Anatomy of *Hevea* and Its Influence on Latex Production

J.B. Gomez

Malaysian Rubber Research
and Development Board

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PREFACE

Latex from which natural rubber is extracted is a milky sap which is manufactured and stored in an intricate network of tubes each of which is approximately one third the diameter of a human hair. These are present throughout the external tissues of *Hevea*, the most successful rubber tree.

In the early part of the 20th century a clear knowledge of the anatomy of the relevant tissues of *Hevea* led to the development of successful methods of harvesting the latex. When Ridley developed the excision method of tapping in the early days of the natural rubber industry, he used a great deal of insight and intuition into the occurrence of latex vessels in the bark tissues, their geometry of distribution in the peripheral tissues and a perspicacious insight into certain aspects of latex physiology. Nearly a century of exploitation of *Hevea* has still not challenged his concepts, although many refinements of the technique have been developed through a better knowledge of the anatomy and physiology of *Hevea.*

Bobilioff in 1923 summarised the existing knowledge at that time in a book on anatomy and physiology of *Hevea.* Much new information has been added to these findings in the last sixty years.

This monograph summarises the present state of knowledge in this field, drawing freely from the early literature as well as from the author's efforts to bring a deeper understanding of the subject for the benefit of students of anatomy, exploitation and breeding of *Hevea.*

The MRRDB supports this type of basic research as it provides the impetus for development of newer concepts of exploitation such as puncture tapping. Just as a knowledge of human anatomy is necessary for successful operations on the body, the knowledge of the structure of the system which is exploited precedes the rationale of exploitation and hence it is hoped that the knowledge presented in this monograph may help the ongoing process of evolving newer latex extraction techniques.

Tan Sri (Dr) B.C. Sekhar
Chairman, MRRDB.

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1. Introduction

Latex occurs in the plant kingdom in a variety of plants distributed in about 12 500 species belonging to 900 genera[1]. These plants belong to about 20 families, mostly of dicotyledons, but a few monocotyledonous families are included together with one genus of Pteridophytes, *Regnellidium* of the Marsiliaceae[2] Of these laticiferous plants only about 1000 species of plants representing 76 families and a few hundred genera contain rubber[3].

Latex is typically contained in tubes and cells which are collectively known as laticifers. These are usually tubular structures which are branched or unbranched, and in many species a very complex laticiferous system is formed by anastomosis between tubes. According to the ontogeny of laticifers they can be classified as the articulated and non-articulated types. Most of the articulated and non-articulated types are often referred to as 'vessels' probably due to their resemblance in origin to that of the conducting elements. In *Hevea* literature one often finds the term 'latex vessels' and this terminology is preferred here in discussing *Hevea* laticifers.

Laticifers may occur in any plant organ[1]. However, Sperlich[4] has noted that in certain plants, the laticifers may be restricted to specific tissues. In *Hevea,* laticifers have been reported in all organs of the plant including the leaves, flowers and fruit. In the root, they occur in bark* tissues. Reports of plugging of xylem vessels with latex have been confirmed by Bobilioff[5,6]. There are occasional reports of laticifers in the pith[5,7]. No laticifers have been reported in the axis of the embryo but copious vessels are present in the inner integument of the seed and in the cotyledons[8].

The *Hevea* tree is exploited commercially for its latex by a systematic excision of the external tissues of the trunk; *viz* bark. Latex is contained mainly in a system of articulated anastomosing latex vessels which are oriented in the bark tissue according to a specific pattern. These latex vessels, form the central theme for anatomical studies on *Hevea*. Studies on the mode of occurrence of latex vessels throughout the plant body made it clear that the principal latex bearing tissue in *Hevea* is the bark of the tree. Numerous studies on the quantitative features of the laticiferous system over the last sixty years have advanced our knowledge of the productivity

*The term 'bark' is used in the popular sense: to include all tissues external to the vascular cambium.

of *Hevea*. In this monograph the main attempt will be to describe the laticiferous system, its quantitative features and relationship to yield and other simple parameters that can be measured. Other significant aspects of morphology and anatomy which have been studied in the past would also be reviewed in the light of their relative importance to the understanding of the productivity of the tree.

