

VARIABILITY, CORRELATIONS AND
PATH CO-EFFICIENT ANALYSIS FOR YIELD IN RELATION
TO ANATOMICAL CHARACTERS IN *HEVEA BRASILIENSIS*
(Willd. ex Adr. de Juss.) Muell. Arg.

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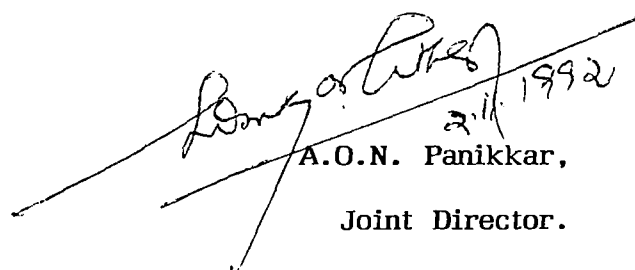
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I further certify that she has passed the Ph.D. qualifying examination conducted by the University in June 1989 (Reg. No. 12) with creditable marks.

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D E C L A R A T I O N

I hereby declare that the thesis entitled "VARIABILITY, CORRELATIONS AND PATH CO-EFFICIENT ANALYSIS FOR YIELD IN RELATION TO ANATOMICAL CHARACTERS IN HEVEA BRASILIENSIS (Willd. ex Adr. de Juss.) Muell. Arg." submitted by me for the degree of Doctor of Philosophy in Botany, of the University of Kerala, embodies the results of original research work carried out by me at the Rubber Research Institute of India under the supervision of Dr. A.O.N. Panikkar, Joint Director, Rubber Research Institute of India, Kottayam. I further declare that this thesis has not previously formed the basis for award of any Degree or Diploma or other title to me.

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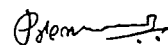
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I. I N T R O D U C T I O N

The domestication of Hevea brasiliensis in the east is the most spectacular event in rubber industry; for, in a short span, a novel plantation enterprise covering an area of over 90,00,000 hectares was created by research and development to meet the new industrial demand. As on 1990, rubber plantations spread on 92,28,700 hectares over the globe and produce 5.10 million tonnes of natural rubber (International Rubber Study Group, 1991). Organised production of natural rubber, the most versatile raw material, is only 100 years old.

Natural rubber is a constituent of latex of certain plants, including Hevea. In the plant kingdom laticifers, which synthesise latex, are present in over 12,500 species belonging to about 900 genera, of which about 1000 species of 76 families contain rubber (Esau, 1965; Metcalfe, 1966; 1967 and Polhamus, 1962). A few monocotyledons like Allium cepa (Hoffman, 1933) and the genus Rognellidium of Marsiliaceae (Pteridophyta) are also reported to have latex.

The nature of laticifers is characteristic of the species. They may be simple or compound in origin, the former developing from a single cell and the latter from more than one. Articulated laticifers are compound in origin and comprise of a series of cells, organised into continuous tubular structure due to partial or complete dissolution of endwalls. Depending on the presence or absence of lateral connections they are further categorised as anastomosing and non-anastomosing

respectively. The non-articulated laticifers are more simple in structure. They may remain as single unbranched cells or branched structures extending throughout the shoot and root system. Non-articulated unbranched laticifers are found in Cannabis, Urtica and Catharanthus. Branched type is characteristic of Asclepias, Cryptostegia and Euphorbia. Achras, Chelidonium, Convolvulus and Ipomea have articulated non-anastomosing laticifers and articulated anastomosing type is found in Argemone, Carica, Cichorium, Hevea, Manihot and Taraxacum.

Hevea

Of all the latex yielding genera, Hevea (Euphorbiaceae) is the most important. The centre of origin of Hevea is the Amazon basins, and the areas adjuscent, of Brazil. Eleven species of Hevea have been identified (Webster & Paardekooper, 1989; Poulo de Souza Goncalves, 1989). They are:-

1. Hevea benthamiana Muller-Argoviensis,
2. Hevea camargoana N.C. Bastos; N.A. Rosa and C. Rosario,
3. Hevea camporum Ducke,
4. Hevea guianensis Aublet var. lutea (Spruce ex Benth) and Hevea guianensis Aublet var. marginata (Duke),
5. Hevea microphylla Ule,
6. Hevea nitida Mart. ex Mueller-Argoviensis var. nitida and Hevea nitida Mart. var. toxicodendroides Schultes and Vinton),

7. Hevea pauciflora (Spruce ex Benth.) and Hevea pauciflora (Spruce ex Benth.) Mueller-Argoviensis var. coriaceae Duke,
8. Hevea rigidifolia (Spruce ex Benth.) Mueller-Argoviensis,
9. Hevea spruceana (Benth.) Mueller-Argoviensis Syn. Hevea discolor (Spruce ex Benth.) Muell Arg.,
10. Hevea brasiliensis (Willd. ex Adr. de Juss.) Muell. Arg.
11. Hevea paludosu Ule Jahrb.

Hevea brasiliensis is the only species being cultivated commercially and about 99 per cent of the world production of natural rubber is obtained from this single species.

Morphology and anatomy

Hevea brasiliensis (Willd. ex Adr. de Juss.) Muell. Arg. is a quick growing perennial tree with straight trunk and greyish brown bark. Bark is fairly smooth, but varies slightly in colour and texture of the surface. It is the tallest species of the genus, which in the natural habitat may grow to over 40 m and live for over 100 years. It winters during December-January and flowers during February-March period. The flowers are found on panicles. Male and female flowers are formed on the same panicle. Fruit is a regma. The chromosome complement is $2n = 36$. Seeds are large and ovoid in shape with a flattened ventral surface. A healthy seed weighs 4-6 g. It has a hard shiny testa which is brown or greybrown in colour with varying types of mottlings. The

endosperm with a papery covering fills the seed. Seed germination is hypogial.

Leaves are trifoliate and spirally arranged. They are glabrous with long petioles (about 15 cm). Mature lamina is shiny dark green on the adaxial surface and paler glaucous green on the abaxial surface. Extra floral nectaries are present at the tip of the petiole where the leaflets are born.

In Hevea, the laticifers exploited commercially for latex are the secondary laticifers. They are differentiated by the activity of vascular cambium. The latex vessels in the bark are formed in concentric rings almost parallel to the cambium, alternating with layers of seive tubes and axial parenchyma. They are articulated, anastomosing and coenocytic type. Non-anastomosing primary laticifers are present in the pith, fruit walls, flower parts etc (Zhao Xiuqian, 1987).

A comprehensive description of the structure of mature bark in Hevea was made by Bryce and Campbell (1917). In the bark, in Hevea, below the protective tissue or cork, there are two distinguishable zones: an inner zone consisting of soft tissues and termed soft bast and an outer zone made up of hard and thick walled cells the major component being sclerified cells or stone cells. Most of the functional latex vessels are present in the soft bast region. Towards the outer portion of the hard bast the latex

vessels, seive tubes, etc. become discontinuous and nonfunctional due to age and senescence.

The latex vessels are oriented in an anti-clockwise direction at an angle of inclination of two to seven degrees. They are produced in discrete rows and the vessels belonging to the same row are inter-connected tangentially. The laticifers, therefore, appear as straight tubes in radial longitudinal sections whereas the structure resembles an expanded meshwork in tangential longitudinal sections. In a cross sectional view latex vessels have more or less circular shape.

Ontogeny of laticifers in Hevea was outlined by Scott (1882). He could identify the latex vessel initials as small elongated cells with characteristic granular contents. According to him, dissolution of cross walls takes place when root growth approaches 3-4 mm. Primary laticifers are observed in the procambial region (Milaniz, 1946; 1948; 1951 and Gomez, 1982). Primary and secondary laticifers follow similar mode of development. The articulated nature results from more or less complete dissolution of cross walls of a row of cells (Bobilioff, 1919; Panikkar, 1974 and Zhao Xiuqian, 1987). Formation of small protuberances on the lateral walls of differentiating laticifers is the first step leading to tangential connections within laticifers of the same row. The tubular projections of adjacent laticifers come in contact and fuse to form the anastamoses.

Gomez (1976) made a comparative study of latex vessels collected at different stages of development, from different portions of a tree and identified five different stages. An embryonic vessel in a leaf petiole, at a stage prior to the fusion of laticifer initials, resembles a normal living paranchyma cell except for the presence of numerous osmiophilic rubber particles. A typical latex vessel from the secondary phloem of green stem has osmiophilic rubber particles ranging from 100 \AA - 5000 \AA in diameter. Lutoids with prominent microfibrils, mitochondria and occasionally Frey-Wyssling complexes, golgi bodies and chloroplasts were observed. A latex vessel from the innermost portion in the secondary phloem of the trunk of an untapped tree at mature age, contained numerous osmiophilic rubber particles of smaller size, 500 \AA - 2 \mu m in diameter. Lutoids, devoid of microfibrils, and mitochondria were present. In a latex vessel under tapping, rubber particles were found in very large numbers. Lutoids and Frey-Wyssling complexes were common and occasionally mitochondria and endoplasmic reticulum (at the periphery) present. Rarely nuclei were detected. In the fifth type, a senescent vessel in the outer bark, rubber particles were comparatively larger in size and the other organelles obscured.

The quantity of laticiferous tissue in a tree is determined by various factors such as the number of latex vessel rows, density ✓ of latex vessels within a ring, distance between vessel rings, size of laticifers and the girth of the tree.

The number of latex vessel rings is a clonal character (Bobilioff, 1923; Sanderson and Sutcliffe, 1929 and Vischer, 1921; 1922) and frequency of laticifer differentiation is genetically controlled. Other influencing factors are age and growth rate of trees. Laticifer diameter is also a clonal character (Gomez et al., 1972; Premakumari et al., 1985a).

In seedling trees the latex vessel rows decrease in number considerably with increasing height of trunk due to the conical shape. Bark thickness also is affected much. Trunk of clonal trees are cylindrical in shape and does not show such wide variations. Gomez (1982) mentioned a difference in the density (number per unit circumference) of latex vessels between two distant positions from the cambium and observed an apparent clonal difference.

Gomez et al. (1972) proposed an index, known as laticifer area index, to approximate the quantity of laticiferous tissue of a tree in terms of cross sectional area. This index is believed to account all the main quantitative factors which are involved in latex production. They could not establish any close correlation between this trait and yielding capacity of clones. /

Tapping and bark renewal

Rubber tree is commercially exploited for latex by a systematic regular excision of bark of the trunk. This process is known as tapping. The economic period of Hevea tree is 20-23 years

from the commencement of tapping by which both virgin and renewed bark are exploited.

During every tapping, a thin slice of bark 1.0-1.5 mm in thickness is shaved off to cut open the latex vessels. The cambium is not injured in this process. More over, a layer of soft bast is also left uncut during tapping which gives protection to the cambium. The protective tissue lost on tapping is replaced by the formation and activity of a new phallogen below the cut surface (Bobilioff, 1923; Panikkar, 1974).

Composition of latex

Hevea latex is a hydrosol and rubber occurs as dispersed discrete particles (Bonner and Galston, 1947). Carbohydrates, proteins, resins, inorganic salts, etc., also form constituents of latex (Archer et al., 1963; 1967; Archer et al., 1982). Latex, being living cytoplasm, contains all cytoplasmic inclusions such as nucleus, mitochondria, ribosomes, various membrane-bound bodies etc. Fresh latex is a polydisperse system in which negatively charged particles of varying types are suspended in an ambient serum (C-serum). The two main particulate phases contained in Hevea latex are rubber particles constituting 30-45 per cent and lutoid particles 10-20 per cent. The third type, on a quantum basis, is the Frey-Wyssling complex.

Rubber particles ususally have a size ranging from 50A to

about 30,000Å (3 mm). A rubber particle of average size about 1000Å would contain hundreds of molecules of hydrocarbon which is surrounded by a surface film of protein and lipids (Gomez and Moir, 1979).

The lutoids are membrane bound bodies and are mostly larger in size. They are 2-5 µm in diameter bound by a unit membrane of about 80Å thick and was suggested as analogous to vacuoles (Ribaillier et al., 1971 and Wiersum, 1957).

The lutoid content (B-serum) has a very rapid flocculating action on aqueous suspension of rubber particles in latex resulting in the formation of microflocs (Southorn and Edwin, 1968). This activity is apparently moderated by the ambient C-serum. Southern and Yip (1968) demonstrated that the fast initial flocculating action of B-serum is an electrostatic one involving the interaction between the cationic content of B-serum and the anionic surface film of rubber particle. However, this enzymic action leading to coagulation of rubber particles is the main point of latex vessel plugging and cessation of flow after tapping. The Frey-Wyssling complexes, first reported by Frey-Wyssling (1929), are more or less spherical bodies in a size range of 3-6 µm diameter and are bound by a double membrane. The complex structure of Frey-Wyssling complexes have been elucidated by Dickenson (1969) and are considered to have vital role in metabolic activities.

Latex flow

Latex vessels are filled with viscous latex under hydrostatic pressure. When the vessels are cut open during tapping, the pressure is released resulting in the exudation of latex. Displacement of latex along the vessel continues due to the cohesive force existing in the liquid phase leading to a fall in pressure in the latex vessel (Riches and Gooding, 1952). As a consequence water passes to the latex vessels from the surrounding tissues causing dilution of latex. This phenomenon, known as 'dilution reaction', reduces the viscosity of latex and enhances flow. Latex flow stops about three hours after tapping. Cessation of flow is effected by an inherent mechanism of clotting (Southern and Yip, 1968; Southern, 1969). An index termed 'plugging index' was proposed by Milford et al. (1969) for measuring the extent of plugging. The latex and rubber lost are regenerated during the interval between two tapplings. Exploitation techniques, such as frequency and intensity of tapping, and stimulation practice govern the productivity of Hevea tree to a large extent. Response of a clone to these factors can be identified only after time consuming experiments.

Importance of the extension of drainage area mediated through dilution reaction after tapping is well elucidated (Sethuraj, 1977). Physiological parameters such as initial flow rate (volume of latex obtained per minute for the first five minutes after tapping) and plugging index received much attention.

Tree improvement

Plant breeding as a single tool has contributed much to the efficiency and economic viability of Hevea tree. When rubber cultivation started the only material used for planting were seedlings from the limited number (22) of base materials available from the Wickham collection. Witby (1919) and Cramer (1940) observed large variability among seedling populations and exploited the source of variability by planting clonal seedlings. Van Helton and Tas during 1916-1918 perfected the techniques of bud grafting (Dijkman, 1951). These early developments resulted in the development of primary clones such as Tjir 1, GT 1, PR 107, Nab 17, PB 86, PB 49 and Pil B 84.

Organised rubber breeding was started during nineteen twenties by hybridization and selection. Selection among large hybrid populations and identifying the best recombinants for elaborate testing before final recommendation of clones for commercial planting, is the major time consuming section of tree improvement programme of this crop. Hence any useful means to reduce the testing time would be of high practical significance. In Hevea polyploidy has been successfully attempted (Markose, 1975; Mendes, 1969; Saraswathy Amma, 1981 and Shepherd, 1969). The type of variability induced and to what extent it is valuable have yet to be studied.

Yield components

Evolving high yielding clones through selective complementation of yield components is an effective method. At the very beginning of tree selection in Hevea, morphological characters had been used for selection of good mother trees. Trunk shape, bark morphology, type of branching and crown size and shape had been considered as important parameters (Peries, 1970).

By later investigations, associated with tree improvement programmes, structural parameters such as the number of latex vessel rows and bark thickness (Ho, 1972; 1976; 1978) and the latex vessel system in leaf (Huang et al., 1981) caught attention as yield contributing factors. The role of physiological (Ho, 1972; 1976; Samsuddin et al., 1986; 1987a,b) and biochemical (Dintinger et al., 1981) factors were also studied to a great extent. Based on a theoretical analysis of yield components Sethuraj (1981) suggested the initial flow rate, panel length, dry rubber content (rubber content as gramme per 100 g of latex) and plugging index as the major ones. The quantitative variation of structural components due to tree age, growth phases or ploidy level have not been well studied. However the inter-relationships among anatomical and physiological traits and their combined role on yield performance have not been fully understood.

Constraints

Jayasekara et al. (1977) used regression analysis to study the genotype-environment interactions in some Hevea clones and reported that the clones can be categorised in to different adaptability groups based on their significant linear components. The summer drop pattern of various clones and some biochemical and physiological factors influencing the seasonal effect of yield variations have been reported. However information on the role of structural parameters on seasonal yield variation is meagre.

Diseases are also constraints which affect yield of Hevea. In India two major leaf diseases have received much attention of rubber planters. These are abnormal leaf fall disease caused by Phytophthora spp. and powdery mildew caused by Oidium heveae. The former is prevalent during monsoon season while the latter occurs during January-March. Disease susceptibility is clone specific and effective selection parameters for disease resistance are lacking. The only method to tackle the problem is proper application of prophylactic measures. Brown bast, a physiological disorder, mostly associated with exploitation, is another serious problem in rubber plantations.

Growth vigour is the most important aspect influencing yield. Growth in terms of girth directly influence the panel length. Tapping retards growth. Templeton (1969) has reported that clones of higher productivity exhibited a more intense depression in growth rate

and Sethuraj et al. (1974) proposed a girth increment index to characterise the yield potential of clones. The extent of growth reduction due to tapping and exploitation is a clonal characteristic and varies due to exploitation techniques and environmental constraints.

The variations in biomass production is mediated through latex flow patterns.

Clone identification is a problem in Hevea. There are some conventional methods based on leaf and seed morphology (Radakrishna Pillai, 1980; Saraswathy Amma et al., 1981).

In any biological system there exists an essential relationship between structure and function. Physiological function and the basic make up of tissue system or organ concerned is intrinsically inter-linked. With this in view the present work was conducted to investigate certain structural aspects, yield and other secondary characters and their variabilities with emphasis to interclonal variations and relationships. Genetic parameters such as genotypic and phenotypic variations, heritability (broad sense) and genetic advance of important characters have also been estimated to observe the suitability of these traits as selection parameters.

This study also analyses clonal variations of a number of bark characteristics, with the view of utilising the information for clone identification purposes.

II. MATERIALS AND METHODS

Materials of Hevea brasiliensis (Willd. ex. Adr. de Juss.) Muell. Arg. at appropriate stages for the observations were collected from the RRII Experiment Station (RRIIES) at Kottayam and from the Central Experiment Station (CES) at Chethackal, near Ranni. The total number of clones involved in the present work was 40. A list of clones, along with brief descriptions, is given in Table 1.

Sampling specificity

(a) Surface ornamentation:- Leaves at bud break stage (bud emerged and just grown to a length of nearly two cm), leaflet stage (leaves of the terminal flush still expanding and copper to reddish in colour), pendent stage (leaves almost completely expanded and green but still limp), hardened stage (leaves of the terminal flush fully expanded but just hardened, lamina in proper position) and fully hardened stage were collected from clone Tjir 1 for studies on surface ornamentation at different stages of development. Fully grown fruits were also collected from the same clone. Fresh leaf pieces from the central position of the middle leaflet and samples from petiole, petiolule, tender green stem and the pericarp of mature green fruits were collected.

Quantitative studies on stomata on different stomatiferous parts were done on six clones, namely RRII 101, RRII 102, RRII 105, RRII 106, PR 107 and Tjir 1. Correlation of percentage leaf retention with the quantitative traits of petiolar stomata was studied with

18 trees, three each belonging to six clones, numbered 456, 455, 301, 416, 417 and 421, raised at RRIIES from the 1954 hand pollinations progenies.

(b) Cambial activity:- Observations on cambial activity and its periodic changes were made on 25 trees of the clone Gl 1 planted, at RRIIES and 40 trees, five each belonging to eight clones namely RRII 101, RRII 102, RRII 105, RRII 106, RRII 109, RRII 111, PR 107 and Tjir 1 planted at CES. One year old twigs were chosen from three branches at random positions and the samples were taken from four cm below the apex.

(c) Variability:- Interclonal variations in bark anatomical traits, leaf anatomical traits, growth characters, intraxylary phloem, primary xylem, latex flow characters, latex yield, rubber yield, dry rubber content, wintering pattern and disease incidences were studied on ten clones namely RRIC 7, RRIC 36, RRIC 45, RRIC 52, RRIC 100, RRIC 102, RRIC 104, RRIC 105, Nab 17 and GT 1 in an RBD trial (with three replications) laid out at CES. Ten normal trees per plot were selected for observations. From the data monthly performances and summer variations of yield and yield factors were computed.

For leaf structure leaf samples have been collected randomly from three branches at random position of the trees. Sample collection was made between 10.00 AM and 11.00 AM. For bark

study one sample per tree at a height of 125-150 cm was collected. Quantification of intraxylary phloem and primary xylem also were made from one twig each chosen from three branches at random positions per tree.

The study to compare and correlate the bark anatomical traits of juvenile plants (three year old) with that of mature plants (eight year old) involved eleven clones, in a trial at CES. Ten of the clones were raised from the progenies of 1970 hand pollinations and numbered as 427, 115, 29, 499, 356, 249, 85, 110, 157 and 16, the remaining one being control clone (GT 1). For the experiment, 10 trees per clone were taken as per availability.

Comparative anatomy of virgin and renewed bark was studied on seven clones, namely RRII 101, RRII 102, RRII 105, RRII 106, RRII 109, RRII 111 and Tjir 1. Bark samples were collected from five trees per clone. Samples of virgin bark were collected at a height of 125-150 cm from the bud union. The samples of renewed bark were of five years regeneration.

To compare drought tolerant and susceptible groups of clones for the bark anatomical traits, on a quantitative basis, six clones were selected from an RBD trial (with three replications) incorporating ten clones. Of the six clones, three (RRIM 601, RRIM 611, RRIM 615) were drought susceptible and the other three (RRIM 501,

RRIM 605 and RRIM 609) drought tolerant in terms of yield drop during summer (February to May).

An induced seedling tetraploid of Tjir 1 obtained by treating seeds with 0.75 per cent aqueous solution of colchicine and cloned later, a tetraploid of GT 1 and another of RRII 105, both obtained by treating the vegetative buds of the respective clones, along with their respective diploids of the same age were taken for comparing the bark anatomical traits at the two ploidy levels. The samples were collected from trees grown at CES.

Fixing and preservation

All the samples were fixed immediately after collection. The fixatives used for bark, leaf and stem samples was formalin-acetic-alcohol. Epidermal peelings were fixed in 70 per cent alcohol after thorough washing with tap water. For SEM study fresh specimens were used.

Maceration

Epidermal peelings were obtained by maceration of the specimens in 40 per cent nitric acid, in a boiling tube along with a pinch of potassium chlorate and gentle heating. On repeated heating and shaking the epidermis got separated. Pieces of peidermis were repeatedly washed in tap water before preserving them in 70 per cent alcohol.

Processing

For leaf study paraffin blocks were prepared by standard methods of dehydration and infiltration through ethyl alcohol-xylene series/ethyl alcohol-tertiary butyl alcohol series. Serial sections were cut at 10-15 μm thickness using a rotory microtome and loaded on slides. Mayer's adhesive was used.

Stem cuttings and bark samples were sectioned using a base-sledge microtome. Samples of stem were cross sectioned at 40 μm thickness. Bark sections were taken at the radial longitudinal plane at 100 μm thickness and at the tangential longitudinal plane at 80 μm thickness. Tangential longitudinal sections were confined to the productive part. For laticifer ontogeny serial sections of the bark at the developing zone were cut at 20 μm thickness.

For SEM study specimen conductivity was improved by painting the edges of the plant tissue against the stub with conductive silver paint (Silver Print, G.C. Electronics, Rodeford, Illinois) and then uniformly coating the specimen with Gold-Palladium (60:40) alloy using the Fine Coat Ion Sputter JFC 1100, for three minutes.

For leaf and stem structure, safranin-fast green staining was done. Bark sections were stained with Sudan III and mounted in glycerine. Epidermal peelings were stained in a mixture of Harri's haematoxylin and phenolic bismark brown in 2:1 proportion after clearing in sodium salicylate (Purvis and Collier, 1966).

For laticifer ontogeny bark sections were stained in Sudan III first. Then washed in tap water and haematoxylin-bismark brown schedule was followed.

The bark sections were mounted in glycerine jelly. For the other materials Canada balsam was used.

Microscopy

Anatomical observations were taken with the aid of light microscope or scanning electron microscope, appropriately for the specific purposes. Data on quantitative aspects were collected using an ocular/eyepiece micrometer and the actual measurements were computed using a stage micrometer.

(a) Surface ornamentation:- The development of epicuticular wax, cuticular ornamentation, stomatal topography and other surface characters of leaf blade, petiole, petiolule, tender green stem and the pericarp of fruits were studied with the aid of a JEOL JSM 36C model scanning electron microscope.

Fruit wall peelings, at different stages of fruit growth, were observed for the ontogeny of stomata. Frequency of stomata per microscopic field was counted and actual numbers/unit area was computed. Frequency of leaf blade stomata is expressed as numbers per mm^2 . Frequency of petiolar stomata is expressed as numbers per 10 mm^2 . Length and width of stomatal aperture were measured using an ocular micrometer.

(b) Strucutre of leaf:- Leaf thickness, height and width of the midrib, cuticle thickness and the height and width of palisade cells were recorded from cross sections of leaves.

(c) Vascular cambium:- Cross sections of one year old stem were observed. Cambial activity was assessed in terms of the number of cambial rows present in each collection of young twigs. The cambial rows were counted from sections taken at four centimeters below the tip. For the observations on periodicity of cambial activity, May to July, August to October, November to January and February to April were treated as first, second, third and fourth periods, respectively.

(d) Intraxylary phloem and primary xylem:- From the cross sections of one year old stem, intraxylary phloem and primary xylem were quantified in terms of the number of points of the respective tissue.

(e) Phloem ray characters:- Phloem ray characters were recorded from tangential longitudinal sections of the bark between 500 μm and 1500 μm away from the cambium. General observations were made on the shape and structure of phloem rays in the laticifer layer and the quantitative traits were recorded.

To study the proportion of ray types in terms of shape and seriation, each type was counted with respect to ten clones.

The height and width of three ray groups at random positions were measured from each section. The ray height and ray width at the longest and broadest part respectively were measured. Diameter of two adjacent cells at the broadest point of three rays per section, with respect to each ray type in terms of seriation, were recorded. Three sections, picked up at random from each sample were observed.

The data were read on a micrometer/projection scale of the projectina and converted to actual measurements. Height/width ratio was also calculated.

(f) Laticifer characters:- The distance of first latex vessel row and the number of latex vessel rows within the first mm from the wood, number of latex vessel rows in the soft bast region and the same in the hard bast region were counted from the radial longitudinal sections. ✓

The density of latex vessels, diameter of latex vessels and the intensity of anastomosing (number of connections, between latex vessels per 0.25 mm height of the same row) were studied from the tangential longitudinal sections. For density, the numbers per unit circumference was counted. Diameter was measured using a micrometer/scale of the projectina. Number of connections between laticifers within a unit height in the anastomosing portions was also counted. Nine observations were recorded from three sections for all characters under study. ✓

Laticifer area index was recorded as per the formula proposed by Gomez et al (1972) for 1/2S d/2 system of tapping: $nfG \pi r^2 .0.3 \sqrt{\quad}$ where 'n' is the number of latex vessel rows, 'f' frequency (density) of latex vessels, 'G' girth and 'r' radius of latex vessels.

Field observations

1. Growth characters

(a) Bark thickness:- Total thickness of the bark was measured directly from the bark samples using a scale and a cord. Thickness of soft bast and hard bast were recorded microscopically. Soft bast refers to the thickness up to the level where sclerification has started. Bark thickness in between the soft bast and cork is referred to as hard bast.

(b) Girth:- Girth at a height of 150 cm from the bud union was recorded using a tailors tape. With respect to ten clones, annual girth recordings were carried out for four consecutive years from 1984 to 1987.

(c) Girth increment on tapping:- From annual girth data percentage increase per year was calculated.

(d) Panel length:- The length of tapping panel was measured using a tailors tape.

2. Flow factors

Monthly recordings were carried out on three trees per plot (a total of 9 trees per clone) from January to December 1987).

(a) Initial rate of flow:- This characteristic indicates the velocity of flow, uninfluenced by the process of latex vessel plugging. It is expressed as average volume (ml) of latex drained per min per panel length for the first five min after the commencement of latex flow on tapping.

$$\frac{\text{Volume of latex (ml) drained for the first 5 min}}{5 \times \text{Panel length}}$$

(b) Duration of flow:- The time of flow from the commencement of latex flow (collection of the first drop) to cessation of flow (min) was recorded at monthly intervals.

(c) Plugging index:- Plugging index (PI) was estimated as per the formula proposed by Milford et al. (1969).

$$\text{PI} = \frac{\text{Mean latex yield per min over the first 5 min}}{\text{Total latex yield}} \times 100$$

3. Yield

The dry rubber yield was collected for four consecutive years from 1984 to 1987. Data on latex volume and dry rubber content were collected for three years only, from 1985 to 1987,

X

(a) Latex yield:- The total volume of latex (ml) of individual trees were measured on normal tapping days at fortnightly intervals. From the data plot means and clone means were calculated.

(b) Dry rubber yield:- Dry rubber yield (g/tree/tap) of individual trees were collected at fortnightly intervals by cup coagulation method. After complete cessation of latex flow, the latex in the collection cup was coagulated using 3.00 per cent formic acid. The individual coagula were collected separately on numbered metal hooks, hung for dripping off the water and then dried in a smoke house for about thirty days. After drying the lump was weighed on a top pan balance. The weight was corrected for 10 per cent moisture content. Plot means and clone means were computed.

(c) Dry rubber content:- The dry rubber content (d.r.c.), which is the quantity of dry rubber contained in the latex expressed as percentage by weight, was estimated at fortnightly intervals. From the pooled samples of latex collected from the ten trees in a plot, a sample of 20 ml of latex was collected and coagulated with formic acid. The coagulum was pressed and dried in an oven and weighed. For each plot d.r.c. was calculated:

$$\frac{\text{Oven dry weight of rubber}}{20} \times 100$$

From this data clonal/annual means were computed.

4. Monthly variations and drought effect

Monthly performance/variations of yield and flow factors have been expressed as percentage of annual means of the respective traits. To assess the performance of each trait during drought period, the mean over four months, from February to May was calculated and expressed as percentage of annual mean.

5. Wintering behaviour

For characterization of clones visual observations were made at fortnightly intervals from December to February for three consecutive years and graded the clones as early, late and partial wintering types.

6. Leaf diseases

To study the correlations of characters of petiolar stomata with leaf retention after the incidence of Phytophthora leaf fall disease, five branches selected at random from each tree were labelled after refoliation and hardening following wintering. Only the branches which had a minimum of hundred leaves were chosen for this purpose. Leaf count was taken before the incidence of Phytophthora leaf fall disease. After the incidence of disease, leaf count was taken again; the percentage leaf retention was assessed.

Interclonal variations for the intensity of abnormal leaf fall disease and powdery mildew among ten clones were observed for two consecutive years and the clones were graded as high (H), medium (M) and low (L). For abnormal leaf fall visual assessment of leaf retention (%) was made. In the case of Oidium, disease incidence associated with leaf fall is referred as high (H), high rate of spotting without leaf fall as medium (M) and low rate of spotting without any leaf fall as low (L).

7. Brown bast incidence

The ten trees selected per plot, for the experiment were observed for brown bast, number of incidence per plot was recorded and the percentage was computed.

Statistical techniques

Standard statistical techniques were used for analysing the data on all metric characters. With respect to the clones in RBD trial, plot means were calculated and used for analysis.

(a) Comparison of means:-

The paired means were compared by paired 't' test as explained by Craxton and Cowden (1966).

$$t = \frac{\bar{D}}{S_{\bar{D}}} \quad \text{with } n-1 \text{ d.f}$$

$$D = x_1 - x_2$$

$$\bar{D} = \bar{x}_1 - \bar{x}_2$$

$$S_{\bar{D}} = \text{S.D. of } D \text{ values}$$

n = Number of pairs of observations.

The significance was tested for $n - 1$ degrees of freedom.

$$\text{The standard deviation for } D \text{ values} = \sqrt{\frac{\sum (D - \bar{D})^2}{n-1}}$$

(b) Analysis of variance:-

Analysis of variance was done by the cross classification system suggested by Singh and Choudhary (1979). For percentage values transformation was done.

$$\hat{\sigma}_e^2 = M_{13}$$

$$\hat{\sigma}_g^2 = M_{12} - M_{13}/r$$

The phenotypic variance ($\hat{\sigma}_p^2$) was obtained by addition.

$$\hat{\sigma}_p^2 = \hat{\sigma}_g^2 + \hat{\sigma}_e^2$$

Coefficient of variation:-

The coefficient of variation was computed as

$$C.V. = \frac{S.D}{\bar{x}} \times 100$$

Phenotypic coefficient of variation (P.C.V.)

$$= \sqrt{\frac{2}{Gp}} \times 100$$

Genotypic coefficient of variation (G.C.V.)

$$= \sqrt{\frac{2}{g}} \times 100$$

The critical difference was calculated as $CD = SE \times t$. SE is the standard error of the difference of the treatment means to be compared which is calculated as $SE = (2MS_{e/r})^{\frac{1}{2}}$ with MS_e as error mean sum of squares and r as the number of replications. For the quantitative traits, varieties were categorised as high, medium and low on the basis of significant difference between varietal mean and grand mean. For this purpose standard error was calculated as $SE = \sqrt{\frac{n-1}{n} + \frac{MS_e}{r}}$. CD at 5 per cent level was calculated.

To compare the drought tolerant and susceptible group of clones the treatment sum of squares (clones) was subdivided into its components. For regression analysis sum of squares due to regression was estimated by the formula:

$$\text{SS due to regression} = \frac{\sum (xy)^2}{\sum x^2}$$

Residual SS = Total SS due to y - SS to regression. The significance of regression SS was tested against the residual SS for 1 and n-2 degrees of freedom.

(c) Heritability (broad sense):-

Heritability, the fraction of total variance which is heritable was estimated in the broad sense. It is the ratio of genotypic variance to phenotypic variance.

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

Genetic advance:- Expected genetic advance, at 5 per cent selection intensity, was estimated by the standard method:

$$\text{Genetic advance} = \frac{i h^2 \sqrt{VP} \times 100}{\text{mean}}$$

where 'i' is a constant, the value of which at 5 per cent selection intensity is 2.06.

(d) Covariance analysis:-

The sum of products of possible pairs of characters and the expectations of mean sum of products were calculated as shown in Table 2.

✓ (e) Simple correlations:-

Possible correlations of characters were estimated as detailed below. As per definition simple correlations were estimated as

$$r(x_1 x_2) = \frac{\text{Cov}(x_1 x_2)}{\sqrt{V(x_1) V(x_2)}}$$

✓ (f) Partial correlations:-

First order partial correlations were computed using

$$r(xy), r^2(xy), 1-r^2(xy) \text{ and } [1-r^2(xy)]^{\frac{1}{2}}$$

$$r_{12.3} = \frac{r_{12} - r_{13} r_{23}}{\sqrt{(1 - r_{13}^2)(1 - r_{23}^2)}}$$

Second order partial correlations were calculated using

$$RAB.C, r^2 AB.C, 1-r^2 AB.C \text{ and } [1-r^2 AB.C]^{\frac{1}{2}}$$

$$r_{12.34} = \frac{r_{12.3} - r_{14.3} r_{24.3}}{\sqrt{(1-r_{14.3}^2)(1-r_{24.3}^2)}}$$

✓ (g) Multiple correlations:-

Multiple correlations were computed using the following formula.

$$R_{1.23}^2 = r_{12}^2 + r_{13}^2 - 2r_{12} r_{13} r_{23}$$

$$R_{1.234}^2 = r_{12}^2 + r_{13.2}^2 (1-r_{12}^2) + r_{14.23}^2 (1-R_{1.23}^2)$$

The significance of multiple correlation was tested by 'F' test,

where,

$$F = \frac{(R_{1.234}^2 \dots m)/m-1}{(1-R_{1234}^2 \dots m)/n-m}$$

with $n_1 = m-1$ and $n_2 = (n-m)$ degrees of freedom, 'm' being the number of variables or characters and 'n' the number of treatment.

✓ (h) Regression coefficient:-

From the variance and covariance analysis simple regression coefficients were worked out.

$$b(y/x) = \frac{\sum yx}{\sum x}$$

$$\hat{y} = \bar{y} - b\bar{x}_1 + bx_1$$

✓ (i) Genotypic correlations and path coefficient analysis:-

Path coefficient analysis was done to study the cause and effect relationships. Data collected from the ten clones namely

RRIC 7, RRIC 36, RRIC 45, RRIC 52, RRIC 100, RRIC 102, RRIC 104, RRIC 105, GT 1 and Nab 17, in R.B.D. trial, were used for estimating genotypic correlations and path coefficient analysis.

Separate analysis was done to examine the effect of (1) girth and bark anatomical traits at the initial year of tapping (1984) on mean yield over three years (1985, 1986 and 1987), (2) girth and bark anatomical traits at the initial year of tapping on girth increase over two years and (3) girth, bark anatomical traits, latex flow characters, volume yield and d.r.c. on dry rubber yield at the same year. Data on all the traits incorporated in the third set were collected in the forth year of tapping (1987).

Using appropriate values from Table 2 genotypic correlations were worked out.

$$\text{Genotypic correlation coefficient } r_{g_1g_2} = \frac{\overline{G_{g_1g_2}}}{\sqrt{\frac{2}{g_1} \cdot \frac{2}{g_2}}}$$

where $\overline{G_{g_1g_2}}$ is the genotypic covariance between the two traits,

$\frac{2}{G_{g_1}}$ is the genotypic variance of the first trait, and

$\frac{2}{G_{g_2}}$ is the genotypic variance of the second trait.

For each study, correlation coefficients of the traits with the respective major characters were partitioned into direct and indirect effects. The method suggested by Wright (1921) and

elaborated by Dewey and Lu (1959) was followed for estimation of direct and indirect effects. The path coefficients were obtained by the simultaneous solution of the following equations which express the basic relationship between correlations and path coefficients.

$$r_{1y} = P_{1y} + r_{12} P_{2y} + r_{13} P_{3y} + \dots + r_{1k} P_{ky}$$

$$r_{2y} = r_{21} P_{1y} + P_{2y} + r_{23} P_{3y} + \dots + r_{2k} P_{ky}$$

$$r_{3y} = r_{31} P_{1y} + r_{32} P_{2y} + P_{3y} + \dots + r_{3k} P_{ky}$$

$$r_{ky} = r_{k1} P_{1y} + r_{k2} P_{2y} + r_{k3} P_{3y} + \dots + r_{k-1, k}^P P_{ky}$$

where r_{1y} to r_{ky} denote coefficients of correlation between causal factors 1 to k and the dependent character y.

r_{12} to $r_{k-1, k}^P$ denote coefficients of correlation among all possible combinations of causal factors, and

P_{1y} to P_{ky} denote direct effects of character 1 to k on the character y.

Path coefficients are obtained as

$$P_{1y} = \sum_{i=1}^k c_{1i} r_{iy}$$

$$P_{2y} = \sum_{i=1}^k c_{2i} r_{iy} \dots \dots \text{etc.}$$

The residual factor (x) which measures the contribution of the rest of the characters not considered in the causal scheme was obtained as

$$P_{xy} = \sqrt{1 - R^2}$$

where,

$$R^2 = \sum_{i=1}^k P_{iy} + 2 \sum_i \sum_{j \atop i < j} P_{iy} P_{jy} r_{ij}$$

The above equations can be written in the matrix form as shown below:

$$\begin{pmatrix} r_{1y} \\ r_{2y} \\ r_{3y} \\ \vdots \\ r_{ky} \end{pmatrix} = \begin{pmatrix} 1 & r_{12} & r_{13} & \dots & r_{1k} \\ & 1 & r_{23} & \dots & r_{2k} \\ & & 1 & \dots & r_{3k} \\ & & & \ddots & \vdots \\ & & & & 1 \end{pmatrix} \begin{pmatrix} P_{1y} \\ P_{2y} \\ P_{3y} \\ \vdots \\ P_{ky} \end{pmatrix}$$

i.e. $\underline{A} = \underline{C} \underline{B}$

Hence $\underline{B} = \underline{C}^{-1} \underline{A}$

Where \underline{C}^{-1} = is the inverse of \underline{C}

let $\underline{C}^{-1} = \begin{bmatrix} C_{11} & C_{12} & C_{13} & \dots & C_{1k} \\ C_{22} & C_{33} & & \dots & C_{2k} \\ & C_{33} & & \dots & C_{3k} \\ & & & \ddots & \vdots \\ & & & & C_{kk} \end{bmatrix}$

III. RESULTS

1. STRUCTURE AND ORGANIZATION

1.1 B a r k

The mature bark of Hevea tree is grey to brown in colour. The colour may slightly vary due to age of the tree and clone. Older trees have rough bark. The extent of roughness is a clonal character and flaky bark is characteristic of certain clones like Gl 1. The thickness of bark depends on various factors such as age of the tree, height of sampling and varietal difference.

The general organization of the mature brown bark of Hevea is comparable to that of a perennial tree except for the presence of laticifers. The tissue outside the cambium is collectively known as bark. The bark comprises of three zones (Figure 1). The inner zone is made up of soft tissues and occupies nearly 40-45 per cent of the total bark. Most of the functional elements, including the functional latex vessels of the secondary phloem region, occur in the soft bast region. The outer zone contains more harder tissues where stone cells in groups are present, which are formed by the sclerification of parenchyma cells. The tissue in outer region of the hard bast become aged and obliterated and form a part of the protective tissue. The outermost zone is the protective tissue made of cork cells.

