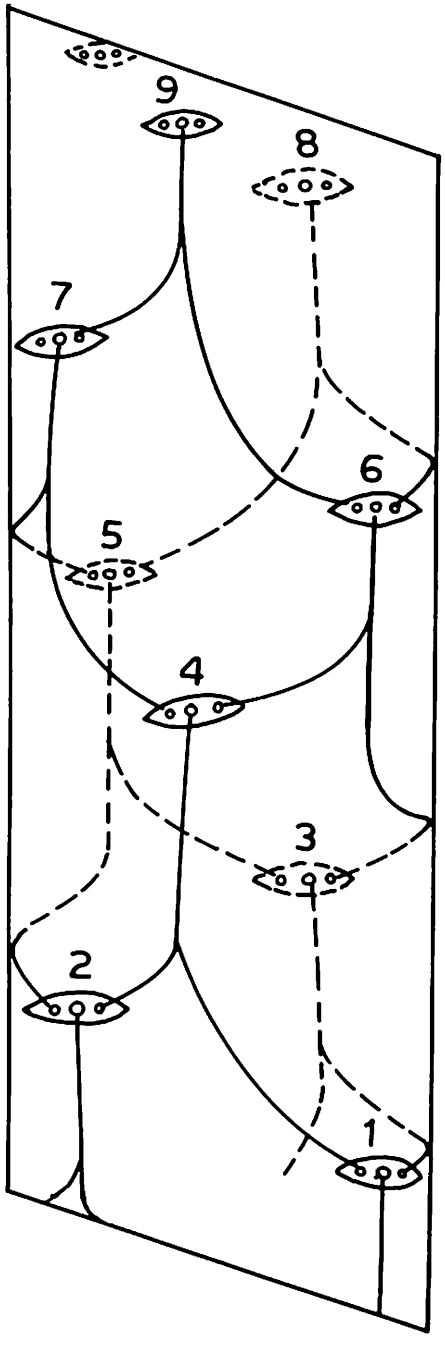


33

PLATE-9

Figs.34-40. Transections showing the nature of nodal pattern.

34 - The median composed of three strands and the laterals of two each. 35 - The traces show divisions. 36,37 - The median composed of seven traces. The laterals have divided and the trace destined to enter the leaf base shows swinging. 38,39,40 - Formation of the vascular crescent at the leaf base composed of adaxial and abaxial elements.

Fig. 41. Diagramatic representation of the nodal structure.

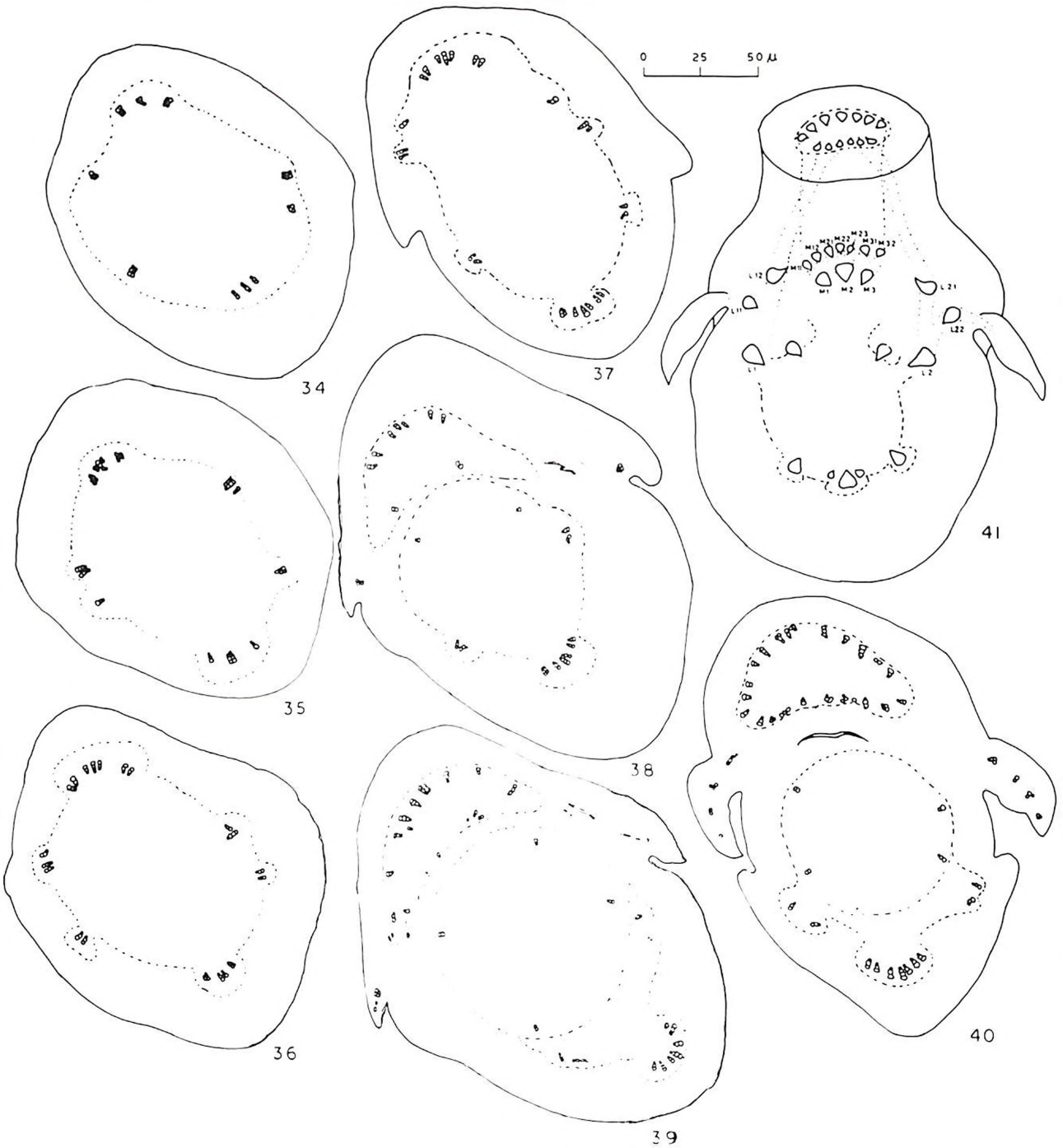

0 25 50 μ
34
37
41
35
38
36
39
40

PLATE-10

Fig. 42. Seeds and seed germination.
A,B - adaxial and abaxial views respectively of the seed.
C-G - show different stages in germination (× 1/2).

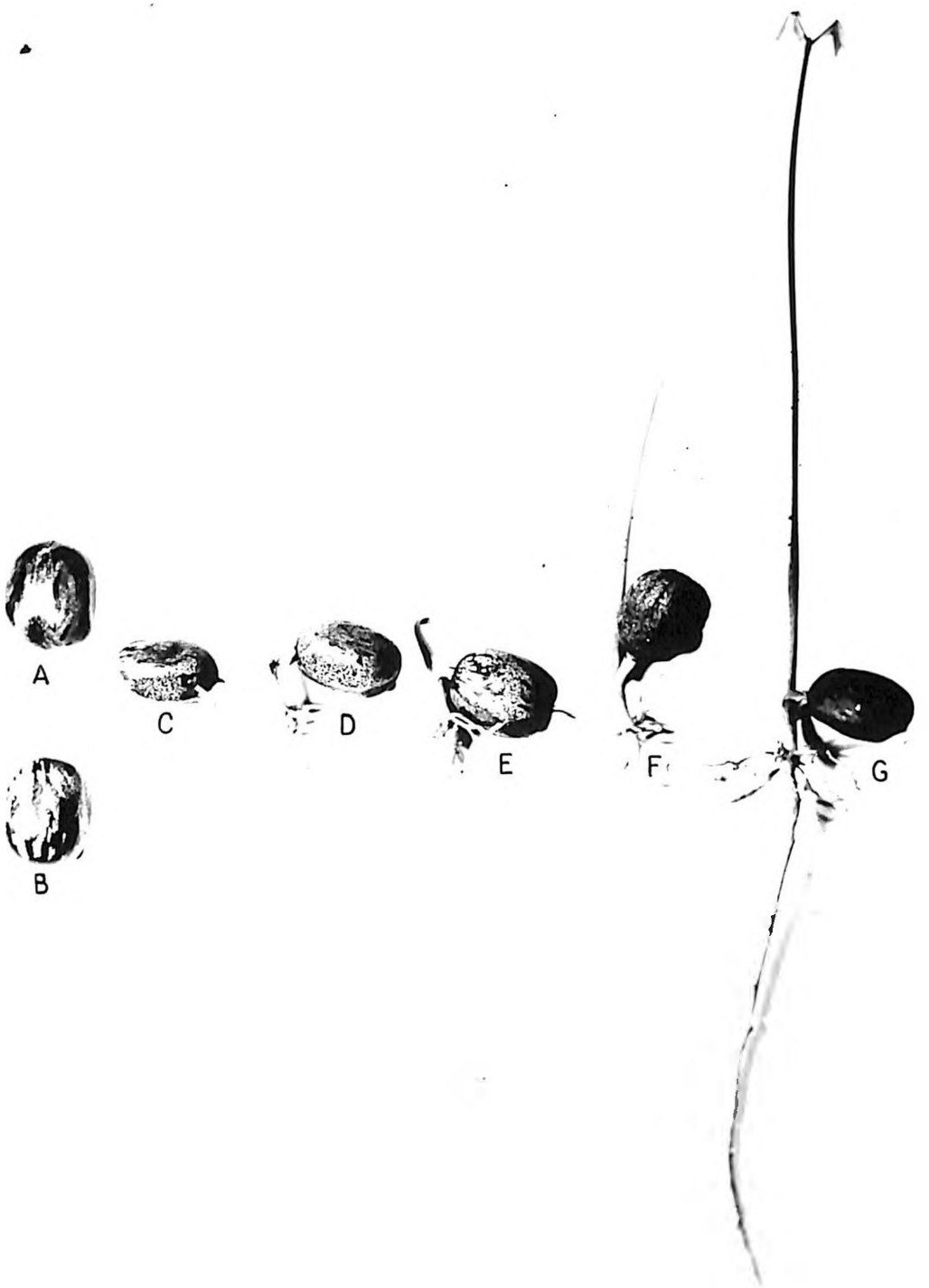

A
B
C
D
E
F
G

PLATE-11

Fig. 43. A-D show shoots developing from the cotyledonary axils when the apical buds get damaged (× 1/2).


A
B
C
D

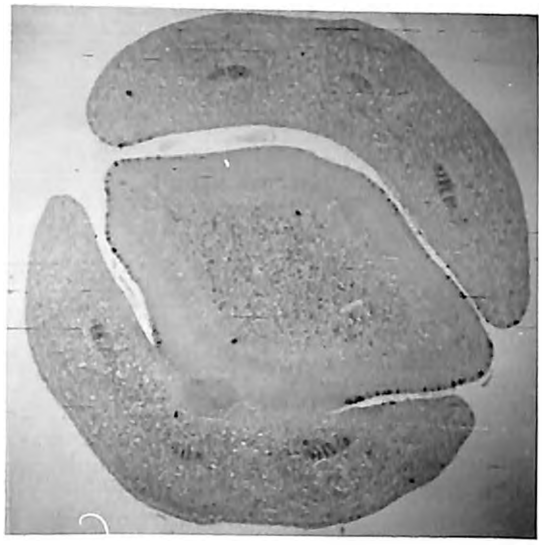
PLATE-12

Fig. 44. Transection of the seedling through the cotyledonary node (× 30).