2. Cell types seen in *Hevea*

Bobilioff[5,9] has considered the various cell types present in *Hevea*. He described the morphology and functions of the cell elements and various tissues such as cork, cork cambium, phelloderm, parenchyma cells, stone cells, medullary rays, laticiferous vessels and sieve tubes.

The cells of a plant are derived from meristems without characteristic differences as seen later, after differentiation and development. Some cells undergo more radical changes than other cells during the course of development, and become specialised into various degrees. Various types of parenchyma cells are relatively less specialised and retain their form and cytological structure not too different from their meristematic initials. Other cells, on the other hand develop thick or rigid walls, become devoid of cytoplasmic contents and cease structural and functional adaptability *eg* sclerenchyma cells. Between these two extreme types, a number of cell types exist which differ in form, shape, function and metabolic activity.

The principal tissue types can be summarised as below (see also *Figure 1*).

Epidermis. A continuous external layer of cells outlining the primary body of the plant is known as epidermis. The main mass of epidermal cells are brick shaped with exceptions in the form of guard cells of the stomata and various trichomes. Leaf epidermal cells have the characteristic cuticle. In tissues subject to secondary growth, the epidermis is replaced by the periderm.

Periderm. Cork tissue or phellum, cork cambium or phellogen and the phelloderm are the three types of cells in the periderm. The phellogen arises in the surface of axial organs having secondary growth. It may arise from the epidermis, cortex or phloem and produces phellum towards the outside and phelloderm towards the inside. The primary regeneration in excised bark tissue after tapping or other forms of wounding is caused by the activity of the phellogen. While the cork cells are suberised and lack protoplasts at maturity, the peridermal cells are mostly parenchymatous.