(a) Latex vessels

The secondary laticifers are differentiated from the cambial derivatives. During the initial stages of development the sieve tube initials and laticifer initials are indistinguishable. In the course of development, the laticifer initials show slow dissolution of the cross walls in the longitudinal course.

Laticifer initial consists of two to seven cells, formed by the division of a fusiform initial. End cells of these laticifer initials have oblique walls. The laticifer initials join, in their longitudinal course by forming connections at the oblique walls of the end cells (Plate I.A). At this stage presence of latex is evidenced by the occurrence of granular substances. Simultaneously dissolution of cross walls of the constituent cells of laticifer initials takes place. At this stage the laticifers are coenocytic (Plate I.B).

Tangential connections also forms at points of contacts between latex vessels. Such tangential connections are formed between latex vessels of the same row. Such connections are concentrated in localized areas of contacts. In the contact regions, on an average, seven connections were recorded within a height of 0.25 mm.

As latex formation proceeds, after the dissolution of cross walls, nucleus seems to be degenerating. However in the mature laticifers where the latex took deep staining of Sudan III, nucleus could not be observed while nucleus was present in the adjacent parenchyma

cells and companion cells of seive tubes.

Laticifer wall is mostly made up of cellulose and is plastic. Plasmodesmatal connections between latex vessels and phloem rays were observed. Pit connections in between young latex vessels are simple but large and conspicuous (Plate I.D), while those in between latex vessels and phloem rays are minute and simple (Plate I.C).

The latex vessels do not have a straight vertical course. They show slight inclination in an anticlockwise direction from base upwards. The running direction is wavy since they are oriented through the sides of the phloem rays.

Latex vessels are distributed in the bark almost in concentric rows alternating with the seive tube layers. The first row originates at a distance of about 500 μm from the cambium. The frequency of laticifer rows depends upon the clone. It is also influenced by the growth rate of the tree. Most of the functional latex vessel rows are present in the soft bast but a few of them occur in the hard bast also.

(b) Phloem rays

The phloem rays are heterogenous and consists of both prostrate and procumbent cells (Plate 2.A-D). Both uniseriate and multiseriate rays occur. The end cells of uniseriate rays are large with conical or dome shape. Multiseriate rays have one to three upright cells

both at the proximal and at the distal ends. The body is two to four cell wide. The cells are procumbent with compact arrangement. They are rectangular or hexagonal in shape. Uniseriate, biseriate, triseriate and tetraseriate rays are present, of which triseriate is the predominant type.

Depending on the shape, four types (Plate 2.E-H) of multiseriate rays were identified.

1. Dumb-bell shaped, with a narrow middle portion.
2. Oval in outline.
3. Spindle shaped, where both ends are long and narrow with unilayered cells.
4. Cricket bat shaped with a broad part and a narrow tail.

Out of these, the bat shaped type is the predominant one.

1.2 Cambial activity

The data on periodicity of cambial activity, expressed as the number of cambial layers comprising the cambium and its immediate derivatives, collected from 25 trees of Gl 1, is shown in Table 3. This trait showed significant seasonal variation. The first two periods (covering May to October) were comparable while the third and fourth periods, covering November, December, January, February, March and April were active growth periods in Hevea.

May, June, July period showed the least growth. In eight other clones namely RRII 101, RRII 102, RRII 105, RRII 106, RRII 109, RRII 111, PR 107 and Tjir 1 also periods 3 and 4 denoted active growth. Maximum number of cambial layers were recorded for the period February to April (Figure 2) for six clones (RRII 101, RRII 106, RRII 109, RRII 111, PR 107 and Tjir I), while two clones (RRII 102 and RRII 105) showed comparable cambial activity during the periods 3 and 4.

1.3 Intraxylary phloem

Occurrence of adaxial (medullary) phloem in Hevea brasiliensis was noticed first during the studies on periodicity of cambial activity. In the stem (one year old branch) intraxylary phloem was identified in the pericentral region as strands associated with the protoxylem groups (Plate 3.A). Each strand consisted of one to three rows of phloem elements flanking the primary xylem elements. This internal phloem resembled the external phloem except for the occurrence of laticifers (Plate 3.B).

In longitudinal sections through the pericentral region, sieve tubes were readily recognised by the presence of terminal and lateral sieve areas and companion cells (Plate 3.C).

1.4 L e a f

In Hevea brasiliensis, the leaves are arranged in stories.

Each storey consists of a cluster of spirally arranged trifoliate leaves. Petiole is long with proximal and distal pulvini of varying size and shape and nectariferous glands are present at the tip. Leaflets are short stalked, elliptic or obovate and entire with green or dark green colour above and glaucous beneath. Venation pattern is of the pinnate type.

(a) Epidermis

The upper epidermis is single layered, composed of brick shaped cells except over the mid-rib where it is dome shaped. The cells are somewhat uniform in shape and arrangement. The component cells recorded a height of 11-19 μm and a width of 17-28 μm . The leaf has a thick cuticle (5-8 μm). Stomata are absent on the upper epidermis.

The lower epidermis also is unilayered but the cells are irregular in shape exhibiting a sinuous outline on surface view (Plate 4.B). Stomata are confined to the lower epidermis. The lower epidermis is cutinized and epicuticular waxes are prominently formed making the lower surface more rough and glaucous (Plate 4.A).

(1) Stomata

Stomata are rubiaceous type. On the veinless portion of the lamina they are distributed more or less at equal distances (Plate 4.B). Stomata occur on the veins, petioles and petiolules and on other plant parts such as fruit walls and young stem.

The stomatal apparatus consists of an outer stomatal ledge aperture, front cavity, the pore, back cavity and the inner ledges. The substomatal chamber is very small (Plate 4.C). Filaments of epicuticular waxes are spread over the aperture. The stomata on leaf blade are sunken.

The topography of stomata in relation to the surrounding cells was very clear in a scanning electron micrograph (Plate 5.E). The guard cells are in level with the lower half of the subsidiary cells. The stomatal aperture is small, oval in shape, seen at the lowest topographic position of the stomatal apparatus. The walls of the guard cell pose slightly bulging to the pore side flanking the pore with the arms of epicuticular wax radiating to the sides. At the sides of the guard cells, subsidiary cells are in a little more raised position, in level with the non-stomatal cells of the epidermis. The whole apparatus looks like a stomatal crypt.

The stomata on foliar veins, petioles, petiolules and fruit walls are slightly raised above the cuticle and hence of the exposed type (Plate 5.A-D). They are comparatively larger in size and fewer in number than those of the lamina. The stomatal density in the petiole and leaf blade in six clones are shown in Table 4. In the leaf blade, stomatal density varied from 297.00 to 348.30 in an area of 1 mm^2 . This is comparable to the range recorded by Senanayake et al. (1970) for rubber clones. For the petiole the range was only 3.00 to 5.25 in 10 mm^2 . The organographic variability

of the length and width of stomatal apertures are shown in Table 5. The aperture length of leaf blade stomata was 10.94 μm against 16.88 μm for the petiole and 14.15 for the vein. The difference was significant at 1 per cent level. The aperture width recorded for leaf blade stomata was 1.93 μm against 3.16 μm for veinal stomata and 4.26 μm for petiolar stomata. For this trait also the three parts differed significantly.

Two types of openings were detected on the fruit wall. They differed in shape, size and ontogeny. One type has oval or elongated aperture with two pear shaped guard cells parallel to the aperture (Plate 6.E). They develop before the fruits attain full size. The ontogeny of this type is analogous to that of leaf blade stomata. The stomatal mother cell divide repeatedly and the resultant cells become arranged in six rows parallel to each other. The central two rows (three cells/row) disintegrate to form the aperture. Cross walls of cells in sides of the aperture fuse to form two pear shaped guard cells. Cells in the adjacent row fuse in the same manner to form the subsidiary cells. Fusion of cell wall is followed by nuclear fusion (Plate 6.A-E). The other type, which are abundant on the fruit wall, are abnormally large in size (Plate 7.D). They are round or irregular in shape with thick walled cells around a giant opening.

Ontogenetically these large openings are analogous to lysegenous cavities. They are formed just before the fruits reach full size.

The first step of development of such cavities is disintegration of a group of cells of the fruit wall (Plate 7.A,B). The internal margins of the cells at the periphery of the cavity become thickened and the cross walls of surrounding cells lyse resulting in the fusion of adjacent cells which assume suitable shape to protect the central opening (Plates 7.C,D). Thus large stomata are formed with a giant opening guarded by thickwalled cells.

(2) Epicuticular wax

On Hevea leaf blade, aggregates of wax coatings, in the form of granules are present on the upper epidermis. It is virgulate in nature and are randomly oriented (Plate 9.F). Owing to an even distribution of virgulate striae, closely entangled without buttresses, upper epidermis has more bloom with shining surface.

The lower surface of leaf blade has mixed type of wax coatings. From the median position of epidermal cells upright plates/buttresses (Plate 9.A,B), with branched filaments at the margins, are observed. The leaf surface become rough and glaucous with a reticulate type of wax ornamentation covering the epidermis and stomata at the mature stage (Plate 9.D,E).

Soft wax coatings without papillae are present on foliar veins, petioles, petiolules, young stem and fruit walls (Plate 5.A-D). Petiole, vein and young stem have comparable type of wax distribution where the folds of waxes are more or less parallelly arranged

into wavy strips, interrupted at the positions of stomata.

(3) Phenology of epicuticular wax

The phenological stages of Hevea leaf are shown in Plate 8. Wax formation was found even at the bud break stage. Folds of wax was observed as a wavy coating on the lower epidermis (Plate 9.A). Thick ridges of wax, median in position and oriented parallel to the long axis of the epidermal cell, producing thin and small filamentous striae, are noticed at the leaflet stage (Plate 9.B). At the pendent stage, the ridges became more prominent. The occurrence of numerous filamentous arms, still elongated and with tapering ends clearly exhibited the reticulate appearance (Plate 9.C). When the leaves get just hardened, the ridges as well as the striae became thicker and prominent. Both showed the same prominence and became clear at the same focus while the epidermal cells were out of focus indicating the position of stomata at a lower level than that of the epicuticular wax layer (Plate 9.D). The stomata were partly covered by wax. At this stage, the cuticular ornamentation looked as a reticulum of buttressed ridges over the epidermis partly overlapping the stomata. As the leaves get more hardened, thickening of the striae continued with more entanglement due to the formation of elongated and parallelly arranged branches and masked the sunken stomata (Plate 9.E).

(b) Mesophyll

The leaf is isobilateral with only one row of pallisade on the adaxial side. The pallisade is not tightly compact in arrangement and the component cells are rod shaped (Plate 4.C). Among ten clones they recorded a size range of 41-71 μm in height and 7-13 μm in width. The spongy layer had four to six rows of cells. The cells are mostly angular or irregular in shape and are not very loosely arranged. Groups of irregularly shaped cells, compactly arranged, are interspersed with small air spaces here and there. The general structure and arrangement of mesophyll does not facilitate high internal surface area.

(c) Vascular system

The vascular system of leaf blade is continuous with the petiole. The mid vein is prominent which abuts the lower surface (Plate 4.D). In cross section it is semicircular to basin shaped in different clones. The cortex consists of two to three layers of collenchyma with a few layers of sclerenchyma below. The stele is crescent shaped. In general, the xylem is lined in the inner margin of the crescent.

At the adaxial side of the vein the phloem is included in the non-vascular tissue (Plate 4.D). The shape of adaxial phloem seems to be a clonal characteristic. In the vein laticifers occur in close association with the phloem.

2. VARIABILITY

2.1 Clonal differences

2.1.1 Bark anatomical traits

(a) Phloem ray characters

Clonal variations in the proportion of ray types in terms of seriation are shown in Table 6. For the proportion of uniseriate, biseriate and tetraseriate types of phloem rays clonal differences were significant at 1 per cent level. For triseriate rays clonal difference was not statistically significant.

Among the ten clones, uniseriate rays ranged from 10.53 to 14.96 per cent of the total number of rays, the general mean being 12.88 per cent. Significantly higher proportion of uniseriate rays, than the general mean, was recorded for three clones namely RRIC 104, RRIC 102 and Nab 17 while low proportions were recorded for RRIC 36, RRIC 105 and RRIC 52. For this trait RRIC 45, RRIC 100, RRIC 7 and GT 1 were comparable to the general mean.

The proportion of biseriate rays ranged from 6.06 to 24.68 per cent with a grand mean of 14.93 per cent of total number of rays. Nab 17, GT 1 and RRIC 100 recorded significantly higher proportions of biseriate rays than the general mean and four other clones namely RRIC 104, RRIC 52, RRIC 36 and RRIC 102 recorded lower proportions. For this trait RRIC 45, RRIC 7 and RRIC 105 were comparable to

to the grand mean.

The highest proportion of phloem rays was the triseriate type, in all clones, though the clonal difference was not significant. Clonal means ranged from 47.12 to 61.26 per cent with a grand mean of 55.95 per cent.

For the proportion of tetraseriate rays the clones recorded a range of 1.81 per cent to 31.48 per cent and the grand mean was 15.97 per cent. Significantly higher proportion of tetraseriate type was recorded for RRIC 36, RRIC 52, RRIC 102 and RRIC 104 and lower proportion for GT 1, RRIC 100, Nab 17 and RRIC 45. With respect to this trait medium type of clones were RRIC 105 and RRIC 7.

Clonal differences in the shape of phloem rays are shown in Table 7. For the proportion of oval shaped rays the clones were highly significant while clonal differences for the dumb-bell, spindle and bat shaped rays were not significant. Oval shaped rays ranged from 10.41 to 29.82 per cent of total number of rays in different clones for which the general mean was 18.14. Only one clone, RRIC 52, recorded significantly higher value than the general mean and two clones, namely RRIC 45 and GT 1 recorded lower values. The remaining seven clones (RRIC 7, RRIC 36, RRIC 100, RRIC 102, RRIC 104, RRIC 105 and Nab 17) recorded values comparable to the general mean.

The major ray type was bat shaped which showed a range of 54.78 to 72.37 per cent in different clones and the general mean was 63.45. Dumb-bell shaped rays ranged from 3.39 to 6.19 per cent with a mean of 4.66 and spindle shaped rays were 12.16 per cent with a range of 10.97 to 13.92 among the clones.

The density, height, width and height to width ratio of phloem rays at the eighth year after planting are presented in Table 8. All the four traits were highly significant clonal characteristics.

Among the ten clones the number of phloem ray groups in an area of 1.25 mm^2 ranged from 28.26 to 39.39 with a grand mean of 32.15. High ray density was recorded for RRIC 105 and RRIC 100 while RRIC 52, RRIC 104 and RRIC 7 recorded low density of phloem rays. The remaining five clones, namely RRIC 36, RRIC 45, RRIC 102, GT 1 and Nab 17 were of the medium type.

The height of phloem rays recorded a range of 302.54 μm to 479.23 μm with a grand mean of 383.09 μm . For this trait RRIC 7 and GT 1 recorded significantly higher values than the general mean while RRIC 52 and RRIC 105 recorded lower values. RRIC 36, RRIC 45, RRIC 100, RRIC 102, RRIC 104 and Nab 17 belonged to the medium range.

The width of phloem rays ranged from 40.36 μm to 53.38 μm in different clones with a grand mean of 46.77 μm . The clones which recorded higher ray width were RRIC 36, RRIC 52 and RRIC 104,

those which recorded lower values being RRIC 45, RRIC 100, Nab 17 and GT 1. The remaining three clones, RRIC 7, RRIC 102 and RRIC 105 were of the medium range.

For the height/width ratio of phloem rays the clones recorded a range of 6.23 to 11.68 and the grand mean of 8.35. RRIC 100, GT 1 and Nab 17 recorded significantly higher values. The clones which recorded lower values were RRIC 52 and RRIC 105. The remaining five clones, namely, RRIC 7, RRIC 36, RRIC 45, RRIC 102 and RRIC 104 recorded values comparable to the general mean of clones.

Clonal variations in the diameter of phloem ray cells are shown in Table 9. For this trait, with respect to uni, bi, tri and tetraseriate types and the mean of all types, clonal differences were highly significant ($P < 0.01$).

The diameter of component cells of uniseriate rays ranged from 21.44 μm to 27.82 μm in different clones with a grand mean of 23.41. Significantly higher diameter was recorded for one clone only, RRIC 104 and for one clone RRIC 100, it was significantly less. For the remaining eight clones the clonal means were on par with the general mean.

Cell diameter of biseriate rays recorded a range of 12.76 μm to 17.14 μm in different clones with a grand mean of 15.04 μm . Two clones, namely RRIC 104 and RRIC 52 recorded higher values. RRIC 100 recorded lower value and for the remaining seven clones,

the values recorded were on par with the grand mean of clones.

Diameter of the component cells of triseriate rays showed a range of 11.54 μm to 16.08 μm among the ten clones and the grand mean of clones was 13.84. Significantly higher diameter was recorded for RRIC 104 and lower diameter for RRIC 100. The remaining eight clones were on par with the grand mean of clones.

With regard to the tetraseriate rays, cell diameter ranged from 9.89 μm to 13.64 μm with a grand mean of 11.98 μm . RRIC 104 and RRIC 52 recorded significantly higher diameter. For this trait also RRIC 100 recorded lower value and the values of all other clones were on par with the mean of ten clones.

For the mean diameter of all the four ray types, clones recorded a range of 12.23 μm to 17.19 μm with a grand mean of 14.87 μm . RRIC and GT 1 recorded significantly higher values and RRIC 104 recorded lower value than the general mean. The ray cell diameter of the remaining seven clones were comparable to the grand mean of clones. Mean diameter of ray cells of uniseriate, biseriate, triseriate and tetraseriate types recorded the values, 23.41 μm , 15.04 μm , 13.84 μm and 11.98 μm respectively. As seriation increased diameter of ray components decreased.

(b) Laticifer characters

Clonal differences of the laticifer characters among ten clones at the eighth year of planting are shown in Table 10. All the five

traits studied, namely the number of latex vessel rows, density of latex vessels, diameter of latex vessels, laticifer area index and intensity of anastomosing were highly significant clonal characters.

For the number of latex vessel rows clones showed a range of 6.45 to 14.35. The grand mean was 10.92. Two clones, RRIC 36 and Nab 17 recorded significantly higher numbers than the grand mean of clones while RRIC 52, RRIC 105 and RRIC 45 recorded significantly lower values. The values recorded for RRIC 100, RRIC 7, RRIC 104, RRIC 102 and GT 1 were comparable to the grand mean.

Latex vessel density ranged from 293.33 to 337.33 in different clones and the mean of ten clones was 316.93. Latex vessel density of RRIC 100 and GT 1 were significantly higher than the general mean while RRIC 7, RRIC 52 and RRIC 104 recorded lower values. RRIC 36, RRIC 45, RRIC 102, RRIC 104, RRIC 105 and Nab 17 were medium type.

Among the ten clones latex vessel diameter ranged from 15.15 μm to 19.59 μm . The clones which recorded significantly higher diameter were RRIC 52 and RRIC 100 and those which recorded lower values were GT 1 and RRIC 105. The other clones, namely RRIC 7, RRIC 36, RRIC 45, RRIC 102, RRIC 104 and Nab 17 recorded values on par with the general mean.

The laticifer area index showed a range of 11.59 mm^2 to 22.44 mm^2 . Four clones, RRIC 100, Nab 17, RRIC 104 and RRIC 36

recorded significantly higher laticifer area index while RRIC 105, GT 1, RRIC 45 and RRIC 52 recorded significantly lower values. The grand mean of clones was 16.78 mm^2 . The values recorded for RRIC 7 and RRIC 102 were on par with the grand mean.

The number of tangential connections between laticifers ranged from 6.01 to 8.23 among the ten clones with a grand mean of 7.13, for a height of 0.25. For two clones, RRIC 100 and RRIC 36, intensity of anastomosing was significantly higher than the general mean and two other clones, RRIC 104 and Nab 17 recorded lower values. For this trait six clones namely, RRIC 7, RRIC 45, RRIC 52, RRIC 102, RRIC 105 and GT 1 were medium type.

2.1.2 Intraxylary phloem

The number of primary xylem points and intraxylary phloem groups were highly significant clonal characters. The data are presented in Table 11.

Among the ten clones RRIC 100 and RRIC 52 recorded significantly higher numbers of primary xylem points and intraxylary phloem points while RRIC 36 recorded lower values for both the traits. For the number of primary xylem points clonal means ranged from 48.21 to 97.67 with a general mean of 62.47. For the number of intraxylary phloem points the grand mean of ten clones was 54.30 and the clones recorded a range of 37.06 to 86.28. For seven clones namely RRIC 7, RRIC 45, RRIC 102, RRIC 104, RRIC 105, GT 1 and

Nab 17 both the traits were on par with the grand mean of the clones.

2.1.3 Leaf anatomical characters

Clonal variabilities of seven leaf anatomical characters were studied and the data are presented in Table 12. Out of the seven traits, width of mid rib (linear measurement at right angle to the length), thickness of cuticle and density of petiolar stomata were significant clonal characters. Among the ten clones differences were not significant for the thickness of mid rib, height and width of cells and frequency of laminar stomata.

For the thickness (depth from one surface to its opposite) of mid rib, clones recorded a range of 0.7160 mm to 1.1083 mm. Numerically the highest thickness was recorded for Nab 17 and the lowest for RRIC 7.

The width of mid rib was significant at 5 per cent level. Clonal means showed a range of 0.8925 mm to 1.3281 mm with a grand mean of 1.0849. Nab 17 recorded significantly higher width of mid rib than the grand mean while RRIC 7 and RRIC 102 recorded lower values. For this trait the remaining eight clones were comparable to the general mean of clones.

Cuticle thickness was highly significant clonal character ($P < 0.01$) and the clone means recorded a range of 5.6550 μm to 7.6728 μm with a grand mean of 6.7664 μm . RRIC 36 and RRIC 102 recorded significantly higher cuticle thickness than the grand mean

of clones, while RRIC 100 and RRIC 104 recorded lower thickness. Values recorded for the remaining six clones were comparable to the general mean of clones.

For the height of palisade cells clones showed a range of 43.8418 μm to 56.2883 μm and the mean of clones was 49.8977. Numerically highest palisade height was recorded for GT 1 and lowest for RRIC 105. Among the clones palisade width varied from 7.9582 μm to 10.4547 μm with a general mean of 9.1210 μm . Highest value was recorded for RRIC 7 and the lowest for RRIC 100.

Stomatal frequency on the leaf lamina and petiole were studied separately. Among the clones density of laminar stomata showed a range of 405.23 to 490.90 per mm^2 with a mean of 437.41. The highest density of laminar stomata was recorded for RRIC 104 and the lowest density for RRIC 7. The clonal means of the frequency of petiolar stomata recorded a range of 1.43 to 3.93 per 10 mm^2 with a grand mean of 2.50. Two clones, RRIC 36 and Nab 17 recorded significantly higher frequency of petiolar stomata than the grand mean of clones while RRIC 7 and RRIC 105 recorded lower frequency. For the remaining six clones, the values recorded for this trait was on par with the grand mean of clones. Interclonal difference was significant at 1 per cent level.

2.1.4 Growth characters

Growth characters such as bark thickness and girth at the

eight year of planting, panel length and percentage girth increase (over two years) are shown in Table 13. For girth and panel length interclonal variability was highly significant ($P < 0.01$). Clonal differences for bark thickness and percentage girth increase over two years were not statistically significant.

(a) Bark thickness

For bark thickness, clones varied from 3.86 mm to 4.69 mm with a general mean of 4.25. Highest bark thickness was recorded for RRIC 36 and the lowest thickness for RRIC 100.

(b) Girth

Girth, ranged from 61.69 cm to 78.54 cm with a mean of 67.02. For two clones, RRIC 52 and RRIC 104, clone means were significantly higher than the general mean. Four clones, namely RRIC 7, RRIC 45, GT 1 and Nab 17 recorded significantly lower girth. The girth recorded for RRIC 36, RRIC 100, RRIC 102 and RRIC 105 were on par with the grand mean of clones.

(c) Panel length

Panel length showed a range of 39.72 cm to 57.44 cm and the grand mean of clones was 45.94 cm. Only one clone (RRIC 104) recorded significantly higher value than the grand mean and one clone (GT 1) recorded lower value. For this trait all the other clones were comparable to the grand mean.

(d) Girth increment on tapping

Clonal differences for percentage girth increase over two years were not statistically significant. Numerically, highest girth increase was recorded for RRIC 104 and the lowest for GT 1. The range among clones was 6.77 to 10.29 per cent with a general mean of 8.57.

2.1.5 Latex flow characters

Data on latex flow characters such as initial rate of flow, duration of flow and plugging index are shown in Table 14. All the three traits were statistically significant.

(a) Initial rate of flow

Initial rate of flow showed a range of 0.07 ml to 0.12 ml among clones with a grand mean of 0.10 ml. Clonal differences were significant at 5 per cent level. RRIC 45, RRIC 7 and RRIC 102 recorded significantly higher values than the general mean and RRIC 104 recorded lower value. The initial rate of flow recorded for RRIC 36, RRIC 52, RRIC 100, RRIC 105, GT 1 and Nab 17 were comparable to the grand mean.

(b) Duration of flow

For duration of flow also clonal differences were significant at 5 per cent level. The clone means ranged from 94.42 min. to 123.18 min. and the general mean was 105.50 min. RRIC 104 and

RRIC 36 recorded significantly higher values while only one clone (RRIC 105) recorded significantly lower value. The values recorded for RRIC 7, RRIC 45, RRIC 52, RRIC 100, RRIC 102, GT 1 and Nab 17 were on par with the general mean.

(c) Plugging index

For plugging index clonal difference was significant at 1 per cent level. The clones showed a range of 3.52 to 6.28 and a grand mean of 4.98. RRIC 45 and RRIC 105 showed higher plugging index than the mean of ten clones while RRIC 104 and RRIC 36 recorded lower values. Clone means comparable to the general mean were recorded for RRIC 7, RRIC 52, RRIC 100, RRIC 102, GT 1 and Nab 17.

2.1.6 Yield

Clonal differences for the annual mean of dry rubber yield (g/tree/tap), total volume of latex (ml/tree/tap) and dry rubber content as the mean over three years (9th, 10th and 11th year of planting) in panel BO-1 are shown in Table 15. All the three traits were highly significant clonal characters.

(a) Dry rubber yield

Among the ten clones mean dry rubber yield ranged from 33.97 g to 64.21 g. Grand mean of the ten clones was 47.10 g. Significantly higher rubber yield was recorded for RRIC 100, RRIC 36 and RRIC 102. Three other clones, RRIC 105, RRIC 52 and GT 1 recorded lower

values than the grand mean.

(b) Total volume of latex

The total volume of latex ranged from 80.61 ml to 145.99 ml and the grand mean of clones was 114.48 ml. Significantly higher values than the general mean were recorded for RRIC 100 and RRIC 36 while lower values were recorded for RRIC 105 and GT 1. Six clones namely RRIC 7, RRIC 45, RRIC 52, RRIC 102, RRIC 104, RRIC 105 and Nab 17 were comparable to the grand mean of clones for this trait.

(c) Dry rubber content

For the dry rubber content clones varied from 31.09 to 36.68 with a general mean of 34.28. The clones which recorded significantly higher dry rubber content were RRIC 100, RRIC 102 and RRIC 105. Those which recorded lower values were RRIC 36, RRIC 104 and GT 1. Dry rubber content recorded for RRIC 7, RRIC 45, RRIC 52 and Nab 17 were comparable to the grand mean.

2.1.7 Diseases

Observations on wintering behaviour and the two major leaf diseases - abnormal leaf fall disease caused by Phytophthora spp. and powdery mildew disease caused by Oidium heveae (Plate 10) - are summarised in Table 16. Data on the incidence of brown bast, which is considered to be a physiological disorder (Plate 11) are

also incorporated.

(a) Brown bast (Tapping panel dryness)

Among the ten clones, brown bast incidence showed a range of 0 to 26.67 per cent. The grand mean was 16.77. Comparatively high incidence was noticed for RRIC 100 and RRIC 36 followed by Nab 17. There was no incidence of brown bast for RRIC 52. Very low incidence of brown bast was recorded for RRIC 7 as well as for GT 1. However the percentage incidence of brown bast was not statistically significant.

(b) Abnormal leaf fall

Based on visual rating, intensity of Phytophthora leaf fall was not very severe during 1986. None of the clones showed more than 50 per cent leaf fall in the 1986 season. Comparatively high leaf fall was observed for Nab 17. Leaf fall was practically nil for RRIC 7 and RRIC 104. During 1987 more than 50 per cent leaf fall was noticed for RRIC 36 and Nab 17 due to Phytophthora leaf fall disease whereas RRIC 7, RRIC 45 and RRIC 105 were showing only mild incidence (below 25 per cent). During this year RRIC 52, RRIC 100, RRIC 102, RRIC 104 and GT 1 were medium for this trait.

(c) Powdery mildew

On the contrary Oidium was very severe during 1986. Four clones namely RRIC 45, RRIC 105, GT 1 and Nab 17 showed high

disease incidence though the intensity of leaf fall was not very severe for the last one. The clones which did not shed leaves but showed severe spotting (recorded as medium range) are RRIC 7 and RRIC 104. The remaining four clones, namely RRIC 100, RRIC 52, RRIC 36 and RRIC 102 had only less intensity of spotting. During 1987 RRIC 45, RRIC 105 and GT 1 repeated leaf shedding due to high incidence of Oidium infection but Nab 17 showed only spotting. RRIC 100 and RRIC 102 continued as less spotting group and two more clones namely RRIC 7 and RRIC 104 showed less spotting. However none of the clones was completely free of the disease.

Wintering behaviour

Only four clones namely RRIC 45, RRIC 52, RRIC 105 and GT 1 showed late wintering and wintering was only partial for RRIC 52. Early wintering was observed for the other clones.

2.2 Comparative bark anatomy

2.2.1 Drought tolerant and susceptible clones

Clonal differences of certain bark anatomical characters among a set of clones, consisting of drought tolerant and susceptible types are shown in Table 17. Six characters showed significant clonal differences. Of this total number of latex vessel rows was significant at 5 per cent level and the other traits namely (1) the proportion of latex vessel rows in the soft bast to total number of latex vessel

rows, (2) proportion of soft bast thickness to total bark thickness, (3) height of phloem rays, (4) width of phloem rays, and (5) the height/width ratio of phloem rays at 1 per cent level. For the diameter of latex vessels and bark thickness clones were not significant.

Comparative mean values of drought tolerant and susceptible groups of clones for the eight anatomical characters are shown in Table 18 and the sub division of clone sum of squares into its components are shown in Table 19.a, b, c, d, e, f, g and h.

For the number of latex vessel rows drought tolerant and susceptible groups were comparable and recorded the mean values 32.55 and 32.33 respectively. Within tolerant group clones were significant at 1 per cent level while the differences between susceptible clones was not statistically significant (Table 19.a). For the diameter of latex vessels and bark thickness, between groups or within group differences were not significant (Tables 19.b and c).

The proportion of latex vessel rows in the soft bast to total numbers was high for susceptible group when compared to the tolerant group. For this trait drought tolerant and susceptible group differed significantly at 1 per cent level (Table 19.d). Within tolerant group clones were not significant while the clones within the susceptible group differed significantly at 1 per cent level.

For the proportion of soft bast thickness to total bark thickness

the tolerant group recorded lower value (28.13 per cent) when compared to the susceptible group (39.42 per cent). Difference between drought tolerant and susceptible groups was significant at 1 per cent level (Table 19.e). Within the susceptible group, clones differed at highly significant level while the clones within the tolerant group were not significant.

The group difference for ray height was not statistically significant (Table 19.f). For this trait, within both groups clones differed significantly at 1 per cent level. For phloem ray width drought tolerant clones recorded lower width (41.19 μm) when compared to the susceptible clones, 47.81 μm (Table 18). Drought tolerant and susceptible groups differed significantly at 1 per cent level (Table 19.g). Within group difference was not significant for both groups.

Drought tolerant and susceptible groups of clones differed significantly for the height to width ratio of phloem rays (Table 19.h). For this trait within group difference was also significant (at 5 per cent level) with respect to both groups. Higher ratio was shown for tolerant group (10.58) than for the susceptible group, 8.52 (Table 18).

2.2.2 Diploids versus tetraploids

Data on bark thickness and number of latex vessel rows in the diploids and tetraploids are shown in Table 20. At the tenth

year of planting GT 1 tetraploid recorded a bark thickness of 1.77 mm. At the same age the respective diploid recorded 7.63 mm thickness. Similar trend was noticed for Tjir 1 for which the bark thickness of tetraploid and the respective diploid were 4.04 mm and 6.93 mm respectively. In the case of RRII 105, four year old tetraploid was comparable to the diploid for bark thickness, the values being 4.11 and 4.44.

The tetraploids of GT 1 and Tjir 1 recorded very low number of latex vessel rows also, the mean values being 3.89 and 6.89 respectively against the corresponding values 16.22 and 19.00 for the respective diploids. RRII 105 did not show such a wide difference between the two ploidy levels with respect to this character.

Density, diameter and intensity of anastomosing of latex vessels are shown in Table 21. Laticifer diameter was higher for the tetraploids of GT 1 and Tjir 1, the mean values being 24.24 μm and 25.16 μm respectively against 21.51 μm and 21.87 μm for their respective diploids. RRII 105 at the two ploidy levels were comparable for the diameter of latex vessels, the values recorded for tetraploid and its diploid being 22.93 μm and 22.60 μm respectively.

In all the three clones laticifer density was low and anastomoses were high for the tetraploids than their respective diploids. The mean laticifer density recorded for the tetraploids of GT 1, Tjir 1 and RRII 105 were 20.83, 21.39 and 22.19 against the corresponding values for the respective diploids 26.33, 25.83 and 26.13 per mm

girth. With respect to the intensity of anastomosing of latex vessels the mean values recorded for the tetraploids of three clones were 11.44, 11.51 and 9.07 in the order mentioned against the values 10.80, 10.44 and 8.87 for the respective diploids.

The height and width of phloem rays are shown in Table 22. Very wide phloem rays was a characteristic feature of the tetraploids in all the three clones under study. The mean values of phloem rays recorded for the tetraploids of GT 1, Tjir 1 and RRII 105 were 74.80 μm , 70.93 μm and 62.03 μm respectively against the corresponding values 52.52 μm , 52.89 μm and 50.58 μm respectively for the respective diploids. Ray height also showed the same trend with respect to two clones, GT 1 and Tjir 1 which recorded 472.60 μm and 392.90 μm heights respectively for the diploids against 736.67 μm and 548.53 μm respectively for the tetraploids, while the third one (RRII 105), did not show such a difference between the two ploidy levels, the value for the diploid and tetraploid being 462.40 μm and 445.13 μm respectively.

2.2.3 Virgin versus renewed bark

A comparative account of the bark anatomical traits of virgin and renewed bark is given in Table 22. Laticifer diameter and intensity of anastomosing in the virgin (17.21 μm and 7.80) and renewed (17.07 μm and 7.38) bark were comparable. Proportion of soft bast was numerically high in the virgin bark (36.63 per cent) compared to the renewed bark (33.17 per cent) though statistically not

significant. The diameter of phloem ray component was numerically high (16.50) for the renewed bark compared to the virgin bark (15.07). The two growth phases of bark varied significantly for the density of latex vessels ($P < 0.05$) with reduced density in renewed bark (7.38) compared to the virgin bark (7.80). The proportion of latex vessel rows in the first mm from the wood (expected residual bark) as percentage of total number of latex vessel rows was higher for the renewed bark ($P < 0.05$) than in the virgin bark, the values being 43.71 per cent and 28.93 per cent respectively.

Significantly lower ray height ($P < 0.01$) and higher ray width ($P < 0.01$) were recorded for renewed bark, the values being 301.00 μm and 56.54 μm against 372.30 μm and 50.65 μm in virgin bark, leading to a more zig zag orientation of latex vessels. The height/width ratio, a character which indicate the orientation of latex vessels in the upward direction, differed between the two growth phases with lower value for renewed bark (5.43 against 7.40 in virgin bark) and the difference was statistically significant ($P < 0.05$).

2.2.4 Juvenile versus mature trees

Girth and certain bark anatomical traits such as number of latex vessel rows, density and diameter of latex vessels, laticifer area index, intensity of anastomosing and width of phloem rays of juvenile (3 year old) and mature trees (8 year old) are shown in Table 24. For all traits, except the intensity of anastomosing

and density of latex vessels, an increase from juvenile to mature age was observed and the differences were significant at 1 per cent level. Girth increased from 13.87 to 59.28 cm. Latex vessel rows increased from 3.54 to 13.48, latex vessel diameter from 17.88 μm to 22.62 μm and the width of phloem rays from 40.59 μm to 62.76 μm . At the third year the laticifer area index was 1.08 mm^2 which increased to 27.01 mm^2 at the eighth year. Density of latex vessels and intensity of anastomosing varied from 281.33 to 269.48 and 6.81 to 6.66 respectively. In both cases the numerical values showed a reduction from juvenile to mature stage but the differences were not statistically significant.

Yearly variations of girth and bark anatomical traits in the virgin bark of tapping trees (pooled data of ten clones) for four consecutive years (from second year to the fifth year of tapping) are plotted in Figure 3. All traits except latex vessel density and intensity of connections showed an increase in the third year. Height of phloem rays increased upto the fourth year and showed a reduction in the fifth year. Latex vessel density recorded a reduction upto the fourth year and showed a deviation in the fifth year. Latex vessel diameter, ray width and density of connections became stable from the third year onwards. Number of latex vessel rows, tree girth and laticifer area index maintained an increasing trend throughout the period of observation.

The rate of increase of girth, number of latex vessel rows and laticifer area index of the ten clones over three years (under

tapping) are plotted in Figure 4. Latex vessel rows increased considerably for RRIC 104 followed by RRIC 102 and RRIC 100. RRIC 52 recorded the least increase. Comparatively high rate of girth increase was recorded for RRIC 104 and RRIC 52 while RRIC 45 and RRIC 105 showed very low rate. RRIC 104 and RRIC 102 followed by RRIC 7 showed remarkable increase in laticifer area index over three years of growth under tapping. Rate of increase of this trait was remarkably low for RRIC 100.

2.3 Monthly variations and the effect of drought

2.3.1 Clone cum monthly variations of rubber yield

The monthly performances of ten clones for the years 1986 and 1987 are shown in Table 25 and 26 respectively. The monthly yield performance of each clone is expressed as percentage of annual mean of the respective clone. In both years the months and clone x month interactions were significant at 1 per cent level.

In 1986 for the pooled data of ten clones months recorded a performance range of 52.72 to 132.05 (Table 25). The highest performance was recorded in December (132.05) and a comparable yield performance was made from September onwards (128.64 to 132.05 per cent). January recorded significantly lower performance (87.84 per cent) which lowered again during February (57.54 per cent), March (52.72 per cent) and April (64.43 per cent) while in May it reached a level comparable to January.

All clones recorded above 100 per cent of the annual mean yield from June to December while the performances were below 100 per cent from January to May. RRIC 45 recorded a range of 27.74 (March) to 157.17 per cent (September) among the months. October was comparable to September and February was comparable to March. RRIC 100 recorded a monthly range of 61.85 (March) to 132.15 (November) per cent. June, September, October and December were comparable to November. From January to May, the monthly performances were comparable. For RRIC 7, monthly performances ranged from 48.53 (March) to 134.49 (December) per cent. From June to December the months were comparable. In February the performance was comparable to that in March. RRIC 104 recorded a range of 50.29 (March) to 141.76 (December) per cent for the months. September was comparable to December while from February to May the months were comparable. For RRIC 105 the monthly performance recorded a range of 37.97 (February) to 136.03 (September) per cent. From August to December and in May yield performances were comparable to that in September while January was comparable to February. RRIC 52 recorded a range of 66.62 (February) to 147.19 (November) per cent. December was also comparable to November. From January to May, the performances were comparable. For RRIC 36, the range was 53.37 (March) to 127.73 (September) per cent. From June to December the monthly performances were comparable. February was comparable to March. The months recorded a range of 37.96 (April) to 143.13 (December) per cent for GT 1. January and

September to December were comparable. The yield performance in March and May were comparable to that in April. Nab 17 recorded a range of 36.32 (March) to 137.29 (December) per cent and the monthly performance in June and September to November were comparable. The contribution in February was comparable to that in March. For RRIC 102 monthly performance recorded a range of 51.81 (April) to 150.12 (November) per cent. From October to December the months were comparable. From February to May also the monthly performances were comparable.