Fig. 45. Transection of a sprouted seed showing a developing lateral root (× 100).

Fig. 46. Transection of seedling showing the arrangement of the primary lateral roots. All the primary lateral roots arise more or less at the same level around the radicular axis (× 28).

Fig. 47. Transection showing the supply to a primary lateral root. Obliteration and degeneration of the centrifugal xylem may also be seen (× 97).



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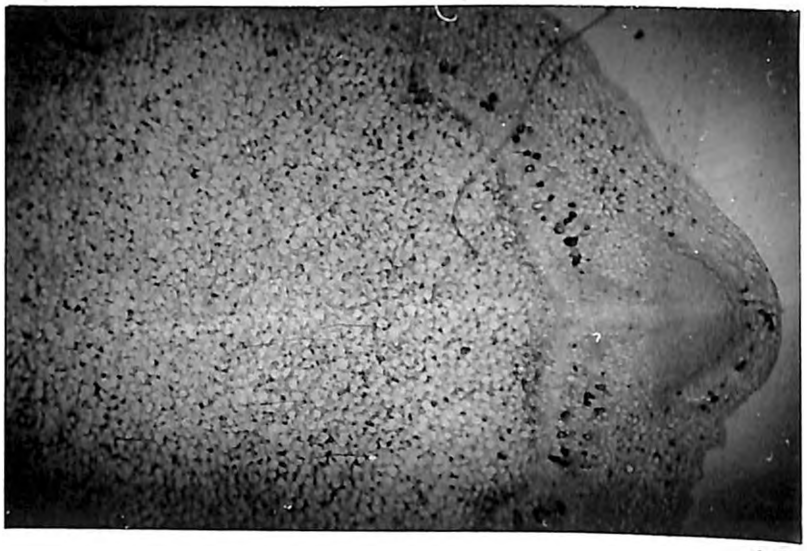

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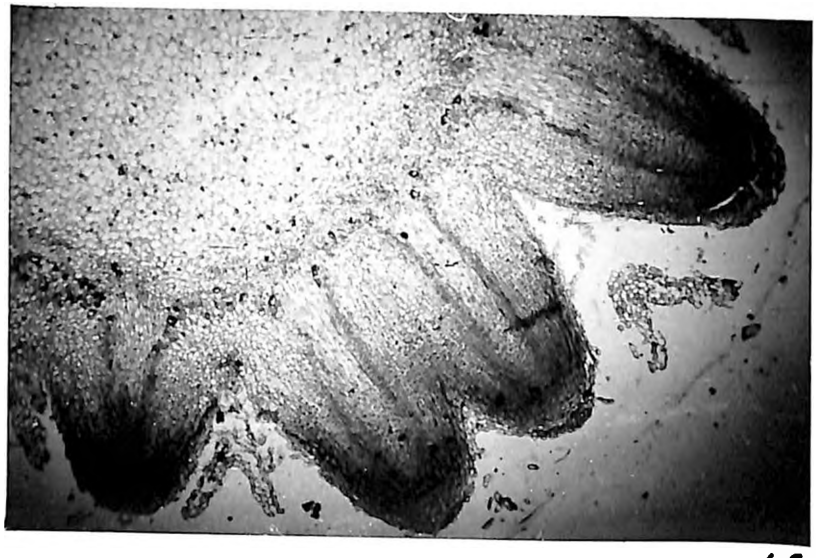

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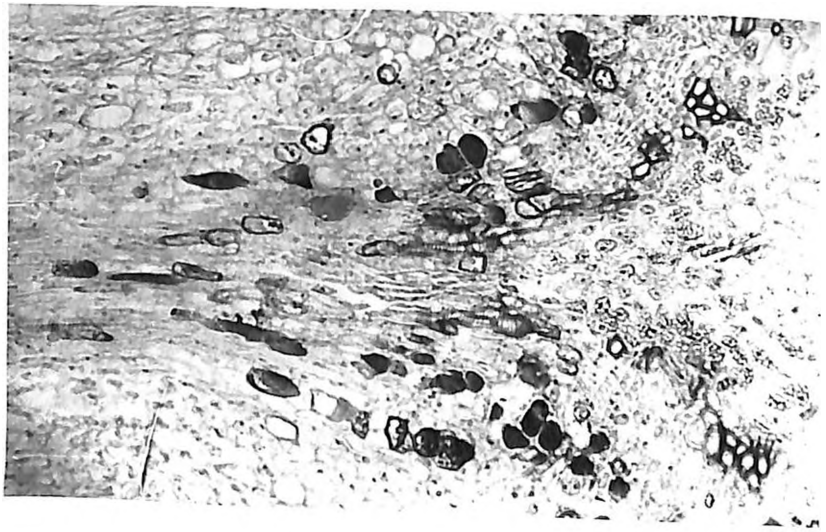


47

PLATE-13

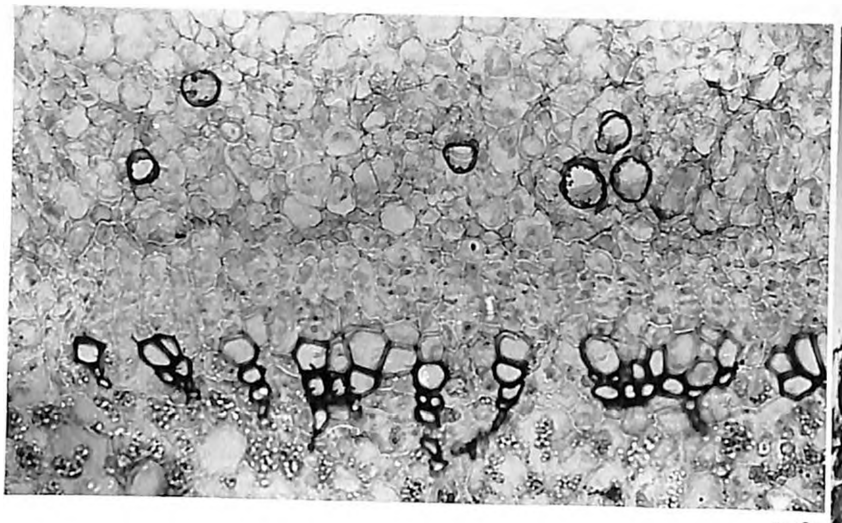
Fig. 48. Transection showing the obliteratio and degeneration of centrifugal xylem at the lower end of the hypocotyl (× 240).

Fig. 49. Longisection of the mature embryo showing the procambial cylinder (× 38).

Fig. 50. Longisection of the radicular apex (× 64).

Fig. 51. Longisection of the apex of a seedling root (× 76).

Fig. 52. Longisection of the embryonic shoot apex. The apex is in the second plastochron (× 64).



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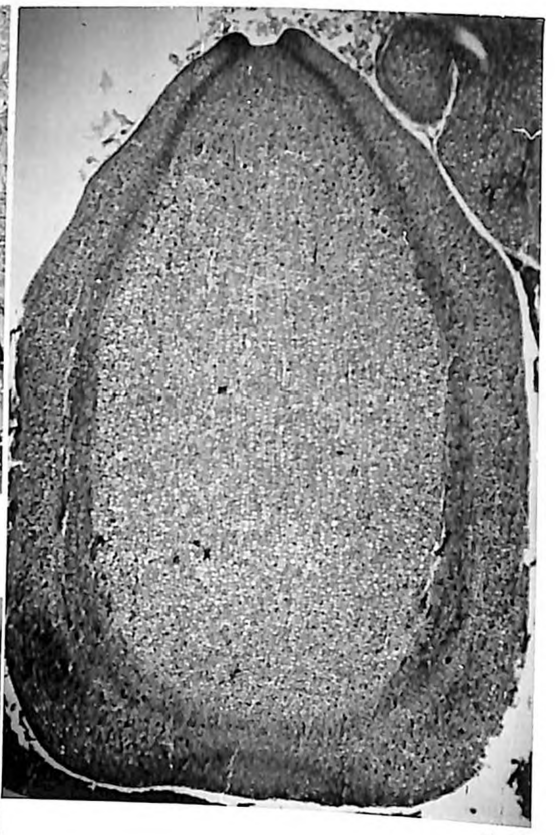

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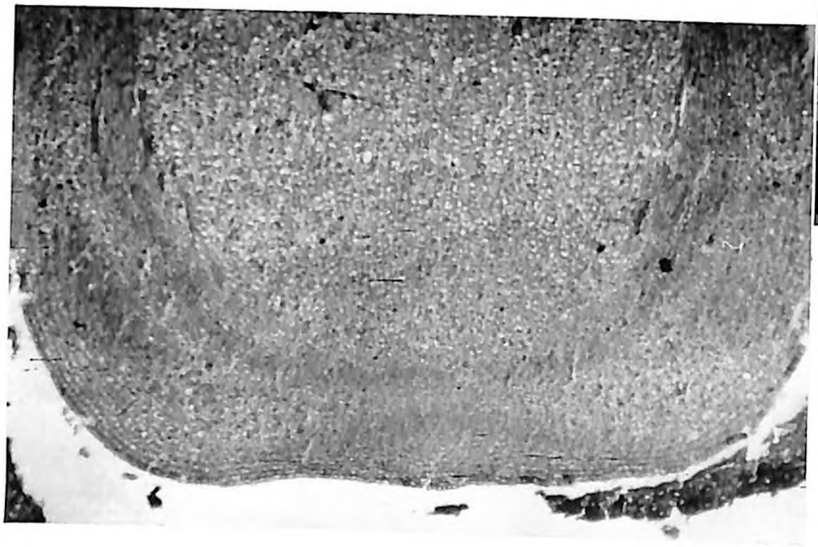

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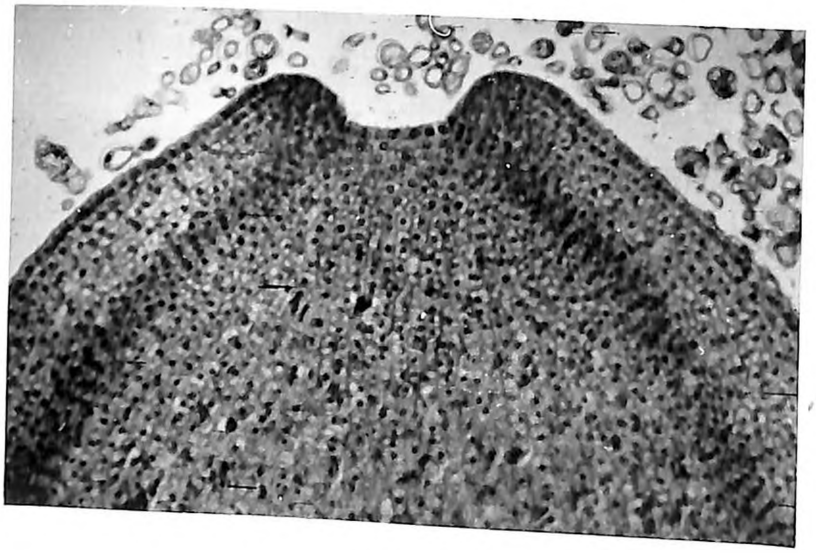


52

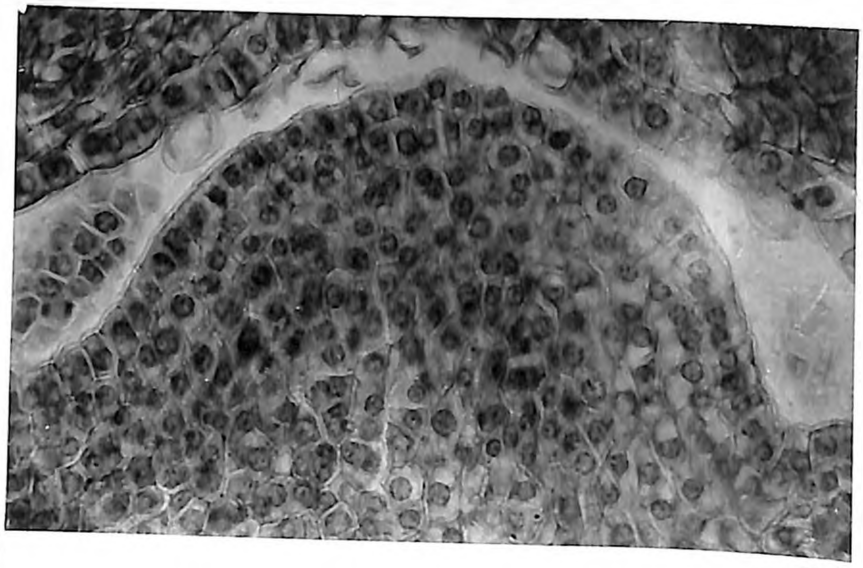
PLATE-14

Fig. 53. Shoot apex of a seedling at the maximal phase of plastochron. The leaf base is sheathing (× 12).