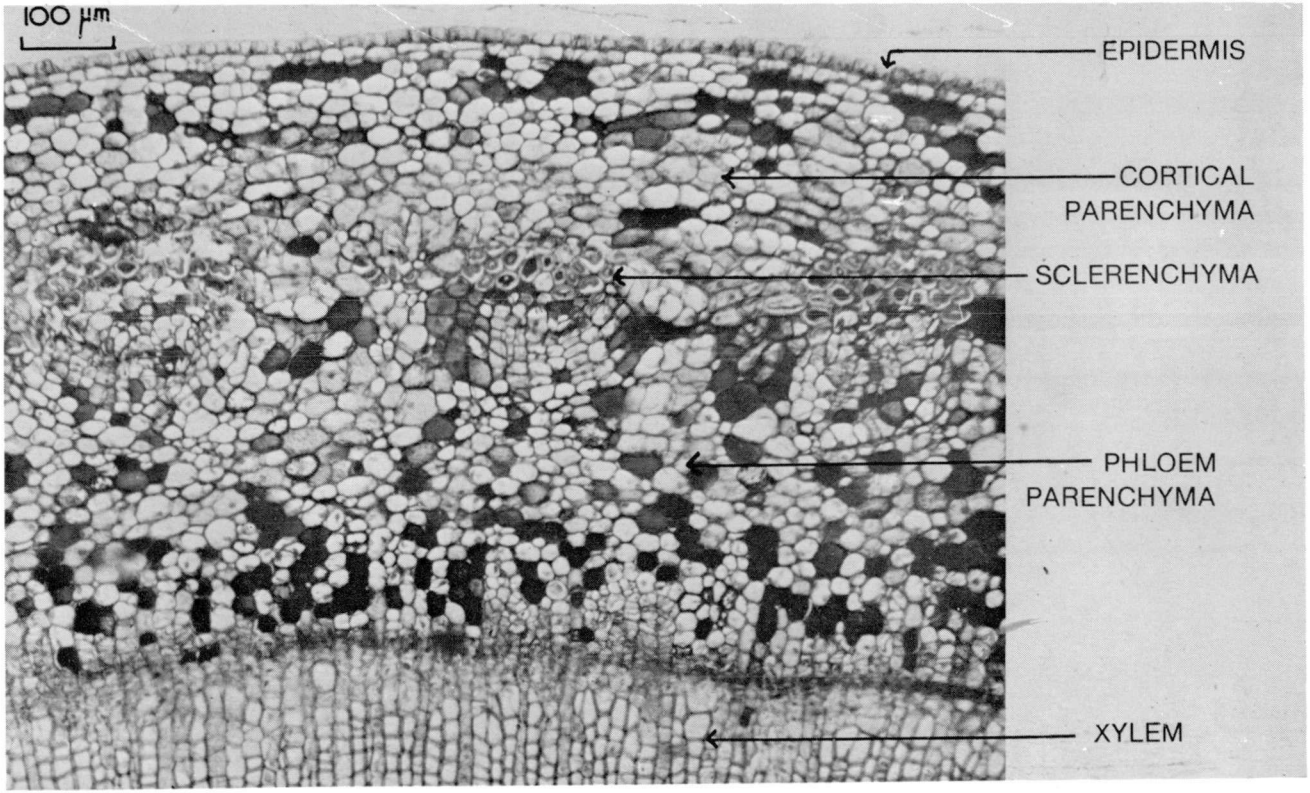

Figure 1. Cell types in Hevea. × 120.

Parenchyma cells. The ground tissue in the cortex of both stem and root and the leaf mesophyll consists of parenchyma cells. They also occur in the medullary rays. Parenchyma cells are living and capable of growth, differentiation and division. Their walls are often primary.

Collenchyma cells. These are a form of parenchyma cells specialised for supportive function in young tissues. Unevenly thickened walls distinguish them from parenchyma cells.

Sclerenchyma cells. In *Hevea* sclerenchyma cells often occur as groups of cells or occasionally individually in the formative stages. They have thick secondary walls which are lignified and commonly are devoid of protoplasts. Two forms of sclerenchyma *viz* sclereids and fibres are recognised.

Xylem. The xylem is the conducting tissue in the wood of the plant. It has also storage and supportive functions. Tracheids and vessel members conduct water and soil elements. Fibres are also present to strengthen the plant body.

Phloem. This tissue is concerned with storage and conduction of assimilates.Sieve cells and sieve tubes specialise in the conducting function, while associated parenchyma have a storage function. Fibres are also present for supportive functions.

Laticifers. The *Hevea* tree is grown for its laticifers which contain latex. A network of anastomosing tubes, sandwiched between phloem parenchyma, constitutes the laticiferous system in the plant. The laticifer cytoplasm is a specialised one containing various ergastic substances and the articulated cells are multinucleate. The nuclei were reported to be bigger than those of other cortical cells[9].

3. The ontogeny of the laticiferous system

A considerable amount of information on the ontogeny of laticifers in other plants was available when Scott[10] investigated germinating *Hevea* seeds. He observed that the latex vessels can be easily detected by their 'characteristic granular contents and by the absence of aleurone grains'. He describes these cells as elongate and smaller in cross section than their neighbours. Cross walls could be detected even at the stage when latex is distinguishable. He could detect the absorption of cross walls in seedlings with root length approaching 3 - 4 mms. In the root, the hypodermal system is more advanced in comparison to the vascular system of laticifers. He observed a similar developmental history in the hypocotyl. The

rate of development of latex vessels in each tissue is determined by the rate of development of the parent tissue itself.

Bobilioff[11] investigated the origin of latex vessels in young cotyledons and the innermost integument of the seed and observed that latex vessels arise in two ways, (1) by absorption of cross walls of a row of cells, (2) by extension or growth of certain cells*. Latex formation takes place in such cells as the vessels originate. He also observed that the property of being able to contain latex was not confined to latex vessels themselves. Under certain conditions parenchyma cells and medullary ray cells contain globules of rubber. Rudimentary latex vessels are shown in *Figure 2*.