In 1987 the monthly performance showed a range of 42.77 (March) to 136.09 (September) per cent. January, July and October were comparable to September. In January and from July onwards, yield was above 100 per cent of annual mean and from February to June it was below hundred per cent. February and April made poor performances but better than March. In 1987, clone x month interaction was more pronounced than that in 1986. RRIC 45 recorded a range of 27.17 (March) to 164.02 (July) per cent among the months. September and December were comparable to July. February, April and May were comparable to March. RRIC 100 showed a range of 38.82 (March) to 143.44 (July) per cent among the months. Monthly performance from June to October and the performance in December were comparable. February and April performances were comparable to that of March. RRIC 7 recorded a monthly range of 57.41 (March) to 147.12 (January). July, September and December performances

were comparable to that of January. February, April and May were comparable to March. RRIC 104 showed a range of 47.10 (March) to 169.82 (January) per cent. February and April performances were comparable to that of March. RRIC 105 recorded a range of 30.13 (March) to 167.07 (December) per cent. July and September were comparable to December. For this clone yield performance in February, April and May were comparable to that in March. For RRIC 52, the monthly yield performance ranged from 36.54 (March) to 151.96 (September) per cent. From July to November the months were comparable. February and April performances were comparable to that of March. RRIC 36 recorded a range of 51.89 (March) to 148.84 (January) per cent. July, September and October performances were comparable to that of January. February and April performances were comparable to that of March. For GT 1 the range was 43.15 (March) to 159.88 (January) per cent. August, September and October performed comparably to that of January. February, April and May were comparable to March. The range of monthly performance of Nab 17 was 38.34 (February) to 159.37 (January). July performance was also comparable to that of January. March and April were comparable to February. RRIC 102 showed a range of 42.23 (February) to 146.68 (August). From August to November, monthly performances were comparable. Yield performance in March and April were comparable to that in February.

2.3.2 Yield in relation to yield factors

A comparative account of the monthly variation of rubber yield and certain major yield contributing factors such as plugging index, initial rate of flow and d.r.c. (pooled data of ten clones) are plotted in Figure 5. The yield per tree per tap had a steep fall from January to February. The trend continued in March and April with slight improvement in May and a rise from June onwards. Plugging index showed an inverse trend with a rise from January to April and a fall from May to July and was almost steady afterwards. The initial rate of flow was considerably low during February, March and April with an improvement during May and a rise from June onwards. The dry rubber content was comparatively a less variable trait which recorded slight increase during drought period.

2.3.3 Drought tolerance of clones

Inter clonal differences for the variations in rubber yield, initial rate of flow, plugging index and dry rubber content during drought period (February-May) are shown in Table 27. Clones were significant for the drop in yield ($P < 0.01$) and initial flow rate ($P < 0.01$) and for the rise in plugging index ($P < 0.05$). For the rise in d.r.c. the clones were not statistically significant.

For yield drop during drought period the clones recorded a range of 25.75 to 54.35 per cent. High drop in rubber yield was recorded for three clones (RRIC 45, GT 1 and RRIC 105) whereas

the least drop was observed for RRIC 36 followed by RRIC 7 and RRIC 100.

The fall in initial flow rate ranged from 6.95 to 32.45 per cent with significant drop for two clones, RRIC 45 and RRIC 105. Three clones (RRIC 36, Nab 17 and RRIC 7) showed significantly low drop in initial flow rate.

For the rise in plugging index clones recorded a high range of 19.99 to 51.89 per cent. RRIC 45 and RRIC 105 had considerable rise in P.I. while RRIC 52 and RRIC 7 had significantly less variation. Rise in d.r.c. varied from 6.37 (GT 1) to 16.08 (RRIC 36) per cent among clones.

2.4 Variability and genetic parameters

The components of variance such as genotypic coefficients of variation (G.C.V.), phenotypic coefficients of variation (P.C.V.) and genetic parameters such as heritability (broad sense) and genetic advance of rubber yield, latex volume, d.r.c., girth, latex flow characters and important anatomical characters were estimated.

2.4.1 Components of variance

For all the traits P.C.V. values were higher than the G.C.V. values. Among yield, girth and latex flow characters (Table 28) total variability was high for rubber yield and latex volume followed by plugging index and initial flow rate. Dry rubber content recorded

the least variability. The P.C.V. values ranged from 7.4032 (d.r.c.) to 21.6234 (latex volume). G.C.V. values ranged from 5.7875 (d.r.c.) to 17.5194 (rubber yield). High G.C.V. values, when compared to the P.C.V. values were recorded for girth, rubber yield, latex volume and dry rubber content. For latex flow characters proportions of G.C.V. values to P.C.V. values were low.

Among anatomical characters (Table 29) laticifer area index, intraxylary phloem points, primary xylem points, latex vessel rows and H/W ratio of phloem rays showed high variability while the variability was low for the density and diameter of latex vessels and intensity of anastomosing. The P.C.V. values ranged from 6.0116 (density of latex vessels) to 30.5959 (laticifer area index). G.C.V. values ranged from 4.5733 (density of latex vessels) to 24.7012 (number of intraxylary phloem points). High G.C.V. values were recorded for the number of intraxylary phloem points, laticifer area index, number of latex vessel rows and the number of primary xylem points.

Variability and genetic parameters for the variations of yield and latex flow characters during drought period were estimated. The data is furnished in Table 30. Total variability was high for the variations of latex flow characters (initial flow rate, plugging index and d.r.c.) for which the P.C.V. values were predominant, at a range of 31.4177 (duration of flow) to 74.5284 (initial rate of flow). For those traits the G.C.V. values ranged

from 15.5103 (duration of flow) to 57.9885 (initial rate of flow). Variations of rubber yield and latex volume also showed fairly good variability, of which the G.C.V. value was high for rubber yield.

2.4.2 Heritability

Among yield, girth and flow characters heritability values ranged from 45.95 per cent (initial rate of flow) to 73.1092 per cent (girth) (Table 28). Rubber yield (65.9459 per cent), latex volume (63.8543 per cent) and d.r.c. (61.1136 per cent) also had fairly good heritability values while the h^2 values for initial flow rate (45.95), duration of flow (48.8572) and plugging index (50.0100) were comparatively low.

For the anatomical characters (Table 29), high h^2 values ranging from 57.8734 per cent (density of latex vessels) to 85.4637 per cent (height of phloem rays) were recorded, of which a value below 60 per cent was recorded for only one trait, latex vessel density. Heritability values were above 70 per cent for the height of phloem rays (85.4637), width of phloem rays (83.8637), H/W ratio of phloem rays (83.0848), number of latex vessel rows (78.2692) and intensity of anastomosing (71.7964).

For the variations of yield and yield factors during drought period (Table 30), heritability values were comparatively low except for the drop in rubber yield (81.3900 per cent) and initial flow rate

(60.3594 per cent). For all other traits such as total volume (48.96), d.r.c. (45.2276), plugging index (41.4893) and duration of flow (49.3680), h^2 values were below 50 per cent.

2.4.3 Genetic advance

Genetic advance for the different traits were estimated as percentage of the respective means. Among yield, girth and flow characters, genetic advance (Table 28) recorded a range of 9.3200 (d.r.c.) to 29.3050 (rubber yield). Fairly good genetic advance was recorded for latex volume (28.4400) also. Genetic advance for anatomical characters (Table 29) showed a more wider range of 7.1666 (density of latex vessels) to 42.2815 (number of intraxylary phloem). Four more traits such as number of latex vessel rows (40.44), laticifer area index (38.8051), number of primary xylem points (37.2847) and height/width ratio of phloem rays (33.5700) recorded high genetic advances. For the variations of yield and latex flow characters during drought period, genetic advance showed a very wide range of 26.8300 (total volume of latex) to 92.9461 (initial rate of flow). Variations in d.r.c. (47.29) dry rubber yield

3. SIMPLE, PARTIAL AND MULTIPLE CORRELATIONS

3.1 Juvenile versus mature plants for girth and bark anatomical traits

Bark anatomical traits and girth at the juvenile stage were correlated with the respective traits at mature stage. The results are shown in Table 31. Significant positive correlations were obtained for the number of latex vessel rows ($r = 0.5619$, $P < 0.01$), laticifer area index ($r = 0.3955$, $P < 0.05$), width of phloem rays ($r = 0.4972$, $P < 0.01$) and girth of the tree ($r = 0.4720$, $P < 0.01$). For the density and diameter of latex vessels the correlation values were not at significant level and for the intensity of anastomosing the correlation was negligible.

3.2 Proportion of uncut latex vessel rows in relation to total number of latex vessel rows and bark thickness

Correlations were estimated to assess the proportion of uncut latex vessel rows on tapping, in relation to total bark thickness and total number of latex vessel rows. The proportions of soft bast and uncut vessel rows are expressed as percentage of total bark thickness and total number of L.V.R. respectively. The data is provided in Table 32. In virgin as well as renewed bark, the proportion of soft bast has no significant correlation with total bark thickness while the proportion of uncut vessel row has negative correlations with total bark thickness, and total number of latex vessel rows ($P < 0.01$). For virgin bark, negative association of

the proportion of uncut vessel rows with total bark thickness was not significant when total number of latex vessel rows was kept constant. For renewed bark the relationship was significant ($P < 0.01$). In both cases, correlation between uncut vessel rows and total number of latex vessel rows was significant ($P < 0.01$) when total bark thickness was kept constant.

Multiple correlation of the proportion of uncut vessel rows, with bark thickness and total number of latex vessel rows was very close and highly significant for virgin ($r = 0.82$, $P < 0.01$) and renewed bark ($r = 0.81$, $P < 0.01$) which explained 67 per cent and 65 per cent variations respectively.

3.3 Leaf anatomical traits versus yield

Using the pooled data of ten Hevea clones correlations of certain leaf anatomical traits such as thickness and width of midrib and the height and width of palisade layer with dry rubber yield were estimated. The results are shown in Table 33. All the four traits showed negative relationships with yield; of which the correlation of midrib width alone was statistically significant.

3.4 Number of intraxylary phloem versus growth characters

Associations of the number of intraxylary phloem with the number of primary xylem points, diameter of one year old twig and rate of girth increment on tapping over the last three years in 17 year old trees were examined by estimating simple correlations

using the pooled data of eight Hevea clones. The results are given in Table 34. With all the three traits it had significant positive correlations. With girth increment rate on tapping the correlation was significant only at 5 per cent level while its correlations with the number of primary xylem points and stem diameter were at 1 per cent level.

3.5 Stomatal characters versus leaf retention after the incidence of Phytophthora leaf fall disease

Stomatal characters such as frequency, aperture length, aperture width and aperture index (product of the other factors) of petiolar stomata were correlated with leaf retention after the incidence of Phytophthora leaf fall. The correlation coefficients are presented in Table 35. Leaf retention percentage had negative correlation with stomatal frequency ($r = -0.7561$, $P < 0.01$), length of stomatal aperture ($r = -0.5883$, $P < 0.05$) and aperture index ($r = -0.7824$, $P < 0.01$) while its correlation with aperture width was not significant. The aperture index had very high positive correlations with stomatal frequency and aperture length while its correlation with aperture width was negligible.

The first and second order partial correlations and multiple correlation are shown in Table 36. The first order partial correlation of leaf retention percentage with stomatal frequency was highly significant when the effect of aperture length or width was eliminated while this trait was not significantly correlated with aperture length

when the influence of stomatal frequency or aperture index was eliminated. The correlations of leaf retention percentage with any of the component traits was not significant when the aperture index was kept constant. With percentage leaf retention, the aperture index showed significant correlation when the aperture length or width was kept constant but the relationship was not significant when the stomatal frequency was kept constant. The second order partial correlations of leaf retention with stomatal frequency and aperture index were highly significant when the aperture length and aperture width were kept constant. Multiple correlation of all these traits with leaf retention percentage recorded a higher value ($r = 0.8233$, $P < 0.01$) than its correlations with each trait, with an R^2 value of 0.6778.

3.6 Brown bast incidence versus yield and anatomical characters

Simple correlation of certain bark anatomical traits and girth with brown bast incidence and percentage girth increase were estimated using the plot means of ten clones (Table 37). Number of latex vessel rows ($P < 0.01$) and laticifer area index ($P < 0.05$) recorded significant positive correlations with brown bast incidence. With girth increase the number of latex vessel rows indicated a negative relationship and laticifer area index a positive relationship. Latex vessel density and height/width ratio of phloem rays showed significant negative correlations with girth increment while those traits indicated positive relationships with brown bast incidence.

Girth showed the same trend but the relationships were not significant. Girth increment on tapping also indicated a negative relationship with brown bast incidence.

Relationship of brown bast incidence with latex volume and rubber yield is furnished in Table 38. Rubber yield showed very high correlation with latex volume ($r = 0.9061$) at highly significant level. Both traits showed significant positive correlations with brown bast incidence at 5 per cent level.

When the effect of one trait is eliminated relationship of the other one is not significant. Both traits together contributed 22 per cent variation of the incidence of brown bast.

Inter relationships among brown bast incidence, number of latex vessel rows, number of intraxylary phloem and latex volume were examined by partial and multiple correlation studies. The results are shown in Table 39 and 40 respectively. Number of latex vessel rows showed highly significant simple correlation ($P < 0.01$) with brown bast incidence. The regression of brown bast incidence on number of latex vessel rows is shown in Figure 8. With latex volume brown bast incidence has positive relationship at a lower level ($P < 0.05$) as showed earlier. Number of intraxylary phloem also showed a negative relationship with brown bast incidence at 5 per cent level. Latex volume showed very high positive correlation with the number of latex vessel rows. The regression of latex volume on number of latex vessel rows is shown in Figure 7. The correlation

between number of latex vessel rows and number of intraxylary phloem was negative and significant at 1 per cent level.

When the effect of latex volume was kept constant, the relationships of brown bast incidence with the number of latex vessel rows and number of intraxylary phloem were not significant but the relationship of latex vessel rows with intraxylary phloem was significant. When the number of latex vessel rows was kept constant, the relationship of brown bast incidence with the number of intraxylary phloem was not significant and with latex volume its relationship was negligible. When the number of intraxylary phloem was kept constant, brown bast incidence was correlated with the other two traits at 5 per cent level.

The second order partial correlation of brown bast incidence with number of intraxylary phloem was highly significant while its relationship with number of latex vessel rows or latex volume were not significant when the effect of two traits were eliminated.

The multiple correlations are shown in Table 40. The multiple correlation of any two of the traits with brown bast incidence was significant at 1 per cent level and contributed to 30 to 40 per cent variation of brown bast incidence. All the three traits together governed 49 per cent of the variation in brown bast incidence.

Dependability of rubber yield on latex volume, latex volume on number of latex vessel rows and percentage brown bast incidence

on number of latex vessel rows were examined by regression analysis. Regression equation were computed and suitable regression lines were fitted (Figures 6, 7 and 8). The equations are shown in the respective order.

$$1. \quad Y = 6.2060 + 0.3772x$$

$$2. \quad Y = 3.6725 + 7.4383x$$

$$3. \quad Y = -110.0098 + 8.0751x$$

The incidence of brown bast (%), rubber yield (g/tree/tap) and latex volume (ml) in ten Hevea clones are shown in Figure 9. The clones which recorded significantly high latex volume (RRIC 100 and RRIC 36) recorded high incidence of brown bast. Out of the two clones which recorded significantly low latex volume, one had no brown bast incidence (RRIC 52) and the other one (RRII 105) recorded average incidence. For six clones which gave average latex volume, brown bast occurrence was low to medium.

4. GENOTYPIC CORRELATIONS AND PATH COEFFICIENT ANALYSIS

4.1 girth and bark anatomical characters at maturity versus subsequent yield

Genotypic correlations of girth and seven anatomical characters at the eighth year of planting on mean yield over subsequent three years of tapping are given in Table 41. Yield showed highly significant positive correlations with laticifer area index ($r = 0.6910$) and total number of latex vessel rows ($r = 0.5888$) at 1 per cent level. It indicated positive relationships with the intensity of anastomosing, latex vessel diameter and latex vessel density and negative relationship with the width of phloem rays. For rubber yield versus girth and height of phloem rays the correlation coefficients were negligible.

Girth of the tree showed significant positive correlation with latex vessel diameter ($r = 0.4990$) and width of the phloem rays ($r=0.4909$) at 1 per cent level and significant negative correlation with latex vessel density ($r = 0.3922$) at 5 per cent level. Positive relationship of this trait with laticifer area index and its negative relationships with intensity of anastomosing, number of latex vessel rows and height of phloem rays were not statistically significant.

Laticifer area index had highly significant positive correlations with latex vessel diameter ($r = 0.5689$) and number of latex vessel rows ($r = 0.7521$) at 1 per cent level and indicated a negative

correlation with latex vessel density. Correlation coefficients for the rest of its pairs were negligible.

Latex vessel diameter showed very significant negative correlation with latex vessel density ($r = 0.6028$). It indicated positive relationships with the width of phloem rays and intensity of anastomosing and a negative relationship with ray height.

Latex vessel density showed highly significant negative correlation with ray width ($r = 0.7254$). It indicated negative association with number of latex vessel rows and positive relationship with intensity of anastomosing. Intensity of anastomosing showed a negative relation with latex vessel rows and width of phloem rays.

Number of latex vessel rows indicated a positive relationship with ray height and negative relationship with ray width. Height versus width of phloem rays has a negative trend.

Direct and indirect effects of the characters on mean yield over three years are shown in Table 42 and the path diagram is provided (Figure 10). Among the eight characters, highest positive direct effect on yield was for laticifer area index (1.8315). Intensity of anastomosing (0.2523) and width of phloem rays (0.1749) showed good amount of positive direct effect while the effects of latex vessel density and height of phloem rays were of negligible magnitudes. Number of latex vessel rows (-0.8315), diameter of latex vessels (-0.6517) and girth of the tree (-0.4806) had high

negative effects on rubber yield. The residual effect was 0.5534.

The indirect effects of certain characters on yield are worth considering. The tree girth has high magnitude of positive effect through laticifer area index (0.4971) and number of latex vessel rows (0.2296) but it is nullified by its negative direct effect and indirect via diameter and density of latex vessels and intensity of anastomosing. The indirect effects of laticifer area index via all other traits were negative but of negligible magnitudes. Latex vessel diameter has high magnitude of positive effect via laticifer area index (1.0402) while its effect on girth, latex vessel density and latex vessel rows were negative. The density of latex vessels has positive effect via girth (0.1885), diameter of latex vessels (0.3928) and number of latex vessel rows which is nullified by its negative effect via laticifer area index (-0.4919). Indirect effects of latex vessel anastomosing on yield via the various traits is negligible. Number of latex vessel rows has very high positive effect via laticifer area index (1.3775) and girth (0.1327). Height of phloem rays has positive effects via girth (0.1303), laticifer area index (0.1123) and diameter of latex vessels (0.1481) but its effects via the other traits are negative. Width of phloem rays have considerable magnitude of positive effect via number of latex vessel rows (0.1079) and a negligible amount via ray height. Its effect through all other traits are negative.

4.2. Rubber yield versus girth, anatomical characters and latex flow characters

Genotypic correlations among rubber yield and fifteen characters including physiological and anatomical traits recorded at the 11th year of planting are shown in Table 43. Yield showed significant correlations with seven characters, of which the relationship of plugging index alone was negative. Correlation of rubber yield with intensity of anastomosing ($r = 0.4505$) was significant at 5 per cent level while its relationships with number of latex vessel rows ($r = 0.5281$), laticifer area index ($r = 0.4977$), duration of latex flow ($r = 0.5509$), plugging index ($r = -0.5838$), total volume of latex ($r = 0.8880$) and initial rate of flow ($r = 0.4072$) were significant at 1 per cent level.

Among the fifteen characters other than rubber yield, correlation coefficients of 24 pairs were statistically significant, of which 14 pairs showed positive and ten pairs negative correlations. Those which showed positive correlations are number of latex vessel rows versus laticifer area index ($r = 0.8234$, $P < 0.01$), duration of flow ($r = 0.3751$, $P < 0.05$) and total volume of latex ($r = 0.5376$, $P < 0.01$); diameter of latex vessels versus laticifer area index ($r = 0.5987$, $P < 0.01$); girth versus width of phloem rays ($r = 0.5211$, $P < 0.01$); laticifer area index versus duration of flow ($r = 0.5445$, $P < 0.01$) and total volume of latex ($r = 0.5744$, $P < 0.01$); intensity of latex vessel anastomosing versus total volume of latex ($r = 0.4792$, $P < 0.01$); height of phloem rays versus H/W ratio of phloem rays ($r = 0.6235$,

$P < 0.01$); width of phloem rays versus diameter of ray cells ($r = 0.4589$, $P < 0.05$); duration of flow versus total volume of latex ($r = 0.6588$, $P < 0.01$); plugging index versus d.r.c. ($r = 0.4349$, $P < 0.05$); total volume of latex versus initial rate of flow ($r = 0.4721$, $P < 0.01$) and d.r.c. versus initial rate of flow ($r = 0.3909$, $P < 0.05$).

The character pairs which showed negative correlations are number of latex vessel rows versus plugging index ($r = -0.4450$, $P < 0.05$); density of latex vessels versus height of phloem rays ($r = -0.4198$, $P < 0.05$) and diameter of ray cells ($r = -0.4776$, $P < 0.01$); girth versus H/W ratio of phloem rays ($r = -0.3668$, $P < 0.05$); laticifer area index versus plugging index ($r = -0.5330$, $P < 0.01$); intensity of anastomosing versus plugging index ($r = -0.3673$, $P < 0.05$); width of phloem rays versus H/W ratio of phloem rays ($r = -0.6775$, $P < 0.01$); duration of flow versus plugging index ($r = -0.8353$, $P < 0.01$) and d.r.c. ($r = -0.4690$, $P < 0.05$) and plugging index versus total volume of latex ($r = -0.6892$, $P < 0.01$).

Direct and indirect effects of the 15 characters on yield at the same year are shown in Table 44 and the path diagram in Figure 11. The highest positive direct effect on yield was obtained for total volume of latex (0.7043) followed by laticifer area index (0.4180), d.r.c. (0.3823), H/W ratio of phloem rays (0.3550), duration of flow (0.3084) and width of phloem rays (0.1957). Laticifer anastomosing, plugging index, rate of flow and diameter of ray cells

have positive effects on yield at small magnitudes. Direct effects of girth (-0.2611) number of latex vessel rows (-0.2511) latex vessel density (-0.2511) and latex vessel diameter (-0.2060) and also the ray height (-0.2060) and also the ray height (-0.2242) were negative and at considerable magnitudes. The residual effect was low (0.3180).

The indirect effect of the number of latex vessel rows on yield is negative while it has strong positive effect via laticifer area index (0.3441), total volume of latex (0.3786) and duration of flow (0.1157). The density of latex vessel has some amount of positive effect via d.r.c. (0.1094) which is nullified by its direct negative effect. Diameter of latex vessels (0.2502) and girth of the tree (0.1132) had fairly good amount of positive effects via laticifer area index which is nullified by its negative direct effect and indirect effects via some other traits. In addition to its direct effect on yield, laticifer area index has high magnitude of positive effects via total volume of latex (0.4046) and duration of flow (0.1680). The effect of laticifer anastomosing via total volume (0.3375) was strong. This trait had small amounts of positive effects via several characters such as latex vessel diameter, laticifer area index, height of phloem rays, H/W ratio of phloem rays, duration of flow, d.r.c. and initial rate of flow. Ray height has considerable amount of positive effects via laticifer area index (0.1251) and H/W ratio of phloem rays (0.2214). Ray width also have good amount of positive effects via laticifer area index (0.1169) in addition to its direct effect which is nullified by its negative effects via

girth and H/W ratio of phloem rays. The positive direct effect of H/W ratio of phloem rays is nullified by its negative effect via ray height (-0.1399). Diameter of ray cells have very small amount of positive direct effect and its positive effects via number of latex vessel rows, density of latex vessels, ray width, duration of flow, plugging index and initial rate of flow were nullified by small negative effects via the other traits. The duration of flow have considerable amount of positive effect on yield via total volume of latex (0.4640) and laticifer area index (0.2276) in addition to its direct effect (0.3084). This trait has some amount of negative effect via d.r.c. (-0.1793). Plugging index has very small positive direct effect on yield and considerable effects via number of latex vessel rows (0.1117) and d.r.c. (0.1663) which is nullified by its strong negative effects via total volume of latex (-0.4854), duration of flow (-0.2577) and laticifer area index (-0.2228). Total volume of latex, which has the highest positive direct effect on yield, has considerable amount of positive effects via laticifer area index (0.2401) and duration of flow (0.2032) and have small effects via girth, latex vessel anastomosing, width of phloem rays and initial rate of flow. The effect of total volume of latex via number of latex vessel rows is negative (-0.1350). A strong positive direct effect of d.r.c. on yield (0.3823) is nullified by its negative effect via duration of flow (-0.1447). The initial rate of flow has a strong effect via total volume of latex (0.3325) and d.r.c. (0.1494) though its direct effect on yield is negligible.

4.3 Girth and anatomical characters at maturity versus girth increment on tapping

Genotypic correlations of girth and anatomical characters at the eighth year of planting with percentage girth increase on tapping over subsequent two years of tapping and the direct and indirect effects are shown in Table 45 and 46 respectively. The path diagram is also provided (Figure 12). Correlations of certain pairs of characters which are common, for Table 41 and 45 have not been explained here.

At genotypic level, percentage girth increase has positive correlation with diameter of latex vessels ($r = 0.4079$) and negative correlation with density of latex vessels ($r = -0.3953$) at significant level. Girth increase on tapping indicated positive relationships with girth, laticifer area index, width of phloem rays, number of intraxylary phloem and number of primary xylem points. With the other traits such as number of latex vessel rows, intensity of latex vessel anastomosing and ray height it indicated negative relationships.

With the number of intraxylary phloem, girth showed significant positive correlation ($r = 0.3846$, $P < 0.05$) and number of latex vessel rows showed negative correlation ($r = -0.5401$, $P < 0.01$). The number of primary xylem points showed significant positive correlations with girth ($r = 0.5114$, $P < 0.01$), number of intraxylary phloem points ($r = 0.9437$, $P < 0.01$) and diameter of latex vessels

($r = 0.4319$, $P < 0.05$).

Laticifer area index showed very high positive direct effect on girth increment on tapping (2.8405). The number of primary xylem points (0.3754) and width of phloem rays (0.1511) also had considerable magnitudes of positive direct effects on girth increment on tapping. Number of latex vessel rows has high magnitude of direct effect (-2.3499) on girth increment but it is negative. The direct effect of girth (-1.1817), diameter of latex vessels (-1.4855), density of latex vessels (-1.1014), intensity of anastomosing (-0.1875) and height of phloem rays (-0.4086) are also negative and in considerable magnitudes. The number of intraxylary phloem recorded very small negative direct effect (-0.0203) on girth increment on tapping. The residual effect was 0.7464.

Considering the indirect effects of the characters on girth increment on tapping, girth has strong positive effect via laticifer area index (0.7709), density of latex vessels (0.4320), total number of latex vessel rows (0.6489), height of phloem rays (0.1108) and number of primary xylem points (0.1920). In addition to a very strong direct effect, laticifer area index has positive effect via density of latex vessels (0.2959) and small effects via latex vessel anastomosing and number of intraxylary phloem. However, this trait has strong negative effects via total number of latex vessel rows (-1.7674), diameter of latex vessels (-0.8438) and girth of the tree (-0.3207) and small negative effects via intensity of latex vessel

anastamosing, ray height, ray width and number of primary xylem points. The latex vessel diameter has very strong positive effect via laticifer area index (1.6133) and density of latex vessels (0.6639). In addition to a high magnitude of negative direct effect, density of latex vessels has strong negative effects via laticifer area index (-0.7630) and width of phloem rays (-0.1096). Intensity of latex vessel anastamosing has positive effect via number of latex vessel rows (0.2591). Number of latex vessel rows has very strong effect via laticifer area index (2.1364), girth (0.3263) and density of latex vessels (0.1351) though its direct effect is negative. The height of phloem rays has good magnitude of positive effect via girth (0.3204), laticifer area index (0.1742) and diameter of latex vessels (0.3376). The width of phloem rays has positive effect of considerable magnitude via density of latex vessels (0.7989) and number of latex vessel rows (0.3048). This trait has considerable magnitude of negative effect via girth (-0.5801) and diameter of latex vessels.

The number of intraxylary phloem has high magnitude of positive effect via the number of latex vessel rows (1.2690) and number of primary xylem points (0.3542), while this trait has high magnitude of negative effects via girth (-0.4545), laticifer area index (-0.4409) and diameter of latex vessels (-0.5157). In addition to the direct effect, number of primary xylem points have very strong positive effect via the number of latex vessel rows (1.2139) which is nullified

by its negative effects via girth (-0.6043), diameter of latex vessels (-0.6416) and laticifer area index (-0.1935).

T A B L E S

Table 1. Experimental materials.

Sl. No.	Clone	Country of origin	Parentage
1.	Tjir 1	Indonesia	Primary clone
2.	GT 1	Indonesia	Primary clone
3.	PR 107	Indonesia	Primary clone
4.	RRIC 7	Sri Lanka	Primary clone
5.	RRIC 36	Sri Lanka	Secondary clone PB 86 x PR 107
6.	RRIC 45	Sri Lanka	Secondary clone RRIC 8 x Tjir 1
7.	RRIC 52	Sri Lanka	Primary clone
8.	RRIC 100	Sri Lanka	Secondary clone RRIC 52 x PB 83
9.	RRIC 102	Sri Lanka	Secondary clone RRIC 52 x RRIC 7
10.	RRIC 104	Sri Lanka	Secondary clone RRIC 52 x Tjir 1
11.	RRIC 105	Sri Lanka	Secondary clone RRIC 52 x Tjir 1
12.	Nab 17	Sri Lanka	Primary clone
13.	RRIM 501	Malaysia	Secondary clone Pil A 44 x Lun N
14.	RRIM 601	Malaysia	Secondary clone Tjir 1 x Gl 1
15.	RRIM 605	Malaysia	Secondary clone Tjir 1 x PB 49
16.	RRIM 609	Malaysia	Secondary clone AVROS 157 x BD 5

Table 1 (contd....)

Sl. No.	Clone	Country of origin	Parentage
17.	RRIM 611	Malaysia	Secondary clone RRIM 504 x Tjir 1
18.	RRIM 615	Malaysia	Tertiary clone RRIM 511 x Tjir 1
19.	RRII 101	India	Secondary clone Tjir 1 x AVROS 255
20.	RRII 102	India	Secondary clone Tjir 1 x Gl 1
21.	RRII 105	India	Secondary clone Tjir 1 x Gl 1
22.	RRII 106	India	Secondary clone Tjir 1 x Mil 3/2
23.	RRII 109	India	Secondary clone Tjir 1 x Mil 3/2
24.	RRII 111	India	Secondary clone Tjir 1 x Hil 28
25.	H.P. 301	India	Secondary clone Tjir 1 x HC 28
26.	H.P. 416	India	Secondary clone Mil 3/2 x HC 28
27.	H.P. 417	India	Secondary clone HC 28 x Mil 3/2
28.	H.P. 421	India	Secondary clone Mil 3/2 x Gl 1
29.	H.P. 455	India	Secondary clone Mil 3/2 x RSY 23

Table 1 (contd....)

Sl. No.	Clone	Country of origin	Parentage
30.	H.P. 456	India	Secondary clone Mil 3/2 x RSY 23
31.	H.P. 16	India	Secondary clone RRII 106 x RRII 33
32.	H.P. 29	India	Secondary clone RRII 6 x Fx 516
33.	H.P. 85	India	Secondary clone RRII 102 x PB 86
34.	H.P. 110	India	Secondary clone RRII 102 x RRII 6
35.	H.P. 115	India	Secondary clone RRII 102 x RRII 6
36.	H.P. 157	India	Secondary clone RRII 12 x RRIM 501
37.	H.P. 249	India	Secondary clone Fx 516 x Gl 1
38.	H.P. 356	India	Secondary clone Fx 516 x RRII 6
39.	H.P. 427	India	Secondary clone Fx 516 x RRII 6
40.	H.P. 499	India	Secondary clone Fx 516 x Gl 1

Table 2. Analysis of variance and covariance table.

Source of variation	d.f.	MSx_1	$MSPx_1x_2$	MSx_2	$E(MSx_1)$	(MSx_1x_2)
Replication	r-1	M_{11}	P_1	M_{21}		
Varieties	V-1	M_{12}	P_2	M_{22}	$\frac{2}{Gc_1} + r \frac{2}{Gg_1}$	$Gc_1c_2 + rGg_1g_2$
Error	(r-1) (V-1)	M_{13}	P_3	M_{23}	$\frac{2}{Ge_1}$	Gc_1c_2

where $E(MSx_1)$ is the expectations of mean squares of character x_1 .

$E(MSPx_1x_2)$ is the expectations of mean sum of products of character x_1 and x_2 .

r is the number of replications.

V is the number of varieties.

$\frac{2}{Ge_1}$ is the variance due to error in character x_1 .

$\frac{2}{Gg}$ is the genotypic variance in character x_1 .

Gc_1e_2 is the covariance due to error in characters x_1 and x_2 .

Gg_1g_2 is the genotypic covariance in characters x_1 and x_2 .

Table 3. Periodic difference in the number of cambial layers in
Gl 1.

Period	Number of cambial layers
1	3.21
2	3.20
3	3.70
4	4.95
SE	0.10
CD: 5%	0.28
CD: 1%	0.37

Table 4. Frequency of leaf blade stomata and petiolar stomata in Hevea clones

Clones	Frequency of stomata	
	Leaf blade Numbers/mm ²	Petiole Numbers/10 mm ²
RRII 101	297.00±13.60	3.00±0.67
RRII 102	343.30±6.60	3.33±0.73
RRII 105	348.30±6.30	3.00±0.43
RRII 106	303.50±6.20	4.63±0.28
PR 107	332.60±11.10	5.25±0.95
Tjir 1	323.10±7.00	4.50±1.19
Mean	324.63±8.548	3.952±0.393

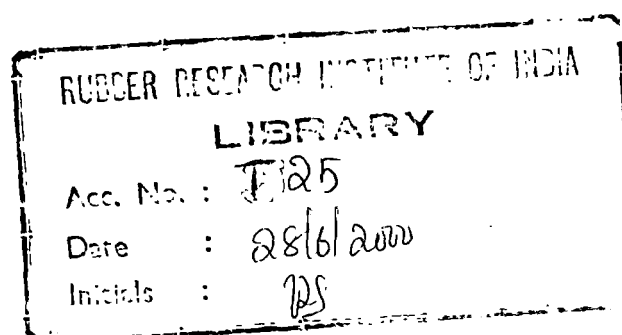


Table 5. Organographic variability in the length and width of stomatal aperture

Character	Leaf blade	Vein	Petiole
Aperture length (μm)	10.94**	14.15**	16.88**

CD at 5% level = 1.26

CD at 1% level = 1.69

Aperture width (μm)	1.93**	3.16**	4.26**
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CD at 5% level = 0.45

CD at 1% level = 0.60

** $P < 0.01$

Table 6. Clonal differences in the proportion of ray types

Clones	Uniseriate** (%)	Biseriate** (%)	Triseriate (%)	Tetraseriate** (%)
	SE = 0.856 CD = 1.798	SE = 2.801 CD = 5.886	SE = 3.957 CD = -	SE = 3.566 CD = 7.492
RRIC 45	13.72	18.02	59.60	8.15 ^L
RRIC 100	13.04	22.95 ^H	59.59	5.63 ^L
RRIC 7	12.12	13.68	59.17	15.02
RRIC 104	14.96 ^H	6.06 ^L	55.93	23.07 ^H
RRIC 105	11.09 ^L	13.65	56.94	17.03
RRIC 52	11.55 ^L	9.46 ^L	53.15	25.81 ^H
RRIC 36	10.53 ^L	10.29 ^L	47.12	31.48 ^H
GT 1	12.70	24.25 ^H	61.26	1.81 ^L
Nab 17	14.45 ^H	24.68 ^H	54.11	6.72 ^L
RRIC 102	14.67 ^H	6.26 ^L	52.64	24.94 ^H
Grand mean	12.88	14.93	55.95	15.97
CD (Grand mean vs individual clones)	1.206	3.948	3.957	2.392

** $P < 0.01$

CD at 5% level.

H = high

L = low

Table 7. Clonal differences in the shape of phloem rays

Clones	Oval**	Bat	Spindle	Dumb-bell
	SE = 4.034 CD = 8.480	SE = 8.490 CD = -	SE = 3.602 CD = -	SE = 1.150 CD = -
RRIC 45	10.63 ^L	71.65	12.43	5.43
RRIC 100	20.02	60.11	13.71	5.21
RRIC 7	15.07	59.87	11.25	4.58
RRIC 104	20.95	62.78	11.14	5.45
RRIC 105	22.49	61.18	10.97	3.39
RRIC 52	29.82 ^H	55.18	11.37	3.65
RRIC 36	22.90	54.78	12.39	3.59
GT 1	10.41 ^L	70.71	11.98	6.19
Nab 17	13.14	72.37	12.50	4.82
RRIC 102	15.93	65.86	13.92	4.28
Mean	18.14	63.45	12.16	4.66
CD (General mean 5.686 vs individual clones)		--	--	--

** $P < 0.01$

CD at 5% level.

H = high

L = low

Table 8. Clonal differences in the density, height, width and height/width ratio of phloem rays

Clones	Density** No/1.25 mm ²	Height** µm	Width** µm	Height/width ratio**
	SE = 1.339 CD = 2.836	SE = 15.498 CD = 32.561	SE = 1.664 CD = 3.453	SE = 0.550 CD = 1.156
RRIC 45	32.54	365.64	43.91 ^L	8.45
RRIC 100	37.01 ^H	370.17	40.36 ^L	9.19 ^H
RRIC 7	29.00 ^L	429.23 ^H	48.69	8.93
RRIC 104	28.80 ^L	398.51	53.38 ^H	7.59
RRIC 105	39.39 ^H	302.54 ^L	48.45	6.23 ^L
RRIC 52	28.26 ^L	346.50 ^L	52.29 ^H	6.73 ^L
RRIC 36	30.72	389.88	49.78 ^H	7.67
GT 1	32.09	479.23 ^H	41.48 ^L	11.68 ^H
Nab 17	32.75	370.26	41.05 ^L	9.21 ^H
RRIC 102	30.94	378.97	48.25	7.99
Mean	32.15	389.09	46.77	8.35
CD (general mean 1.887 vs individual clones)		21.843	2.316	0.775

** P < 0.01

CD at 5% level.

H = high

L = low

Table 9. Clonal differences in diameter (μm) of ray cells

Clones	Uni- seriate**	Bi- seriate**	Tri- seriate**	Tetra- seriate**	Mean of the four types**
	SE = 1.268 CD = 2.665	SE = 0.950 CD = 1.995	SE = 0.817 CD = 1.717	SE = 0.825 CD = 1.734	SE = 0.836 CD = 1.763
RRIC 45	21.77	14.76	13.07	12.47	14.78
RRIC 100	21.44 ^L	12.76 ^L	11.54 ^L	9.98 ^L	12.23 ^L
RRIC 7	22.81	15.60	13.73	11.44	14.62
RRIC 104	27.82 ^H	16.74 ^H	16.08 ^H	13.64 ^H	17.19 ^H
RRIC 105	22.43	14.72	13.62	11.63	14.21
RRIC 52	25.19	17.14 ^H	14.91	13.52 ^H	15.99
RRIC 36	22.39	15.07	14.61	12.80	14.44
GT 1	23.80	15.59	14.69	10.82	16.06 ^H
Nab 17	22.73	14.22	12.93	11.15	14.65
RRIC 102	23.77	14.04	13.21	11.68	14.55
Mean	23.41	15.04	13.84	11.98	14.87
CD (general mean vs individual clones)	1.788	1.339	1.152	1.163	1.184

** $P < 0.01$

CD at 5% level.

H = high

L = low

Table 10. Clonal differences in laticifer characters

Clones	Number of latex vessel rows**	Density of latex vessel** (No/0.25 mm girth)	Diameter of latex vessel** (µm)	Laticifer area index (mm)**	Intensity of anastomosing** (No/0.25 mm height)
	SE = 0.73 CD = 2.17	SE = 0.73 CD = 2.15	SE = 0.50 CD = 1.49	SE = 1.84 CD = 5.46	SE = 0.22 CD = 0.65
RRIC 45	9.12 ^L	328.00	16.73	12.02 ^L	7.17
RRIC 100	11.43	337.33 ^H	18.72 ^H	22.44 ^H	8.23 ^H
RRIC 7	12.06	298.27 ^L	17.88	17.27	7.27
RRIC 104	11.35	293.33 ^L	18.42	20.92 ^H	6.01 ^L
RRIC 105	7.85 ^L	329.87	16.53 ^L	11.59 ^L	7.04
RRIC 52	6.45 ^L	298.07 ^L	19.59 ^H	12.92 ^L	7.52
RRIC 36	14.35 ^H	312.00	17.94	20.74 ^H	7.56 ^H
GT 1	10.56	334.07 ^H	15.15 ^L	11.84 ^L	7.41
Nab 17	13.98 ^H	314.00	18.09	21.51 ^H	6.24 ^L
RRIC 102	12.02	324.40	16.62	16.55	6.88
Grand mean	10.92	316.93	17.57	16.78	7.13
CD (general mean vs individual clone)	1.44	14.301	1.00	2.06	0.42

** P < 0.01

CD at 5% level.

H = high. L = low

Table 11. Clonal differences in primary xylem groups and intraxylary phloem points

Clones	Number of primary xylem points**	Number of intraxylary phloem points**
	SE = 7.62 CD = 16.00	SE = 7.33 CD = 15.41
RRIC 45	54.86	50.07
RRIC 100	77.48 ^H	77.78 ^H
RRIC 7	57.45	53.37
RRIC 104	65.83	51.72
RRIC 105	54.58	44.57
RRIC 52	97.67 ^H	86.28 ^H
RRIC 36	48.21 ^L	37.06 ^L
GT 1	57.65	50.74
Nab 17	54.80	44.20
RRIC 102	56.13	53.21
General mean	62.47	54.30
CD (General mean vs individuval clone)	10.73	10.34

** $P < 0.01$

CD at 5% level.