Fig. 54. Shoot apex at the maximal phase of plastochron (× 327).

Fig. 55. Shoot apex at the minimal phase of plastochron (× 327).

Fig. 56. Shoot apex at maximal phase. Also shows the developing stipules (× 300).



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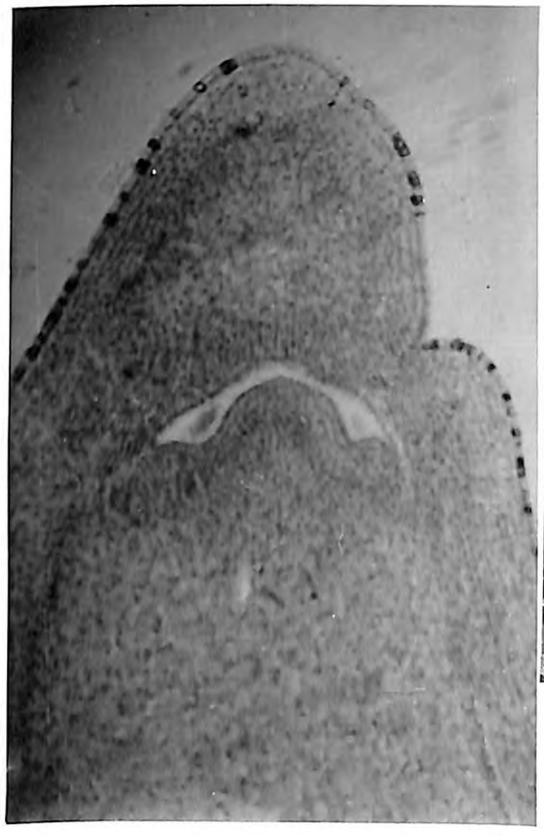

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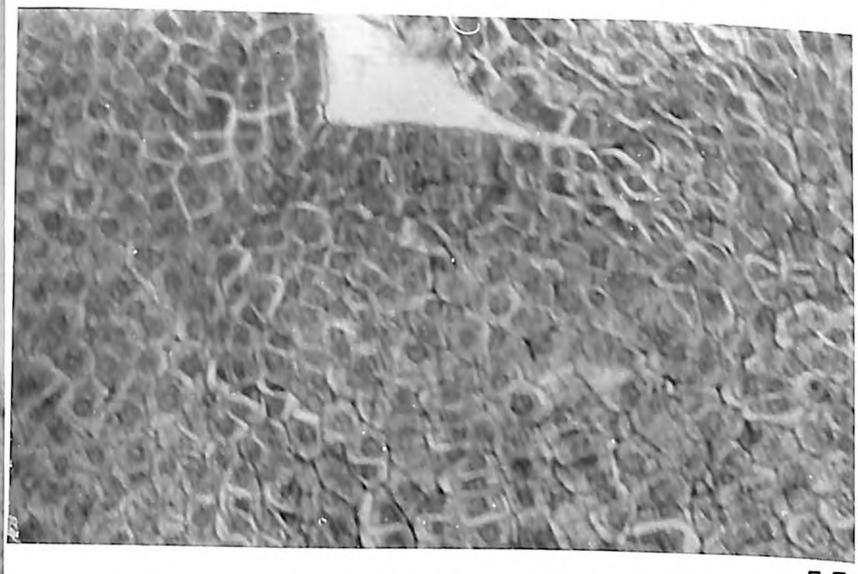

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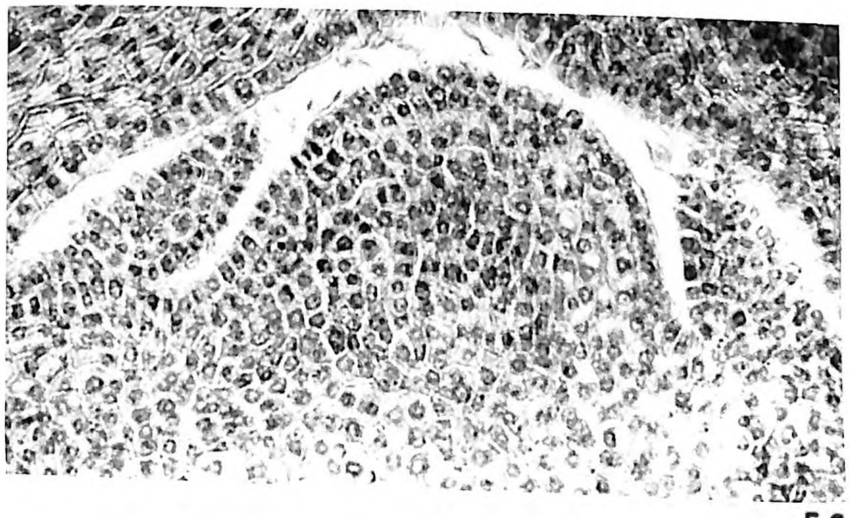


56

PLATE-15

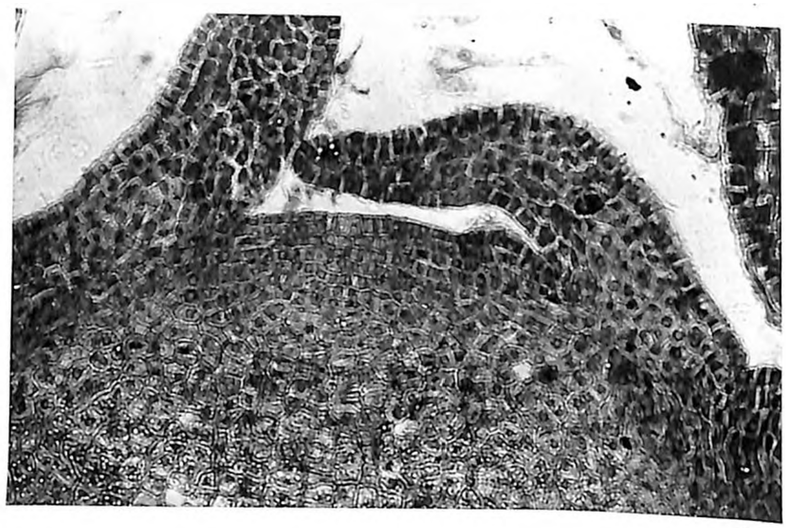
Fig. 57. Longisection at the maximal phase of 10th plastochron. Also shows the initiation of a leaf (× 105).

Fig. 58. Longisection through a leaf base showing the attachment of the stipule (× 98).

Fig. 59. Transection of a petiolule. The petiolules have adaxial and abaxial vascular elements (× 52).

Fig. 60. Paradermal section of the lower epidermis showing the reticulate cuticle (× 225).

Fig. 61. Transection of a leaf (× 400).



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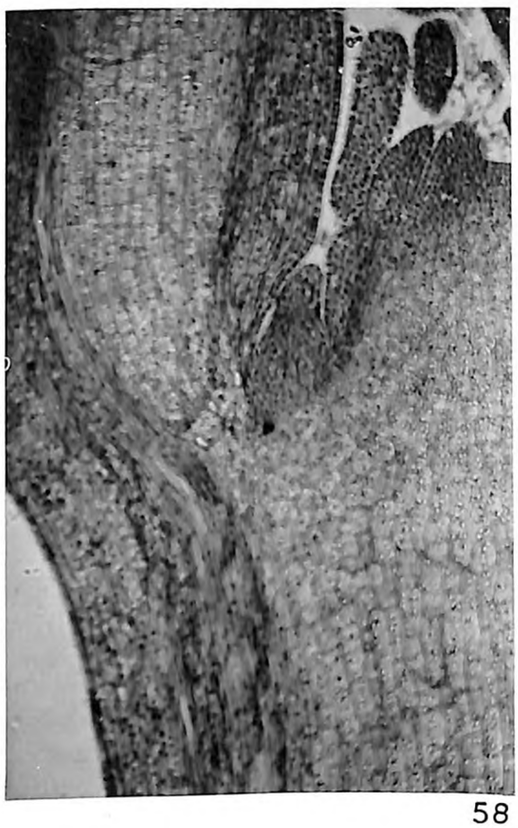

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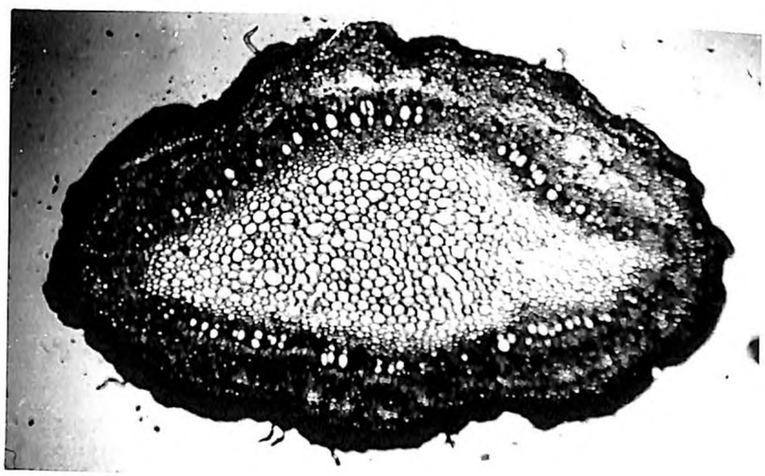

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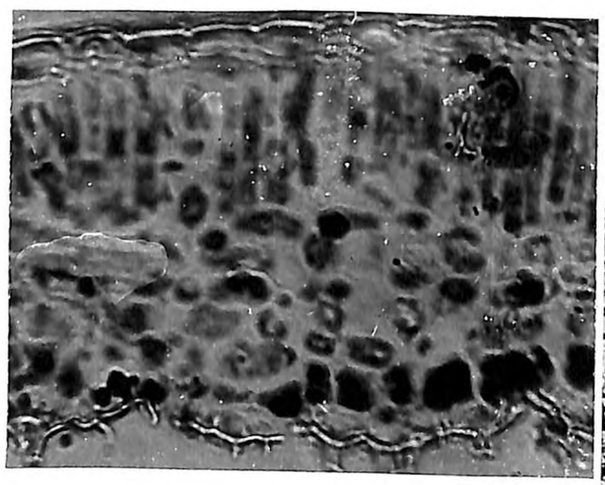