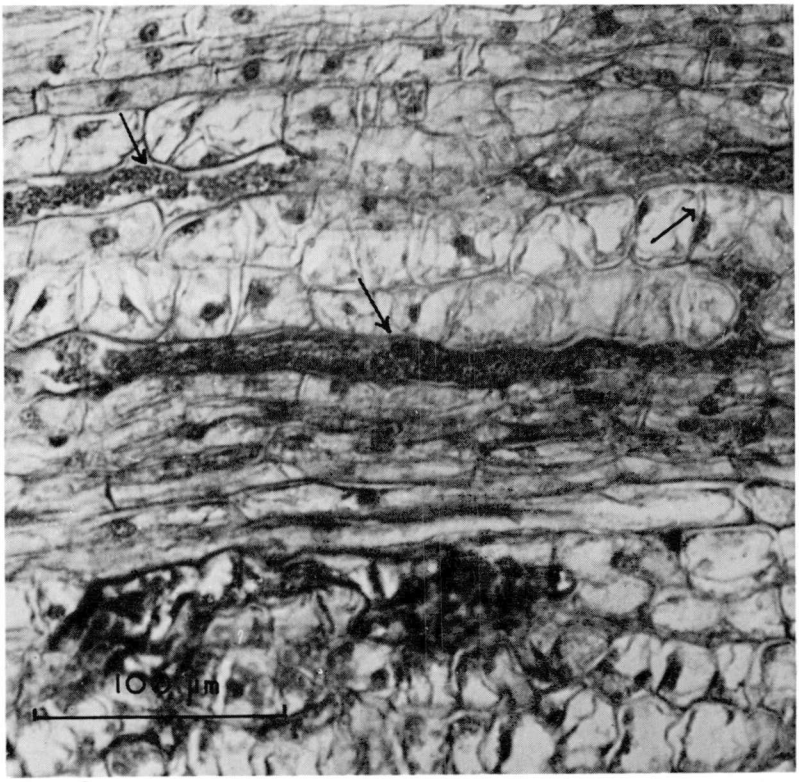

Figure 2. Rudimentary latex vessels from young primordium (arrows) × 320 (Ref. 19).

4. Developmental anatomy of laticifers in the fruit and seed

Maximum size of fruit is attained in about seven to eight weeks after fertilization[12]. Ovary, at fertilization is approximately 2 mm long and

* For a recent study of the problem, see ref. 113.

1.2 mm wide and almost cylindrical in shape. Pericarp is soft and laticiferous until maximum size is obtained, but is more or less cartilaginous about ten weeks after fertilization. The exocarp remains laticiferous until 10 - 14 days before maturity, when it dries up and becomes membraneous. Most of the laticiferous tissue arises after capsule reaches a considerable size. Laticiferous tissue is absent at the time of fertilization. At maturity, the fruit dehisces septicidally and later bursts with a loud report. Seeds are sometimes thrown as far as 100 feet away. Sometimes, the seeds germinate within the fallen fruit.

Clonal seeds have characteristic shape, size and morphology. The following account is limited to a description of Tjir 1 clonal seed[13]. They have a characteristic oblong shape. The external circumference along the equatorial plane is an average of 7.2 cm and along the polar plane, 8.3 cm. The seed is slightly broader at the antipodal end (*Figure 3*). The testa is hard and impermeable, except at the micropyle. It has a characteristic chestnut brown colour. There are a large number of darker mottles on the testa. On the dorsal sur-