H = high

L = low

Table 12. Clonal differences in leaf anatomical characters

Clones	Thickness of midrib	Width of midrib* (mm)	Cuticle thickness** (µm)	Height of palisade cells (µm)	Width of palisade cells (µm)	Density of laminar stomata No/mm ²	Frequency of petiolar stomata** No/10 mm ²
	SE = 0.127 CD = -	SE = 0.129 CD = 0.250	SE = 0.404 CD = 0.840	SE = 5.720 CD = -	SE = 1.910 CD = -	SE = 23.02 CD = -	SE = 0.270 CD = 0.566
RRIC 45	0.8854	1.0932	6.8055	52.2628	8.7385	440.77	1.92 ^L
RRIC 100	0.8647	1.0670	5.6550 ^L	47.8524	7.9582	449.96	2.87
RRIC 7	0.7160	0.9100 ^L	6.8488	49.6625	10.4547	405.23	1.43 ^L
RRIC 104	0.8067	1.0179	6.1723 ^L	46.9318	8.2771	490.90	2.78
RRIC 105	0.8025	1.1663	7.0810	43.8418	9.7250	422.22	1.70 ^L
RRIC 52	1.0008	1.2459	6.5695	55.5850	9.5703	425.20	2.73
RRIC 36	0.8557	1.0671	7.4517 ^H	51.8352	8.4268	439.80	3.28 ^H
GT 1	0.8457	1.0611	6.4522	56.2883	10.0493	426.05	2.30
Nab 17	1.1083	1.3281 ^H	6.9552	45.2980	8.2988	452.81	3.93 ^H
RRIC 102	0.7656	0.8925 ^L	7.6728 ^H	49.4208	9.6910	421.09	2.00
Mean	0.8719	1.0849	6.7664	49.8977	9.1210	437.41	2.50
CD (General mean vs individual clone)	--	0.168	0.563	--	--	--	0.380

* P < 0.05. ** P < 0.01. CD at 5% level. H = high L = low

Table 13. Clonal differences in growth characters

Clones	Girth** (cm)	Panel length** (cm)	Percentage girth increase (trans- formed figures)	Bark thickness (mm)
	SE = 2.665 CD = 6.000	SE = 3.359 CD = 6.988	SE = 0.120 CD = -	SE = 0.285 CD = -
RRIC 45	61.69 ^L	39.72	8.50 (3.00)	4.35
RRIC 100	69.28	49.83	8.77 (3.03)	3.91
RRIC 7	62.64 ^L	45.44	9.00 (3.08)	4.32
RRIC 104	78.54 ^H	57.44 ^H	10.29 (3.28)	3.86
RRIC 105	70.31	43.55	8.57 (3.01)	4.63
RRIC 52	74.30 ^H	49.25	9.33 (3.13)	4.02
RRIC 36	63.36	45.06	7.42 (2.81)	4.69
GT 1	62.17 ^L	39.94 ^L	6.77 (2.69)	4.31
Nab 17	62.64 ^L	43.06	9.01 (3.08)	4.14
RRIC 102	65.20	46.06	8.07 (2.92)	4.25
Mean	67.02	45.94	8.57 (3.00)	4.25
CD (General mean vs individual clone)	3.756	4.688	--	--

** $P < 0.01$

CD at 5% level

(SE is of transformed figures)

H = high L = low

Table 14. Clonal differences in latex flow characters

Clone	Initial rate of flow* (ml)	Duration of flow* (min)	Plugging index**
	SE = 0.01 CD = 0.03	SE = 5.44 CD = 16.16	SE = 0.42 CD = 1.25
RRIC 45	0.12 ^H	97.91	5.87 ^H
RRIC 100	0.11	114.99	4.27
RRIC 7	0.12 ^H	109.10	5.11
RRIC 104	0.07 ^L	123.18 ^H	4.07 ^L
RRIC 105	0.09	94.42 ^L	6.28 ^H
RRIC 52	0.10	97.79	5.39
RRIC 36	0.10	120.57 ^H	3.52 ^L
GT 1	0.08	102.68	4.77
Nab 17	0.10	96.93	5.45
RRIC 102	0.12 ^H	97.40	5.03
General mean	0.10	105.50	4.98
CD (General mean vs individual clone)	0.016	10.73	0.830

* $P < 0.05$ ** $P < 0.01$

CD at 5% level.

H = high

L = low

Table 15. Clonal differences in dry rubber yield, total volume of latex and dry rubber content (mean over three years)

Clone	Dry rubber yield** (g/tree/tap) SE = 4.842 CD = 10.071	Total volume** (ml/tree/tap) SE = 12.152 CD = 25.277	Dry rubber content** SE = 1.292 CD = 2.688
RRIC 45	46.05	115.07	35.07
RRIC 100	64.21 ^H	145.99 ^H	36.57 ^H
RRIC 7	49.03	120.57	33.50
RRIC 104	45.52	119.37	31.40 ^L
RRIC 105	39.49 ^L	90.90 ^L	36.68 ^H
RRIC 52	33.97 ^L	80.61 ^L	35.65
RRIC 36	54.55 ^H	143.98 ^H	31.09 ^L
GT 1	37.97 ^L	96.07 ^L	32.12 ^L
Nab 17	46.17	106.99	34.11
RRIC 102	54.09 ^H	127.20	36.65 ^H
General mean	47.10	114.48	34.28
CD (General mean vs individual clone)	6.756	16.956	1.803

** $P < 0.01$

CD at 5% level

H = High L = low

Table 16. Clonal differences in percentage incidence of brown blast, wintering pattern and intensity of *Phytophthora* leaf fall and powdery mildew

Clones	Percentage incidence of brown blast SE = 1.125 CD = -	Intensity of <i>Phytophthora</i> leaf fall		Intensity of Oidium disease		Wintering behaviour
		1986	1987	1986	1987	
RRIC 45	16.67 (4.08)	M	L	H	H	Late
RRIC 100	26.67 (5.16)	M	M	L	L	Early
RRIC 7	10.00 (3.24)	L	L	M	L	Early
RRIC 104	13.33 (3.67)	L	M	M	L	Early
RRIC 105	20.00 (4.47)	M	L	H	H	Late
RRIC 52	0.00 (0.50)	M	M	L	M	Late & partial
RRIC 36	26.67 (5.16)	M	H	L	M	Early
GT 1	10.00 (3.24)	M	M	H	H	Late
Nab 17	23.33 (4.83)	H	H	H	M	Early
RRIC 102	20.33 (4.51)	M	M	L	L	Early
Mean	16.77 (3.89)	-	-	-	-	-

The mean in paranthesis and the standard error given are of transformed values.

H = high. M = medium. L = low

Table 17. Clonal differences in bark anatomical characters among drought tolerant and susceptible clones

Clones	Total No.* of latex vessel rows	Proportion** of latex vessel in soft bast (%)	Diameter** of latex vessels (μ m)	Thickness of bark bark (mm)	Proportion of soft bast (%)	Height of*** phloem rays (μ m)	Width of*** phloem rays (μ m)	Height/width** ratio of phloem rays
RRIM 501 (T ₁)	24.21	45.74	20.88	6.02	24.16	369.34	40.12	9.20
RRIM 605 (T ₂)	32.21	42.78	20.59	5.66	30.89	500.09	43.49	11.46
RRIM 609 (T ₃)	41.22	35.01	20.65	6.84	29.33	442.03	39.95	11.08
RRIM 601 (S ₁)	32.33	67.34	22.67	4.65	54.35	471.77	48.47	9.74
RRIM 611 (S ₂)	27.77	54.23	19.76	4.80	34.27	344.39	47.18	7.32
RRIM 615 (S ₃)	36.89	35.27	21.47	6.35	29.63	405.73	47.77	8.50

T - tolerant

S - susceptible

* P < 0.05

** P < 0.01

CD at 5% level.

Table 18. Bark anatomical characters of drought tolerant and susceptible groups of clones

Characters	Drought tolerant	Drought susceptible
Total number of latex vessel rows	32.55	32.33
Proportion of latex vessel rows in the soft bast (%)	41.77	52.28
Diameter of latex vessels (μm)	20.71	21.30
Total thickness of bark (mm)	6.17	5.27
Proportion of soft bast thickness (%)	28.13	39.42
Height of phloem rays (μm)	437.15	373.96
Width of phloem ray (μm)	41.19	47.81
H/W ratio of phloem rays	10.58	8.52

Table 19. Subdivision of clone sum of squares into its components for anatomical traits

(a) Number of latex vessel rows

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	0.2113	0.2113	1.00
Between tolerant	2	434.1868	217.0934	8.92**
Between susceptible	2	124.5793	62.2897	2.56

(b) Diameter of latex vessels

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	1.5724	1.5724	1.00
Between tolerant	2	0.1419	0.0710	1.00
Between susceptible	2	12.8013	6.4007	3.71

(Table contd.....)

(Continuation of Table 19)

(c) Bark thickness

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	3.6901	3.6901	4.32
Between tolerant	2	2.1975	1.0988	1.29
Between susceptible	2	5.3181	2.6590	3.11

(d) Proportion of vessel rows in the soft bast to total number of latex vessel rows

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	568.2944	568.2944	21.29**
Between tolerant	2	184.1121	92.0561	3.45
Between susceptible	2	1519.6331	759.8166	28.47**

(Table contd.....)

(Continuation of Table 19)

(e) Thickness of soft bast as percentage of total

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	973.7014	573.7014	14.75**
Between tolerant	2	74.4795	37.2395	<1.00
Between susceptible	2	1036.0101	518.0061	13.32**

(f) Height of phloem rays

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	4011.69	4011.69	2.50
Between tolerant	2	25749.01	12874.51	8.01**
Between susceptible	2	24352.09	12176.05	7.57**

(Table contd....)

(Continuation of Table 19)

(g) Width of phloem rays

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	197.2760	197.2760	62.94**
Between tolerant	2	23.9174	11.9587	3.82
Between susceptible	2	2.4897	1.2449	< 1.00

(h) Height/width ratio of phloem rays

Source of variation	d.f.	S.S.	M.S.	V.R.
Tolerant vs susceptible	1	19.0344	19.0344	22.14**
Between tolerant	2	8.8317	4.4158	5.14*
Between susceptible	2	8.7864	4.3932	5.11*

* $P < 0.05$ ** $P < 0.01$

Table 20. Bark thickness and number of latex vessel rows in induced tetraploids and the respective diploids (Mean \pm S.D)

Clones	Bark thickness		Number of latex vessel rows	
	Diploid	Tetraploid	Diploid	Tetraploid
GT 1 (10 years)	7.63 \pm 0.97	1.77 \pm 0.46	16.22 \pm 3.03	3.89 \pm 0.35
Tjir 1 (10 years)	6.93 \pm 1.23	4.04 \pm 0.64	19.00 \pm 3.00	6.89 \pm 1.27
RRII 105 (4 years)	4.44 \pm 0.48	4.11 \pm 0.48	5.44 \pm 1.51	5.00 \pm 0.50

Age of the tree is indicated in paranthesis.

Table 21. Density, diameter and intensity of anastomosing of latex vessels in induced tetraploids and the respective diploids (Mean \pm S.D)

Clone	Density of latex vessel (No/mm girth)		Diameter of latex vessel (μ m)		Intensity of Anastomosing (No/0.25 mm height)	
	Diploid	Tetraploid	Diploid	Tetraploid	Diploid	Tetraploid
GT 1 (10 years)	26.33 \pm 3.67	20.83 \pm 1.44	21.51 \pm 1.23	24.24 \pm 1.22	10.80 \pm 0.82	11.44 \pm 0.53
Tjir 1 (10 years)	25.83 \pm 2.50	21.39 \pm 2.20	21.87 \pm 1.55	25.16 \pm 1.69	10.44 \pm 0.76	11.51 \pm 0.11
RRII 105 (4 years)	26.13 \pm 1.81	22.19 \pm 1.60	22.60 \pm 0.71	22.93 \pm 0.63	8.87 \pm 0.43	9.07 \pm 0.15

Age of the tree is indicated in paranthesis.

Table 22. Height and width of phloem rays in induced tetraploids and the respective diploids

Clones	Height of phloem rays (μm)		Width of phloem rays (μm)	
	Diploid	Tetraploid	Diploid	Tetraploid
GT 1 (10 years)	472.6 \pm 67.91	736.67 \pm 130.15	52.52 \pm 3.00	74.80 \pm 3.39
Tjir 1 (10 years)	392.50 \pm 47.23	548.53 \pm 66.30	52.89 \pm 8.69	70.93 \pm 5.13
RRII 105 (4 years)	462.40 \pm 73.32	445.13 \pm 68.14	50.58 \pm 2.84	62.03 \pm 5.06

Age of the tree is indicated in paranthesis.

Table 23. Comparison of virgin and renewed bark for nine structural traits

Characters	Virgin bark Mean \pm SD	Renewed bark Mean \pm SD	Computed t value
Diameter of latex vessels (μm)	12.21 \pm 2.47	17.07 \pm 1.63	0.3775
Density of latex vessels (No/0.25 mm girth)	7.80 \pm 0.71	7.38 \pm 0.55	2.4046*
Anastamosing (No/0.25 mm height of L.V)	6.47 \pm 1.12	6.66 \pm 1.01	-1.0039
Proportion of soft bast (% of total bark thickness)	36.63 \pm 9.98	33.17 \pm 10.52	1.2253
Proportion of uncut vessel rows (% of total L.V.R.)	28.93 \pm 10.41	43.71 \pm 18.72	3.1899**
Diameter of ray cells (μm)	15.07 \pm 2.60	16.50 \pm 3.05	1.0323
Height of phloem rays (μm)	372.30 \pm 54.00	301.00 \pm 38.12	6.2709**
Width of phloem rays (μm)	50.65 \pm 5.59	56.54 \pm 6.67	3.16118*
Height/width ratio of phloem rays	7.40 \pm 1.50	5.43 \pm 0.91	3.8674**

* $P < 0.05$ ** $P < 0.01$

Table 24. Girth and bark anatomical traits of juvenile and mature trees

Character	Juvenile	Mature	t
Girth (cm)	13.87±2.88	59.28±6.37	5.7206**
Laticifer area (mm ²)	1.08±0.61	27.01±10.83	14.0493**
Intensity of anastomosing (No/0.25 mm)	6.81±0.73	6.76±0.96	-0.4423
Number of latex vessel rows	3.54±1.44	13.48± 4.56	3.6407**
Latex vessel density (No/cm girth)	281.33±38.29	269.48±25.21	1.7026
Diameter of latex vessel (µm)	17.88±2.04	22.62±2.56	5.0920**
Width of phloem ray (µm)	40.59±5.65	62.76±8.93	15.9972**

** P < 0.01

Table 26. Monthly variations in yield performance of ten clones during 1987 (percentage of annual mean)

	RRIC 45	RRIC 100	RRIC 7	RRIC 104	RRIC 105	RRIC 52	RRIC 36	GT 1	Nab 17	RRIC 102	Mean = 3.53 CD = 9.78
January	120.99	97.16	147.12	169.82	83.34	88.69	148.84	159.88	159.37	88.14	126.34
February	38.67	72.39	80.12	65.12	31.55	56.21	74.03	59.03	38.34	42.23	55.77
March	27.17	38.82	57.41	47.10	30.13	36.54	51.89	43.15	47.01	48.46	42.77
April	41.40	47.34	65.19	58.55	40.00	58.61	63.54	52.60	68.78	55.54	55.15
May	53.78	82.18	74.37	92.66	59.28	75.78	106.67	60.80	74.54	79.34	75.94
June	106.83	120.27	99.44	100.23	92.28	87.77	101.98	74.10	113.34	98.77	99.50
July	164.02	14.344	119.26	124.17	144.80	124.71	126.02	106.78	143.64	110.66	108.75
August	126.16	132.26	105.01	122.90	121.70	123.48	107.76	138.38	120.72	146.68	124.50
September	148.27	123.37	129.56	123.08	162.21	151.96	123.76	138.25	122.71	137.70	136.09
October	131.48	125.03	108.39	107.29	134.67	150.02	120.15	146.39	118.34	140.17	128.19
November	106.61	97.30	92.85	91.82	133.14	127.62	78.50	100.95	91.09	134.36	105.43
December	134.58	120.45	121.16	97.22	167.07	118.67	96.95	119.68	105.22	116.58	119.76

For means in the body of the table SE = 11.15. CD = 39.91.

CD at 5% level.

Table 25. Monthly variations in yield performance of ten clones during 1986 (percentage of annual mean

	RRIC 45	RRIC 100	RRIC 7	RRIC 104	RRIC 105	RRIC 52	RRIC 36	GT 1	Nab 17	RRIC 102	Mean
											SE = 2.32 CD = 6.43
January	85.02	79.42	82.01	88.55	56.82	75.93	93.32	139.68	101.92	75.72	87.84
February	32.12	73.24	51.78	68.76	37.97	66.62	70.25	72.02	50.23	52.39	57.54
March	27.74	61.85	48.53	50.29	62.27	71.28	53.37	51.51	36.32	63.99	52.72
April	53.22	69.54	77.72	68.57	68.95	67.90	84.32	37.96	64.33	51.81	64.43
May	74.48	79.92	85.85	61.68	123.24	76.25	77.96	48.13	82.83	72.05	78.24
June	126.95	114.97	122.27	110.20	115.56	115.95	110.94	103.08	108.08	112.84	114.08
July	109.04	106.36	108.19	118.58	113.60	107.13	105.02	117.11	120.15	109.94	111.51
August	122.36	105.39	114.26	102.16	116.37	105.02	122.32	105.54	114.42	120.36	112.82
September	157.17	122.52	131.12	137.80	136.03	114.88	127.73	128.32	129.30	116.12	130.10
October	154.38	124.22	117.75	128.53	121.92	119.49	120.97	125.26	129.03	144.84	128.64
November	131.00	132.15	126.04	122.97	130.54	147.19	116.78	128.29	123.35	150.12	130.84
December	128.23	130.43	134.49	141.76	116.91	132.31	126.21	143.13	137.29	129.77	132.05

For means in the body of the table SE = 7.33. CD = 20.32.

CD at 5% level.

Table 27. Interclonal differences for the variations of rubber yield (y initial rate of flow (F), plugging index (PI) and dry rubber content (d.r.c.) during drought period (variations as % of annual mean)

Clones	y** SE = 3.219 CD = 6.764	F** SE = 5.860 CD = 12.31	PI* SE = 9.428 CD = 19.807	d.r.c. SE = 3.894 CD = -
RRIC 45	54.35 ^H	29.95 ^H	51.89 ^H	15.00
RRIC 100	32.42 ^L	15.00	35.63	7.10
RRIC 7	30.32 ^L	7.11 ^L	20.92 ^L	7.00
RRIC 104	35.82	7.49	26.77	14.20
RRIC 105	41.98 ^H	32.45 ^H	51.00 ^H	11.97
RRIC 52	33.75	20.73	19.99 ^L	8.13
RRIC 36	25.75	5.07 ^L	25.63	16.08
GT 1	48.87 ^H	10.90	25.75	6.37
Nab 17	38.56	6.95 ^L	21.50	8.02
RRIC 102	34.46	17.65	33.48	11.48
Mean	37.01	15.33	31.26	10.56
CD (general mean vs individual clones)	4.537	8.110	10.287	--

* $P < 0.05$

** $P < 0.01$

CD at 5% level

Table 28. Estimates of variability and genetic parameters for yield, girth and latex flow characters

Characters	G.C.V.	P.C.V.	Heritability %	Genetic advance %
Dry rubber yield	17.5194	21.5738	65.9459	29.3050
Latex volume	17.2790	21.6234	63.8543	28.4400
Dry rubber content	5.7875	7.4032	61.1136	9.3200
Initial rate of flow	13.0384	19.1485	45.9500	18.2100
Plugging index	14.6700	20.7200	50.0100	21.3740
Duration of flow	8.7281	12.4869	48.8572	12.5683
Girth	8.2967	9.6743	73.1092	14.5702

Table 29. Estimates of variability and genetic parameters for anatomical characters

Characters	G.C.V.	P.C.V.	Heritability %	Genetic advance %
Number of latex vessel rows	22.0232	24.8934	78.2692	40.1400
Density of latex vessels	4.5733	6.0116	57.8734	7.1666
Diameter of latex vessels	6.8137	8.4048	65.7220	11.3787
Intensity of anastomosing	8.5416	10.0806	71.7964	14.9100
Laticifer area index	24.0061	30.5959	61.5656	38.8051
Height of phloem rays	12.0114	12.9928	85.4637	22.8735
Width of phloem rays	9.8203	10.7235	83.8637	18.5250
Height/width ratio of phloem rays	17.8780	19.6137	83.0848	33.5700
No of primary xylem points	21.9058	26.5155	68.2734	37.2847
No. of intraxylary phloem points	24.7012	29.7291	69.0355	42.2815

Table 30. Estimates of variability and genetic parameters for the variations of yield and latex flow characters during drought period

Characters	G.C.V.	P.C.V.	Heritability %	Genetic advance %
Dry rubber yield	22.3260	24.6700	81.9300	41.6300
Total volume of latex	18.6166	26.6047	48.9600	26.8300
d.r.c.	22.9571	50.7591	45.2276	47.2900
Initial rate of flow	57.9885	74.5284	60.5394	92.9481
Plugging index	31.1034	48.8553	41.4893	41.6700
Duration of flow	15.5103	31.4177	49.3680	31.9525

Table 31. Simple correlations of juvenile versus mature trees for bark anatomical characters and girth

Characters	Correlation coefficient
Number of latex vessel rows	0.5619**
Density of latex vessels	0.2724
Diameter of latex vessels	0.1461
Laticifer area index	0.3955*
Intensity of latex vessel anastomosing	-0.0680
Width of phloem rays	0.4972**
Girth of the tree	0.4720**

* $P < 0.05$

** $P < 0.01$

CD at 5% level

Table 32. Associations of certain structural traits in virgin and renewed bark

Simple correlation			Partial correlation		Multiple correlation		R^2
Source	r		Source	r	Source	r	%
a_1 b_1	-0.28		d_1 $a_1.c_1$	-0.27	R $d_1.a_1$ c_1	0.82**	67.24
a_1 d_1	-0.59**		d_1 $c_1.a_1$	-0.71**			
c_1 d_1	-0.81**						
a_2 b_2	-0.12		d_2 $a_2.c_2$	-0.49*	R d_2 $a_2.c_2$	0.81**	65.61
a_2 d_2	-0.69**		d_2 $c_2.a_2$	-0.59**			
c_2 d_2	-0.74**						

* $P < 0.05$ ** $P < 0.01$

a) Total bark thickness

b) Proportion of soft bast

c) Total number of latex vessel rows

d) Proportion of uncut latex vessel rows

Table 33. Association of certain leaf anatomical traits with yield

Thickness of midrib	Width of midrib	Height of palisade cells	Width of palisade cells
-0.2407	-0.3758*	-0.0650	-0.1280

* $P < 0.05$

Table 34. Correlations of the number of intraxylary phloem with certain growth characters

Number of primary xylem points	Diameter of one year old twig	Rate of girth incre- ment on tapping
0.8158**	0.5067**	0.4231*

* $P < 0.05$

** $P < 0.01$

Table 35. Simple correlations among leaf retention percentage and stomatal characters

Characters	x_1	x_2	x_3	x_4	x_5
Leaf retention (%) (x_1)	1.0000	-0.7561**	-0.5883*	-0.0637	-0.7824**
No. of stomata/10 mm ² (x_2)		1.0000	-0.4644	-0.2043	0.9319**
Aperture length (x_3)			1.0000	0.2465	0.7410**
Aperture width (x_4)				1.0000	-0.0692
Aperture index (x_5)					1.0000

* $P < 0.05$ ** $P < 0.01$

Table 36. Partial and multitude correlations of leaf retention percentage and stomatal characters

First order		Second order	
Characters	Correlation value	Characters	Correlation value
$r_{12.3}$	-0.6743**	$r_{12.34}$	-0.6885**
$r_{12.4}$	-0.7873**	$r_{12.35}$	-0.3724
$r_{12.5}$	-0.1194	$r_{12.45}$	-0.2128
$r_{13.2}$	-0.5920*	$r_{13.24}$	-0.3182
$r_{13.4}$	-0.5920*	$r_{13.25}$	-0.3558
$r_{13.5}$	-0.0204	$r_{13.45}$	0.0727
$r_{14.2}$	-0.3405	$r_{14.23}$	-0.2139
$r_{14.3}$	0.1038	$r_{14.15}$	-0.2575
$r_{14.5}$	-0.1897	$r_{14.35}$	-0.2017
$r_{15.2}$	-0.3277	$r_{15.23}$	0.2530
$r_{15.3}$	-0.6381**	$r_{15.24}$	-0.2392
$r_{15.5}$	-0.7903**	$r_{15.34}$	-0.6520**

- * P 0.05 $R^1_{.2345} = 0.8233$ ** 1. Leaf retention %.
- ** P 0.01 $R^2_{.2345} = 67.7816$ 2. No. of stomata/10 mm².
3. Length of stomatal aperture.
4. Width of stomatal aperture.
5. Aperture index.

Table 37. Simple correlations of certain bark anatomical characters and girth on brown bast incidence and percentage girth increase

Characters	% incidence of brown bast	% girth increase over two years
Number of latex vessel rows	0.5561**	-0.1053
Density of latex vessels	0.2812	-0.4367*
Diameter of latex vessels	-0.2184	0.4768**
Laticifer area index	0.3898*	0.2599
H/W ratio of phloem rays	0.0831	-0.3919*
Intensity of anastamosing	0.0979	-0.3274
Girth	-0.0586	0.3547
% girth increase over 2 years	-0.1673 0.4372	-- 0.1841

* $P < 0.01$

** $P < 0.05$

Table 39. Simple and partial correlations among brown bast incidence (x_1), total volume of latex (x_2), number of latex vessel rows (x_3) and number of intraxylary phloem (x_4)

Simple correlation		First order partial correlations		Second order partial correlations	
Source	r value	Source	r value	Source	r value
$rx_1 x_2$	0.4620*	$rx_1 x_3 \cdot x_2$	0.3507	$rx_1 x_4 \cdot x_2 x_3$	-0.5431**
		$rx_1 x_4 \cdot x_2$	-0.3352		
$rx_1 x_3$	0.5561**	$rx_1 x_4 \cdot x_3$	-0.2381		
		$rx_1 x_2 \cdot x_3$	0.0371		
$rx_1 x_4$	-0.4372*	$rx_1 x_2 \cdot x_3$	0.371		
		$rx_1 x_3 \cdot x_4$	0.4409*	$rx_1 x_2 \cdot x_3 x_4$	0.0451
$rx_2 x_3$	0.7981**	$rx_1 x_2 \cdot x_4$	0.3703*		
$rx_2 x_4$	-0.3415	$rx_2 x_4 \cdot x_3$	0.0228		
$rx_3 x_4$	-0.4726**	$rx_3 x_4 \cdot x_2$	-0.3834*	$rx_1 x_3 \cdot x_2 x_4$	0.3454

* $P < 0.05$

** $P < 0.01$

Table 38. Simple, partial and multiple correlations of brown bast incidence (x_1) with latex volume (x_2) and rubber yield (x_3)

Simple correlations		Partial and multiple correlations	
Source	r value	Source	r value
$r_{x_1 x_2}$	0.4621*	$r_{13.2}$	-0.0997
$r_{x_1 x_3}$	0.3812*	$r_{12.3}$	0.2981
$r_{x_2 x_3}$	0.9061**	$R_{1.23}$	0.4703*

$$R^2_{1.23} = 0.2212$$

* $P < 0.05$

** $P < 0.01$

Table 40. Multiple correlations of brown bast incidence (x_1), total volume of latex (x_2), number of latex vessel rows (x_3) and number of intraxylary phloem (x_4)

Source	R	R^2
$R_{1.23}$	0.6279**	0.3942
$R_{1.24}$	0.5493**	0.3018
$R_{1.34}$	0.6183**	0.3823
$R_{1.234}$	0.6992**	0.4889

* $P < 0.05$

** $P < 0.01$

Table 41. Genotypic correlations among rubber yield (mean over three years from the ninth year of planting) and the girth and bark anatomical characters at maturity (eighth year of planting).

Characters	Rubber yield	Girth	Laticifer area index	Latex vessel diameter	Latex vessel density	Intensity of anastomosing	Total No. of latex vessel rows	Height of phloem rays	Width of phloem rays
Rubber yield	1	-0.0336	0.6910**	0.2033	0.1809	0.3022	0.5888**	0.0528	-0.2541
Girth		1	0.2714	0.4990**	-0.3922*	-0.1709	-0.2762	-0.2712	0.4909**
Laticifer area index			1	0.5680**	-0.2686	-0.0151	0.7521**	0.0613	-0.0007
Latex vessel diameter				1	-0.6028**	0.1002	0.0325	-0.2273	0.3524
Latex vessel density					1	0.3433	-0.1226	-0.0441	-0.7254**
Intensity of latex vessel anastomosing						1	-0.1102	-0.0233	-0.2376
Total number of latex vessel rows							1	0.2959	-0.1297
Height of phloem rays								1	-0.1994
Width of phloem rays									1

Table 42. Direct and indirect effects of bark anatomical characters and girth at maturity (8th year of planting) on subsequent yield (mean over three years from the ninth year of planting).

Characters	Girth	Laticifer area index	Diameter of latex vessels	Density of latex vessels	Intensity of latex vessel anastomosing	Total No. of latex vessel rows	Height of phloem rays	Width of phloem rays	Genotypic correlations with rubber yield
Girth	<u>-0.4806</u>	0.4971	-0.3252	-0.0108	-0.0431	0.2296	0.0135	0.0858	-0.0336
Laticifer area index	-0.1304	<u>1.8315</u>	-0.3702	-0.0074	-0.0038	-0.6254	-0.0031	-0.0001	0.6910**
Diameter of latex vessels	-0.2398	1.0402	<u>-0.6517</u>	-0.0166	0.0253	-0.0271	0.0114	0.0616	0.2033
Density of latex vessels	0.1885	-0.4919	0.3928	<u>0.0275</u>	0.0866	0.1020	0.0022	-0.1268	0.1809
Intensity of latex vessel anastomosing	0.0821	-0.0276	-0.0653	0.0095	<u>0.2523</u>	0.0917	0.0012	-0.0415	0.3022
Total number of latex vessel rows	0.1327	1.3775	-0.0212	-0.0034	-0.0278	<u>-0.8315</u>	-0.0148	-0.0227	0.5888**
Height of phloem rays	0.1303	0.1123	0.1481	-0.0012	-0.0059	-0.2461	<u>-0.0499</u>	-0.0349	0.0528
Width of phloem rays	-0.2359	-0.0013	-0.2297	-0.0200	-0.0599	0.1079	0.0100	<u>0.1749</u>	-0.2541

Residual effect 0.5534. The direct effects are underlined.

Table 44. Direct and indirect effects of structural and latex flow characters on rubber yield at a specific year.

Characters	No. of L.V.R. of L.V.	Density of L.V.	Diameter of L.V.	Girth index	Laticifer area index	Inten-sity of anastomosing	Height of phloem rays	Width of phloem rays	H/W ratio of phloem rays	Diameter of cells	Duration of flow	Plugging index	Total volume of latex	d.r.c.	Initial rate of flow	Genotypic correlation with rubber yield
No. of latex vessels	-0.2511	0.0327	-0.0587	0.0508	0.3441	0.0016	-0.0566	-0.0247	0.0831	-0.0220	0.1157	-0.0295	0.3786	-0.0399	0.0036	0.5281**
Density of latex vessels	0.0398	-0.2060	0.0673	0.0085	0.0562	0.0026	0.0941	-0.0005	-0.0965	-0.0391	0.0075	0.0127	0.0385	0.1094	0.0012	-0.0167
Diameter of latex vessels	-0.0723	0.0680	-0.2039	-0.0847	0.2502	-0.0038	-0.0514	0.0640	-0.0410	0.0274	0.0497	-0.0100	0.0450	-0.0386	-0.0005	-0.0018
Girth	0.0489	0.0068	-0.0662	-0.2611	0.1132	0.0033	-0.0080	0.1020	-0.1302	0.0158	0.0881	-0.0119	0.1206	0.0119	-0.0029	0.0302
Laticifer area index	-0.2067	0.0277	-0.1221	-0.0707	0.4180	0.0011	-0.0671	0.0547	-0.0159	-0.0023	0.1680	-0.0353	0.4046	-0.0585	0.0023	0.4977**
Intensity of anastomosing	-0.0166	-0.0222	0.0321	-0.0363	0.0188	0.0239	0.0010	-0.0337	0.0417	-0.0101	0.0884	-0.0243	0.3375	0.0481	0.0022	0.4505*
Height of phloem rays	-0.0634	0.0865	-0.0467	-0.0093	0.1251	-0.0001	-0.2242	0.0268	0.2214	0.0220	0.0473	-0.0135	0.0810	-0.1306	0.0004	0.1127
Width of phloem rays	0.0316	0.0005	-0.0667	-0.1360	0.1169	-0.0041	-0.0308	0.1957	-0.2405	0.0376	0.0527	-0.0027	0.0831	-0.0353	0.0005	0.0025
H/W ratio of phloem rays	-0.0588	0.0560	0.0235	0.0958	-0.0188	0.0028	-0.1399	-0.1326	0.3550	-0.0137	-0.0185	-0.0064	-0.0331	-0.0685	-0.0006	0.0503
Diameter of ray cells	0.0675	0.0984	-0.0682	-0.0504	-0.0115	-0.0029	-0.0601	0.0898	-0.0593	0.0819	0.0009	0.0031	-0.0610	-0.0567	0.0011	-0.0274
Duration of flow	-0.0942	-0.0050	-0.0328	-0.0746	0.2276	0.0069	-0.0344	0.0334	-0.0121	0.0002	0.3084	-0.0553	0.4640	-0.1793	-0.0019	0.5509**
Plugging index	0.1117	-0.0394	0.0308	0.0471	-0.2228	-0.0088	0.0458	-0.0080	-0.0344	0.0038	-0.2577	0.0662	-0.4854	0.1663	0.0010	-0.5838**
Total volume of latex	-0.1350	-0.0113	-0.0130	-0.0447	0.2401	0.0115	-0.0258	0.0284	-0.0167	-0.0071	0.2032	-0.0456	0.7043	-0.0007	0.0057	0.8880**
d.r.c.	0.0262	-0.0589	0.0206	-0.0091	-0.0640	0.0030	0.0766	-0.0181	-0.0636	-0.0121	-0.1447	0.0288	-0.0012	0.3823	0.0047	0.1715
Initial rate of flow	-0.0798	-0.0198	0.0080	0.0636	0.0815	0.0043	-0.0081	0.0088	-0.0186	0.0072	-0.0494	0.0055	0.3325	0.1494	0.0120	0.4972**

Residual effect is 0.3180. The direct effects are in diagonals and underlined.

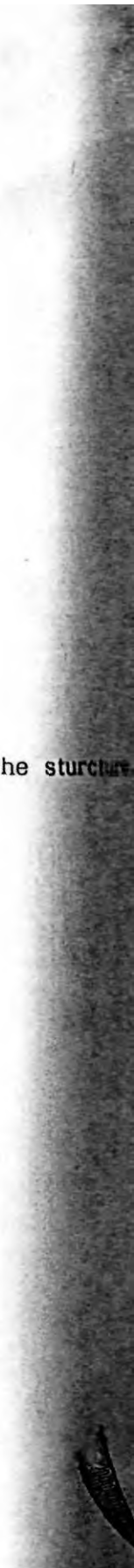
Table 46 Direct and indirect effects of girth and anatomical characters at maturity (8th year of planting) on percentage girth increase on tapping (mean over three years from the 9th year of planting).

Characters	girth	Laticifer area index	Diameter of latex vessels	Density of latex vessels	Intensity of anastomosing	No. of latex vessel rows	Height of phloem rays	Width of phloem rays	No. of intraxylary phloem	No. of primary xylem groups	No. of primary xylem points	Genotypic correlations with girth increase
Girth	-1.1817	0.7709	-0.7413	0.4320	0.0320	0.6489	0.1108	0.0742	-0.0078	0.1920	0.3300	
Laticifer area index	-0.3207	2.8405	-0.8438	0.2959	0.0028	-1.7674	-0.0251	-0.0001	0.0032	-0.0256	0.1597	
Diameter of latex vessels	-0.5897	1.6133	-1.4855	0.6639	-0.0188	-0.0765	0.0929	0.0532	-0.0071	0.1621	0.4079*	
Density of latex vessels	0.4635	-0.7630	0.8954	-1.1014	-0.0644	0.2882	0.0180	-0.1096	-0.0006	-0.0216	-0.3953*	
Intensity of anastomosing	0.0219	-0.0428	-0.1489	-0.3781	-0.1875	0.2591	0.0095	-0.0359	-0.0060	0.0898	-0.2389	
No. of latex vessel rows	0.3263	2.1364	-0.0484	0.1351	0.0207	-2.3499	-0.1209	-0.0196	0.0110	-0.1939	-0.1031	
Height of phloem rays	0.3204	0.1742	0.3376	0.0486	0.0044	-0.6954	-0.4086	-0.0301	0.0030	-0.0679	-0.3137	
Width of phloem rays	-0.5801	-0.0020	-0.5235	0.7989	0.0445	0.3048	0.0815	0.1511	0.0001	0.0418	0.3170	
No. of intraxylary phloem	-0.4545	-0.4409	-0.5157	-0.0299	-0.0549	1.2690	0.0605	-0.0006	-0.0203	0.3542	0.1668	
No. of primary xylem groups	-0.6043	-0.1935	-0.6416	0.0632	-0.0448	1.2139	0.0739	0.0168	-0.0192	0.3754	0.2399	

Residual effect is 0.7464. The direct effects are in diagonals and underlined.

FIGURES

Fig. 1. Hevea bark: a three dimensional view of the structure



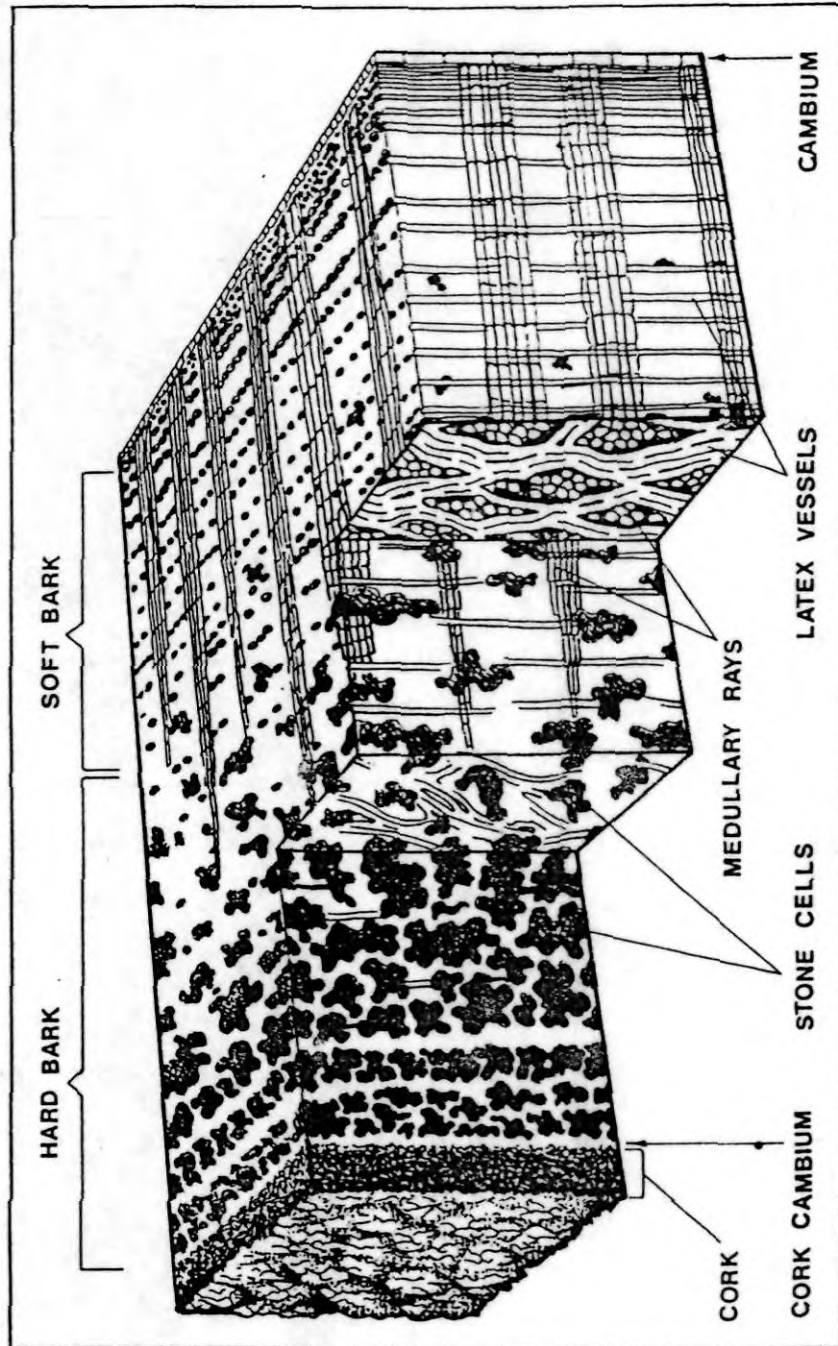


Fig. 2. Periodicity in cambial activity in eight Hevea clones.