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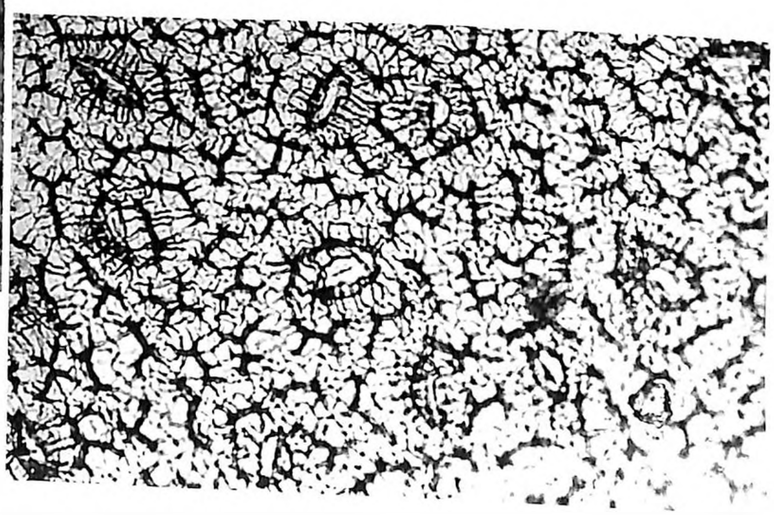


60

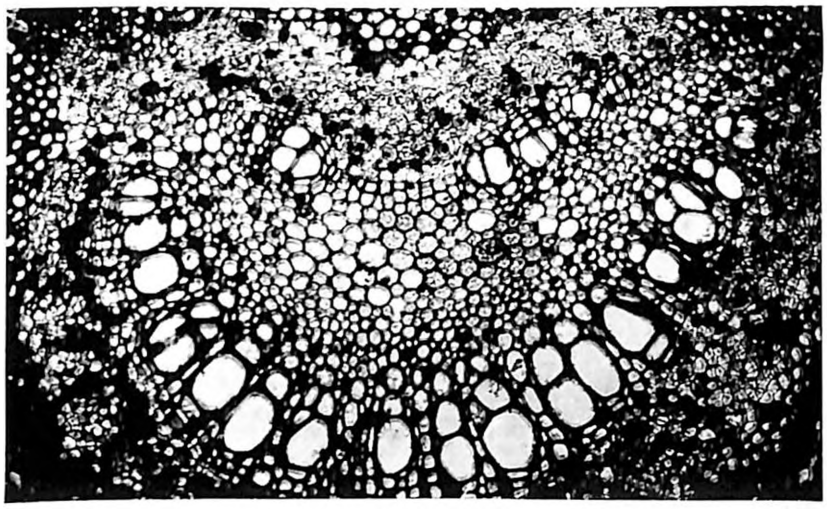
PLATE-16

Fig. 62. Transection of the mid vein showing the abaxial and adaxial vascular elements (× 113).

Fig. 63. Transection of a secondary vein. The secondary veins also possess abaxial and adaxial vascular elements (× 50).

Fig. 64. A cleared leaf showing the pattern of venation (× 1/2).

Fig. 65. Longisection of the shoot apex at the onset of the dormant phase (× 300).



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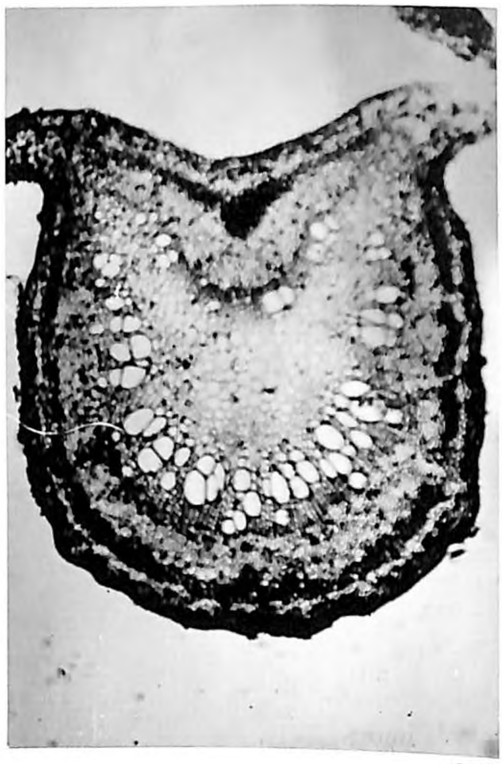

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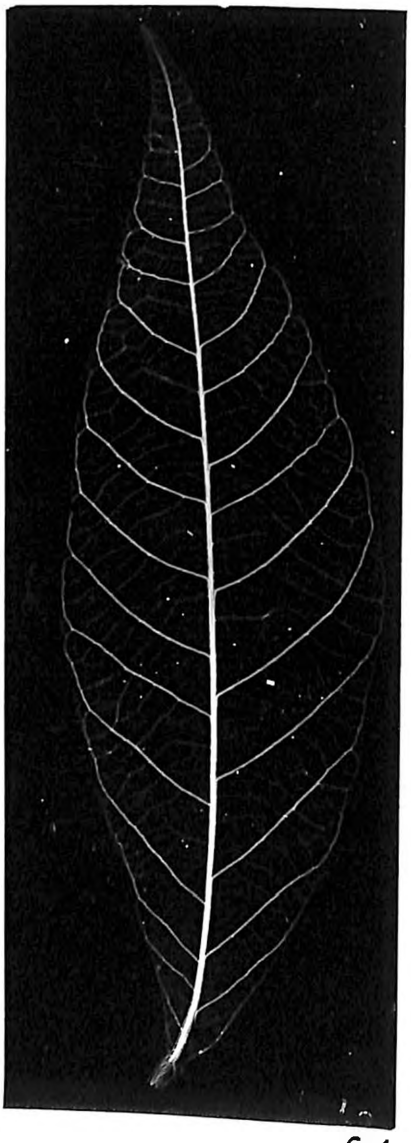

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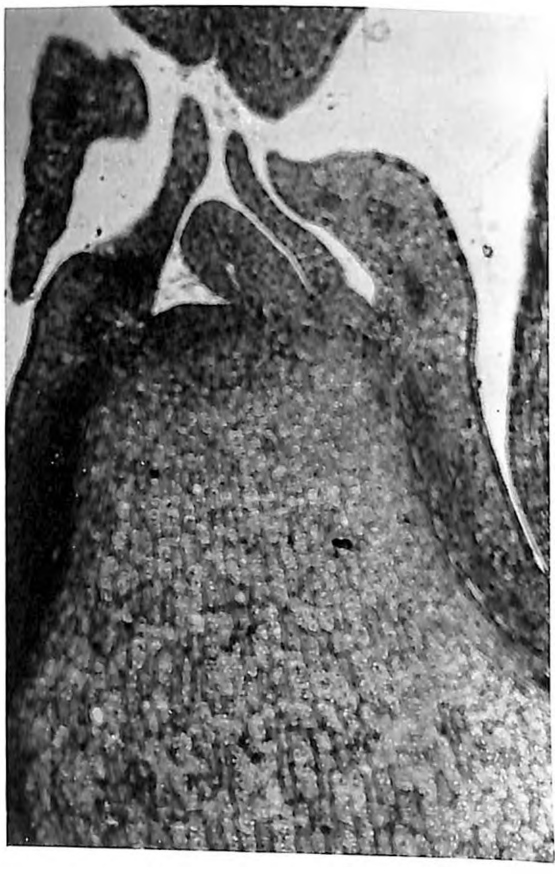

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PLATE-17

Fig. 66. Longisection of shoot at the dormant stage. 3-4 layers of cells show tunica-like appearance (× 328).

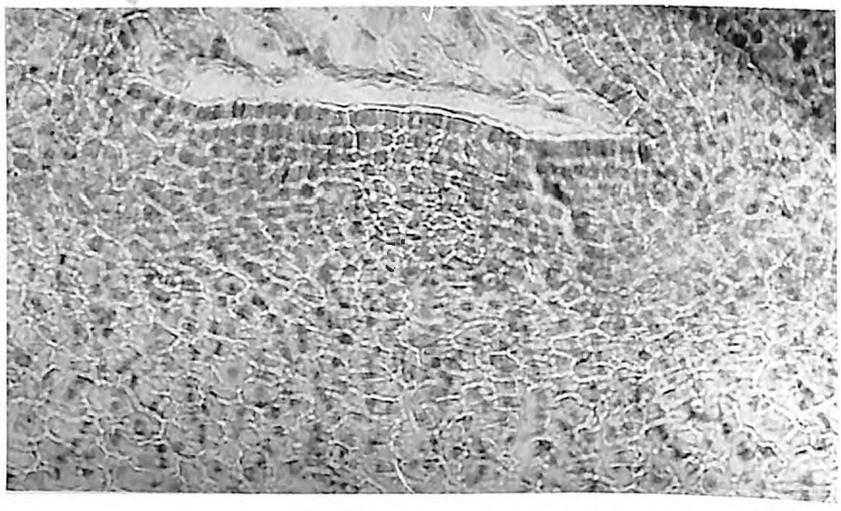
Fig. 67. Shoot apex at the dormant stage. The apex is concave, which results from the development of the cataphylls (× 328).

Fig. 68. Longisection through a leaf scar showing well-developed periderm beneath the abscission zone (× 56).

Fig. 69. Transection showing complete blocking of petiolar traces (× 85).

Fig. 70. Longisection, about one mm away, of a dormant apex showing the cork cambium and vascular cambium (× 262).