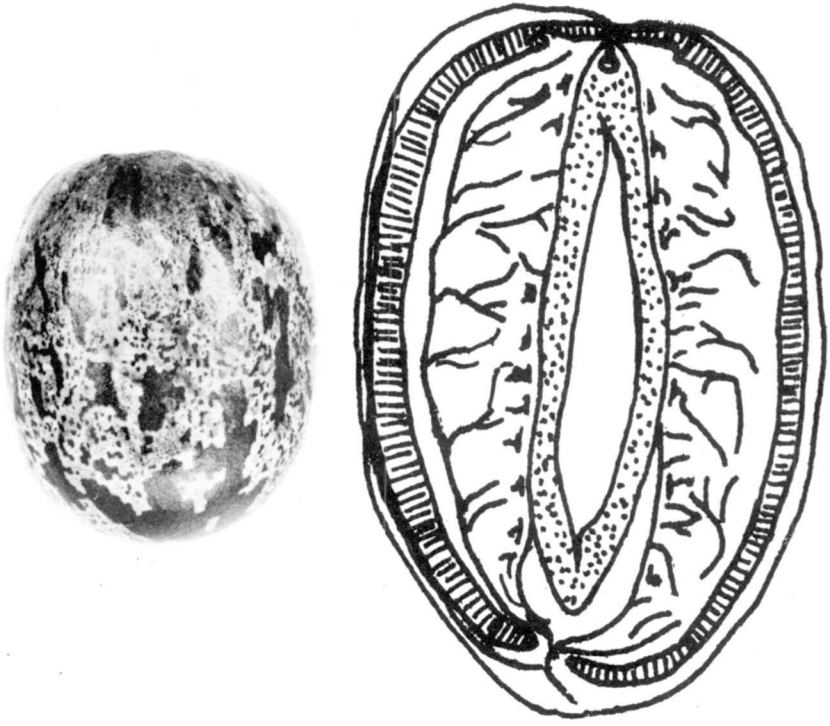

Figure 3. a) Whole Tjir 1 seed. b) longitudinal section. × 2 (Ref. 8).

face (the ventral surface is the side where the hilum is situated) of the micropylar pole, these mottles converge towards the hilar depression. The colour of these mottles darkens as they converge. Towards the antipodal end, these mottles gradually fade and disappear. The mottles are extremely rare at the ventral surface. The hilum is situated at the micropylar pole on the ventral side of the seed. The hilar region is distinct as a shallow pit, nearly circular in shape, measuring 3 - 4 mm across. This depression, however, should not be confused with one present at the antipodal region, on the ventral side, which is caused by the locular surface of the endocarp jutting inwards. The hilar depression, on the other hand, is influenced by the manner of placental attachment. There is a thin layer of cuticle 2 mm broad, which can be peeled off from the hilar end to a short distance, medianly along the ventral surface.

Inner to the testa is the many layered tegmen which is very soft, papery and light. The tegmen is attached to the inner walls of the testa as well as to the endosperm. This tissue has generous air spaces, especially in a resting seed. The tegmen appears to have brown veins converging to the antipodal end of the seed.

The embryo is oriented inside the endospermal tissue in such a way that the radicle faces the micropyle. The axis is not enclosed by the cotyledons except at the plumular end. There are two white, distinctly veined cotyledons situated dorsiventrally flat inside the endosperm so that tangential sections made along the dorsal surface or ventral surface will reveal the cotyledons in full. In a fresh seed the cotyledons are close together and somewhat crumpled, following the undulations of the endospermal surfaces which contact them. In a resting seed, there is considerable space between the inner surfaces of the cotyledons, caused by the inward and outward shrinkage of the endospermal halves.