- | PERIODS | |
|---------|---------------------|
| | 1. May-July |
| | 2. August-October |
| | 3. November-January |
| | 4. February-April |

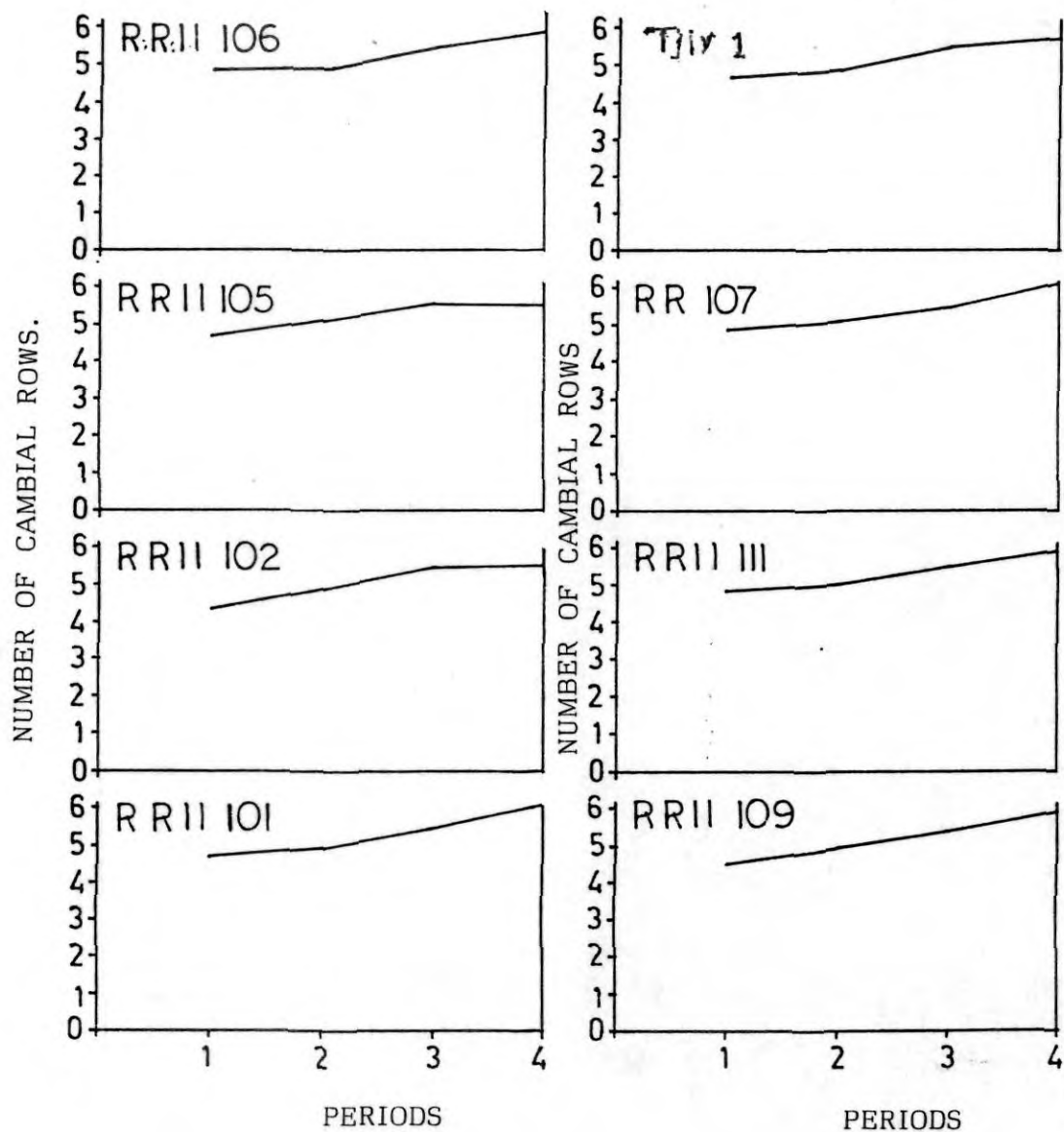


Fig. 3. Yearly variations in certain structural traits and girth, on tapping.

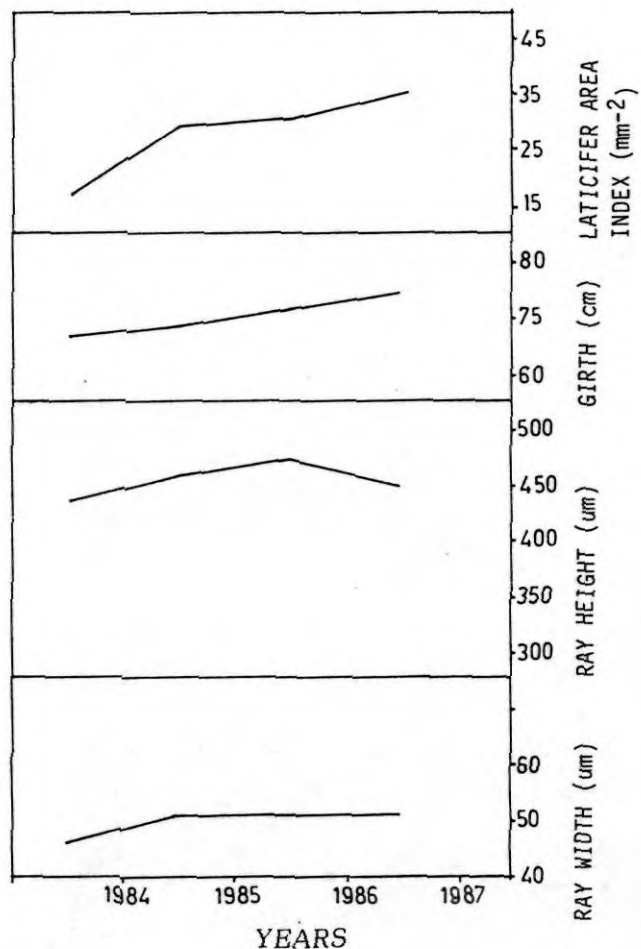
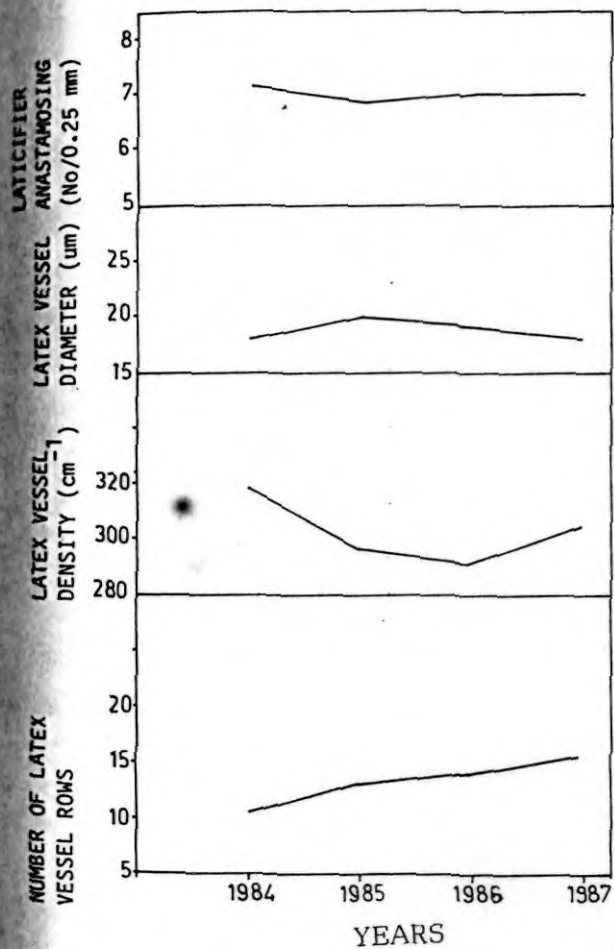
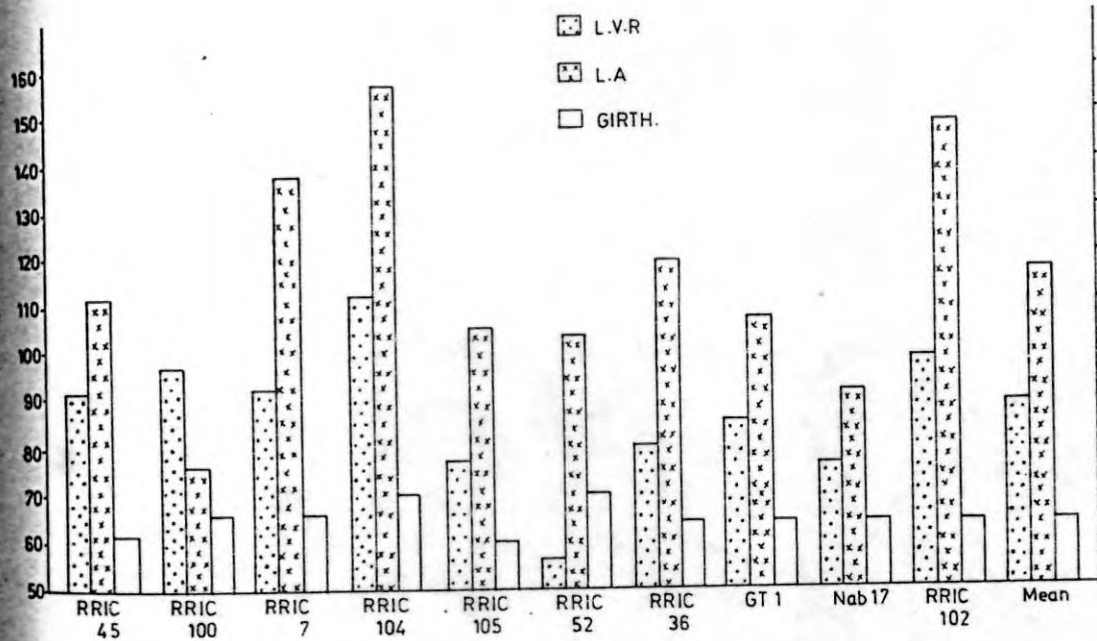


Fig. 4. Rate of increase in girth, number of latex vessel rows and laticifer area index over three years on tapping in ten Hevea clones.

PERCENTAGE INCREASE IN THE NUMBER OF LATEX
VESSEL ROWS AND LATICIFER AREA INDEX



PERCENTAGE INCREASE IN GIRTH

Fig. 5. Monthly variations of yield, d.r.c. and latex flow characters in Hevea.

Yield (◻)

d.r.c. (◼)

Plugging index (●)

Initial rate of flow (△)

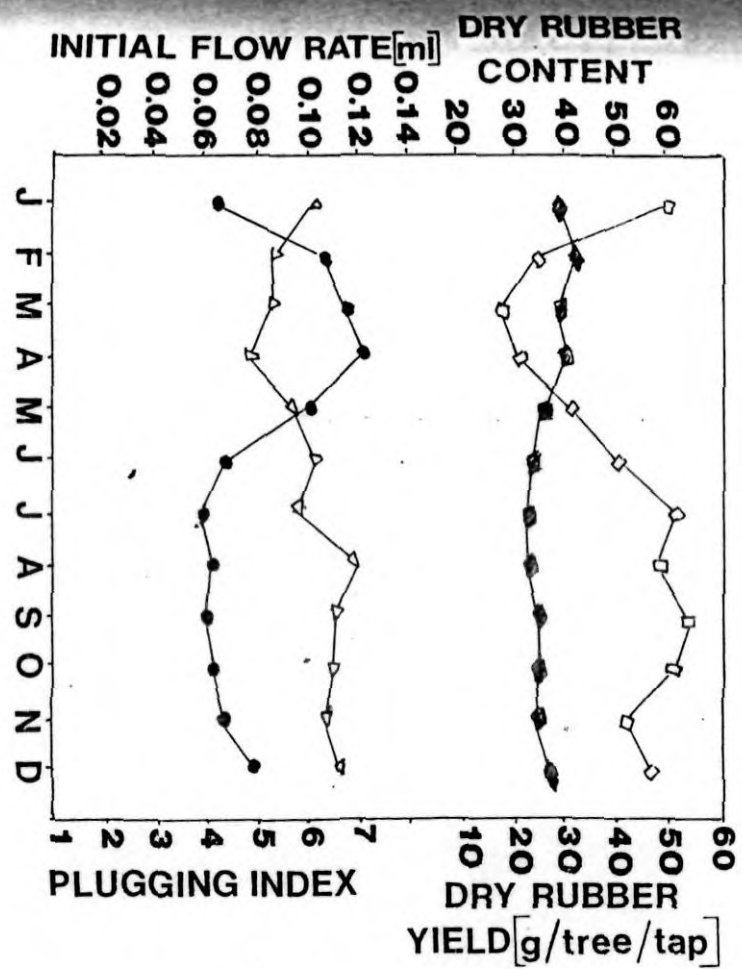


Fig. 6. Regression of yield on latex volume.

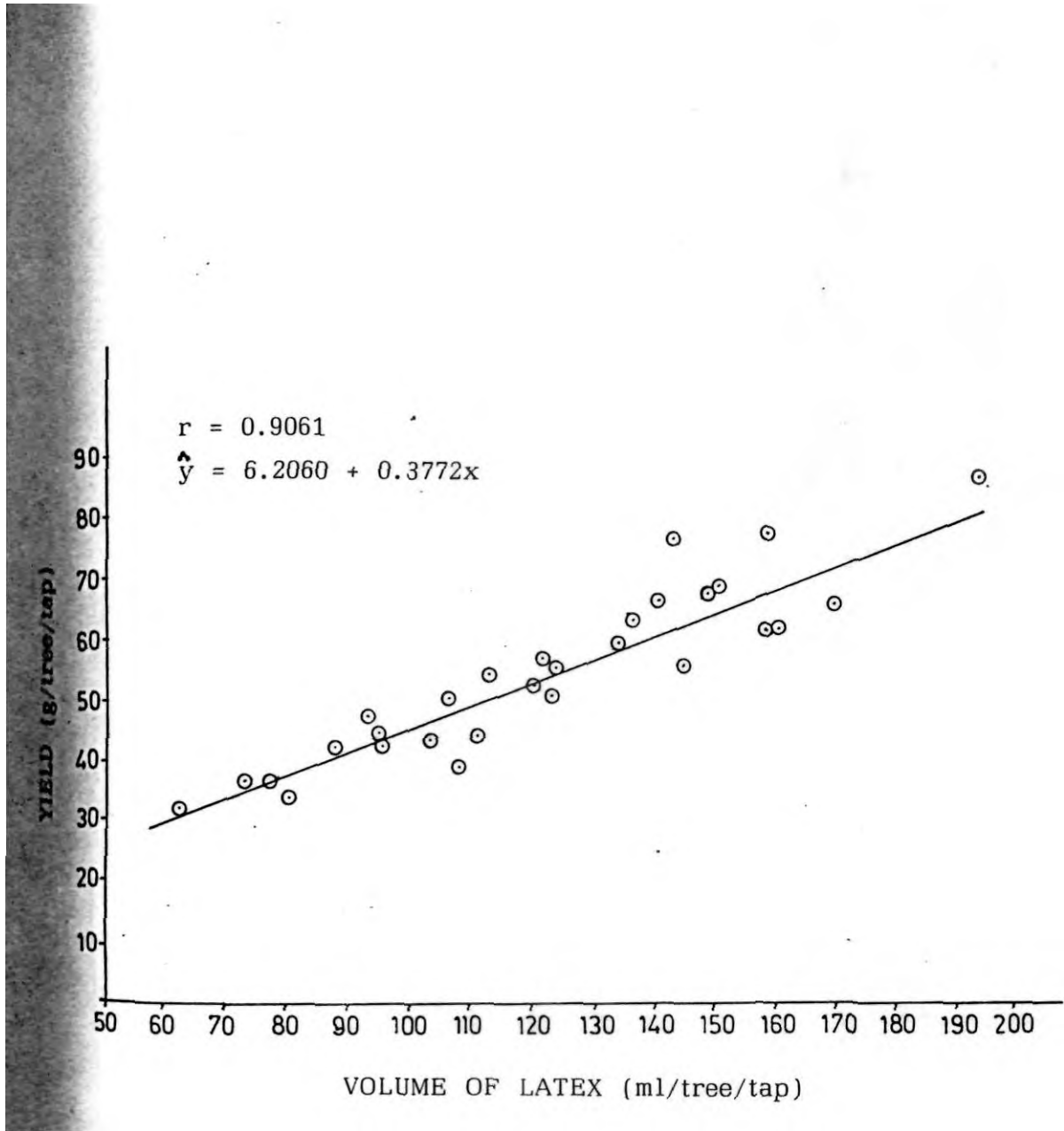


Fig. 7. Regression of latex volume on number of latex vessel rows.

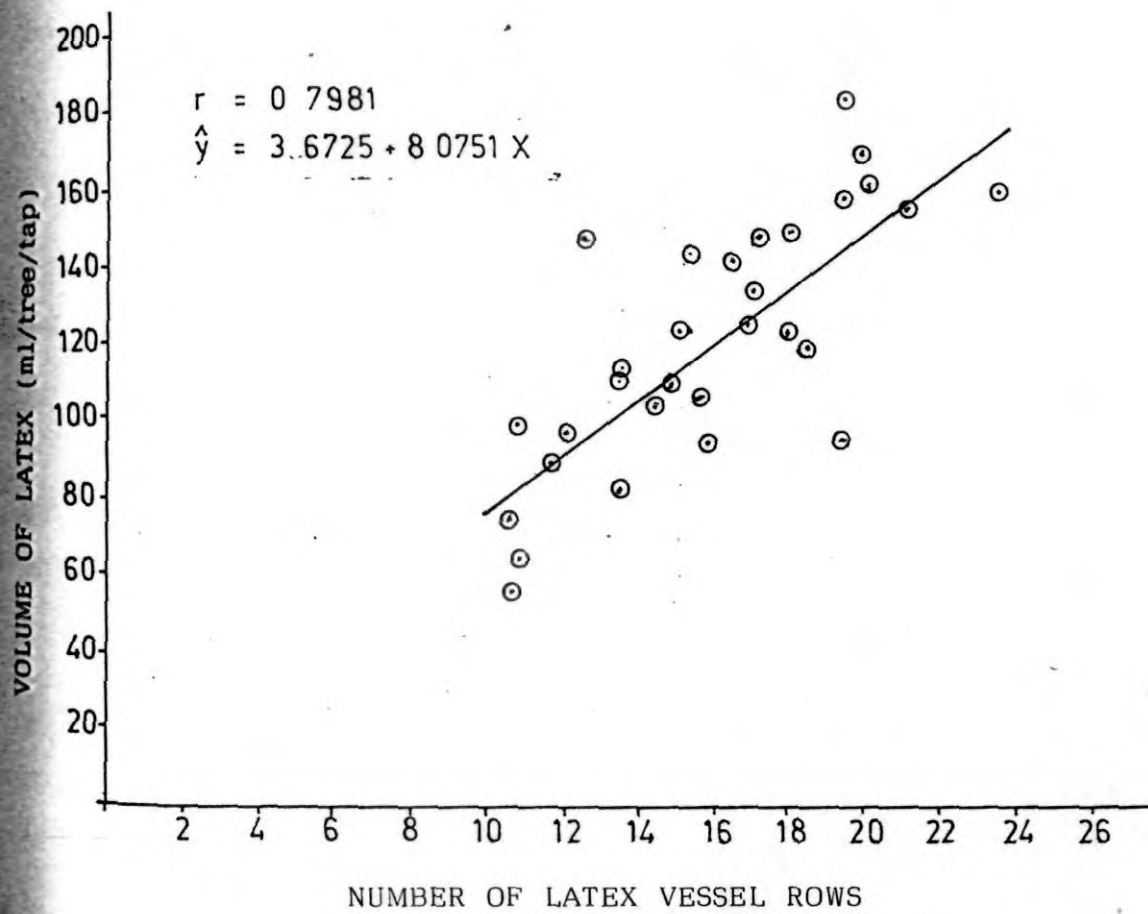


Fig. 8. Regression of brown bast incidence on number of latex vessel rows.

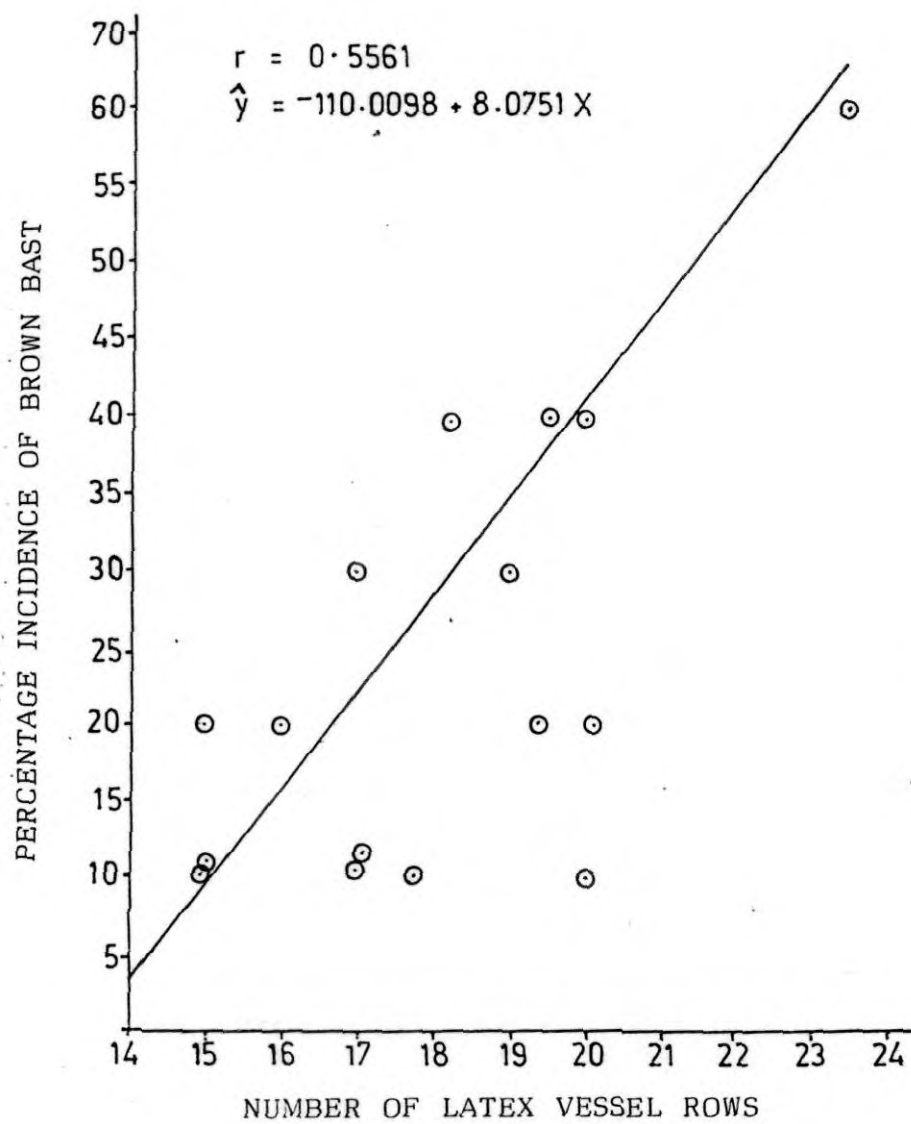


Fig. 9. Incidence of brown bast (%), rubber yield (g/tree/tap) and latex volume (ml/tree/tap) in ten Hevea clones.

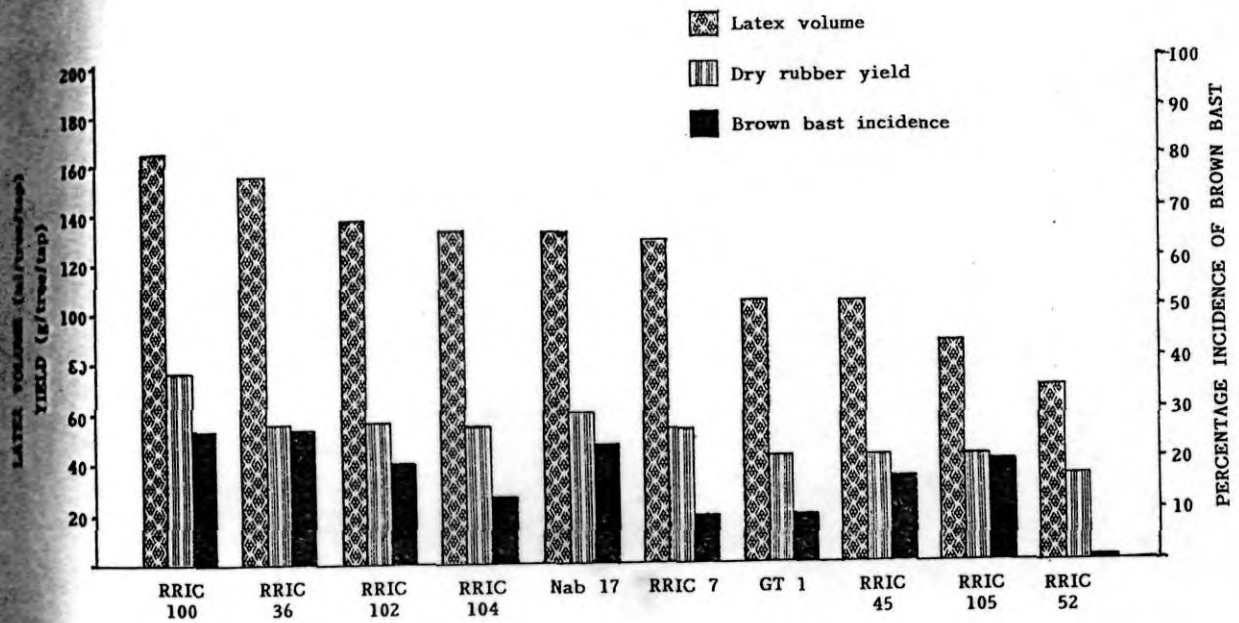
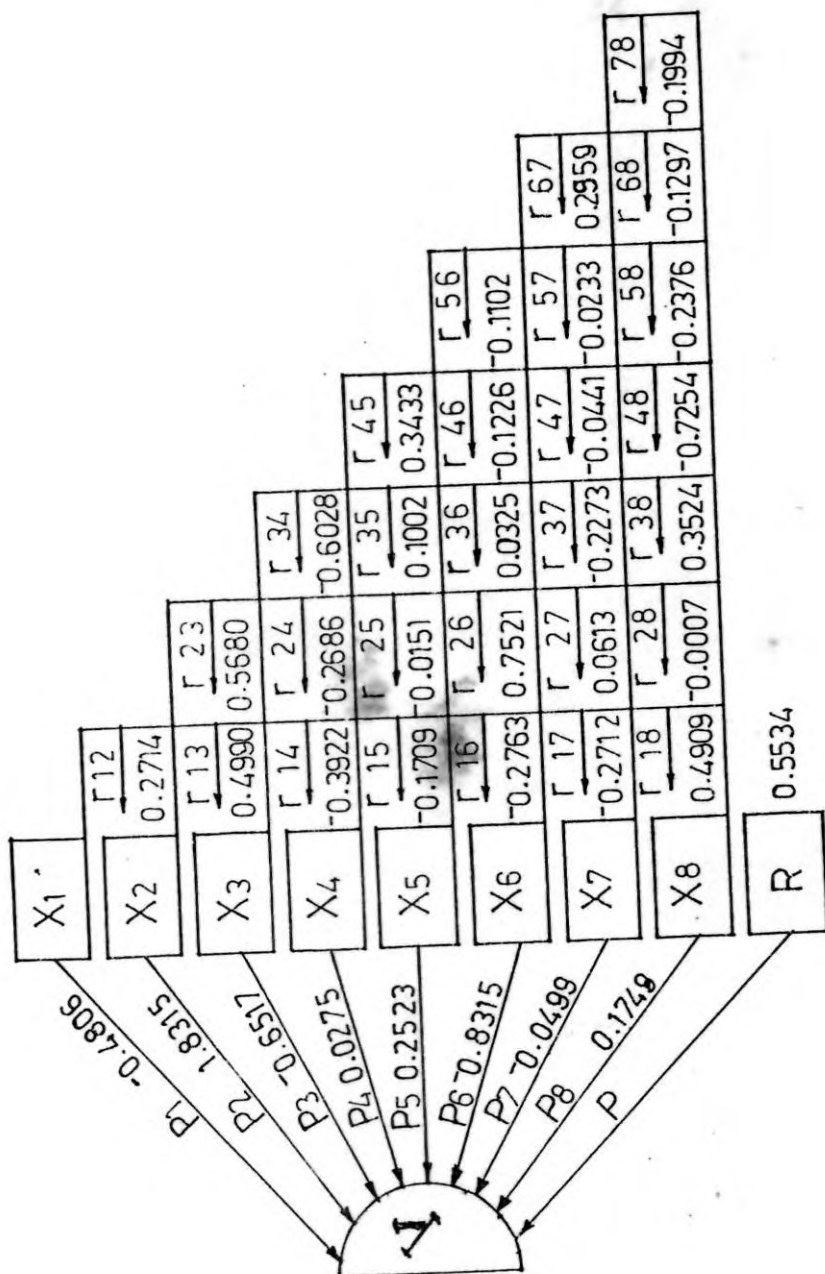


Fig. 10. Path diagram showing the direct effects of girth and bark anatomical characters at initial maturity (eighth year of planting) on rubber yield (mean over three years from the ninth year) and the inter-relationships of the characters.

- y - Yield
- x_1 - Girth
- x_2 - Laticifer area index
- x_3 - latex vessel diameter
- x_4 - latex vessel density
- x_5 - Intensity of laticifer anastamosing
- x_6 - Total number of latex vessel rows
- x_7 - Height of phloem rays
- x_8 - Width of phloem rays



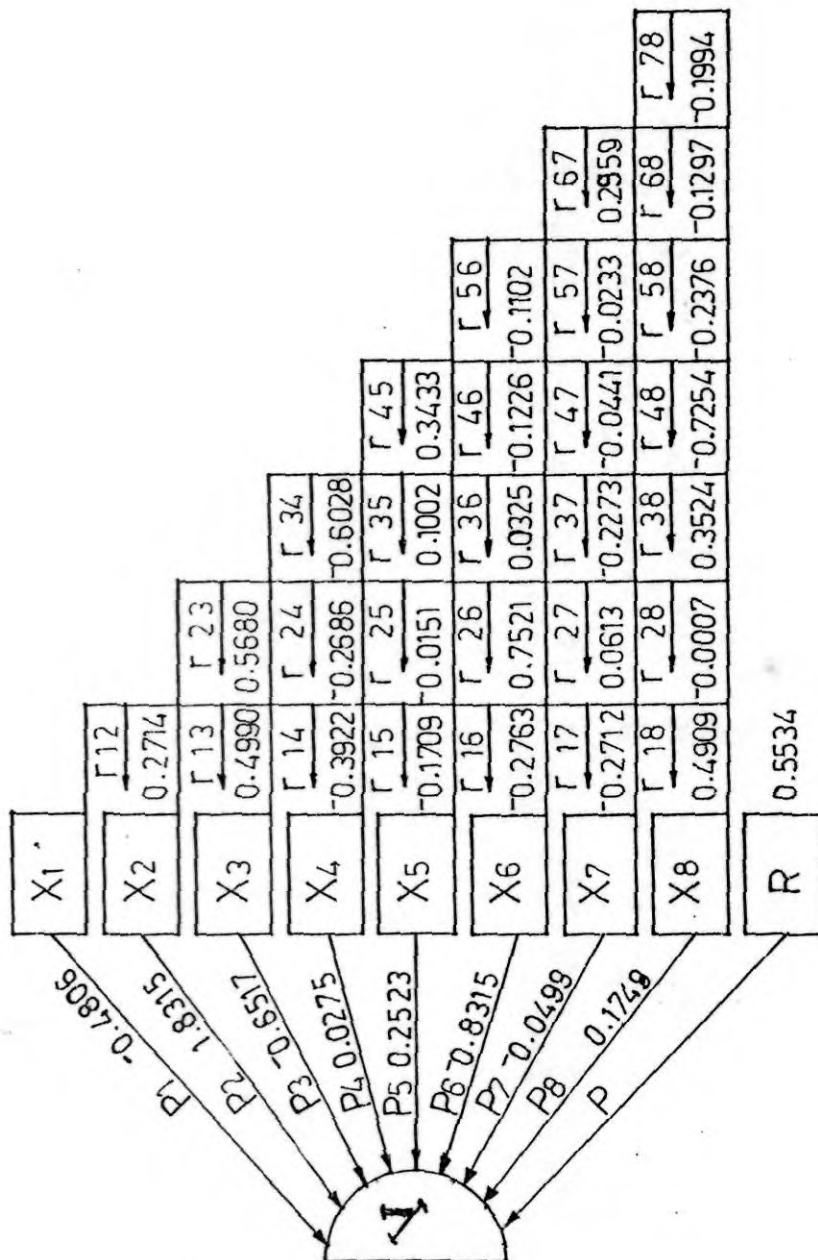


Table 41. Genotypic correlations among rubber yield (mean over three years from the ninth year of planting) and the girth and bark anatomical characters at maturity (eighth year of planting).

Characters	Rubber yield	Girth	Laticifer area index	Latex vessel diameter	Latex vessel density	Intensity of anastomosing	Total No. of latex vessel rows	Height of phloem rays	Width of phloem rays
Rubber yield	1	-0.0336	0.6910**	0.2033	0.1809	0.3022	0.5888**	0.0528	-0.2541
Girth		1	0.2714	0.4990**	-0.3922*	-0.1709	-0.2762	-0.2712	0.4909**
Laticifer area index			1	0.5680**	-0.2686	-0.0151	0.7521**	0.0613	-0.0007
Latex vessel diameter				1	-0.6028**	0.1002	0.0325	-0.2273	0.3524
Latex vessel density					1	0.3433	-0.1226	-0.0441	-0.7254**
Intensity of latex vessel anastomosing						1	-0.1102	-0.0233	-0.2376
Total number of latex vessel rows							1	0.2959	-0.1297
Height of phloem rays								1	-0.1994
Width of phloem rays									1

Fig. 11. Path diagram showing the direct effects of structural and latex flow characters on rubber yield at a specific year (11th year of planting) and the inter-relationships of the character.

- y - Yield
- x_1 - Number of latex vessel rows
- x_2 - Density of latex vessels
- x_3 - Diameter of latex vessels
- x_4 - Girth
- x_5 - Laticifer area index
- x_6 - Intensity of laticifer anastomosing
- x_7 - Height of phloem rays
- x_8 - Width of phloem rays
- x_9 - Height/width ratio of phloem rays
- x_{10} - Diameter of ray cells
- x_{11} - Duration of flow
- x_{12} - Plugging index
- x_{13} - Total volume of latex
- x_{14} - Dry rubber content
- x_{15} - Initial rate of flow

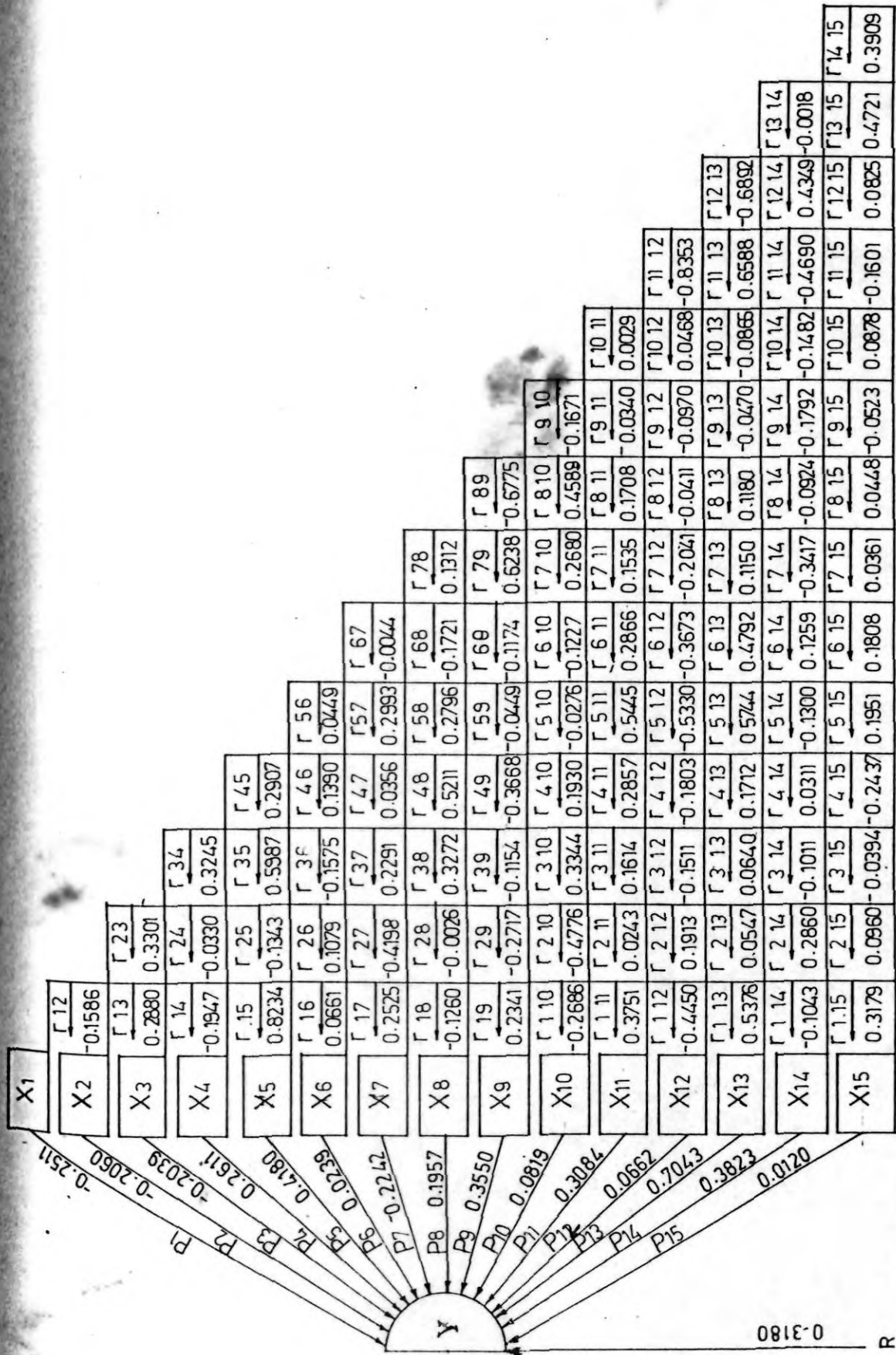
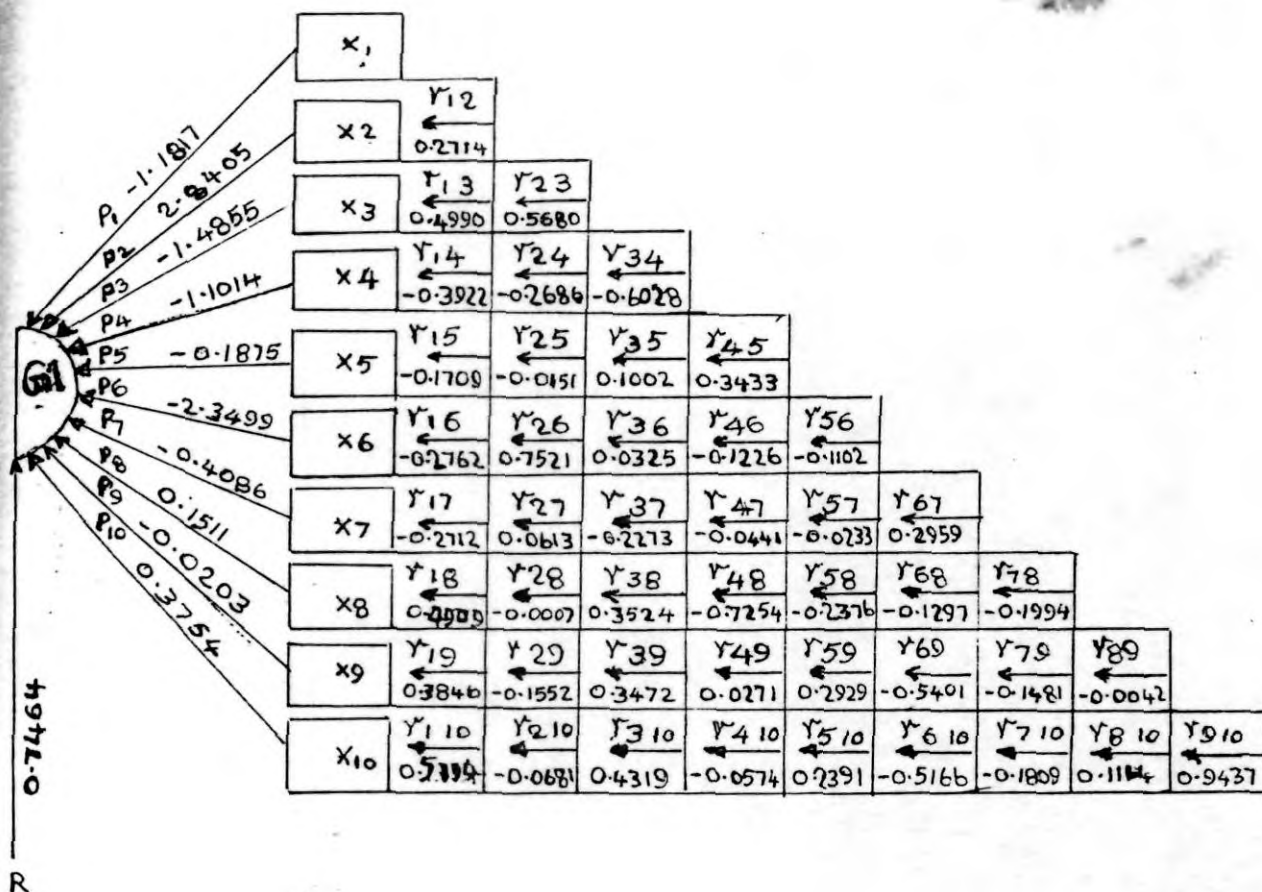


Fig. 12. Path diagram showing the direct effects of girth and bark anatomical characters at initial maturity (8th year of planting) on percentage girth increase on tapping (mean over three years from the 9th year of tapping).