68



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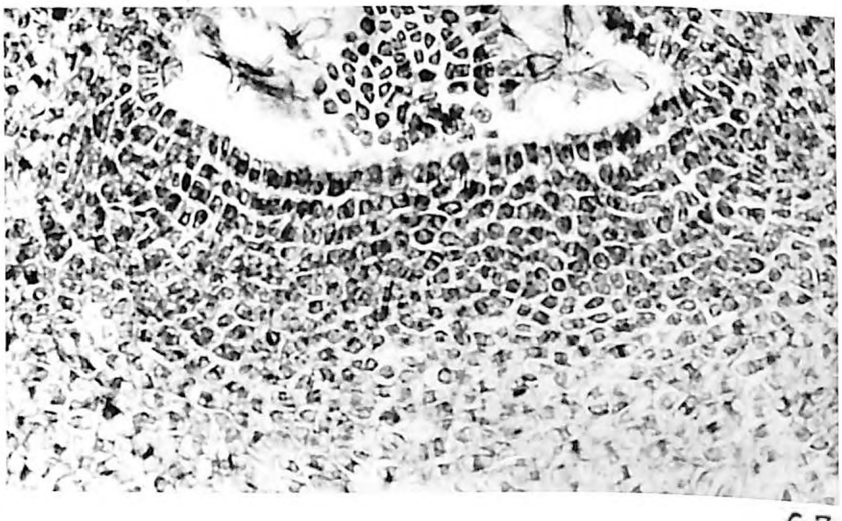

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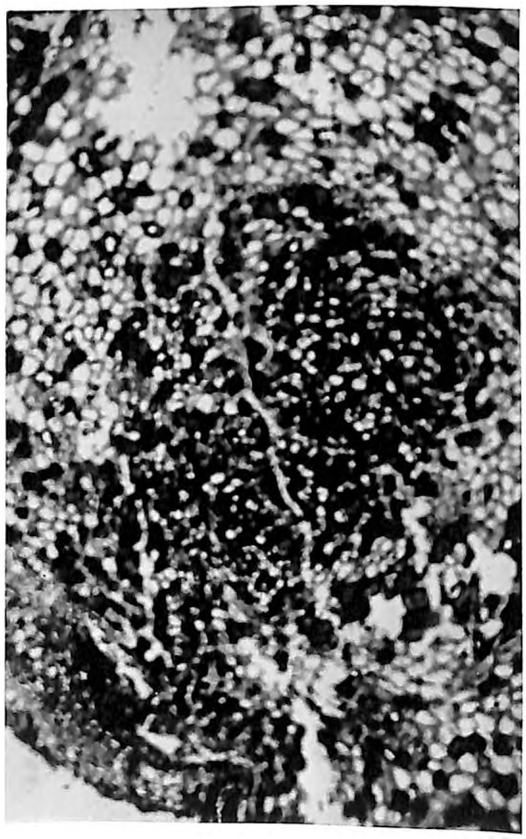

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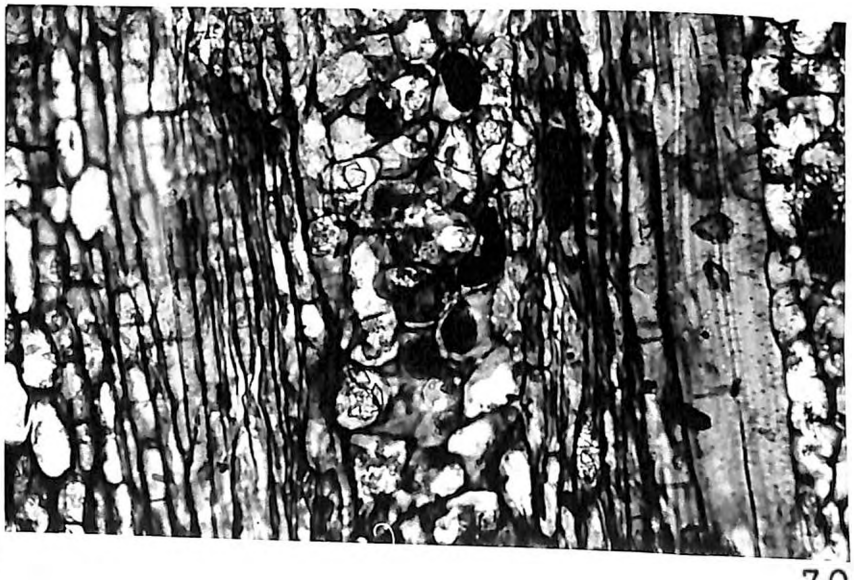


70

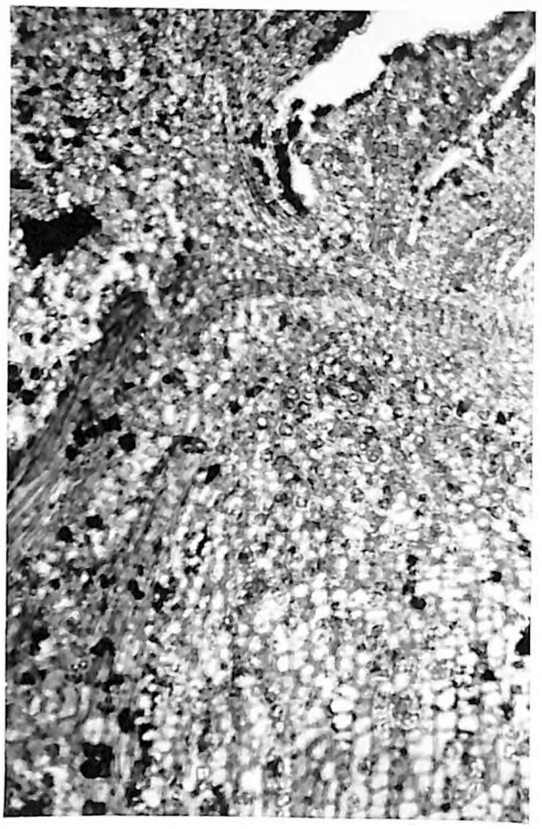
PLATE-18

Fig. 71. Longisection of dormant apex showing the cork cambium and vascular cambium which bend acroscopically and reach near the summit (× 82).

Fig. 72. Longisection of a cataphyll, formed just prior to the breakage of dormancy, showing glandular cells on the adaxial surface and a single trace (× 120).

Fig. 73. A cataphyll in longisection showing periderm beneath the abscission zone (× 77).

Fig. 74. Shoot apex at the break of dormancy (× 153).



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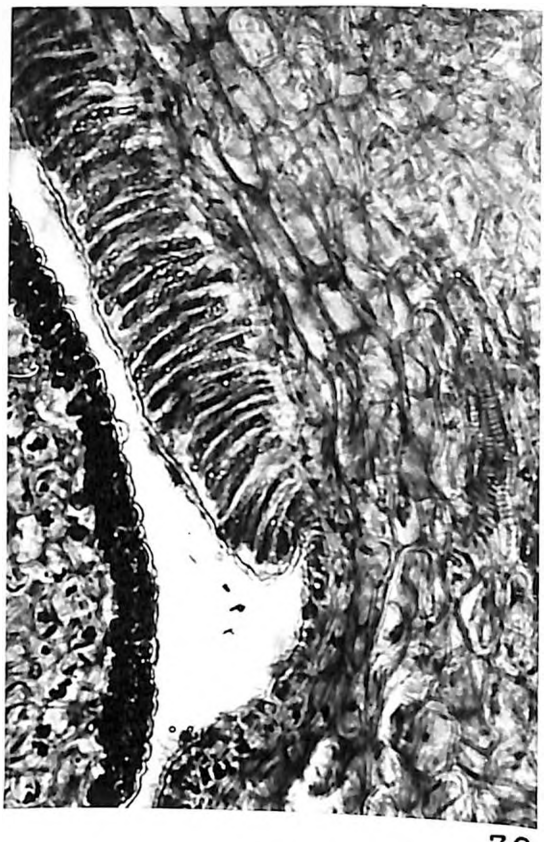

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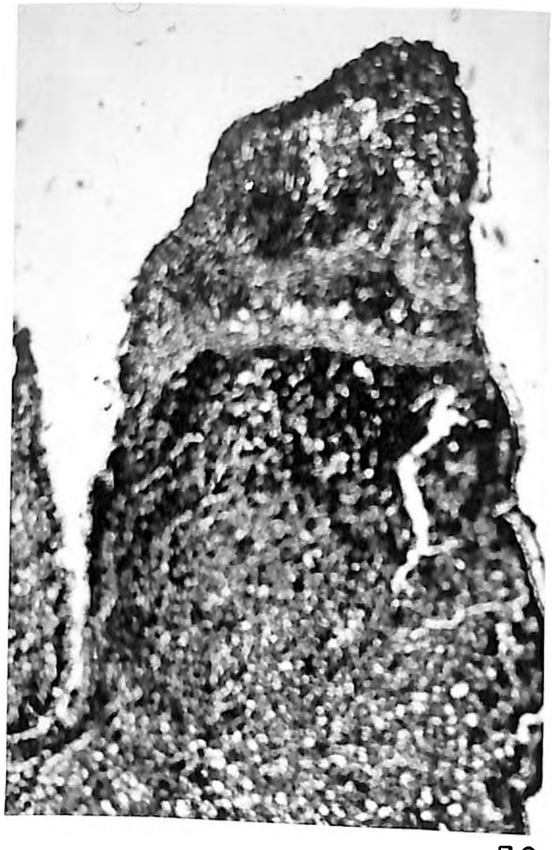

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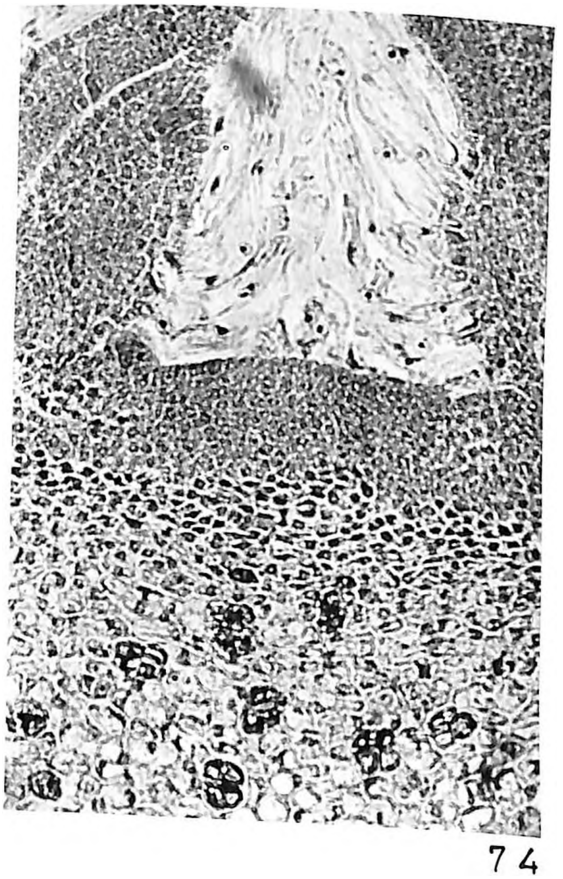


74

PLATE-19

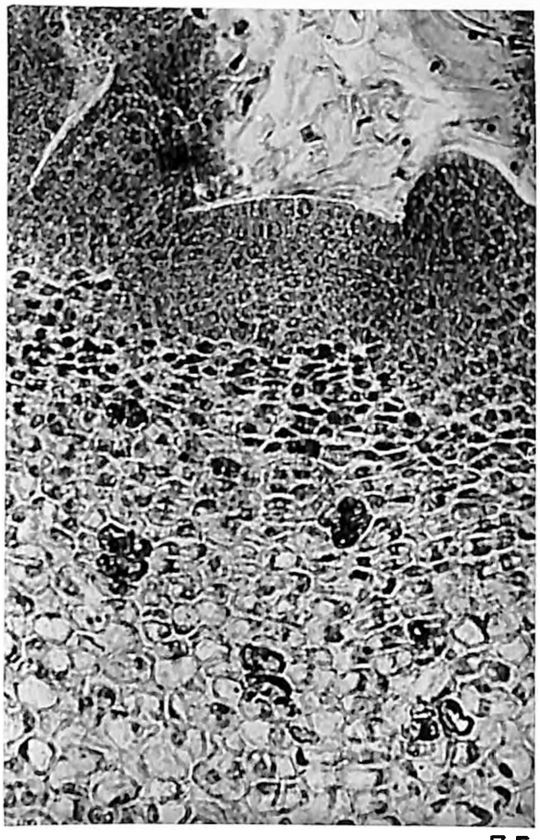
Fig. 75. Shoot apex at the break of dormancy showing the initiation of scale leaves and elevation of the apical dome (× 153).

(Figs. 65, 66, 67, 74 and 75 show successive stages from the onset to break of the dormant phase).

Fig. 76. Transection of a tender stem, showing primary structure and the formation of perivascular sclereids (× 95).

Fig. 77. Development of perivascular sclereids (× 250).