5. Germination and early growth of the seedling

The hypocotyl emerges from the seed through the hole left by the operculum which is formed by a circular abscission layer in the seed coat[12,14]. This operculum lifts completely before the hypocotyl emerges but remains attached to one side, usually the top, and sometimes persist for several weeks. The adventitious roots develop rapidly, while the primary root grows slowly. The cotyledons remain in the seed and the plumule emerges, forming a hump at first, which straightens out later (*Figure 4*). The plumule is about 5 cm long when it straightens up after emergence. Although the cotyledons do not emerge, they sometimes turn green or partially green at the micropylar end. Cork formation occurs in the hypocotyl within four days of germination. It is often delayed under

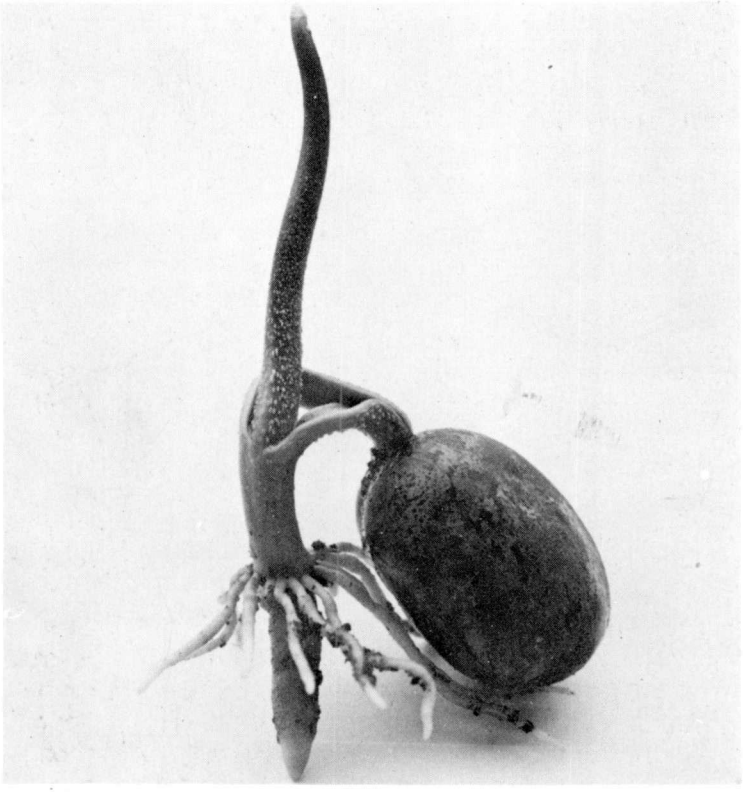

Figure 4. Seedling with cotyledons inside seed and emerged plumule and radicle.

each node. Seedlings usually remain attached to the cotyledons for 14 - 18 days, but attachment can be prolonged to four months by repeatedly excising buds. Approximately 75% of growth in height of these seedlings takes place at night.

Working on *Hevea brasiliensis* in culture, Muzik[15] has observed that the typical hump shape of the emerging plumule was retained even when pressure on the plumule was removed by cutting away half of the endosperm. He further reports that mature or nearly mature cotyledons, 10 - 14 weeks after fertilization, formed roots readily in nutrient media or in damp chamber. These roots showed no consistent geotropic response.

The present writer's observations[13] are somewhat different from those described above. The radicle emerges through the circular opening formed around the hilar depression in the ventral micropylar pole of the testa. Twenty four hours after germination, this radicle would have become 1 - 1.5 cm long. Immediately preceding the apex of the primary root primordium, a circular ring of

nodules appear, which are the primordia of the lateral roots. Muzik's description of these roots as adventitious should be questioned as these laterals arise at least two millimetres below the transition zone from shoot to root, as shown by vascularization patterns. The laterals usually number around 12. The ring of laterals grow rapidly while the primary tap root remains in the primordial condition. However, when the laterals reach lengths of 2 cm or more, the tap root grows vigorously again.