- GI - Girth increase
- x_1 - Girth
- x_2 - Laticifer area index
- x_3 - Diameter of latex vessels
- x_4 - Density of latex vessels
- x_5 - Intensity of anastomosing
- x_6 - Number of latex vessel rows
- x_7 - Height of phloem rays
- x_8 - Width of phloem rays
- x_9 - Number of intraxylary phloem
- x_{10} - Number of primary xylem points



P L A T E S

Plate 1. Sections of Hevea bark, at the differentiating zone, in tangential plane.

A. Laticifer initials x 346.

B. Coenocytic latex vessels. The latex vessels at the stage just after the dissolution of cross walls x 624. Tangential connections between latex vessels have been formed (→).

C. Pit connections between latex vessels (L.V) and phloem rays (P.R) x 346.

D. Pit connections between latex vessels x 346.

Rocky

A



Plate 2. Variations in ray shape and clonal differences in the orientation of latex vessels in Hevea.

A. Tangential section of the bark of RRIC 105 x 300.

B. Tangential section of the bark of RRIC 104 x 300.

C. Tangential section of the bark of RRIC 45 x 300.

D. Tangential section of the bark of RRIC 100 x 300.

E-H. Ray types in terms of shape x 300.

E. Dumb bell

F. Oval

G. Spindle

H. Cricket bat shape



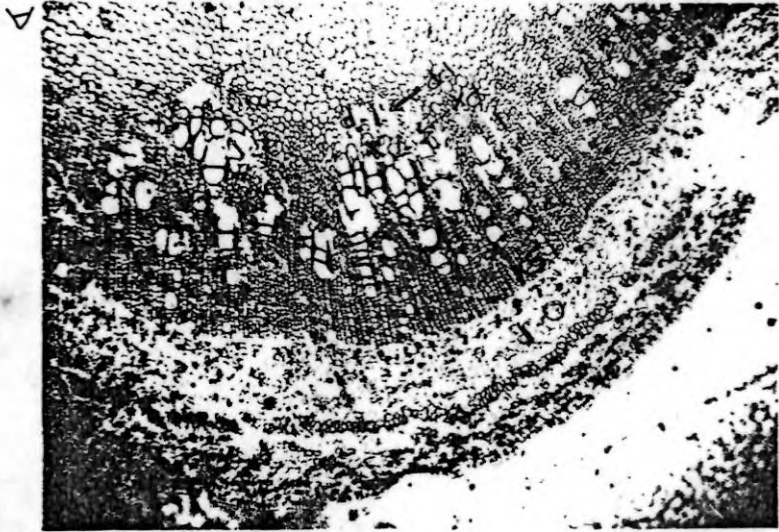
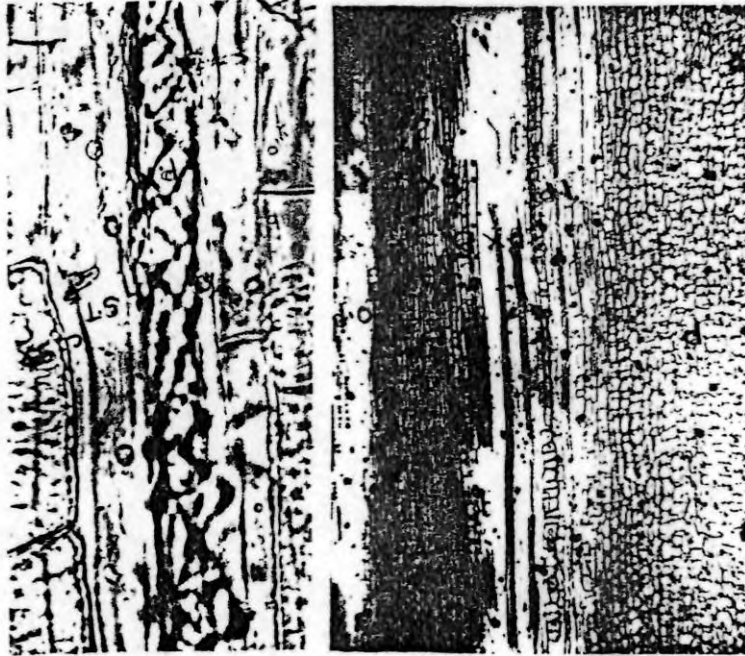
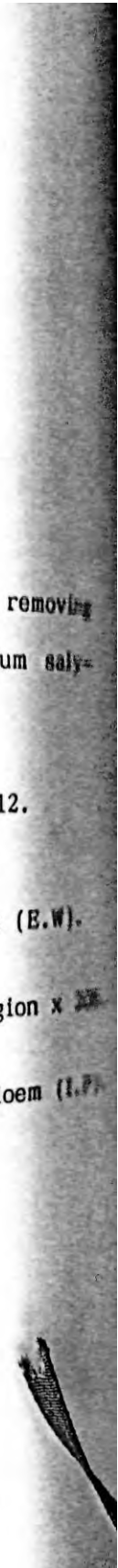


Plate 4. Leaf structure.

- A. Surface view of lower epidermis x 1178.
- B. Surface view of lower epidermis after removing the epicuticular wax by clearing in sodium salicylalex x 1178.
- C. Cross-sectional view of the leaf blade x 512.
Palisade layer (P.L); Spongy layer (S.L);
Stomata (St); Filaments of epicuticular wax (E.W).
- D. Cross section of the leaf at the midrib region x 250.
Xylem (X); Outer phloem (O.P); Inner phloem (I.P);



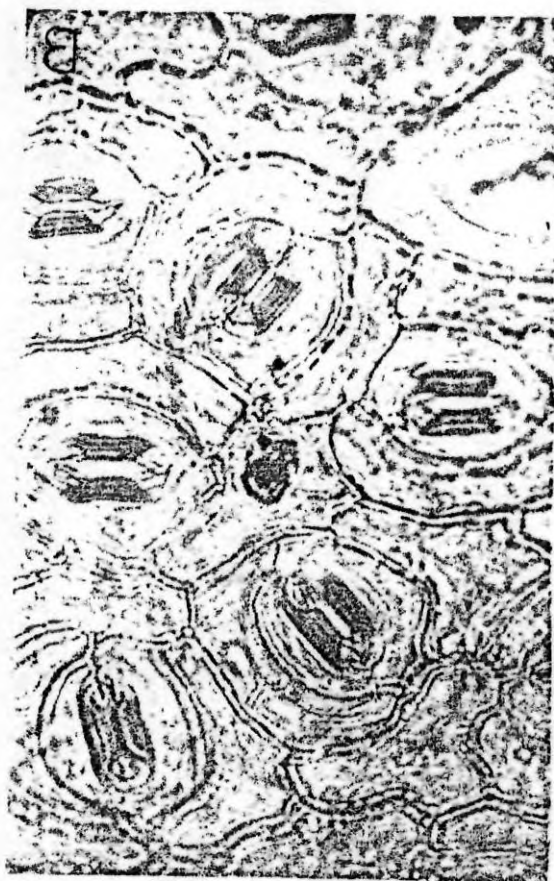
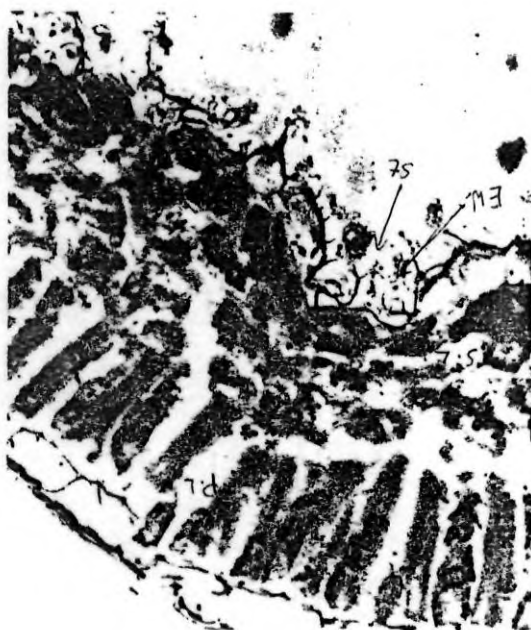


Plate 5. Scanning electron micrographs showing part to part differences in surface ornamentation.

- A. Surface of the petiole x 1000.
- B. Surface of the vein x 1000.
- C. Surface of the petiolule x 1000.
- D. Surface of the fruit wall x 1000.
- E. A stomata on the leaf blade x 4800.

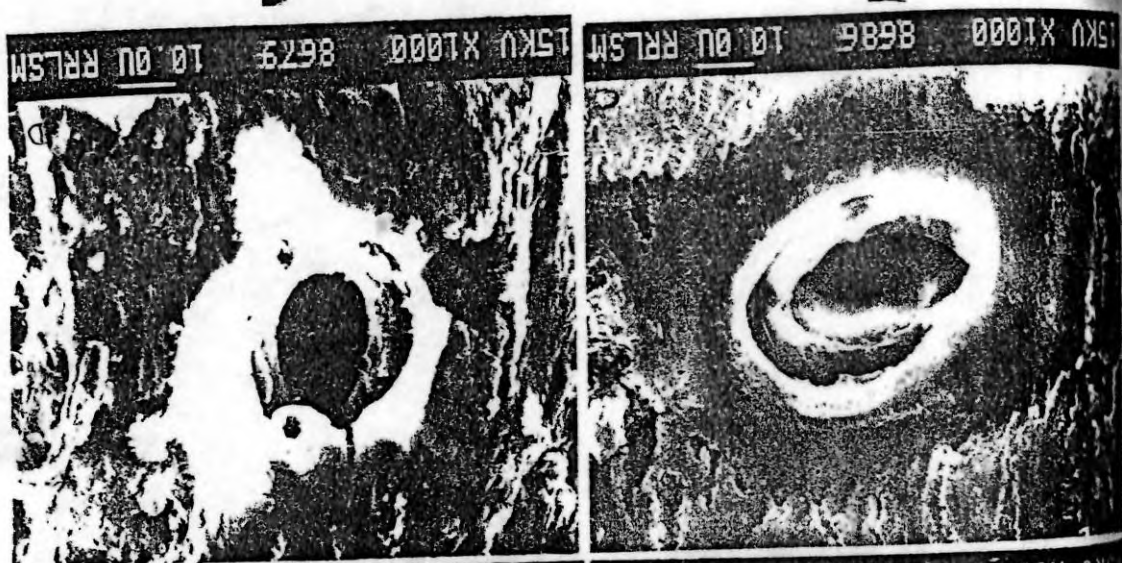
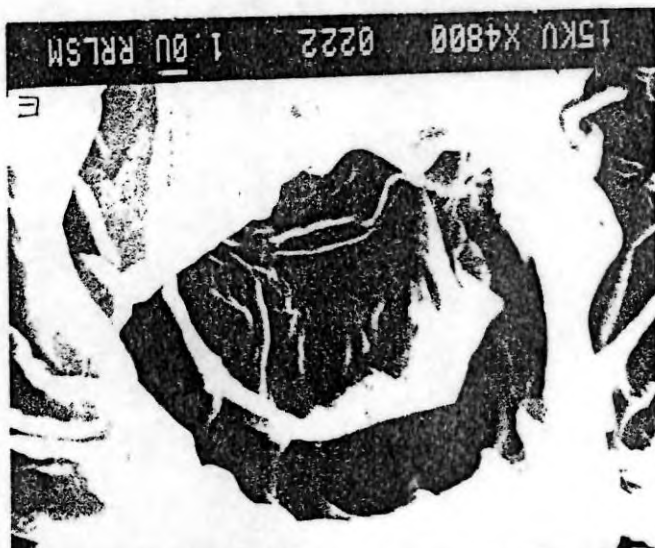
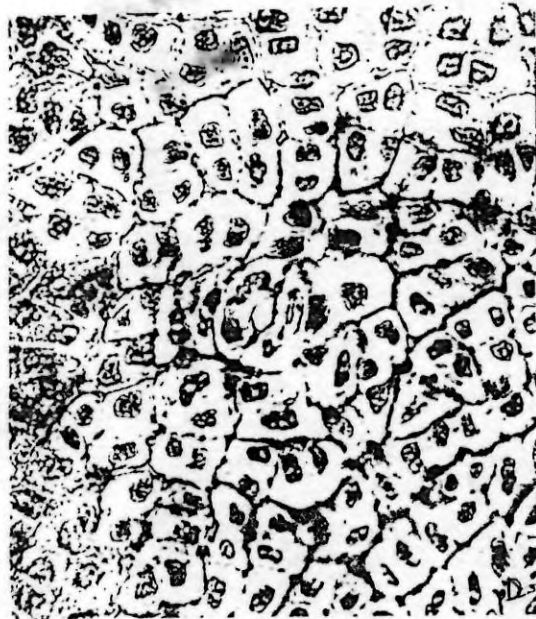
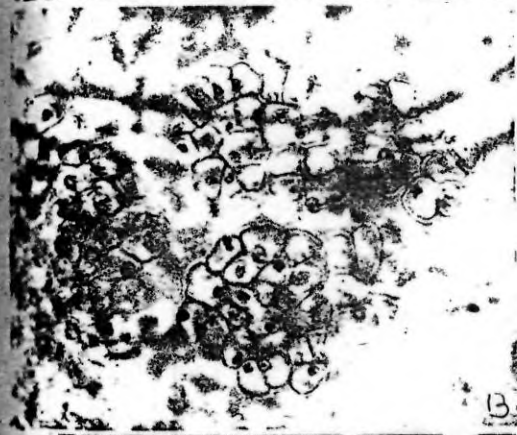
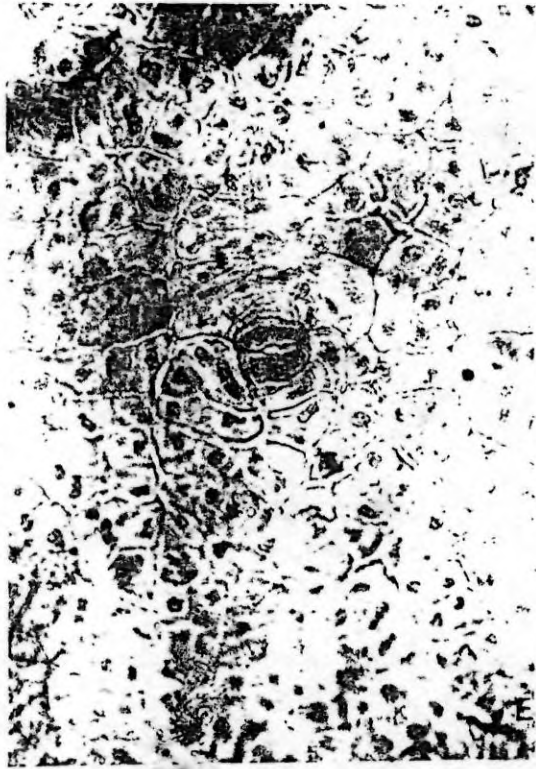
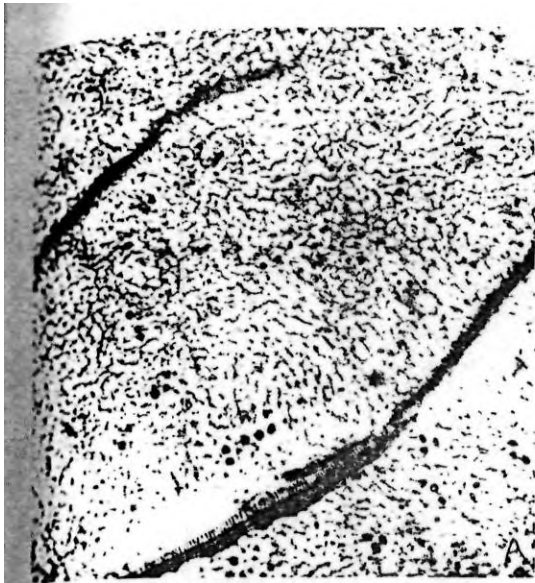


Plate 6. Ontogeny of the normal stomata.

- A. Division of stomatal mother cell of leaf blade
x 300.
- B. The resultant cells being arranged in rows x 300.
- C. Disintegration of central rows; initiation of fusion
of cells of side rows (leaf blade) x 300.
- D. A normal stomata on fruit wall just before nuclear
fusion x 300.
- E. A normal stomata on fruit wall after nuclear
fusion x 300.



disc

Plate 7. Ontogeny of the giant stomata on fruit wall.

- A. Initial stage of cell disintegration x 300.
- B. The area of cell lysing well marked x 300.
- C. Cell lysing almost completed; cell fusion and wall thickening at the periphery of the cavity started x 300.
- D. Guard cells have developed around the giant opening x 300.

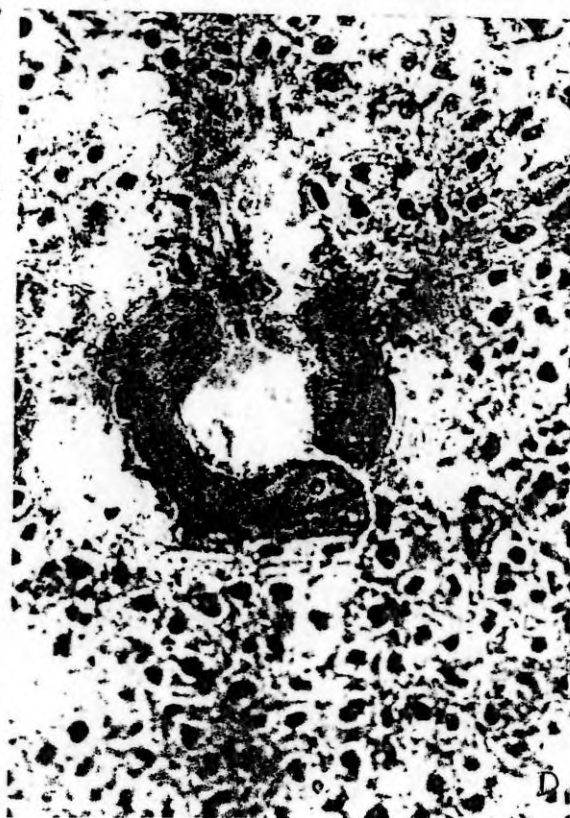
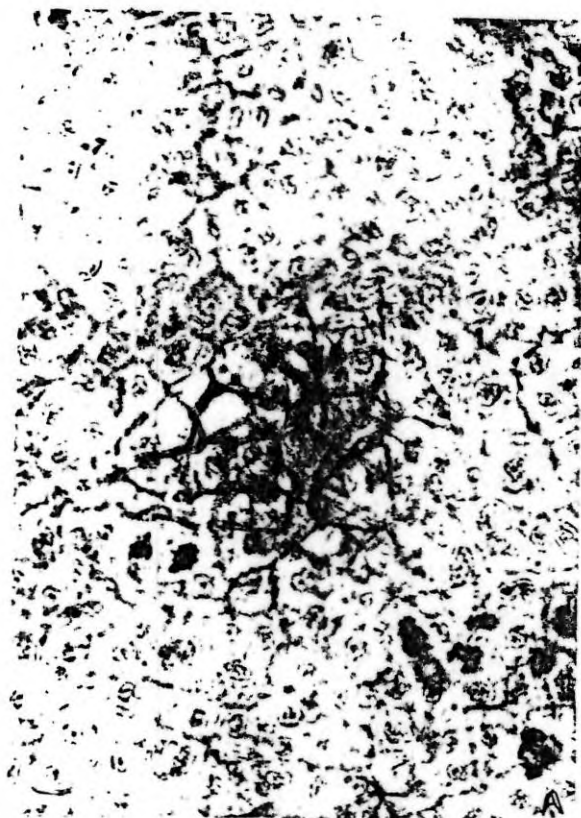


Plate 8. Different stages of leaf growth and development

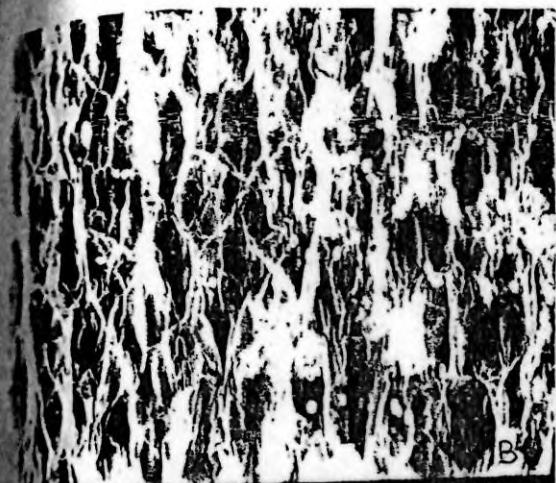
Hevea.

- A. Bud break stage.
- B. Leaflet stage.
- C. Pendent stage.
- D. Mature hardened foliage.

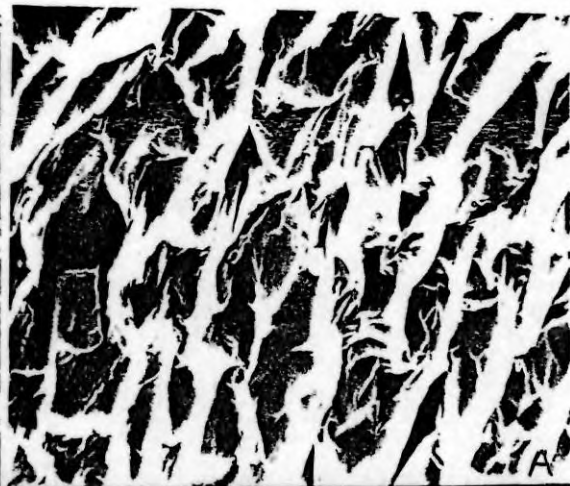


Plate 9. Scanning electron micrographs of the developmental stages in the formation of apicuticular wax pattern on the abaxial side of Hevea leaf.

- A. Bud break stage x 1000.
- B. Leaflet stage x 1000.
- C. Pendent stage x 1000.
- D. Hardened stage x 1000.
- E. Later stage of hardening x 1000.
- F. Upper epidermis of hardened leaf.



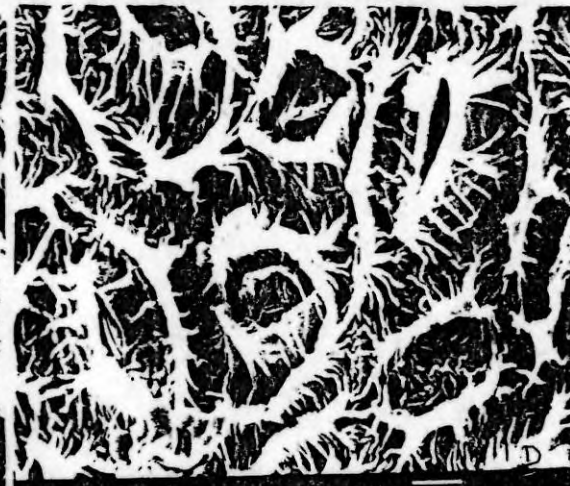
15KV X1000 8660 10.0U RRLSM



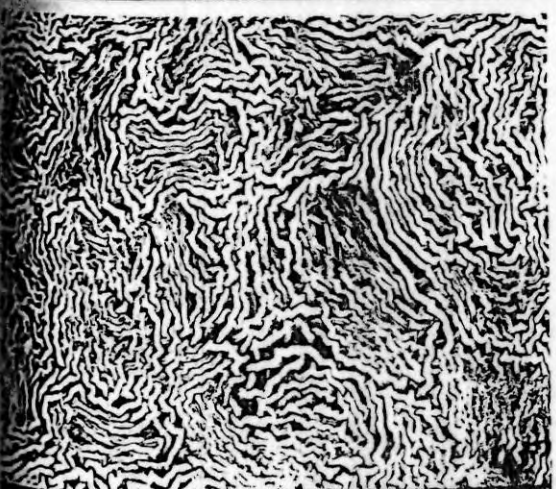
15KV X1000 8653 10.0U RRLSM



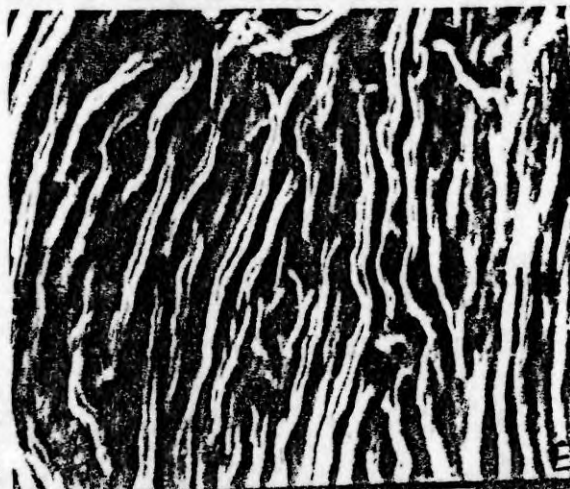
15KV X1000 8662 10.0U RRLSM



15KV X1000 0221 10.0U RRLSM



15KV X1000 0224 10.0U RRLSM



15KV X1000 8674 10.0U RRLSM

Plate 10. Major leaf diseases in Hevea.

- A. An estate view showing both severe incidence of Phytophthora leaf fall and unaffected area.
- B. A branch after the incidence of powdery mildew.



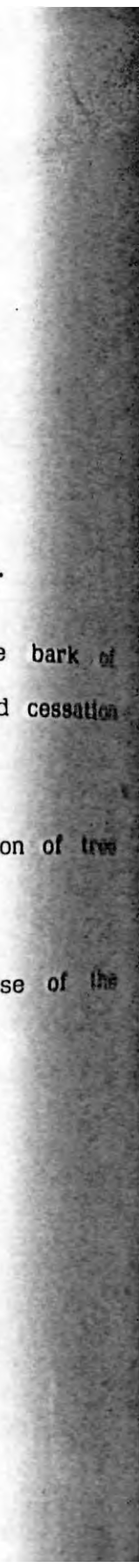
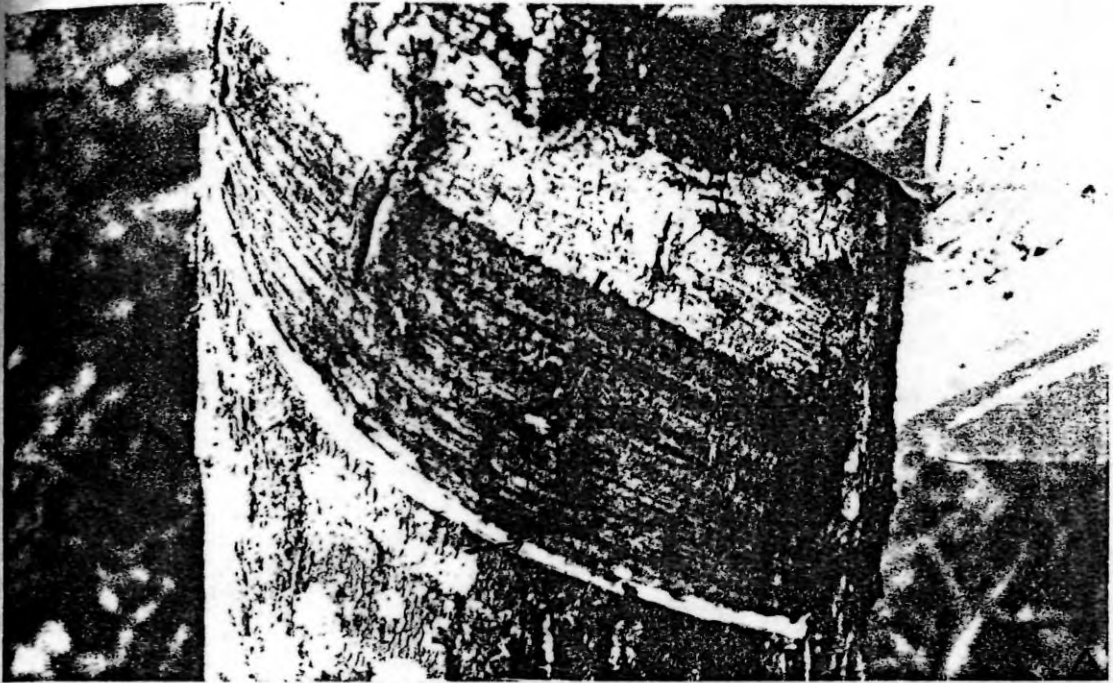


Plate 11. Brown bast (Tapping panel dryness) incidence.

- A. A tree showing partial drying of the bark of the tapping panel (→) and localised cessation of latex flow.
- B. Abnormal growth of the exploited portion of tree trunk.
- C. Cracking and flaky bark at the base of the tapping panel.



IV. D I S C U S S I O N

Productivity of a rubber tree or a population is measured in terms of the dry rubber recovered. Rubber yield is a very complex trait governed by large number of major and minor components involving genetic and environmental factors and their interactions (Jayasekara et al., 1977 and Pardeecooper, 1964a,b).

Populations exhibit large variability in productivity. Hybridization and clonal selection is the conventional method of crop improvement in Hevea. An assessment of the relationships between the basic make up of the plant and its physiological function is obvious to understand the causes and the consequences thereon. With these in the background the observations of this study have been discussed with emphasis to variability and relationships.

1. STRUCTURE AND ORGANIZATION

1.1. Latex vessels

Articulated and non-articulated laticifers are present in Hevea. The primary laticifers found in the leaf, primary stem, perianth lobes, fruit walls, etc. are non-articulated. This is in agreement with the observations of Zhaoxiugian (1987). Secondary laticifers which are commercially exploited are produced by the activity of vascular cambium and are distributed in the bark in rings. In the course of development fusiform initials divide anticlinally and laticifer initials are formed. The laticifer initials join end to end

and the cross walls dissolve forming tubular latex vessels. Latex vessels of the same ring are inter-linked by tangential connections formed at points of contacts between them. Such connections contribute for the extent of drainage area after tapping. A similar mode of ontogeny have been reported by earlier workers (Bobilioff, 1923; 1930, Gomez, 1982 and Panikkar, 1974).

The young latex vessels are coenocytic. In the present study the coenocytic condition of latex vessels was clearly observed (Plate I.B). As the latex vessels become mature, the nucleus seemed to be obscure. Presence of nuclei in young latex vessels was observed by Bobilioff (1923). Dickenson (1965) observed nuclei in the electron micrographs of young differentiating laticifers and developed latex vessels of the tender parts of the tree. Gomez (1976) observed the presence of nucleus only in the embryonic vessel in ultra thin sections, while multinucleate condition of tapped vessels was occasionally noted (Gomez and Moir, 1979).

The present study revealed that primary pit fields with protoplasmic connections are present in between young latex vessels and phloem rays. At maturity of the wall the plasmodesmatal connections become obscure or beyond the limit of resolution of light microscope. In such cases the wall of functional latex vessel in certain areas are more adhered to the wall of phloem rays, especially at the unilayered portion of the phloem rays and such cells gradually become aged and discoloured. It is common that more colouring

materials are seen in uniseriate rays and the tail cells of the phloem rays. Plasmodesmatal connections between latex vessels are numerous and clear. Plasmodesmata play an important role in the transport of materials and relay of stimuli. Hebant and Ede Fay (1980) have demonstrated clearly the location and limits of long distance translocation of assimilates in Hevea and the importance of short distance radial transport through phloem rays for providing the latex vessels with metabolites needed for the biosynthesis of rubber. Occurrence of protoplasmic connections between latex vessels and phloem rays have been reported by Dickenson (1969). In contrast d'Auzac (1984) reported that laticifer cells do not have any pitfields connecting the neighbouring paranchyma. He found perforations connecting laticifers with each other and suggested that the outer membrane of laticifer or the plasmalemma might be selectively accumulating ions or solutes from the secondary medium and capable of accumulation of nutrients and removal of toxic substances.

Observations of the present study agree with those of Brice and Campbell (1917) for the spacial organization of bark. Hevea bark comprises of three zones. The inner zone (soft bast) occupies 40-45 per cent of total bark and contains most of the functional elements including the rings of functional latex vessels. The rings, towards the inner region are more closely packed. As reported by Gomez (1982) nearly 40 per cent of the total number of latex vessel rows are present at the first millimeter from the cambium. The first latex vessel row originate within 200-500 μm from the wood

in different clones. The proportion of latex vessel rows very near to the cambium signifies the relationship of tapping depth and yield. However, this structural organization of the soft bast indicates that a higher proportion of latex vessel rings at the inner bark may tax on the proportion of functional conducting tissue in the phloem.

A slight inclination of latex vessels to the right in relation to the axis of the tree has been taken into consideration for fixing the slope of tapping cut in seedlings and buddings. On detailed observation Gomez and Chen (1967) found that the deviation need not always be to the right and the angle of inclination within a clone varies much.

The outer zone (hard bast) contains harder tissues where stone cells, in groups, are abundant. Some of the functional latex vessels are present in the hard bast region. They are more mature and has higher rubber content. Higher rubber content in more mature latex vessels was observed by Gomez (1976). The outermost ones however are nonfunctional and contains flocks of rubber particles contributing little to productivity. The outermost zone is the protective tissue made of cork cells.

1.2. Phloem rays

The rays of wood and phloem have vascular origin and are together known as vascular rays. The vascular rays have been

classified as (1) homogenous when composed of procumbent cells only and (2) heterogenous when composed of procumbant and upright cells (Kribs, 1935; Metcalfe and Chalk, 1950; Committee on nomenclature in 1957). Both group comprises different types according to the occurrence of uniseriate and multiseriate rays and the combination of cell types. The ray type and its dimensional variations are useful traits for systematic studies and identification purposes (Metcalfe and Chalk, 1950).

The phloem rays of Hevea are heterogenous and consists of both prostrate and procumbent cells. Both uniseriate and multiseriate rays occur. End cells of the uniseriate rays are large with conical dome shape. Multiseriate rays have one to three upright cells at both ends. The body cells are procumbent type and two to four cell wide with compact arrangement.

Based on the shape, four types of multiseriate rays were identified. In the longitudinal course the latex vessels are running by the sides of the phloem rays in close aposition with their walls. Hence the type and proportion of rays and their dimensional variations decide the orientation of latex vessels in their upward path (Premakumari, 1985a). Broad and short rays in high density leads to a more zig-zag orientation which may affect the rate of latex flow and thereby the yield (Premakumari, 1988a).

According to the classification of rays by Chalk (1938), and accepted by the International Association of Wood Anatomist (1939),

the rays of Hevea are fine (25-50 um) to medium (50-100 um) type.

1.3. Cambial activity

There are plants in which the cambium is active throughout the year and those in which the cambium is dormant for a very long period and there are intermediate types also. In Hevea seasonal variation in cambial activity was significant and nine clones showed almost the same pattern. This observation was in full agreement with earlier reports on seasonal cambial activity, in eight trees of Hevea by Rao (1975) and in 25 trees by Premakumari et al. (1981). Cambial activity is the least during May to July under the climatic conditions of central Kerala. An increased rate of cambial activity from August onwards with the peak in November-January was indicated by higher number of cambial rows. Significant association of cambial activity with bark thickness, girth number of latex vessel rows and the pattern of crop production has been reported (Premakumari et al., 1981). However, February, March and April, a very active growth period, shows summer drop in yield which is attributed to a reduced rate of latex flow and an early plugging of latex causing cessation of flow. Sethuraj (1977), George et al. (1980), Yeang and Paranjothy (1982) and Devakumar et al. (1988) have made similar observations. Comparatively less or little activity of cambium in Hevea during June-July, the time of south-west monsoon with a cloudy atmosphere, indicates that sun light might be an important limiting factor in the growth activity of this plant species. Temporary

inactivity of cambium during July-August period and an enhanced activity from September onwards has been reported in Eucalyptus spp. and Tamarix aphylla (Fahn, 1979).

1.4. Intraxylary phloem

There are reports on the occurrence of internal phloem in the xylem of the shoot system in certain families of dicotyledons including Euphorbiaceae although there was no reference of such anomalous structures in Hevea before Premakumari et al. (1985) reported it. Occurrence of intraxylary phloem in some other plants such as Macrotylome uniflorum (Kuo and Pate, 1981) and Nicotiana tabacum (Zamski and Tsivion, 1977) and its importance in the translocation of photosynthates and growth substances and its functional changes under varying conditions had been reported. In tobacco girdling activated the internal phloem to take on the functions of external phloem for transporting assimilates. It has also been reported that the internal phloem translocates endogenous auxins in girdled stems. Hevea tree is exploited by controlled wounding, a process known as tapping, resulting in partial girdling of the tree. Considering the active role of intraxylary phloem in translocation in girdled stems occurrence of adaxial phloem in Hevea deserves more attention.

1.5. L e a f

Hevea leaf is isobilateral with thick cuticle and epidermal

and mesophyll characters which signifies its functional importance. Hevea leaf has a thick cuticle. Epicuticular wax on the lower epidermis is reticulate and that of upper epidermis has even distribution of virgulate striae. Stomata are present only on the lower epidermis.

(a) Stomata

The functional significance of stomata is usually related to photosynthesis, transpiration, adaptability to environmental constraints and disease occurrence. Stomata in leaves with a dorsiventral lamina either occur in both surfaces (amphistomatic) or more often they are present exclusively on abaxial side (hypostomatic). In Hevea leaf blade it is hypostomatic and are almost equally distributed over the whole abaxial surface except the midrib and lateral veins where the frequency is very low. Spinner (1936) observed high proportion of amphistomatic species in high altitudes and hypostomatic species in plane land. However the laminal stomata in Hevea exhibited certain xeromorphic characters such as sunken stomata atleast partly covered by the filaments of epicuticular wax.

Metcalf and Chalk (1979) have mentioned that fruit walls in some species possess stomata atleast at early stages of development which later give rise to lenticels and often mark the site where periderm is initiated. Ramayya and Jagannatha Rao (1969) had emphasised the importance of investigating the entire stomatiferous area of a plant and the response of a given part to a function

according to its stomatal variations. The present study brings to the fore the occurrence of stomata on veins, petioles and petiolules and on other plant parts such as fruit walls and young stem, in addition to those on the leaf blade. Premakumari et al. (1979) had reported the occurrence of stomata on the petiole, vein and fruit wall of Hevea.

Before discussing the organographic differences of stomata and its functional significance in detail it is relevant to discuss a little on the stomatal type and its ontogeny. The laminal stomata of Hevea is paracytic type. This has reference to earlier report (Panikkar, 1974). Florin (1933) reported two types of stomatal development, the perigenous type in which the two guard cells originate by a single division of the stomatal initial while some of the neighbouring cells become modified independently as subsidiary cells and the mesogenous type wherein the subsidiary cells and guard cells are produced from the same initial. In this context the salient features of the major types may be briefly mentioned and the differences observed in Hevea are discussed. In Pant's classification (1965) based on stomatal development in various families the perigenous group is subdivided into three types and the mesogenous into four main groups. The present study revealed that stomatal ontogeny in Hevea is different from any of the two major groups discussed above. On the fruit wall, in addition to the normal stomata, giant stomata are formed, the origin of which shows some similarity to that of lyseogenous cavities. Such giant type of stomata

on the fruit wall may or may not have the typical morphology of the paracytic stomata.

The two peculiarities worth of special mention regarding the stomatal ontogeny in Hevea are (1) formation of stomatal aperture by lysing of cells and (2) development of guard cells by the fusion of more than one cell. In the normal type of stomata the stomatal mother cell divide repeatedly and the cells resultant of the division become arranged in six rows parallel to each other. From this the central two rows (three cells per row) disintegrate to form the aperture. Three cells each in two rows at the two sides of the aperture fuse to form two pear shaped guard cells. Pear shaped subsidiary cells are also formed in the same manner. Nuclear fusion also takes place resulting in a large elongated nucleus in the guard cells. Bobilioff (1923) observed large elongated nucleus in the guard cells in Hevea. The ontogeny indicates the possibility of polyploid nature of stomatal guard cells.