Fig. 78. Longisection of the soft bark showing the compound sieve plates (× 125).



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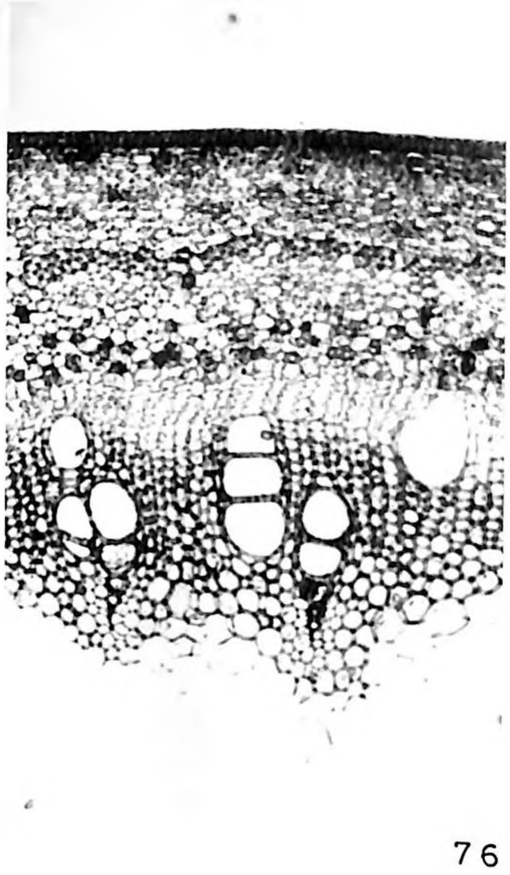

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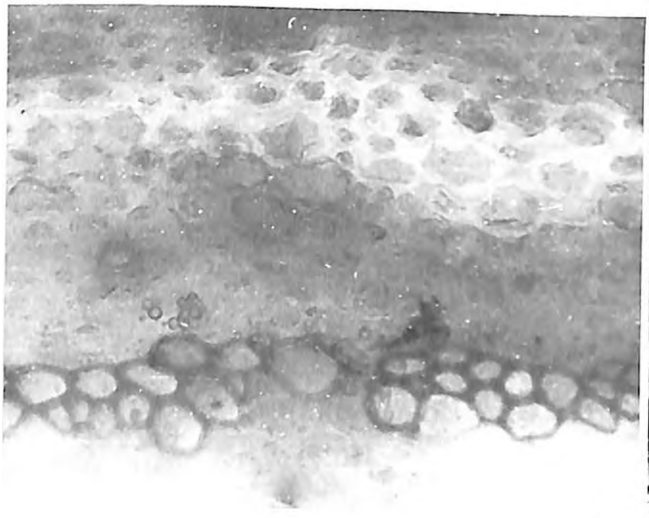

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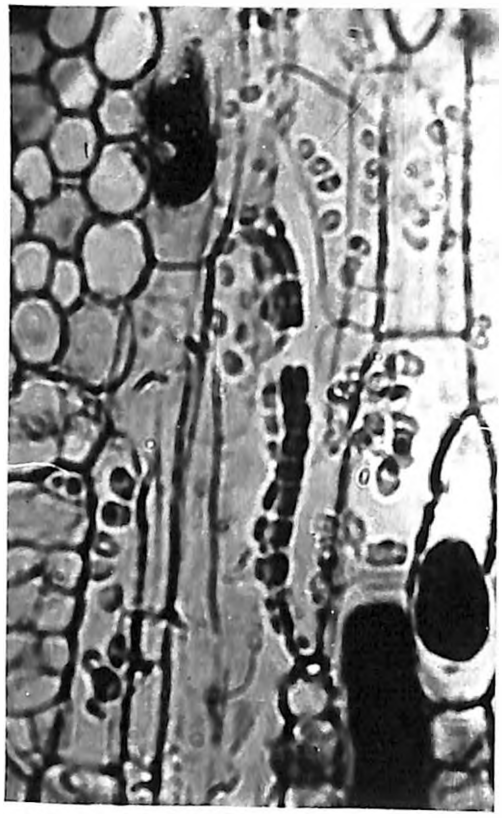
PLATE-20

Fig. 79. Tangential longisection through soft bark showing the steeply oblique sieve plate (× 337).

Fig. 80. Tangential longisection of the bark showing uni, bi, tri and four seriate phloic rays (× 125).

Fig. 81. Splitting of a phloic ray as seen in tangential plane (× 337).

Fig. 82. A group of sclereids in the outer bark (× 337).



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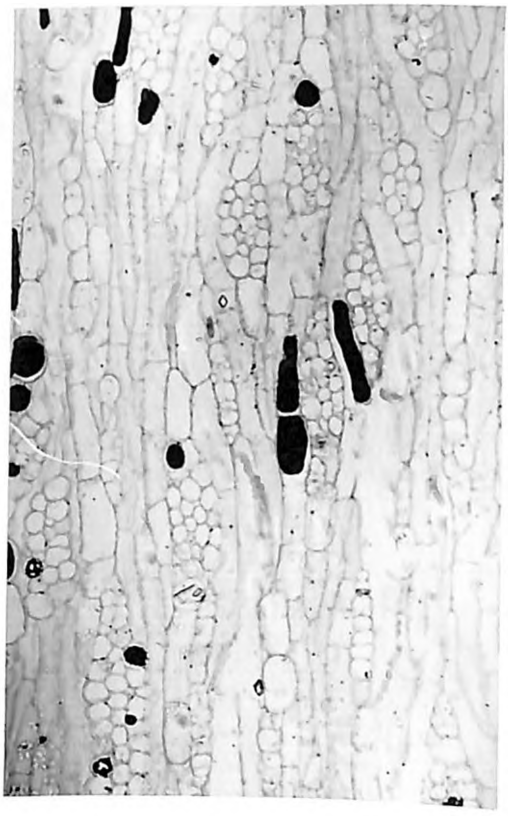

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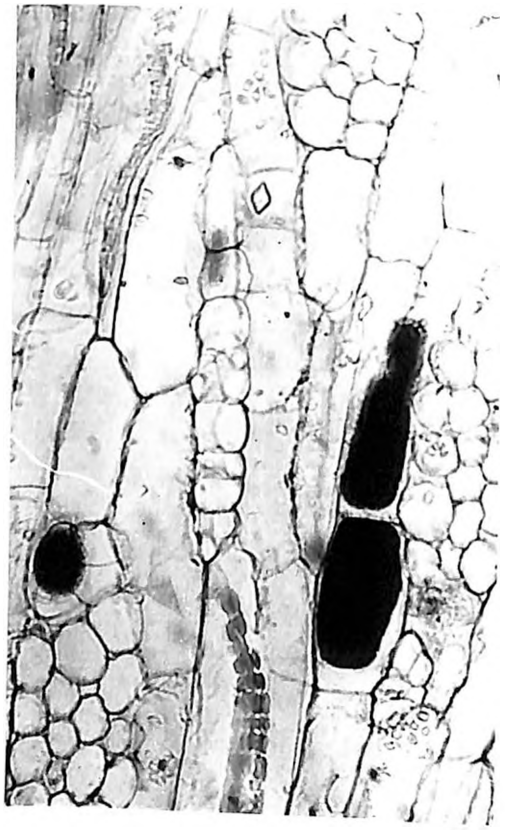

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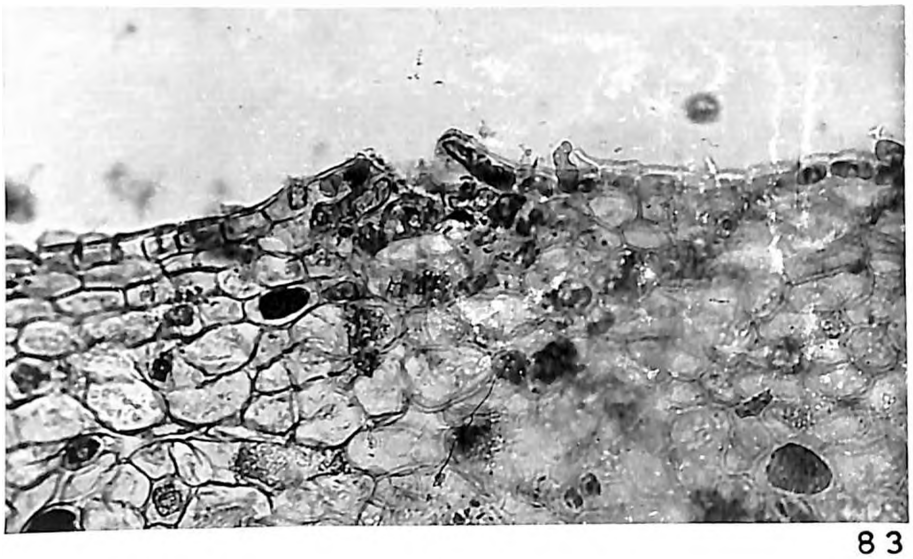
PLATE-21

Fig. 83. A lenticel. Development of lenticels start before the initiation of periderm (× 192).

Fig. 84. Transection of bark showing development of first periderm which initiates in the subepidermal layer (× 120).

Fig. 85. Transection of bark showing the second periderm which is initiated in the secondary phloem (× 192).

Fig. 86. A tree under tapping, showing the nature of the tapping cut. The portion just above the cut is the regenerating bark (the tree is about 66 cm in girth).



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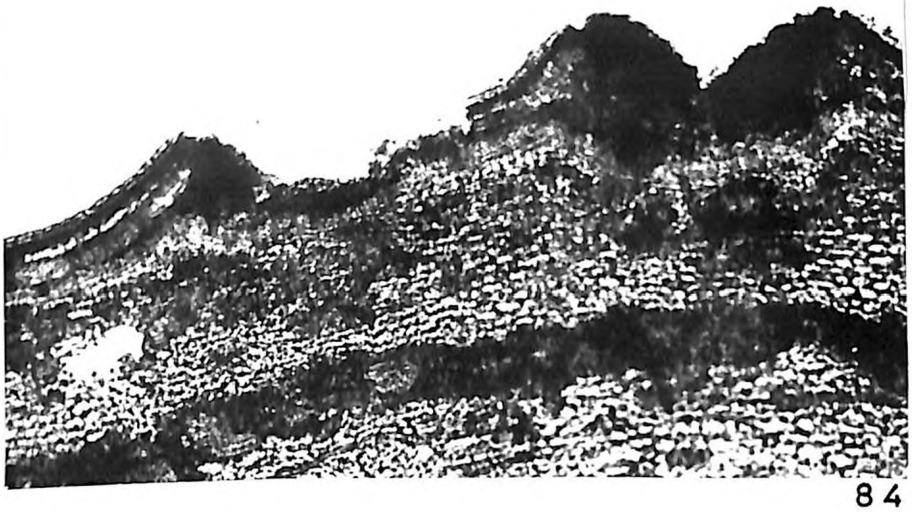

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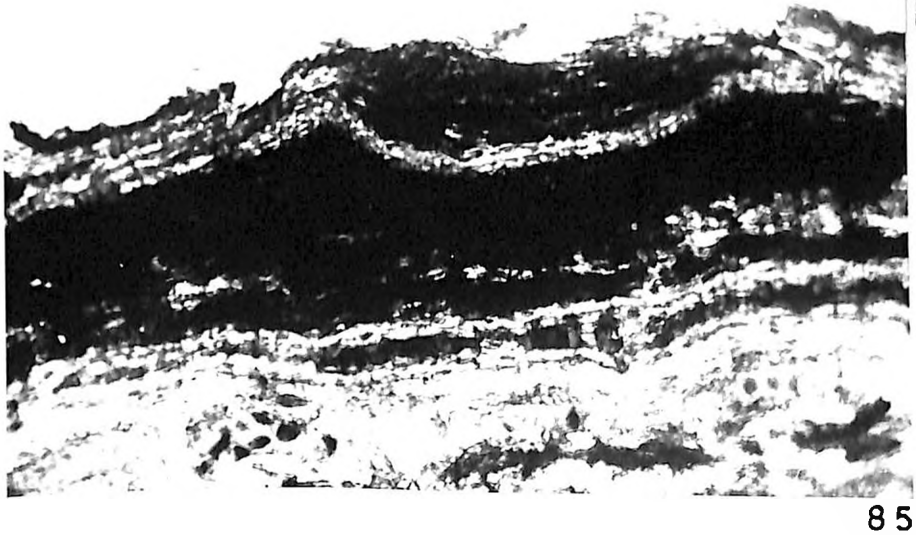

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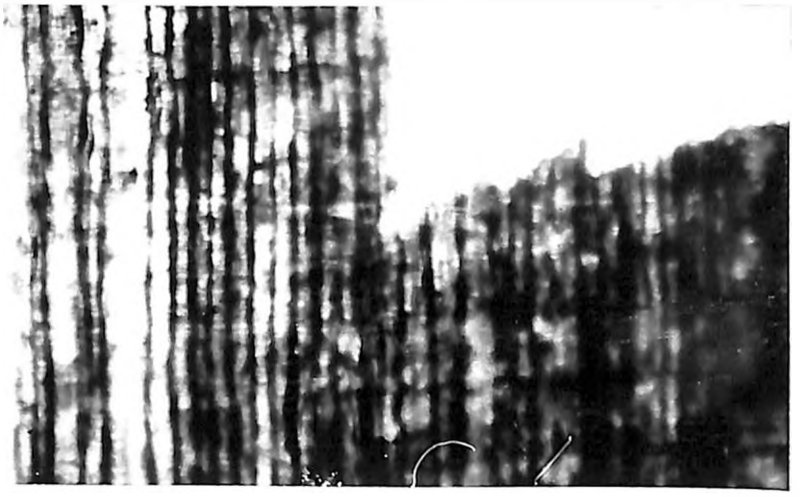
PLATE-22

Fig. 87. Longisection of the soft bark after the tapping cut is made, showing the residual bark. Arrangement of the laticifers may also be noted (× 30).

Fig. 88. Section of bark collected and fixed soon after tapping. The immediate response to wounding is the shrinkage and necrosis of the ruptured cells (× 337).

Fig. 89. Section of bark showing early stage of regeneration (× 337).



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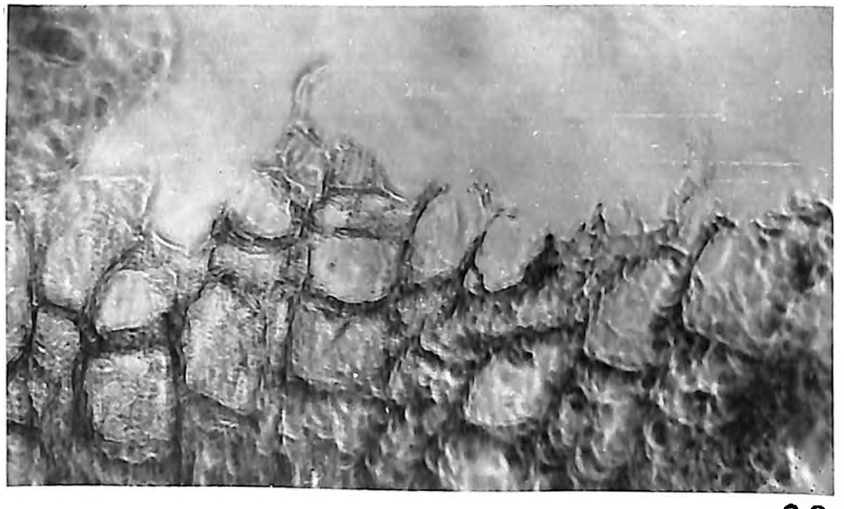

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PLATE-23

Fig. 90. Section of the regenerating bark showing the wound periderm initiated close to the cut surface and the second periderm beneath. Cells close to the first periderm have undergone sclerosis (× 337).

Fig. 91. Longisection of young stem showing laticifer initials (× 255).

Fig. 92. Longisection of young stem. The young laticifer has established longitudinal and tangential connections. The cross walls show dissolution (× 255).

Fig. 93. Transection of tender stem showing the developing secondary laticifers. The nature of pith cells is also seen (× 96).

Fig. 94. Transection showing a ring of secondary laticifers (× 255).

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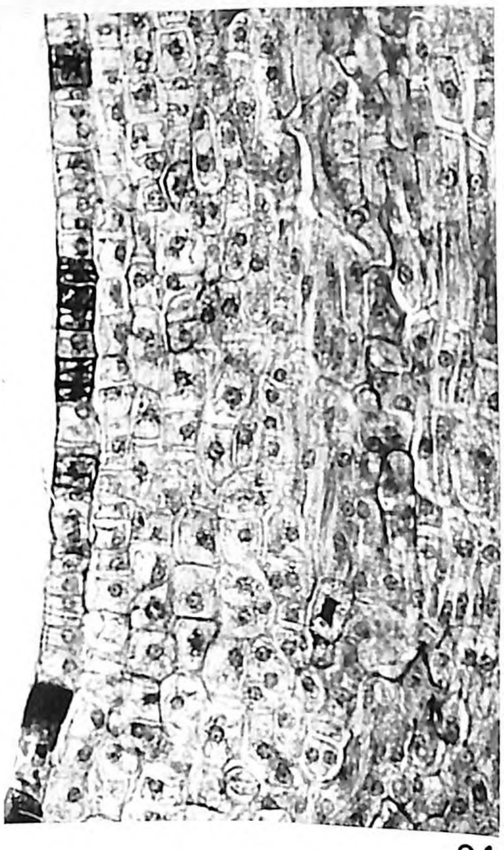

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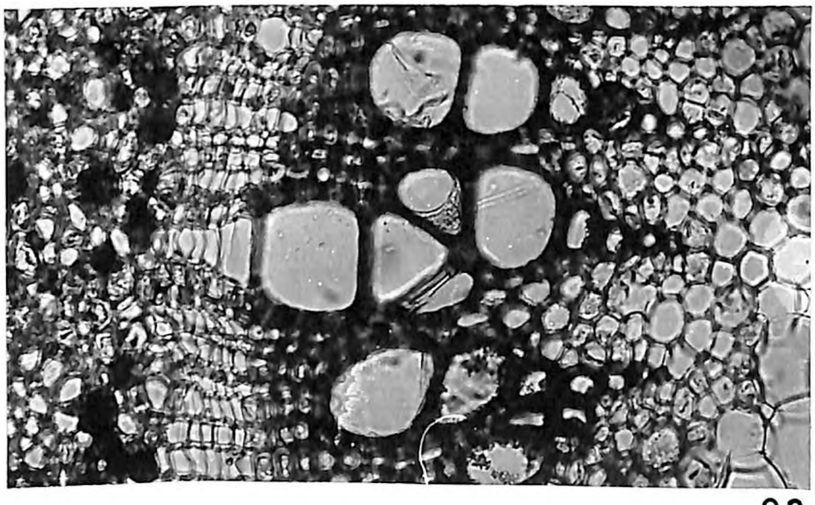

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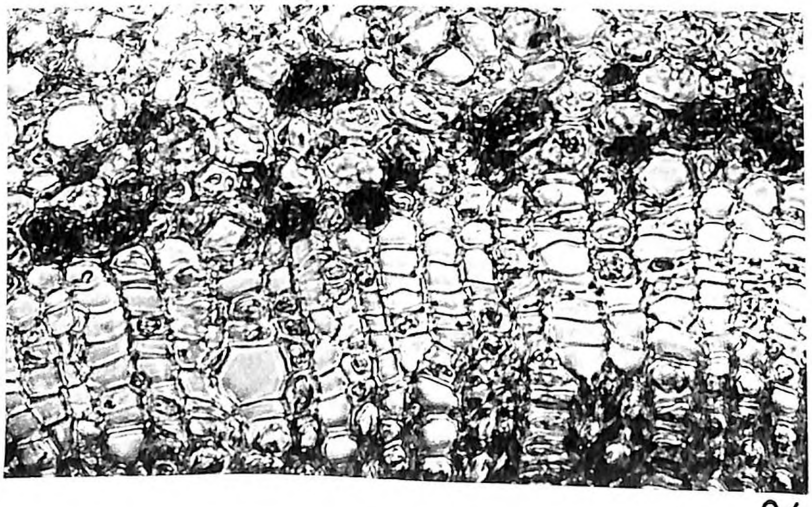

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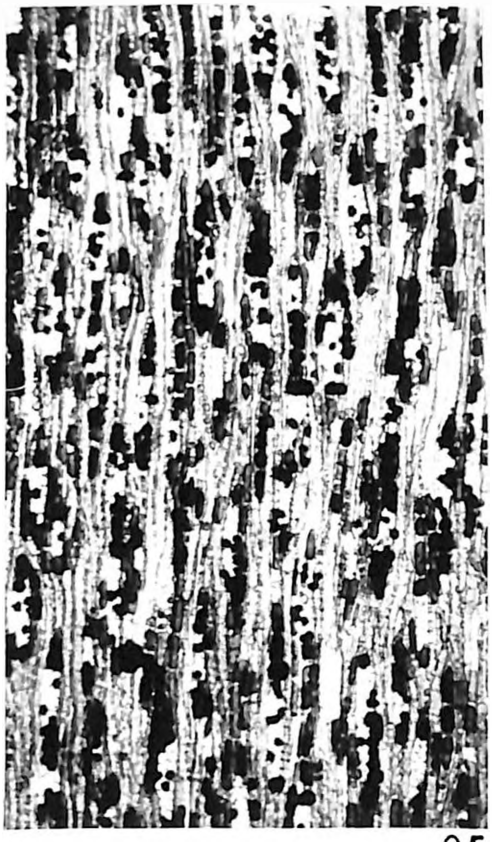
PLATE-24

Fig. 95. Tangential section of bark showing laticifers (× 120).

Fig. 96. Transection of wood showing diffuse porous nature (× 192).

Fig. 97. A vessel showing the nature of pitting. The pits are oblong and borders angular (× 358).