The abnormally large stomata are formed at a later stage of fruit development. Large openings are formed first by the distingegation of epidermal cells. Then the walls of peripheral cells become thickened followed by cell fusion to form giant cells which function as guard cells. This type of ontogeny seems to be novel in stomatal development. The giant stomata of fruit wall are preferential sites of Phytophthora infection which causes pod rot. Subsequently infection takes place on the petiole, petiolule and ultimately on the leaf blade causing severe leaf fall.

Phytophthora leaf fall disease is one of the major leaf diseases of Hevea which causes high yield loss, unless controlled by prophylactic spraying (Kuruvilla et al., 1989 and Radhakrishna Pillai, 1980). Certain clones show more susceptibility to the disease (Ramakrishnan et al., 1961). The causal organism enters the host through the stomata (Thankamma et al., 1975). Hence part to part differences in the size, distribution, topography and exposure of stomata observed in this study provides explanation to the organographic preference for infection.

Phytophthora leaf fall is prevalent during June-July by the onset of south-west monsoon. By that time the leaves of rubber tree matures. Leaf blade has the last preference as infection site, which should be attributed to the sinuous wall of lower epidermis and sunken stomata with small apertures and masking of stomatal aperture by the reticulum of buttressed waxes in completely hardened leaves. In contrast the stomata present on the petiole, petiolule, vein and young stem have large apertures though the frequency is very low. Being situated in a raised topographic position they are exposed and hence advantageous for disease causing organisms. The functional importance of structural variabilities has opened a new path in the host parasite relationship in Hevea (Premakumari et al., 1989).

(b) Epicuticular wax

The reticulate type of lower epidermis in Hevea is due to

the reticulate pattern of epicuticular wax. Similar observations have been reported earlier by Rao (1963) and Sanier and d'Auzac (1986).

Metcalf and Chalk (1979) reviewed the pattern of epicuticular wax in plants and the usefulness of wax morphology as an additional diagnostic character for taxonomists. This character is under strong genetic control (Mueller, 1966) which can produce recombination on hybridization. The thick wax layer and its reticulate pattern indicated some functional importance. Gururaja Rao et al. (1988) quantified the epicuticular wax in Hevea and discussed its role in drought tolerance of Hevea. They found very high correlation between the amount of epicuticular wax and light reflectance.

Phenological observations in this study showed that before the pendent stage of leaf development, the wax is thin and interrupted without filamentous striae. At full maturity, the lower epidermis become striated and the stomata are mostly covered by the filaments of wax. Discussions on the occurrence of certain leaf diseases has relevance in this context. In Hevea infestation of Colletotrichum gleosporoides and Oidium heveae is on young leaves. The time of refoliation and disease incidence in Hevea synchronizes (Sharples, 1926 and Anon., 1971). Yves Senechal et al. (1987) found that clonal differences in the resistance to Colletotrichum gleosporoides in Hevea was significant only when the lower epidermis was inoculated. There is clonal differences in the defoliation/refoliation time. Susceptibility

to the above diseases is also clone specific. Usually early wintering clones escape the disease which might be connected to the phenology of epicuticular wax. A complete spread of wax foldings and filaments over the whole surface on the abaxial side of hardened leaf and masking of the stomata at a very advanced stage of leaf hardening has been discussed elsewhere in relation to some sort of tolerance of leaf blade to Phytophthora leaf fall disease. The epicuticular wax on the leaf vein, petiole, petiolule, young stem and fruit wall, the preferential parts of Phytophthora infection are not striated type where the wax has interruptions at the positions of stomata. Samsuddin and Impens (1979a,b) have studied the photosynthetic efficiency of clonal seedlings and buddings in relation to the age of the leaf. According to them photosynthesis commences at least a week after leaf emergence and increased upto 23-30 days and thereafter declined slowly to a constant rate at 50-60 days. The authors suggested that the maximum photosynthetic rate is sustained for only a short period in the life of the leaf. This has reference to the phenology of epicuticular wax and stomatal development and their inter-relationships which attach a great importance to the photosynthetic efficiency of Hevea leaves. There is thus a possibility that clones with high quantity of epicuticular wax may suffer for low photosynthetic efficiency.

(c) Mesophyll

In leaves the inter-cellular space between the palisade cells

limits water transport in the plane parallel to the leaf surface (Wylic, 1943). In Hevea the palisade cells are not very compactly arranged while the intercellular spaces of spongy tissue are small. Small volume of intercellular spaces and reduced internal surface area are detrimental to the photosynthetic efficiency. Turrell (1936) has reported such traits as xeromorphic characters.

(d) Vascular system

The petiole has circular stele and the internal phloem continues from the leaf to the stem through the petiole. Hevea leaf has a prominent mid vein which abuts the lower surface. Primary, secondary and tertiary veins and the quaternaries with minute branches constitute the venation in Hevea in a reticulate pattern. According to the classification of Ettinghausen (1961) it is 'camptodromous type' wherein the secondary veins curve acroscopically to form a series of loops with adjacent secondaries and their branches.

The stele of midvein is somewhat crescent shaped. Among clones slight variations occur in the distribution of vascular tissues, prominence of vein and its shape in cross section. Such characters were found to be useful for clone identification.

2. VARIABILITY

For quantitatively inherited characters which are controlled by a large number of genes of similar but small individual effects, the effect of individual gene is so small compared to the environmental fluctuations which influence the character that it becomes impossible to assess the contribution of each and every gene to the total genetic variation. The characters of economic importance, in general, are such metric characters for which the average effects of the gene complexes as a whole should be estimated with their inter relationships and relative roles. The very limited base of the Wickham germplasm (22 seedlings) which covers the whole rubber producing areas in the world exhibits very wide variability. Accountability of different sets of major factors in controlling rubber yield of Hevea clones vary at different growth phases (Ho, 1975) and at different environments (Jayasekara et al., 1977, Rajeswary Meenattoor et al., 1992 and Thomas et al., 1992). Variability of certain phenotypic characters governing rubber yield and its contributing factors have been discussed below.

2.1. Interclonal variations

2.1.1. Phloem ray characters

In terms of seriation of phloem rays triseriate type is the major one in Hevea for which the clones are not significant. predominance of triseriate rays in Hevea wood has been observed by

Panikkar (1974). Proportion of the other types, uniseriate, biseriate and tetraseriate were highly significant clonal characters. For the proportion of uniseriate rays the range among clones is not very wide and hence the other two types, biseriate and tetraseriate rays, are more useful to differentiate clones and hence good anatomical criteria for clone identification. Predominance of biseriate or tetraseriate rays and the diameter of their component cells decide the width of phloem rays in a clone.

Premakumari (1985) studied the shape of phloem rays and identified four types in Hevea. The present study showed that bat shaped ray is the predominant type and proportion of dumb bell shaped ray is negligible. Clones are significant only for oval shaped rays and this can also be utilized for clone identification. Utility of phloem ray characters for identification of plant species has been suggested by Metcalfe and Chalk (1950). The present studies indicate that phloem ray characters would be useful for identification of H. brasiliensis at clonal level.

The height, width and H/W ratio of phloem rays showed highly significant clonal differences. The size, shape and density of phloem rays have been reported as clonal characteristics (Premakumari et al., 1985). It has also been suggested that these traits govern the orientation of latex vessels and contribute to the yield of Hevea clones (Premakumari et al., 1988a). The ratio of phloem ray height to its width is an indicator of the extent of the zig-zag orientation

of latex vessels in its upward direction, weaving the phloem rays. Hence the influence of phloem rays on yield is related to the orientation of latex vessels possibly mediated through the rate of flow of latex.

The diameter of component cells of uniseriate to tetraseriate types of rays individually and the average of four types showed highly significant clonal differences. In biological system turgor pressure maintenance and cell volume keeps a linear relationship mediated through cell wall elasticity. Small cells are more elastic (Steudle and Zimmerman, 1977), thereby leading to turgor maintenance. Maintenance of latex flow depends on maintenance of turgor pressure in the latex vessels by a dilution reaction which is the influx of water from the neighbouring cells into the latex vessels to restore equilibrium disturbed by tapping (Frey-Wyssling, 1932; Riches and Gooding, 1952 and Sethuraj, 1977) and this osmotic adjustment depends on the turgor pressure of surrounding cells also. Therefore small diameter of phloem rays favours turgor maintenance in latex vessels. This structure and function relationship influence the yield through dilution reaction and the extent of drainage area of bark, especially at conditions when water status in plant tissue is a limiting factor. d'Auzac et al. (1989) has referred the continuity of ray cells through the cambium towards the wood and its possible bearing on dilution reaction. Cell diameter is also a factor deciding the width of phloem rays and hence the orientation of latex vessels.

2.1.2. Laticifer characters

All the laticifer characters such as number of latex vessel rows, density and diameter of latex vessels, laticifer area index and intensity of anastomosing showed highly significant clonal differences and the clones vary for the combination of laticifer traits. There are earlier reports on clonal differences of such quantitative traits. Vizher (1921; 1922), Sanderson and Sutcliffe (1929), Gomez (1982) and Premakumari et al. (1988) reported clonal differences in the number of latex vessel rows. This trait varies due to age and height of sampling and therefore demands care in collection of samples. Gomez (1982) indicated clonal variation in the density of latex vessels while Premakumari et al. (1985) reported significant clonal differences for the density and diameter of latex vessels. Gomez (1982) found significant differences for the density of latex vessels at two distances from the cambium. There are reports on the influence of various laticifer characters such as number of latex vessel rows (Gomez, 1982; Gomez, Narayanan and Chen, 1972; Ho, 1975; Premakumari, 1988), latex vessel diameter (Ashplant, 1927; 1928a,b,c) and latex vessel density (Premakumari et al., 1988) on yield of Hevea clones.

Laticifer area index as described by Gomez et al. (1972) approximately represents the total quantity of laticifer tissue under exploitation in terms of cross sectional area. Number of latex vessel rows, density of latex vessels per row and diameter of latex vessels

contribute to this index. Along with the length of tapping cut, it reveals the total effect and interaction of the individual contributing factors. Premakumari (1988) observed highly significant clonal differences for this trait and suggested it as a major yield component. In the present study also all the high yielders were high/medium for this trait.

The tangential connections of laticifers are expected to assume importance as it contributes to the efficiency of the laticiferous system as a biological drainage system after the commencement of latex flow on tapping. Panikkar (1974) quantified the anastomosing in Hevea seedlings where he observed 98 to 124 connections/mm² at the inner bark and 82 to 98 connections/mm² in the outer bark. He attributed this reduction in number of connections in the outer bark to the expansion of tissues of the bark. Premakumari et al. (1985) observed highly significant clonal differences of this trait where the density ranged from six to nine within 0.22 mm height. In the present study also clonal differences for this trait was significant at 1 per cent level and the clones showed a range of six to eight connections per 0.25 mm height at the anastomosing portions of latex vessels. A comparable data has been reported by Zhaoxiuqian (1987). The high yielding clones recorded high/medium intensity of anastomosing.

2.1.3. Intraxylary phloem

Identification of adaxial phloem in Hevea (Premakumari, Panikkar and Sankar Sobhana, 1985) created a new interest in the structure and function relationship of clones. The first attempt to quantify such tissue in Hevea clones recorded a range of 52 to 72 primary xylem points and 41-65 intraxylary phloem points among eight clones and this trait showed significant positive correlation with girth increment on tapping (Premakumari and Panikkar, 1988). In the present study the ten clones recorded a range of 48 to 98 primary xylem points and 37 to 86 intraxylary phloem points. For both traits clonal differences were highly significant.

2.1.4. Leaf anatomical characters

Studies on the interclonal variations of leaf anatomical characters in Hevea are meagre. In the present study, out of the seven characters recorded three traits (width of the midrib, thickness of cuticle and density of petiolar stomata) showed significant clonal differences. For the thickness of midrib, height and width of palisade cells and frequency of laminar stomata clonal differences were not significant. For the height and width of palisade cells the clones showed wide range and lack of significance might be due to high error variance. For laminar stomata the clones were comparable. Senanayake and Samaranayake (1970) observed intra specific variation of stomatal density in Hevea brasiliensis and found a wide range of stomatal

density per unit leaf area among 25 cultivars. Premakumari et al. (1979) found significant clonal differences for the petiolar stomata of budwood plants. In further studies (Premakumari et al., 1984; 34; 1989) occurrence of wide range of stomatal density among clones for the leaf blade and petiolar stomata of mature trees and the importance of stomatal characters in clonal susceptibility to Phytophthora leaf fall disease were discussed. In the present study also the clones which recorded high frequency of petiolar stomata recorded high intensity of abnormal leaf fall and vice versa. Gomez and Samsidar Hamzah (1980) studied 11 clones and observed significant clonal differences for a number of characters such as stomatal density, cell number in the upper epidermis, thickness of leaf, thickness of palisade layer, number of cells in unit palisade layer and the number of cells in unit spongy tissue.

2.1.5. Growth characters

In this study girth and panel length, the two traits relative to each other, showed highly significant clonal differences. Significant clonal variability of those traits have been reported earlier (Paardekooper and Samosorn, 1969; Sethuraj and George, 1980).

It has been observed that the annual girth increment of a tapped tree is substantially less than that of an untapped tree (Dijkman, 1951). For the rate of girth increment on tapping significant clonal differences has been reported (Markose, 1984; Premakumari et al., 1988, Schweizer, 1949 & Vollema, 1941). For percentage

birth increase on tapping, the clones observed in this study showed a range of 6.77 to 10.29. However, the differences were not statistically significant.

Bark thickness have been observed as a clonal character in different studies (Markose, 1984; Tan et al., 1975) while the clones taken for this study were comparable for bark thickness.

2.1.6. Latex flow characters

The latex flow characters such as initial rate of flow, duration of flow and plugging index were significant clonal characters. However the significance was only at 5 per cent level. The rate and duration of latex flow determine the amount of latex volume obtained from a tree on each tapping. Sethuraj (1981) has suggested a formula, $y = \frac{F.l.C_r}{p}$ on theoretical basis to explain yield where F represent initial flow rate, l represent length of tapping cut, C_r percentage of rubber content and p the plugging index. Saraswathyamma and Sethuraj (1975) and Sethuraj (1977) elucidated interclonal variations of latex flow characters. According to Simmonds (1982) plugging index is a clonal character but it hardly provides an objective for the breeder. On the contrary Wycherley (1975) observed that low plugging results in long flow leading to reduced growth and increased risk of dryness or breakage but in practice selection for unstimulated early yield must imply unconscious selection for low plugging index.

2.1.7. Rubber yield, latex volume and dry rubber content

Productivity of a clone is expressed as the rubber yield which is the total effect of latex volume and dry rubber content. Rubber yield and the contributing characters are clonal characteristics. For all the three traits the ten clones under study varied significantly at 1 per cent level. For rubber yield three clones, RRIC 100, RRIC 36 and RRIC 102 were superior. For the highest yielder (RRIC 100) both latex volume and dry rubber content contributed significantly. For another high yielder (RRIC 36) the high rubber yield was contributed by significantly high latex volume. For this clone dry rubber content was significantly less. On the contrary for the third one (RRIC 102) an average latex volume and significantly high d.r.c. contributed to high yield. Thus for the extent of influence of major components and their subcomponents on dry rubber yield, clones vary widely. This has been indicated by earlier workers (Ho, 1975; Premakumari et al., 1988 & Sethuraj, 1985) also. Hence the genetic make up of a clone for the various desirable and undesirable traits is very important factors to be considered than the yield itself when planting materials are chosen for specific environment.

2.1.8. Diseases

In Hevea abnormal leaf fall disease caused by Phytophthora spp. and powdery mildew disease caused by Oidium spp. (Ismail Hashim, 1980; Peries and Soloman, 1963 & Kuruvilla Jacob et al.,

1992) are two major leaf diseases causing crop loss. In South India, abnormal leaf fall disease is very severe causing 30-50 per cent crop loss under unsprayed conditions (Radhakrishna Pillai, 1977). To a certain extent at least the crop loss depends on clone (Young, 1950) and tree age (Kuruville et al., 1989).

For disease intensity the two years differed. Phytophthora leaf fall was more severe in 1987 compared to the incidence in 1986 while powdery mildew was severe in 1986 when compared to 1987. Such a mutually contrasting effect in the case of these two diseases has been noticed in rubber plantations though specific studies are meagre. This phenomenon is justified by the differences in the mode of infection by the respective causative organisms.

Phytophthora infection starts on fruits while fruit production is hindered by Oidium. Clones varied to a certain extent for tolerance to both diseases. Nab 17 and RRIC 36 were highly susceptible to Phytophthora leaf fall. RRIC 7 showed fairly good tolerance, while RRIC 45, RRIC 104 and RRIC 105 recorded medium to low rate of infection. At the same time Oidium was severe for RRIC 45, RRIC 105 and GT 1 while RRIC 102 and RRIC 100 had fairly good tolerance. RRIC 36, RRIC 7, RRIC 104 and RRIC 52 recorded medium to low rate of infection. Nab 17 showed medium to high rate of Oidium infection also. Leaf diseases are severe constraints of yield in Hevea clones and hence disease management and judicious selection for specific environment with respect to disease occurrence is essential

to reduce the incidence of diseases and for improvement in productivity. This has agreement with the statement that the rubber breeders objective should be to reduce the natural incidence of leaf diseases (Webster, 1989).

Wintering observations indicated high incidence of powdery mildew in late wintering clones. This is due to the synchrony of infestation time and early phenological stage of the leaves. Year to year variation in the severity of powdery mildew has been related with wintering behaviour of the clones (Sharples, 1926). Trees refooliating early invariably escape severe infection and consequent leaf fall (Anon, 1971). Control measures to *Oidium* leaf fall in *Hevea* based on wintering pattern has been suggested by Lim and Sripathy Rao (1975). Phenology of epicuticular wax is the basic factor governing such a host parasite relationship (Premakumari et al., 1989).

Brown bast (Tapping Panel Dryness - TPD) is very often related to the level of exploitation (Ng et al., 1966; Rands, 1921 & Taylor, 1926). Different morphological expressions of the disorder are observed for which specific clone effect have not been ascertained. But the general concept is that the extent of this disorder is clone specific and also that high yielding clones are generally more susceptible to tapping panel dryness (Sivakumaran, Haridas and Abraham, 1988). Kuswanhadi et al. (1992) observed clone specificity in the occurrence of tapping panel dryness in response to periodic tapping. In the present study also the clones showed a wide range

of 00-26.67 for percentage incidence of tapping panel dryness. Out of the three high yielding clones, two showed the highest percentage of TPD Incidence. Among the medium and low yielding clones, varying trend was observed. This result agree with the planters experience that most of the high yielding clones are susceptible to tapping panel dryness. Differential expression of TPD among the medium and low yielding clones indicates that factors other than the yield, are also involved in the expression of this syndrome.

2.2. Comparative bark anatomy

2.2.1. Drought tolerant and susceptible clones

The rate of yield depression during drought period varies from clone to clone (pardekooper, 1965). The extent of variation is attributed to the variation in latex flow pattern (Sethuraj, 1977). In the present study the clones were significant for the number of latex vessel rows, proportion of soft bast, proportion of latex vessel rows in the soft bast region, height of phloem rays, width of phloem rays and the ratio of height to width. The importance of structural parameters as yield contributing factors are well known though the significance of such structural aspects on seasonal yield variation has not been ivnvestigatd. However, the clones involved in this study were comparable for total bark thickness and diameter of latex vessels. Sethuraj et al. (1974) has reported a positive correlation between initial flow rate and number of latex vessel rows

in the progeny of Hevea brasiliensis derived from the crosses involving Tjir 1 as female parent. The influence of such a relationship was not reflected in the materials taken for the present study since the difference between drought tolerant and susceptible group of clones did not differ significantly for the total number of latex vessel rows.

When the proportion of soft bast and proportion of latex vessel rows in the soft bast were taken into consideration group differences were highly significant. For both traits the clones within tolerant group were not significant though the clones within susceptible group showed significant differences. High proportion of soft bast was recorded for drought susceptible clones. This results recall the role of environmental factors such as soil moisture and atmospheric temperature on the turgor pressure variation in the laticifers which can influence the expression of yield during different seasons, mediated through total volume of latex as proposed by George et al. (1980) and Sethuraj and George (1976).

Stone cell formation is influenced by environmental and seasonal factors (Bobiliooff, 1923; Gomez, 1982 & Premakumari et al., 1990). But this study showed that it is a clonal character also. The drought tolerant clones showed high sclerification resulting in low proportion of soft bast thickness indicating the potentiality of such clones to resist the drought conditions.

Clone to clone differences for the size and distribution of phloem rays is in agreement with the observations of earlier studies (Premakumari et al., 1985; 1988). The influence of such traits on the orientation of latex vessels and thereby on the latex flow pattern has been suggested. In the present study, the drought tolerant and susceptible groups did not show significant differences for ray height. Within both groups the clones differed significantly indicating that this trait cannot be relied upon for drought tolerance.

The width of phloem rays was significantly high for the drought susceptible clones and the group difference was significant at 1 per cent level. For both groups within group differences were not significant indicating that it is the most reliable criteria. The ratio of phloem ray height to its width was also a very significant clonal character for which drought tolerant versus susceptible groups of clones differed significantly at 1 per cent level. For this trait, the clones within group were significant which might be due to the influence of ray height.

The results of this study lead to the conclusion that the drought tolerant and susceptible groups of clones differ significantly for certain bark anatomical characters such as phloem ray width, H/W ratio of phloem rays, the proportion of soft bast to total bark thickness and proportion of latex vessel rows in the soft bast to total number of latex vessel rows. For lesser yield drop during drought, the former two traits might be mediating through the

orientation of latex vessels and the latter traits through maintenance of turgor pressure in the functional latex vessels. However, the yield drop during drought is a complex multifactorial trait and further detailed studies incorporating more clones and still more variables would be rewarding.

2.2.2. Polyploids and diploids

H. brasiliensis, which is considered as a diploid (Bouharmont, 1960 & Ong, 1976) has a chromosome complement of $2n = 36$. Polyploidy usually cause an increase in cell size but it need not always increase the whole plant size as the increase in cell size may be associated with a reduction in cell number (Indira and Abraham Susan, 1977 & Stebbins, 1971). Retarded bud growth after colchicine treatment, as in many plants, has been reported in Hevea (Shepherd, 1969). Reduced number and increased size of stomata associated with tetraploidy in Hevea (Mendes, 1969; Mendes and Mendes, 1963 & Saraswathy Amma et al., 1988) is also an indication of the tendency for reduction in cell number and increase in cell size at higher ploidy level. Most of the species in Euphorbiaceae have a chromosome complement of $2n = 18$ and H. brasiliensis is suspected to be a tetraploid adapted to the environment (Majumdar, 1964 & Shepherd, 1969).

In this study, reduction in stem girth, bark thickness, number of laticifer rows, laticifer density and tree height were noticed

for the mature trees of GT 1 and Tjir 1 polyploids. In the case of RRII 105, differences between the two cytotypes were not very pronounced when the trees had just attained the canopy stage of closure. As reported for the autotetraploids of RRII 105 (Saraswathy Amma et al., 1984) and IAN 45 837 (Mendes, 1969) at young age tetraploids may show vigorous growth, but when the plants face competition for space, food and environment those with higher cell size likely to be affected more. Markose (1975) observed higher stem index for young plants of GT 1 tetraploids but the clone showed reduced growth in the field.

Considerable reductions in the number of laticifer rows and laticifer density along with low girthing in the tetraploids assure a steep fall in the total cross sectional area of laticifers in the tetraploids. A slight increase in laticifer diameter cannot be the least adequate compensation for this effect. Highly zig-zag orientation of laticifers due to broad rays may affect the rate of latex flow atleast at drought conditions.

The technique of polyploidy is usually employed to induce genetic variability and exploit the useful traits directly or by further breeding and selection. As far as Hevea is concerned, the anatomical traits and the general tendency discussed above do not promise improvement of yield or growth by this technique though the possibility of inducing other desirable traits cannot be ruled out.

2.2.3. Virgin and renewed bark

Tapping is controlled wounding of the bark. The wound reaction may cause some variations in the quantitative aspects of the renewed bark.

The two growth phases, virgin and renewed, of the bark varied significantly for the density of latex vessels, proportion of uncut vessel rows and the height and width of phloem rays. Lower density of latex vessels, high proportion of uncut latex vessels, on tapping, and short but broad rays were characteristics of renewed bark.

Laticifer area and orientation of laticifers are very important factors affecting the yield of Hevea clones (Premakumari et al., 1988). High negative association between phloem ray width and latex vessel density has been reported (Premakumari et al., 1984). Hence significantly reduced density of latex vessels associated with an increased ray width in the renewed bark is growth oriented. Certain clones record high yield from the renewed bark (Nazeer et al., 1986 & Premakumari et al., 1988) which can be attributed to a high rate of girth increment on tapping. Premakumari et al. (1986) observed high influence of girth increment, than actual girth, on yield increment after tapping. The above observation highlight the importance of girth increment on tapping for maintaining the yield in renewed bark.

Higher proportion of uncut latex vessels also contributes to a reduced yield from renewed bark. Therefore deeper tapping of

renewed bark can be adopted to improve the yield, by cutting more number of latex vessel rows. Wounding and nodule formation is not a barrier since exploitation of bark of second renewal is not expected.

2.2.4. Juvenile and mature trees

Biological yield is one of the major objectives of any breeding programme and Hevea is not an exception. Exploitation and associated factors are equally relevant in this regard. The changes in component factors due to age is very important for a breeder in the efforts to make early prediction of yield (Ho, 1975 & Premakumari et al., 1989). Templeton (1968; 1969) studied the growth of Hevea clones at pre-exploitation and under exploitation as well as the photosynthetic rate and leaf area index under different growth periods. He observed varying trends due to age for the different traits. Girdling continues for the major part of the economic life period but the rate is reduced at the exploitation period in Hevea.

In the present study the girth, number of latex vessel rows, latex vessel diameter, laticifer area index and width of phloem rays recorded significant increase from juvenile to the mature age. Density of latex vessels and intensity of latex vessel connections recorded reduced values at mature age but there was no statistical significance. Premakumari et al. (1984) have reported a negative correlation between phloem ray width and latex vessel density.

Hence the reduction in latex vessel density due to age can be attributed to the increase in phloem ray width. The increase in girth, number of latex vessel rows and latex vessel diameter from juvenile to mature age contributed to a very significant increase in laticifer area index which can contribute well to an increased yield. To a limited extent at least the increase in ray width which may cause a more zig-zag orientation of latex vessel may counteract this. It is worth to remember that the correlation of juvenile yield to mature yield is only 0.50 or below (Dijkman, 1951 & Premakumari et al., 1988). Ho (1975) observed that the total contribution of latex vessel rows, girth and plugging index to the yield at juvenile age was reduced at the mature age. A clear knowledge on the variation in yield contributing traits due to age would help researchers to exploit those traits in a judicious way.

For the trees under exploitation also latex vessel rows, girth and laticifer area index recorded an increase from year to year. Latex vessel density showed a reducing tendency but fluctuated. Latex vessel diameter stabilized from the third year of tapping after a rise from the second year. The observations indicate that the quantity of laticifer area of a tree under exploitation is solely depended on the variation in latex vessel rows and girth, the two sinks other than latex regeneration in the partitioning of metabolites. Among ten Hevea clones, those which had high initial girth (RRIC 52 and RRIC 104) continued high rate of girth increase under exploitation, while the clones under medium group showed fluctuations. For the

number of latex vessel rows, medium to high girthing clones with medium number of latex vessel rows at the initial years of tapping (RRIC 104, RRIC 102, RRIC 7) picked up and contributed to an increased laticifer area on tapping. The clones which had very high number of latex vessel rows, initially (RRIC 36 and Nab 17) with medium to low girth showed a reduced rate of girth increment on tapping. Further detailed study in this regard would be beneficial.

2.3.1. Clone cum monthly variations of yield

Tan (1980) demonstrated genotype - environment interaction in Rubber. For the pooled data of ten clones, in the present study, monthly yield performance showed a range of 52.72 to 132.05 per cent of the annual mean in 1986 and 42.77 to 136.09 per cent in 1987. For maximum monthly performances the years varied. The minimum performance was in March in both years. February and April performances were comparable to that in March. Sethuraj (1977) has reported that February to April is the period of high moisture stress in South India and moisture stress is the major factor to govern the extent of summer drop of Hevea clones. The impact of climatic and water deficit conditions on the yield of Hevea clones have been advocated by Sanjeeva Rao (1991) and he observed minimum precipitation in March in the traditional rubber growing regions of South India. Differential adaptability of clones to non-traditional rubber tracts in India (Rajeswary Meenattoor et al., 1991) have also be reported.

In the present study, clones varied significantly for the monthly performance of yield in both years while all clones performed significantly less during February to April, the drought prevailing months. Certain clones such as RRIC 45, RRIC 105, GT 1 and Nab 17 recorded a wider range for the monthly performance which was mainly due to their performance in drought affected months. For those clones duration of poor performance was also longer. During wet months clonal differences for yield performance was not so pronounced. This result combined with the clonal variations of yield performances among the ten clones under study showed that variations in clonal performances of rubber yield is highly influenced by the variations in drought affected months than the performance in wet months.

2.3.2. Summer drop in yield

Summer drop in yield in Hevea is a very complex phenomenon caused by soil moisture stress and a synchrony of various other physiological complexities due to defoliation, flowering, refoliation (Chua, 1970) and the occurrence of powdery mildew disease on the new flushes. A reduction in initial flow rate and a rise in plugging index during drought period, causing considerable drop in yield was observed in the present study. This is agreeable to earlier reports (Chandrasekhar et al., 1990; Devakumar et al., 1988; George et al., 1980; Premakumari et al., 1979; Sherief and Sethuraj, 1978 & Yeang and Paranjothy, 1982). Clonal differences were significant for yield drop during summer period. Three clones namely RRIC 45,

RRIC 105 and GT 1 recorded very high drop in dry rubber yield while the least was recorded for RRIC 36 followed by RRIC 7. In general, the clones where high laticifer area index is the major component of yield, recorded only medium to less drop in yield during summer period. Such an effect can be justified since this trait influencing yield is not much variable due to seasonal moisture stress when compared to the flow characters.

Significant clonal differences were observed for the variations in plugging index and initial flow rate, of which the latter was more significant. Seasonal variation of plugging index and the drought effect in Hevea clones have been studied by Premakumari et al. (1991). Considerable drop in initial flow rate was recorded for two clones, RRIC 45 and RRIC 105 which had only low laticifer area associated with medium to low H/W ratio of phloem rays; i.e. more zig-zag orientation of latex vessels. Premakumari et al. (1992) found significantly high H/W ratio for drought tolerant clones. GT 1 had the highest H/W ratio but was associated with low laticifer area. Significant negative correlation of summer drop in yield with the laticifer area index and variation of initial flow rate, during summer, and positive correlation with rise in plugging index during summer have been reported (Premakumari, 1991). The same study indicated a negative relationship of H/W ratio of phloem rays with the variation of initial flow rate in summer. These structural traits have high heritability coupled with high genetic advance suggesting

predominance of additive gene action and hence selection based on this character would be most advantageous. Laticifer area index being less variable due to season is the most reliable criteria to reduce seasonal yield variation in clones.

All the clones which recorded high yield drop for a prolonged period after January (RRIC 45, RRIC 105 and GT 1) were highly susceptible to Oidium and showed considerable rise in plugging index. Hence Oidium and drought together contributed to an extreme condition of summer drop. GT 1 recorded high leaf fall due to Oidium and recorded good rise in plugging index also. RRIC 52 which was tolerant to Oidium, recorded the least rise in plugging index during summer period and hence recorded fairly good summer yield in spite of its high drop in initial flow rate.

The facts discussed above show that (a) in traditional areas where Oidium is prevalent, only a part of the summer drop in yield is due to the impact of drought and at least a part of it is due to Oidium, (b) to the impact of drought condition on yield, initial flow rate has major role while the influence of plugging index might be intensifying summer drop of yield through the disease. However the clones which have high laticifer area index combined with high H/W ratio of phloem rays have comparatively high tolerance to drought, in terms of summer drop in yield.

2.4. Variability and genetic parameters

2.4.1. Components of variance

In crop improvement programmes, one of the fundamental aspects that a breeder should know about the breeding material is the adequacy of genetic variation (Falconer, 1960 & Mather and Jims, 1977). This is not directly accessible to measurement, as phenotypic characters which are external expression of genetic values as modified by environment are measurable. Genetic variation is estimated by partitioning the phenotypic values into its components, genotypic and environmental (Johnson, 1909; Henderson, 1953 & King and Henderson, 1954).

Though the genetic base of commercially cultivated rubber is very limited it shows very wide variability (Comstock and Robinson, 1949; Fyfe and Gilbert, 1963 & Gilbert et al., 1973). In the present study, rubber yield and latex volume showed comparatively wider variability than the dry rubber content. Initial rate of flow and plugging index recorded better variability than the duration of flow but not upto the yield, the major trait. Girth also showed less variability than rubber yield. When compared to P.C.V. values, G.C.V. values were more for girth, rubber yield, latex volume and dry rubber content indicating more involvement of genetic factors in the expression of those traits.

Among the anatomical characters, high variability was observed for the laticifer area index, number of intraxylary phloem points, number of primary xylem points and number of latex vesse rows. For all anatomical traits, in general proportion of G.C.V. values were high indicating high genetic control for the expression of those traits.

Variability was more for the variations of latex flow characters and d.r.c. during drought period indicating the importance of those traits in yield variations during drought period. The proportion of G.C.V. values to P.C.V. values were high for the variations of rubber yield and initial rate of flow indicating that such variations are genetically controlled. For the other traits P.C.V. values were very high indicating that the expression of those traits are more governed by factors other than genetic.

2.4.2. Heritability

Heritability is the fraction of the observed or phenotypic variance which is caused by differences between the genes or the genotypes of individuals in a population. In the broad sense it refers to the functioning of the whole genotype as a unit and is used in contrast with environmental sources of variation (Lerner and Michael, 1950). It is estimated as the ratio of genotypic variance to phenotypic variance.

Among rubber yield, girth and latex flow characters (Table 28) highest heritability was recorded for girth followed by rubber yield, latex volume and d.r.c. For the latex flow characters such as initial rate of flow, plugging index and duration of flow heritability values were comparatively low. Several workers (Gilbert et al., 1973; Licy et al., 1992; Nga and Subramaniam, 1974; Simmonds, 1969; Tan et al., 1975 & Tan, 1981) have suggested that yield and girth variation can be largely accounted for by additive genetic variance. Anatomical characters in general showed very high heritability values when compared to the latex flow characters (Table 29) indicating the more dependability of structural parameters as selection criteria for yield than the latex flow characters. Height and width of phloem rays and the height/width ratio recorded very high heritability values. High heritability for such anatomical traits was observed in a different population in an earlier study (Premakumari et al., 1984). Number of latex vessel rows, a well established yield component and laticifer area index a more balanced system of laticifer trait and the intensity of laticifer anastomosing are highly heritable characters. Licy et al. (1992) observed only moderate heritability and low genetic advance for the F_1 progenies of RRII 105 x RRIC 100 at immature age. The number of intraxylary phloem points, a trait having very high heritability has high functional importance (Premakumari et al., 1988) when the physiology of tapping tree is concerned.

When the percentage variations of yield, latex volume, d.r.c. and latex flow characters during drought period were considered (Table 30), heritability was very high for the variation in rubber yield followed by the variation in initial rate of flow. Variations of total volume, d.r.c., plugging index and duration of flow recorded comparatively low heritability values indicating that percentage variations in rubber yield itself is the most reliable parameter for selecting the breeding material for drought tolerance in rubber. Variations in initial flow rate during drought period also is a better criteria than the variation of other traits.

2.4.3. Genetic advance

Johnson et al. (1955) suggested that heritability along with genetic advance, expressed as percentage of the mean furnishes a better picture than heritability alone. High heritability associated with high genetic advance indicate high involvement of additive gene action and hence shows further scope for improvement by breeding and selection. Important anatomical traits such as number of latex vessel rows, laticifer area index, height/width ratio of phloem rays, *number of intraxylary phloem and number of primary xylem* points recorded very high genetic advance associated with high heritability indicating better scope for improvement by breeding and selection. High heritability associated with low genetic advance was recorded for d.r.c., girth, diameter of latex vessels density of latex vessels, intensity of laticifer anastamosing and width of

hloem rays. Such condition indicates involvement of non-additive gene action (Panse, 1957) and hence those traits can be exploited by heterosis. High estimates of heterosis for girth (Kavitha et al., 1990), bark thickness and girth increment rate (Licy et al., 1992) for Hevea clones have been reported. High heritability associated with low genetic advance for density and diameter of latex vessels has been reported in another set of Hevea clones (Premakumari et al., 1984). The latex flow characters such as plugging index, initial flow rate and duration of flow recorded comparatively low heritability and genetic advance indicating lesser scope for improvement by selection. Variations of rubber yield and initial rate of flow during drought period also recorded high heritability combined with high genetic advance indicating high involvement of additive gene action.

3. SIMPLE, PARTIAL AND MULTIPLE CORRELATIONS

3.1. Juvenile and mature plants

The breeding cycle of Hevea is very long which make the need of early prediction techniques obvious in clone selection. Juvenile yield is an indication of mature yield but its correlation with mature yield is below 0.5 (Dijkman, 1951; Ong et al., 1986; Premakumari et al., 1988 & Tan et al., 1981). Hence information on the correlations between juvenile and adult stage for the component traits will be useful to strengthen the feasibility of early prediction.

In the present study, highest correlation was recorded for the number of latex vessel rows followed by width of phloem rays and girth of the tree. Laticifer area index also showed significant correlation but the relationship was at a lower level of significance which might be due to the influence of the density and diameter of latex vessels. Girth is a very important trait governing juvenile yield (Ho, 1975; Licy et al., 1988 ; Annamma Varghese et al., 1992 & Premakumari et al., 1989), though its importance at the mature phase is variously suggested (Markose, 1984 & Napithupulu, 1973). The width of phloem rays influences summer drop in yield and thereby the annual mean yield (Premakumari, 1992).

This study indicated that preliminary selection for latex vessel rows, width of phloem rays, girth of the tree and laticifer area index can be made at juvenile stage itself. Such early selection

on component basis may provide some additional clue on the sustenance of yield at the mature age via a prediction on the possible response to drought conditions and chances of brown bast occurrence.

3.2. Proportion of uncut latex vessel rows versus total bark thickness and total number of latex vessel rows.

On tapping, a portion of the inner bark is left uncut. The functional latex vessel rows present in the residual bark is thus unexploited. The proportion of latex vessel rows present at this region thus influences the yield per tree per tap which varies due to clone and growth phases (Bobilioff, 1923 & Gomez, 1982). Relationship of this trait with total bark thickness can be of practical utility to manage the depth of tapping in a judicious way.

The present study showed that total bark thickness and total number of latex vessel rows are negatively correlated with the proportion of vessel rows in a unit thickness of residual bark. Both the traits together contribute to 67 per cent variations in virgin bark and 65 per cent variation in renewed bark. This result imply that for thicker bark, deeper tapping would not do much benefit and in the reverse situation shallow tapping will not be economic.

3.3. Leaf anatomical traits versus yield

As latex is the cytoplasm of latex vessels (Milanez, 1946; Cook and Sekhar, 1953 & Moir, 1959) and photosynthetic efficiency

of the plant is an essential factor in providing the substrates for latex production, limitations in the water conducting and photosynthetic tissues may influence the yield. In the present study, all the four traits showed negative relationships with yield. To explain such phenomena further detailed study is needed.

3.4. Intraxylary phloem versus growth characters

Occurrence of intraxylary phloem in Hevea and clonal differences for its quantity have been discussed elsewhere in this thesis. As such tissue is formed in association with the primary xylem, a very high correlation with the quantities of those two tissues, as obtained in this study, is quite natural.

The growth rate of Hevea tree is affected by tapping (Dijkman, 1951; Markose, 1984 & Sethuraj, 1977). Wounding of tissues on tapping affects the normal functioning of the external phloem and thereby further growth of the plant. Intraxylary phloem is a supplementary source of phloem tissue which can compensate, to a certain extent, the disturbances in the functioning of the external phloem (Zamski and Tsivion, 1977). Significant correlations of the quantity of intraxylary phloem with the growth aspects such as stem diameter and girth increment on tapping support the theory. To assess the extent of its effect at varying conditions and tree age further study is needed.

3.5. Stomatal characters versus leaf retention after the incidence of Phytophthora leaf fall disease

According to the definition of Robinson (1969) disease resistance is the ability of the host to hinder a pathogen or disease causing agent. Attempts have been made to define the resistance in terms of the anatomical, morphological, physiological and biochemical features of the host plant which are responsible for its expression and are termed as resistance mechanism (Russel, 1978). Resistance could be due to existing structures and conditions before penetration of the host which is called passive resistance or due to phenomena induced in response to infection, known as active resistance (Hare, 1966 & Kue, 1967). In Hevea the stomatal characters control such a resistance mechanism in the case of Phytophthora spp. causing abnormal leaf fall disease mediated through poor establishment of the fungus in the host plant and the mechanism decides the part specificity of infection as discussed in a previous chapter.

In this study the percentage leaf retention after the incidence of abnormal leaf fall disease was related to the quantitative traits of stomata such as frequency, aperture length, aperture width and the aperture index which indicate the size, in general, of the aperture. The study is based on petiolar stomata. Stomatal frequency and aperture size influences establishment of the fungus in the host plant since the germ pore enters the host plant through the stomata (Thankamma et al., 1975). This assumption is supported by the

results obtained in the correlation study. The leaf retention percentage has very high negative association with the frequency of stomata and a higher association with aperture index where the size and frequency together are accounted. When stomatal frequency, aperture length and aperture width were treated separately, stomatal frequency was observed as the first preference to consider as a criteria for selecting disease resistant materials. Aperture length has the second preference.

3.6. Brown bast incidence versus yield and anatomical characters

Brown bast is a physiological syndrome familiar to Hevea researchers from 1912 onwards (Gomez and Gandhimathy, 1990). The general symptoms are absence of latex flow on tapping followed by partial or complete dryness of the bark. Late dripping may precede. Bark formation with woody nodules in the bark as a result of an increased meristematic activity in some advanced cases cause morphological deformities. The trees kept under rest due to the onset of dryness usually show sloughing off of the external bark. Seedlings succumb more to this disease (Rands, 1921). Researchers on exploitation of Hevea repeatedly ascertained its relationship with tapping intensity (Rands, 1921; Taylor, 1926; Ng et al., 1969 & Vijayakumar, 1990).

Morphological, anatomical and biochemical changes occurring in brown bast affected trees at the affected region have been demonstrated well (Bealing and Chua, 1972; Chua, 1965; Paranjothy et al.,

1975; Gomez, 1982; Christin et al., 1985; Jacob and Prevot, 1989; Gomez and Ghandimathy, 1990, Gomez et al., 1990 & Vidya Shiva Swamy, 1992). All agree to the point that it is a physiological disorder affecting the laticiferous system. The causative factors triggering the disorder is not very clear though it is variously suggested as disturbed water balance (Sharples and Lambourne, 1924); impairment of phloem transport (Horne, 1925), a reaction of wound healing (Rands, 1921 & Rhodes, 1930) and a wound reaction leading to a reduction in the permeability of latex vessel wall (Bealing and Chua, 1972). Pushpadas et al. (1975) has suggested a connection of brown bast incidence with nutritional imbalance, mediated through a prolonged flow and withdrawal of a critical quantity of latex from the tree. The work by Bolton and Shorrocks (1961) and Collier and Lowe (1969) on the influence of mineral nutrients support this view. Recently Sivakumaran and Haridas (1989) have connected it with agroclimatological factors. Nugavela et al. (1992) observed high incidence of tapping panel dryness in dry regions and they suggested that the tappers skill could also contribute to this disorder. All these reports denote a stress condition associated with brown bast incidence. Hence it should be assumed that physiological disturbances due to some sort of stress conditions induces histochemical changes, increased meristematic activity and growth abnormalities leading to the disorganization of laticiferous system and ultimately bark dryness.

In the present study, the latex volume and rubber yield showed positive relationships with percentage incidence of brown bast at significant level. Onset of brown bast due to prolonged flow, even under normal tapping system is a common experience in the field. The general concept also is that high yielding clones are more susceptible to tapping panel dryness (Sivakumaran et al., 1988) which support the above result. Since latex volume keeps a very high correlation (above 0.90) with dry weight yield, influence of the two on brown bast incidence overlaps. However, the partial correlations indicated comparatively a little higher importance of latex volume than the rubber yield.

Before going to further results it would be relevant to discuss certain salient points on latex flow. Latex flow is an induced physiological phenomenon by tapping. The tree regenerate the latex lost on tapping. Hence, in a tapping tree, more photosynthates are partitioned for latex production than in an untapped tree and hence the girth increment rate retards (Wycherly, 1975; 1976 & Sethuraj, 1985). When the level of exploitation exceeds the physiological capability of the tree for regeneration of rubber, the tree succumbs to brown bast (Sethuraj, 1988).

The latex volume recovered on each tapping under a specific system depends on certain genetic traits and its interaction with the environment. This can be manipulated by adjusting the length and depth of tapping cut, frequency of tapping and stimulation.

In the present study, the influence of certain inherent characteristics of the tree such as grith, number of latex vessel rows, density and diameter of latex vessels, laticifer area index, height/width ratio of phloem rays, intensity of anastamosing of latex vessels and the number of intraxylary phloem with brown bast incidence and percentage girth increase over two years of tapping under 1/2S d/2 system in panel BO/1 is interesting. The number of latex vessel rows and laticifer area index showed significant positive correlations with percentage incidence of brown bast with a higher degree of relationship for the number of latex vessel rows. The number of intraxylary phloem showed negative correlation with brown bast incidence at significant level. Brown bast incidence indicated a positive relationship with the density and a negative relationship with the diameter of latex vessels. In general the characters which showed a positive relationship with brown bast incidence showed a negative trend with percentage girth increase and vice versa except for the laticifer area index.

The results discussed above confirm the possibility that some common stress factors are involved in increasing the frequency of brown bast and reducing girth increment on tapping.

The loss in biomass production due to tapping termed 'k', is considered to be the fraction of photosynthate converted to latex, which is an important factor of yield potential (Simmonds, 1982). It is not fully accounted for by the rubber yield even if the high

energy content of rubber, as suggested by Templeton (1969) is taken into account (Sethuraj, 1985). This proportion of biomass potential in a tree $(1-k)$ that is not realised, but not accounted for by the rubber yield, should be explored with a view to reduce 'k' and to achieve a sustained upward yield trend for many years on tapping.

Theoretically $(1-k)$ might be due to some loss or some disturbances in CO_2 assimilation or in translocation. Sethuraj (1985) has suggested an enhanced respiratory activity and consequent loss of biomass in response to tapping as one of the reasons.

In the present study, brown bast incidence showed significant positive correlation with number of latex vessel rows and latex volume and negative correlation with the number of intraxylary phloem. The number of latex vessel rows was negatively correlated with the number of intraxylary phloem and positively correlated with latex volume. Since the latex volume is highly depended on the number of latex vessel rows, influence of the two traits on brown bast incidence overlaps to a certain extent. But the result shows that brown bast incidence have higher degree of relationship with the number of latex vessel rows at highly significant level, than its relationship with latex volume at the normal tapping intensity. When the influence of latex volume and number of latex vessel rows were eliminated the negative relationship of number of intraxylary phloem with percentage incidence of brown bast was intensified. This result indicated that tapping checks translocation and the internal

core of phloem tissue is capable of minimising the effect of tapping on translocation. This might be one of the major factors causing the unexplained part of k . Hence k can be reduced by selecting clones with high number of intraxylary phloem which will reduce the chances of brown bast incidence. In the present study expression of brown bast incidence in medium and low yielding clones ascertain this assumption. Premakumari et al. (1988c) observed that atleast in the latter part of the economic life, the quantity of intraxylary phloem has significant positive correlation with girth increment in tapping. Since the latex vessel rows are more concentrated in the functional phloem, the higher influence of the number of latex vessel rows with brown bast incidence, in addition to its influence through latex volume, might also be mediated through a check in translocation. It is relevant to remember that RRII 105, a very popular clone in India is very susceptible to brown bast incidence. Very high number of latex vessel rows and very low number of intraxylary phloem is combined in this clone and the girth increment rate also is very low (Premakumari et al., 1988). Under higher levels of exploitation the influence of latex volume on the incidence of brown bast need not be the same. However in the present study, the latex volume, number of latex vessel rows and number of intraxylary phloem together contributed to nearly 50 per cent of the variation in brown bast incidence. Of this, 38 per cent was the combined effect of latex vessel rows and intraxylary phloem. A recent observation that the incidence of dryness may not be related

to the level and intensity of stimulation, provided it is coupled with low intensity of tapping system (Sivakumaran, 1992) and earlier report that depression of girth increment is more marked by lengthening of tapping cut than by increasing the frequency of tapping (Luckman, 1980) also support the detrimental effect of repeated wounding.

This study reveals that a check in translocation might also be one of the reasons for the loss of biomass production due to tapping. Selection for a very high number of latex vessel rows involve the risk of brown bast incidence even under normal tapping system. Occurrence of high number of intraxylary phloem can nullify the effect. A high laticifer area should be associated with medium girth and medium width of latex vessels. A judicious selection for the genotype is essential to avoid the incidence of tapping panel dryness.

4. GENOTYPIC CORRELATIONS AND PATH COEFFICIENT ANALYSIS

The concept of path coefficients suggested by Wright (1921) and elaborated by Dewey and Lu (1959) has been well applied in population genetics (Kamalam et al., 1977; Li, 1956 & Li Liang, 1965) though this technique has not been well exploited for structural traits in Rubber. In Hevea direct selection for yield during the last decade could not achieve improvement in yield higher than 2500-3000 kg and the attention of plant breeders are being diverted to introducing new germplasm (Mohd Noor, Ong and Tan, 1980 & Subramaniam and Ong, 1973) for further improvement of planting materials. Still there exists a wide gap between the present potential of 2500-3000 kg and the estimated potential (Templeton, 1969) of above 9000 kg/ha/year. A concept of ideal plant type developed by Sekhar and Subramaniam (Subramaniam, 1980) and selection for specific environment based on regression analysis proposed by Jayasekara et al. (1977) form part of the efforts to fill the gap.

In a perennial tree like rubber direct selection for yield for a long time is not feasible and plant breeding programmes should be based on an understanding of correlations between yield and various yield determining factors (Swaminathan, 1975). Earlier researchers have worked out some simple correlations of latex yield with bark thickness, number of latex vessel rows, girth and plugging index (Narayanan et al., 1975; Ong, 1982; Saji T Abraham et al.,

1992 & Ong et al., 1983) though estimation of genetic correlations are meagre. However, the total effect of those traits, which explained 75 per cent of the variation in yield between clones at the nursery stage accounted only 40 per cent in the adult stage (Ho, 1975). This clearly indicate the variable role of component traits due to growth phase. Other studies on early prediction of yield (Henon et al., 1984; Jacob et al., 1975; Molly Thomas et al., 1990 & Zhongyu et al., 1983) also provide some simple correlations or quantitative differences between juvenile and mature plants.

In rubber the conventional method of direct selection was based on the first five years yield and now it is viewed that the first three years yield data is adequate for selecting superior clones (Ong, 1980 & Swaminathan, 1975) to shorten the testing time. Since the exploitation period is nearly 20 years the response of tapping on yield is very important. A sustainable yield on tapping is highly dependant on girth increment on tapping (Dijkman, 1951; Templeton, 1969; Simmonds, 1982 & Sethuraj, 1985). Premakumari et al. (1989) reported high correlation between girth increment on tapping and yield increment on tapping. Sethuraj et al. (1974b) have proposed a girth increment index to characterise the yield potential of clones in relation to girth increment. The genotypic correlation and direct and indirect effects of different characters on yield, obtained in the present study have been discussed below with a view to understand the value of each component trait as selection parameters at maturity as well as for early prediction.

4.1. Girth and bark anatomical characters at the initial maturity versus mean yield over subsequent three years

Total number of latex vessel rows and laticifer area index showed high degree of positive relationship with yield over three subsequent years at highly significant level. Gomez (1982), after a review of the past studies on the relationship of the structural traits and yield, have suggested that number of latex vessel rows is the most important single factor related to yield. High correlation coefficients, often in excess of 0.8, have been found in earlier studies for trees within a clone while between clones the coefficients have usually been between 0.35 and 0.57 (Narayanan et al., 1973; 1974) when number of latex vessel rings and yield of the same year were correlated.

In the present study the correlation coefficients for yield versus number of latex vessel rings and laticifer area index, at genotypic level, were within a range of 0.50 to 0.70 with a better value for laticifer area index. However, this study implied that these two traits, recorded three years in advance, could be made use of for predicting subsequent yield and hence involve a special advantage of early prediction. A lesser importance for density and diameter of latex vessels as single factors is in agreement with earlier reports (Gomez, 1982 & Webster and Baulkwill, 1989).

The intensity of latex vessel anastomosing showed a positive trend and width of phloem rays a negative trend though not at

significant level. The former trait contributes to the efficiency of laticiferous system as a drainage system and the latter for less yield drop during summer season.

In the present study the correlation coefficient of tree girth with yield was negligible and negative. Negative correlation of girth with yield have been reported by Narayanan et al. (1973) and Ho et al. (1973). Ho (1976) and Premakumari et al. (1989) found yield to be correlated with growth at juvenile age while at maturity girth assumed lesser role in determining yield. Wycherley (1969) found that at opening of the tree for tapping, yield and girth were positively correlated but on subsequent tapping the relationship declined and gradually reversed.

Considering the laticifer area index versus its individual factors, number of latex vessel rows and latex vessel diameter showed positive correlations with laticifer area index at 1 per cent level while girth and latex vessel density showed a negative trend. In this context the relationships among the contributing factors is relevant. Girth of the tree has significant positive correlation with latex vessel diameter ($P < 0.01$) and negative correlation with latex vessel density ($P < 0.05$). This might be mediated through the positive relationship of phloem ray width to girth and its negative relationship with latex vessel density.

However the study indicated that the relationships of individual traits with yield is very complicated due to the mutual interference.

Unfavourable association between yield and other secondary characters is a problem in rubber (Wycherley, 1969 & Ho, 1972). Laticifer area index, a balanced system of several important factors is more associated with yield at genotypic level. Swaminathan (1975) has suggested the need of such a mutually complemented trait as parameter for predicting a sustainable yield in rubber. Among the individual factors number of latex vessel rows show the highest degree of relationship with yield.

Cause and effect relationships

The cause and effect relationships of girth and bark anatomical characters on mean annual yield per tree per tap over subsequent three years at panel BO-1 is very interesting. Direct effect of laticifer area index is positive and at the highest magnitude. This pair showed the highest positive correlation also and hence is the most suitable parameter for direct selection. The intensity of latex vessel anastomosing had considerable amount of direct effect on yield. This trait which is independent of laticifer area index showed a positive trend of association with yield and hence deserve attention as a good parameter. The width of phloem rays also showed considerable amount of positive direct effect on yield though its correlation with yield showed a negative trend.

Direct effect of girth, number of latex vessel rows and diameter of latex vessels on yield were of considerable magnitude but negative and the positive effect of latex vessel density was of a negligible

magnitude. This result, in general, indicate that partitioning for tissue differentiation will affect latex production and only a complementary balanced system can function in a proper way. Even the number of latex vessel rows which is positively correlated with yield showed a high magnitude of negative direct effect on yield. Markose (1984) observed a negligible amount of positive direct effect of number of latex vessel rows on rubber yield.

Though the direct effect of girth, number of latex vessel rows and diameter of latex vessel on yield are negative, those traits assume importance as their indirect effects via laticifer area index are positive and of very high magnitudes.

The results conclude that laticifer area index is the most effective criterion and represents a complementary balanced system of the laticiferous tissue of Hevea. Intensity of latex vessel anastomosing and width of phloem rays are also important anatomical parameters for direct selection. The other traits such as girth, number of latex vessel rows and diameter of latex vessels contribute to yield via laticifer area index. The anatomical characters recorded from one sampling collected three years in advance can predict the yield trend in the same panel for the subsequent years and hence are capable of shortening the long testing time before selection.

4.2. Rubber yield versus girth, anatomical characters and latex flow characters at the respective year

Attempts to relate structural characters, tree girth and latex

flow characters with yield in rubber is not new. In the present study genotypic correlations among rubber yield and 14 characters, including tree girth, laticifer characters, phloem ray characters, flow characters, latex volume and dry rubber content, recorded at the 11th year of planting (5th year of tapping), were estimated. The cause and effect relationships have been discussed.

Correlation of yield versus girth and structural traits

Regarding the relationships of yield with girth and structural traits, number of latex vessel rows and laticifer area index showed highly significant positive correlations with rubber yield. There are several reports on simple positive correlation of the number of latex vessel rows with yield at juvenile age (Ho, 1972; 1975 & Tan, 1987) and mature age (Ho, 1976; Samsidar Hamzah and Gomez, 1980 & Wycherley, 1969), though the laticifer area has not been well studied.

When data of the same year were considered, correlations of the intensity of latex vessel anastomosing with rubber yield improved to the significant level. No other reports are available on the correlation of yield with this trait. Compared to the results in the previous data, correlation coefficients of phloem ray characters with yield were lesser.

Rubber yield versus latex volume, d.r.c. and latex flow characters

As expected, rubber yield showed highly significant positive

correlations with duration of flow, initial rate of flow and total volume of latex and negative correlation with plugging index at genotypic level. Negative simple correlation of rubber yield with plugging index and its positive relationship with initial rate of flow and duration of flow are well known (Paardekooper and Samosorn, 1969; Sethuraj, 1977 & Samsidar Hamzah and Gomez, 1980). Ho (1975) have elucidated the importance of plugging index in early prediction of yield. Contrary to this, he has also suggested that selection of high yielders with high plugging index is advantageous since low plugging index subsequently causes high incidence of dryness and wind damage and also low rate of girth increment on tapping and response to stimulation. Markose (1984) also obtained very high correlation of rubber yield with total volume of latex at genotypic level.

The relationship of dry rubber content with yield shows a positive trend but the correlation coefficient is very low (0.1715). This is in agreement with the observations of Sethuraj (1977) in a population of clonal mother trees. He attributed the low correlation to the negative relationship of d.r.c. with total volume of latex. Paardekooper and Samosorn (1969) also could not observe significant correlation between yield and d.r.c.

Among girth and structural traits

Considering the girth and structural traits, relationships of the number of latex vessel rows, diameter of latex vessels and

girth with laticifer area index kept the same trend as in the previous data. The positive relationship of girth with diameter of latex vessels and its negative relationship with latex vessel density became insignificant at the fifth year of tapping. Simultaneously, the negative correlation of latex vessel density with rubber yield also have been lessened to an insignificant level.

At the initial maturity period girth showed a negative trend with the intensity of latex vessel anastomosing while this was reversed at the fifth year of tapping. This might also be mediated through the density of latex vessels.

As opined by Ho (1975), this study also showed that the relationships among yield, girth and certain structural traits vary as tapping proceeds. Still the number of latex vessel rows and laticifer area index maintained highly significant positive relationships with yield. The intensity of anastomosing, another trait influencing yield is independent of the other two traits.

Girth and structural traits versus latex volume, d.r.c. and latex flow characters

Girth did not show any significant correlations with rubber yield, latex volume, d.r.c. or any of the latex flow characters at the fifth year of tapping. This is in agreement with the statement of Ho (1975) that tree girth has significant influence on the yield of Hevea clones only at the immaturity period and after opening for tapping, only the rate of girth increment has significant role.

The same observation was recorded by Premakumari et al. (1989) in a seedling population.

The number of latex vessel rows and laticifer area index maintained significant positive correlations with total volume of latex and duration of flow and negative correlation with plugging index. Any relationship between latex vessel diameter and rate of flow of latex as suggested by Frey Wyssling (1930) was not evident in this study. Little information is available on the laticifer area index, while simple negative correlation between the number of latex vessel rows and plugging index, at significant level, has been reported in mature trees (Samsidar Hamzah and Gomez, 1980). Tan and Subramaniam (1975) did not observe any significant correlation between those two traits in young Hevea seedlings. Between number of latex vessel rows and initial rate of flow, Sethuraj et al. (1974) found positive correlation in the progenies involving Tjir 1 as a parent. In the present study the correlations of initial rate of flow with the number of latex vessel rows, laticifer area index and intensity of anastomosing showed positive trends, although the values were not statistically significant.

A very interesting result is that the intensity of latex vessel anastomosing showed significant negative correlation with plugging index ($P < 0.05$) and positive correlation with total volume of latex ($P < 0.01$). This trait showed positive trend with duration of flow, initial rate of flow and d.r.c. also. It is very important that this

character keeps highly significant positive relationships with total volume of latex keeping a positive trend with d.r.c. and duration of flow. High intensity of latex vessel connections might be favourable for an extended drainage area. Sethuraj (1977) suggested lowering of plugging index due to the extension of drainage area. Hence the laticifer connections which has not been well studied earlier deserve great attention as an yield component. It is relevant to say that this trait is a significant clonal character which has high heritability combined with good genetic advance and hence is governed by additive gene action.

This study clearly shows highly significant association of major structural traits such as number of latex vessel rows, laticifer area index and intensity of anastomosing with total volume of latex. The structural and functional parameters are highly complemented.

Among total volume of latex, d.r.c. and latex flow characters

The total volume of latex, d.r.c. and latex flow characters were highly inter-related. As expected, the duration of flow showed highly significant negative correlations with plugging index and d.r.c. and positive correlation with total volume of latex while this trait had a negative trend with initial rate of flow. The negative correlation of plugging index with latex volume ($P < 0.01$) and its positive correlation with d.r.c. ($P < 0.05$) is also well expected. The initial rate of flow showed significant positive correlation with total volume of latex ($P < 0.01$) and d.r.c. ($P < 0.05$). The concepts

on the mechanism of latex flow on tapping reviewed by Sethuraj (1977) support this relationship of initial rate of flow and d.r.c. The viscous latex filled in the vessels, under hydrostatic pressure, exudes as a result of release of pressure. Subsequent displacement of latex before the onset of a dilution reaction is due to the cohesive force existing in the liquid phase and is mostly free of latex dilution. Hence in case the initial flow is a major component of yield there is chances of high rubber content.

However the results ascertain that latex volume has the highest degree of association with dry rubber yield at highly significant level. The latex volume is governed by the rate and duration of flow which are mostly independent of each other.

Cause and effect relationships

When the anatomical and latex flow characters were considered together for the influence of yield of the respective year (at the fifth year of tapping) residual effect was low (0.3184). The highest positive direct effect was for total volume of latex (0.7043) indicating the prime importance of this trait for direct selection. Laticifer area come in the second rank for the direct positive effect on yield. In general, the latex flow characters such as duration of flow, plugging index and initial rate of flow showed positive direct effect on yield, though the magnitude of effect for the latter two traits were negligible indicating that duration of flow is a better

parameter for direct selection. Though the direct effect of plugging index is positive it is over ruled by its negative indirect effect via total volume of latex, laticifer area index and number of latex vessel rows and keeps a negative relationship with yield. In addition to a small magnitude of direct effect, initial rate of flow has good positive indirect effect via total volume and keeps a significant positive correlation with yield revealing its suitability as a parameter.

The dry rubber content also have high magnitude of direct effect (0.3823) on yield which is nullified by its negative effect via duration of flow and small negative effects via structural traits and hence its correlation with yield is not significant.

In addition to the laticifer area index, the H/W ratio of phloem rays and intensity of latex vessel anastomosing showed direct effect on yield while correlation of the former trait with yield was negligible.

In addition to the small magnitude of direct effect, intensity of latex vessel anastomosing have considerable magnitude of indirect effect via total volume of latex, keeping significant positive correlation with yield. Therefore this trait also can be considered as a good parameter for yield.

Similar to the previous data the direct effect of girth, number of latex vessel rows and the density and diameter of latex vessels

on yield were negative. Of this the number of latex vessel rows is worth considering since it has positive indirect effects via laticifer area index, total volume of latex and duration of flow and keeps positive correlation with yield. However, this trait is not suitable for direct selection. Laticifer area has good magnitude of positive direct effect on yield and in addition, it has positive effect via total volume of latex keeping highly significant positive correlation with yield. Hence this trait is a very good parameter for direct selection of high yielding materials.

Effective selection is not based on correlation alone. It is well known that progressive selection through generations is successful only when the character selected is highly heritable and determined by additive gene action. Only at such situation selection is effective, response is rapid and continuous, family performance is predictable and correlation between parental genotype and breeding behaviour is high (Simmonds, 1969; 1979 & Swaminathan, 1975). In Hevea though clone selection is practical, such aspects assume special importance when parents are selected for polyclonal seed gardens. The heritability values discussed elsewhere in this thesis shows that important anatomical parameters such as laticifer area index intensity of latex vessel anastomosing and H/W ratio of phloem rays which have high magnitude of direct effect on rubber yield are highly heritable traits combined with high genetic advance. The heritability values of total volume of latex and duration of

flow are only medium though these traits showed high correlations with yield and positive direct effects.

Another advantage of structural traits is that only one sampling was required for characterization. Latex volume, d.r.c. and latex flow characters, being highly variable due to environment and season, need monthly recordings.

This study, in general, showed that structural traits such as laticifer area index intensity of latex vessel anastomosing and H/W ratio of phloem rays should be considered as very important selection parameters for yield in Hevea. Those traits can effectively be used for direct selection of elite clones and good parents. The number of latex vessel rows cannot be used for direct selection while this trait can be considered for indirect selection, for high volume of latex.

Direct selection based on total volume of latex and duration of flow would also be effective for yield but this requires comparatively long period of testing in varying environments.

4.3. Girth and anatomical characters at initial maturity versus girth increment on tapping

The relative importance of yield determinants vary at different phases in the physiological age of the tree. Ho (1975) has attributed this to the different dominant functions of the tree at its various stages.

Genotypic correlations of structural traits possessed at early maturity on girth increment on tapping was examined. Percentage girth increase on tapping showed significant positive correlation with diameter and negative correlation with density of latex vessels.

Sethuraj (1977) and Markose (1984) observed positive relationships between girth and girth increment. In the present study also the relationship showed positive trend.

Width of phloem rays, laticifer area index, number of primary xylem points and number of intraxylary phloem points showed a positive trend with percentage girth increase while the intensity of latex vessel anastomosing, total number of latex vessel rows and height of phloem rays a negative trend. It is very interesting that most of the anatomical traits, except laticifer area index, which showed a negative trend with plugging index in panel BO-1 showed a negative trend with girth increment also. Low girth increment on tapping associated with low plugging index in panel A have been reported by earlier researchers (Milford et al., 1969 & Wycherley, 1975). They have attributed this to excess removal of latex beyond the capacity of the tree to replenish the loss. Higher number of primary xylem points and intraxylary phloem are highly inter-related and are favourable traits for strengthening the upward and down-ward translocation respectively. In more aged trees of Hevea clones these traits showed significant correlations with girth increment rate (Premakumari, 1988). As the trees become

aged, growth rate is retarded and more photosynthates are partitioned for latex. Adaxial phloem is usually activated as the function of normal phloem is hindered (Zamski and Tsivion, 1977). The results imply that the extent of influence of different traits vary at different stages of its growth.

Cause and effect relationships

Considering the cause and effect relationships, a high residual effect (0.7464) shows that the undefined factors contributed much to the girth increase at the initial years of tapping. However, among the characters under consideration the highest positive direct effect with a positive trend of correlation was observed for laticifer area index and hence can be considered for direct selection.

The primary xylem points showed positive direct effect of considerable magnitude and had a good magnitude of positive effect via the number of latex vessel rows. Its correlation with percentage girth increase showed a positive trend also assuming its importance as a criterion for good girth increment on tapping. Though this trait had significant negative correlation with the number of latex vessel rows, it was independent of laticifer area index. Hence both traits together can be considered as parameters for early prediction of girth increment on tapping. High number of primary xylem points might be a factor maintaining strong conduction in the upward direction to maintain the source of metabolites.

The correlation between percentage girth increase and phloem ray width showed a positive trend and this trait had positive direct effect on percentage girth increase indicating its importance for direct selection.

All the laticifer traits except laticifer area index had negative direct effects on percentage girth increase on tapping, of which the effects of the number of latex vessel rows, density of latex vessels and diameter of latex vessels were of considerable magnitudes. All those traits except the diameter of latex vessels showed negative trends of correlations also. The positive correlation of latex vessel diameter with percentage girth increase was manifested through its positive effects via laticifer area index, density of latex vessels and number of primary xylem points. However this trait can be considered for indirect selection.

Though the girth contributes positively via various traits such as laticifer area index, density of latex vessels, number of latex vessel rows, height of phloem rays and number of primary xylem points, its direct effect on percentage girth increase is negative and of a considerable magnitude. Markose (1984) also obtained the same result in a study involving 20 clones. Hence this trait cannot be considered as a reliable criterion for high girth increment on tapping. The direct effect of intraxylary phloem was also negative though the magnitude was very small. This trait has good magnitude of positive effect via the number of primary xylem points.

This study showed that the structural traits at the initial years of tapping have some hold on the girth increase on tapping though the major part is not explained. Laticifer area index is the best anatomical criteria for direct selection for high girth increase on tapping. Along with this the width of phloem rays and number of primary xylem points can also be considered. The diameter of latex vessels can be considered as a good criteria for indirect selection.

V. S U M M A R Y

This study was conducted to explore the variability and relationships among traits with emphasis to structural traits with a view to identify parameters for early prediction of yield and major yield constraints such as leaf diseases, drought and tapping panel dryness. Secondary laticifers which are commercially exploited are produced by the activity of vascular cambium and are arranged in rows in the bark. Fusiform initials divide anticlinally and the laticifer initials thus formed join end to end followed by the dissolution of cross walls (becoming coenocytic) and formation of tangential connections between vessels of the same ring. Pit fields with protoplasmic connections are present in between young latex vessels and phloem rays. At maturity of the wall the plasmodesmatal connections and nuclei become obscure. In such cases the wall of functional latex vessels are more adhered to the wall of phloem rays to facilitate short distance radial transport. Between the latex vessels plasmodesmatal connections are numerous and clear.

The phloem rays are heterogenous consisting of both prostrate and procumbent cells. Both uniseriate and multiseriate rays occur. Uni to tetra seriate types are common and they are fine to medium in width. End cells of uniseriate rays are large with conical dome shape. Multiseriate rays have one to three upright cells at both ends. The body cells are procumbent and two to four cell wide with compact arrangement. Based on the shape four types (Dumb-bell, oval, spindle and bat shaped) of multiseriate rays were identified.

Seasonal cambial activity is significant and the clones show almost the same pattern. Cambial activity is the least during May to July under the climatic conditions of central Kerala with an increasing trend from August onwards with the peak in November to January. The trend is continued during February-April.

Occurrence of intraxylary phloem was identified. Groups of such internal phloem occurs in association with the protoxylem at the pericentral region of the stem. Considering the active role of intraxylary phloem in translocation in girdled stems significance of adaxial phloem in Hevea deserves more attention.

The surface ornamentation of leaf has high influence on the major leaf diseases in Hevea, such as abnormal leaf fall disease caused by Phytophthora spp. and powdery mildew disease caused by Oidium heveae. Hevea leaf blade is hypostomatic and the stomata are almost equally distributed over the whole abaxial surface except the midrib and lateral veins where the frequency is very low. In lower frequency, stomata are present on other plant parts such as petiole, petiolule, young stem and fruit wall. Morphologically the stomata are paracytic (rubiaceous) type and those on the leaf blade are sunken.

The present study revealed that the stomatal ontogeny in Hevea is a special type, different from any of the two major types (perigenous/mesogenous) described earlier. The specialities of stomatal

ontogeny in Hevea are (1) formation of stomatal aperture by lysing of cells and (2) development of guard cells by cell fusion. Pear shaped subsidiary cells are also formed by the fusion of more than one cell. Followed by cell fusion nuclear fusion takes place resulting in a large elongated nucleus in the guard cell. On the fruit wall, in addition to the normal stomata, giant stomata are formed the origin of which shows some similarity to that of lyseogenous cavities. The giant stomata on the fruit wall may or may not have the typical morphology of the paracytic stomata. Such abnormally large stomata are formed, at a later stage of fruit development. The giant opening is formed by the disintegration of epidermal cells. The guard cells are developed subsequently by cell fusion and thickening of side walls. The giant stomata of fruit wall are preferential sites of Phytophthora infection which causes pod rot which subsequently leads to abnormal leaf fall disease.

Part to part differences in the size, distribution, topography and exposure of stomata, observed in this study provides explanation to the organographic preference for Phytophthora infection. Leaf blade has the last preference as infection site which should be attribute to the sinuous wall of lower apidermis, sunken stomata, small apertures and masking of stomatal apertures by the reticulum of buttressed waxes. In contrast, the stomata on the petiole, vein and young stem have large apertures though the frequency is very low. Being situated in a raised topographic position they are exposed and hence advantageous for disease causing organisms.

The reticulate ornamentation of the lower epidermis in Hevea is due to the reticulate pattern of epicuticular wax. On the upper epidermis the wax distribution is even and it is vermiculate type. Observations on the phenology of epicuticular wax on the lower epidermis showed that the reticulum of wax is developed at the pendent stage before which the wax is thin and interrupted without filamentous striae which facilitate Oidium infection. Hence the structural basis of the intensity of powdery mildew in relation to leaf phenology in Hevea is the wax pattern. Clonal differences in wintering and refoliation time results in clonal susceptibility/resistance to powdery mildew disease. Such a relationship was indicated in the clones under observation.

Analysis for interclonal variations of quantitative traits showed that in terms of seriation of phloem rays, triseriate is predominant, irrespective of the clones, while clonal difference is significant for the other types only (uni, bi and tetra seriate). The proportion of bi and tetraseriate types is very useful criteria for clone identification.

In terms of ray shape bat shape is the predominant type in all clones and clonal difference is significant only for the proportion of oval shaped rays which can also be used for clone identification. For this purpose the density, height, width and height/width ratio of phloem rays are also useful. The ratio of phloem ray height to its width is a good indicator of the extent of the zig-zag

orientation of latex vessels in the longitudinal direction. Hence clonal differences in the ray characteristics decides the orientation of latex vessels which influences yield. The cell diameter of ray component is another clonal characteristic which can influence turgor maintenance in latex vessels and thereby latex flow. This trait influences the orientation of latex vessels also via the width of phloem rays.

Rubber yield, latex volume, dry rubber content, growth characters such as girth and panel length, latex flow characters such as initial rate of flow, plugging index and duration of flow and structural characters such as number of latex vessel rows, density and diameter of latex vessels, intensity of laticifer anastomosing, laticifer area index, number of primary xylem points, number of intraxylary phloem points, density of petiolar stomata, width of leaf midrib and cuticle thickness are significant clonal characters. For the combination of different traits clones vary widely and the extent of contribution of different yield contributing traits vary in different high yielding clones. However, in all high yielders latex volume was medium to high. A combination of medium to high laticifer area and intensity of laticifer anastomosing was observed in all high yielders. Clonal differences were pronounced for the intensity of abnormal leaf fall and powdery mildew disease and also for the wintering pattern. Late wintering clones showed high intensity of powdery mildew disease when compared to the early

wintering clones. The clones which recorded high density of petiolar stomata were highly susceptible to abnormal leaf fall disease and vice versa. Clonal differences for the incidence of brown bast was not statistically significant but the clones recorded a wide range of 00-26 per cent. Among the clones under study the top yielders showed high incidence of tapping panel dryness. Among the medium and low yielding clones varying trend was observed. Differential expression of brown bast incidence among the medium and low yielding clones indicate that factors other than yield are also involved in the expression of this syndrome.

Monthly yield performances and clone x month interaction are statistically significant. Clonal differences for monthly yield performance is governed by clonal variation in summer drop of yield. During wet months clonal performances are more or less comparable. Summer variations in rubber yield, latex volume and latex flow characters are significant clonal characters. Clonal differences in summer drop of yield is a combined effect of drought and the incidence of powdery mildew. It is associated with a drop in initial flow rate and a rise in plugging index. To the impact of drought condition on yield initial flow rate has major role while the influence of plugging index might be intensifying summer drop of yield via powdery mildew also. The extent of effect of both these factors vary in clones. The clones which have high laticifer area as major yield contributing factor and where high H/W ratio is associated

(more or less straight orientation of latex vessels) the impact of drought condition on yield drop is less pronounced and showed less variation in initial rate of flow. Hence these structural traits are reliable parameters of drought tolerance. The drought tolerant and susceptible groups of clones showed significant differences for structural traits such as phloem ray width, H/W ratio of phloem rays, proportion of soft bast to total bark thickness and proportion of latex vessel rows in the soft bast to total number of latex vessel rows which can also be used as supporting parameters for drought tolerance. However the genetic make up of a clone for the various desirable and undesirable component traits is the important factor to be considered than the yield itself when planting materials are chosen for specific environment.

Variations of bark anatomical characters between juvenile and mature trees and thereafter on tapping, between virgin and renewed bark and between the two ploidy levels (diploid and tetraploid) were studied. From juvenile to mature age significant increases in latex vessel diameter, laticifer area index, phloem ray width, girth and number of latex vessel rows were evident. The differences in latex vessel density and intensity of anastomosing were not statistically significant but a fall in numerical values were observed. For the trees under exploitation also latex vessel rows, girth and laticifer area index recorded an increase from year to year in panel BO-1. Latex vessel density showed a reducing tendency with fluctuations.

Latex vessel diameter showed a rise up to the third year of tapping and stabilized. Hence the quantity of laticifer area of a tree under exploitation is solely depended on the variation in latex vessel rows and girth (the two sinks) in addition to latex regeneration, in the partitioning of metabolites.

The two growth phases of bark (virgin and renewed) differ significantly for certain bark structural traits such as density of latex vessels, proportion of latex vessel rows and the height/width ratio of phloem rays. The observations highlights the importance of girth increment of clones on tapping and the need of deeper tapping of renewed bark for a more economic yield.

The technique of polyploidy is usually employed to induce genetic variability and to exploit the variability for crop improvement. This study indicated that the structural variability induced in Hevea by polyploidization do not promise yield improvement. The same trend was observed for growth also.

Information on the correlations of juvenile versus adult trees for the component traits will be useful to support the feasibility of early prediction based on juvenile yield. The correlation study showed that preliminary selection for latex vessel rows, ray width, tree girth and laticifer area index can be made at juvenile stage itself. Early selection on component basis may provide some clue on the sustenance of yield at the mature age via a further prediction

on the possibility of drought tolerance and chances of brown bast occurrence.

Correlation studies revealed the relationships among bark thickness, total number of latex vessel rows and the proportion of latex vessel rows left uncut in the residual bark. The results implied that on thicker bark deeper tapping would not make much benefit and in the reverse situation shallow tapping will not be economic. Thus for economic yield tapping depth should be adjusted according to the bark thickness.

The influence of stomatal characters with respect to the petiolar stomata was also examined by correlation studies. The percentage leaf retention after the incidence of abnormal leaf fall disease showed high negative correlation with frequency of petiolar stomata and the aperture size which explained nearly 68 per cent of the variation. Stomatal frequency alone accounted the major part of the influence and hence is a reliable parameter for field escape from abnormal leaf fall disease.

The quantity of intraxylary phloem is closely associated with the quantity of primary xylem points and this trait showed significant associations with stem diameter and girth increment on tapping in 17 year old trees. Genotypic correlation of this trait with girth increment on tapping on panel BO-1 was not at significant level. Hence further study is needed to assess the extent of its effect on growth at varying conditions and tree age.

Correlation studies revealed that a judicious selection for the genotype is essential to avoid the incidence of tapping panel dryness. A check in translocation might also be one of the reasons for the loss of biomass production on tapping. Selection for high initial yield and high numebr of latex vessel rows involve the risk of brown bast incidence even under normal tapping system. A high laticifer area should be associated with medium girth, latex vessel rows and width of latex vessels.

Component analysis for yield and its early prediction and for early prediction of girth increment on tapping was made employing the estimation of genotypic correlations and path coefficient analysis. Estimates of variability and genetic parameters of yield, latex flow characters, structural characters and also the variations of yield and latex flow characters during drought period were taken. Rubber yield is a very complex trait governed by a very large number of factors and their interactions. Laticifer area index, a well balanced system of the different factors, is the best parameter for early prediction of yield and girth increment on tapping. Laticifer anastomosing directly contributes to subsequent yield and the genotypic correlation with yield is positive though not up to the significant level. These two traits are independent of each other and hence both together can make a better contribution to yield. These structural traits are suitable parameters for direct selection for a sustainable yield. For subsequent yield and girth increment on tapping, girth,

number of latex vessel rows and diameter of latex vessels contribute via laticifer area though their direct effects are negative and hence can be considered for indirect selection. In addition to laticifer area index number of primary xylem points also showed high magnitude of positive direct effect on girth increment on tapping and the correlation also was positive. These two traits are independent of each other and hence both together can be considered for early prediction of girth increment on tapping. The structural traits alone contributed more or less 50 per cent to the early prediction for yield and girth increment.

When structural traits and physiological traits were considered together for yield in a specific year (11th year of tapping) the residual effect was low and the characters taken into consideration contributed to more than 85 per cent. Total volume of latex and laticifer area index were the major components of yield. Duration of flow contributed directly to rubber yield and showed significant positive correlation also. Though the correlation was not significant direct effect of d.r.c. on yield was positive and of high magnitude and hence can be considered for direct selection. Intensity of anastomosing, initial rate of flow and plugging index which showed significant correlations with yield contributed via total volume.

For the inheritance of rubber yield, latex volume, number of latex vessel rows, laticifer area index, height/width ratio of

phloem rays, quantity of intraxylary phloem and primary xylem points and summer variations of rubber yield and initial flow rate additive gene action predominates. Hence these traits are effective parameters for parental selection. For the inheritance of d.r.c., girth, diameter and density of latex vessels, laticifer anastomosing and width of phloem rays non-additive gene action predominates and hence can be considered for phenotypic selection. For latex flow characters h^2 was only medium. The structural traits as parameters have a special advantage that monthly/seasonal variations are negligible and hence a single recording is sufficient while monthly/seasonal observations are needed for yield, latex volume and latex flow characters. Laboratory observations, though time consuming and laborious, are also more accommodating than field observations.

VI. REFERENCES

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