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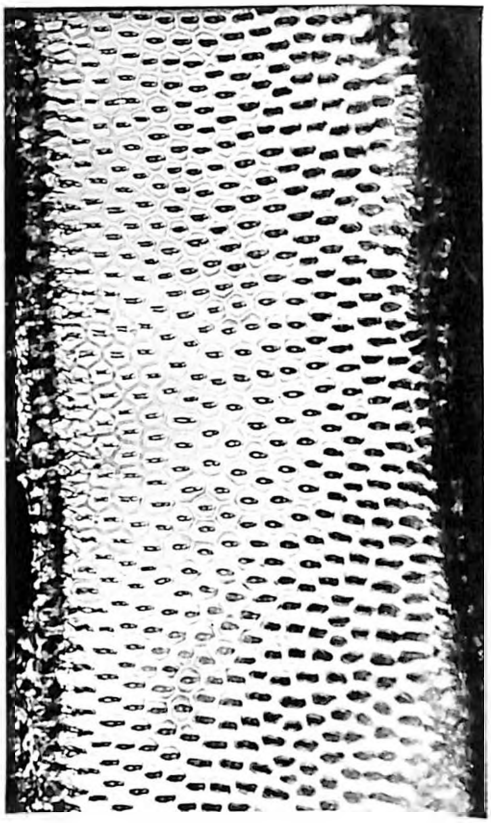

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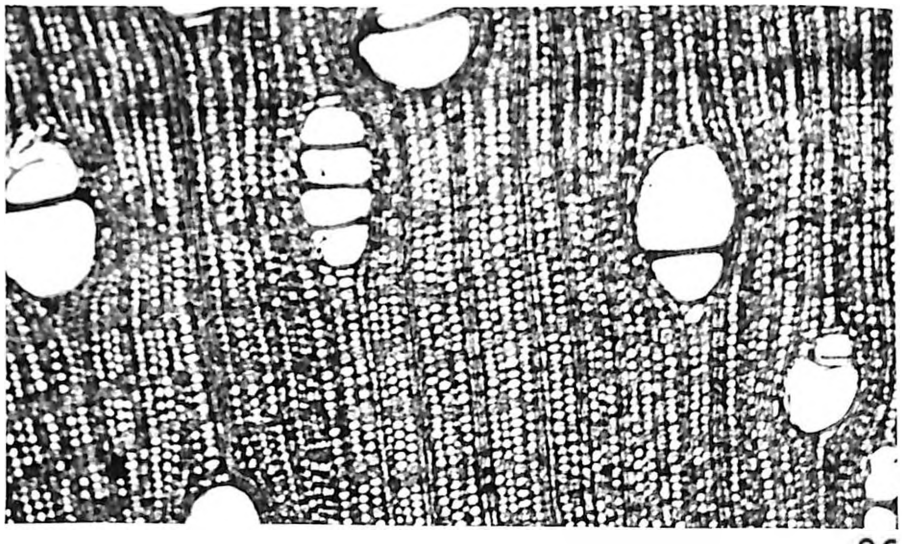

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PLATE-25

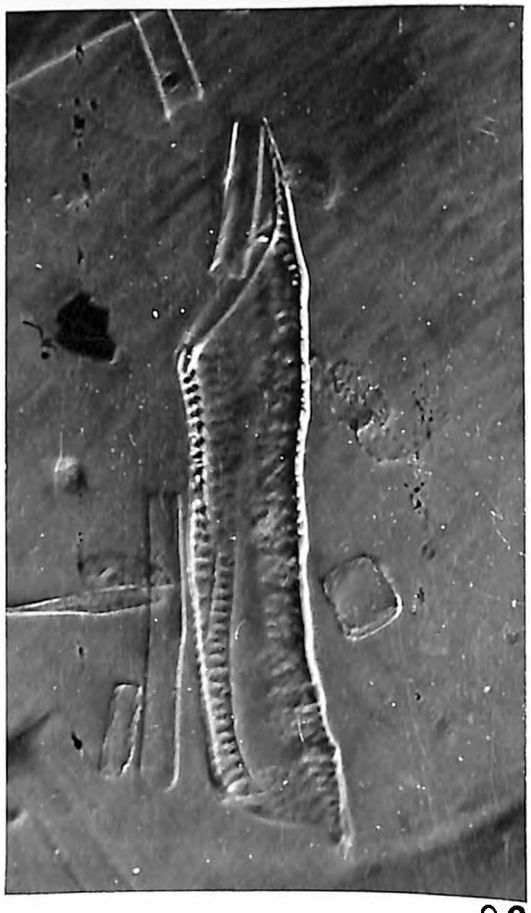
Fig. 98. Wood fibres after maceration. A vessel is also seen (× 90).

Fig. 99. A vessel with steeply oblique perforation plate (× 192).

Fig. 100. A vessel with slightly oblique perforation plate (× 288).

Fig. 101. An aggregate of vessels in transection. The presence of tyloses is seen in this and Fig. 100 (× 192).

98



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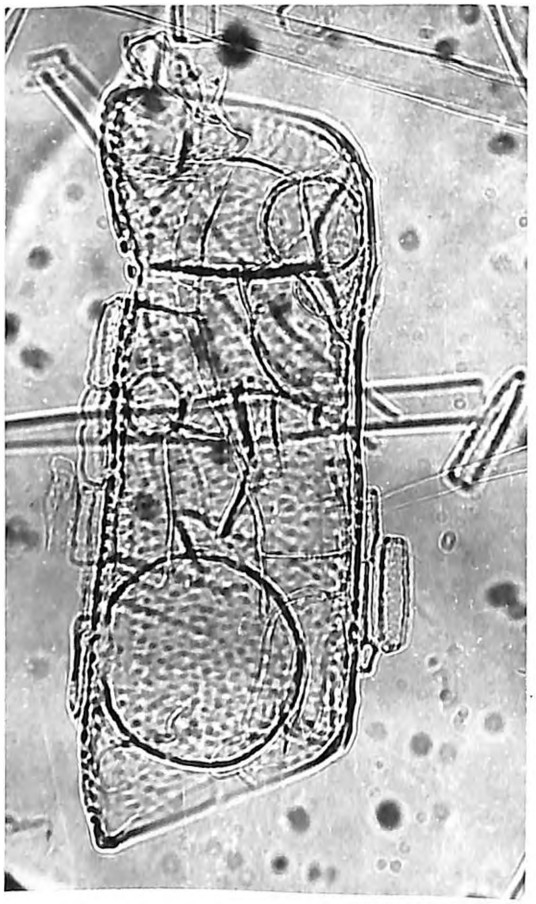

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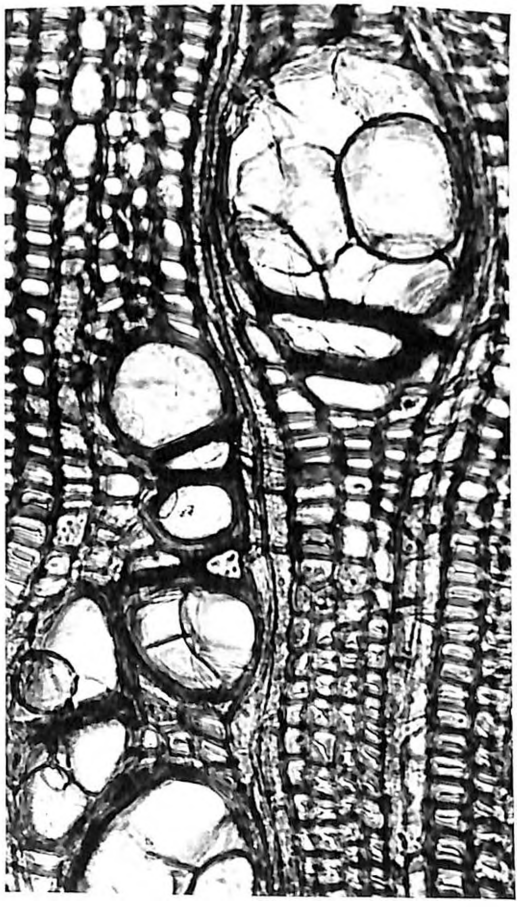

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PLATE-26

Fig. 102. Tangential longisection of wood showing the vascular rays (× 120).

Fig. 103. Dissection of a multiseriate ray in wood. Tangential longisection (× 337).

Fig. 104. Transection of a leaning stem showing bands of tension wood (× 2).

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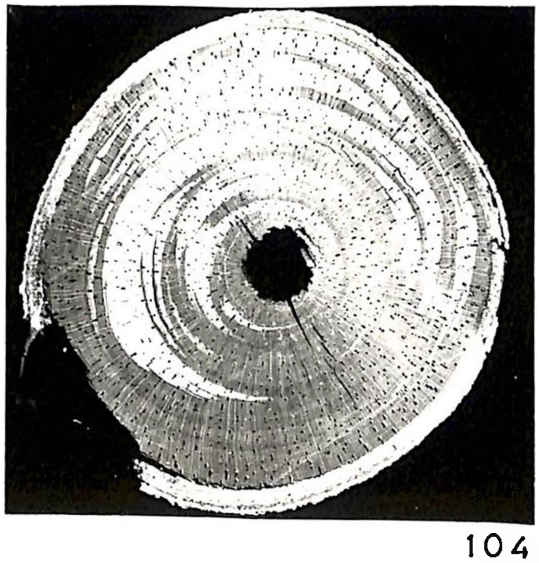

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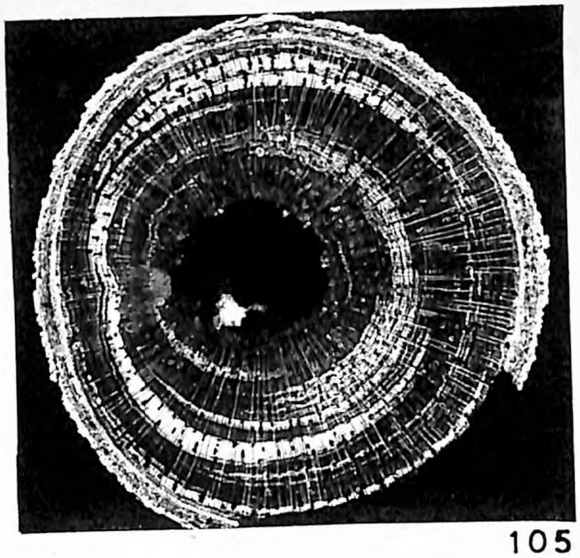
PLATE-27

Fig. 105. Transection of a leaning stem showing tension wood all around (× 2).

Fig. 106. Transection of tension wood (× 192).

Fig. 107. Tension wood fibres in transection showing massive gelatinous wall and narrow lumen (× 480).



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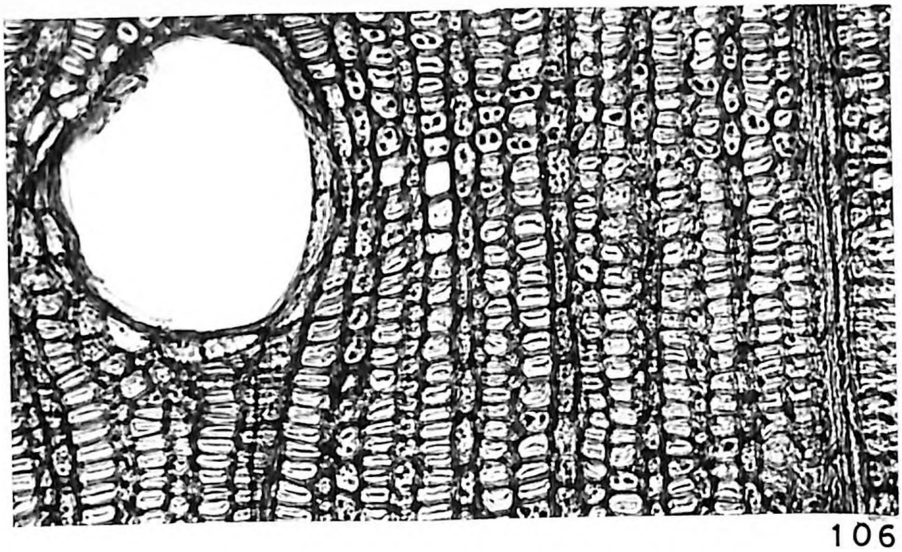

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