The plumule begins to elongate soon after germination. At the two-day-old stage, the plumule is observed to be enclosed between the cotyledonary stalks which have elongated considerably and have partially emerged normally bent so that, together with the hypocotyl, they resemble an inverted J. At the three-day stage, the plumule is still enclosed within the emerged cotyledonary stalks but the apical part of the plumule is well within the seed. At the four-day-old stage, one observes the base of the plumule distinctly displayed between the cotyledonary stalks which appear to be thinner. The middle part of the plumule is hump-shaped and shows a tendency to withdraw its tip from within the seed. Once the tip is free, the plumule gradually straightens up, simultaneously growing with vigour. By this time, the plumule, visible above the junction of the hypocotyl with cotyledonary stalks is 4 - 5 cm long. The hypocotyl region of the ring of lateral roots is 1 - 2 cm long, the primary tap root is 3 - 4 cm long and the laterals 5 - 6 cm long.

The cotyledons never emerge from the seed. The seed is hence hypogeal. The cotyledonary stalk emerges due to its elongation and twisting, and turns green. The upper cotyledonary stalk (on the dorsal side) grows more rapidly than the lower. The cotyledons themselves turn yellowish to light green towards the micropylar region as light seeps through. The plumule has a distinct pinkish colour, which slowly turns green on exposure to sunlight.

When the seedling is eight-days old the first pair of leaves begin to open out to expose the apical meristem. The leaves are small and reddish. The lateral roots are more than 8 cm long at this stage. They do have plenty of root hairs distributed approximately 1 cm from the tip. The basal part of the stem and the hypocotyl region and the outer surfaces of the cotyledonary stalks are covered with small patches of corky tissue which exhibit lenticels.

Even on the fourteenth day, the leaves have not fully expanded, they are small, but green. The tap root is still growing very fast, and no laterals have appeared below the first ring of laterals. By the sixteenth day after germination, other lateral roots arise from the tap root and tertiary roots appear in the original laterals. The lateral

roots newly formed are not distributed regularly except as an incomplete ring nearly 4 cm below the first ring of laterals. The leaves are larger and opposite.

Internode formation above the first pair of leaves is during the third week of growth and the first flush of three leaves appear above.

6. Primary structure of embryo

The embryo in the mature seed consists of a round mass which resembles the scutellum of *Cocos*, with the radicle flat where it contacts the hilar depression at the micropylar end and the plumular end of the axis enclosed between the cotyledons facing the antipodal end of the seed. A longitudinal section through the axis and cotyledons reveals the mass of parenchymatous cells in the axis with a densely staining tissue situated nearly parallel to the margin of the axis approximately 160 μ inside the margin. The tissue at the promeristem is 120 μ wide at the widest part (radicular end) and narrows at the plumular end (*Figure 5*). Continuation of this densely staining promeristem is observed in both the cotyledons. The ground tissue is made up of more or less isodiametric cells with thin walls, dense cytoplasm and generous inclusions of starch grains. The distribution of starch grains in the embryo is not even at all places, the parenchymatous ground tissue having dense inclusions except at the plumular apex. The promeristem is nearly devoid of starch inclusions. The continuation of the promeristem into the cotyledonary stalks show gradual differentiation into vascular tissue as it proceeds upwards from the embryonic axis. This shows that vascular development is basipetal in the embryo.

The promeristem contributes to the development of the protoderm, the primary dermal tissue of the plant. The protoderm in a germinating embryo consists of a layer of epidermal cells on the outside, enclosing cortical parenchyma ten layers thick, when the seedling is less than 24 hours old, the cells appear more or less rectangular in longitudinal section.

The inner layers of the promeristem should be termed the procambium which cuts off cells towards the inside which later differentiate to form the vascular tissue. The origin of the pith is from the ground meristem in the interior.

The organisation of the root apex shows clearly one layer of actively dividing superchromatic cells, which is the calyptrogen. This layer cuts off many cells towards the outside, forming the many layered calyptra, or root cap. The outer layers of calyptra show suberisation even at a very early stage.

Hyperchromicity to basic dyes was observed in several cells distributed along the epidermis at the plumular end of the axis and the leaf primordia. These cells showed increased vacuolation, hypochromatic nuclei and had lesser number of nucleoli. Some of these cells show dense cytoplasm full of inclusions which stain heavily.

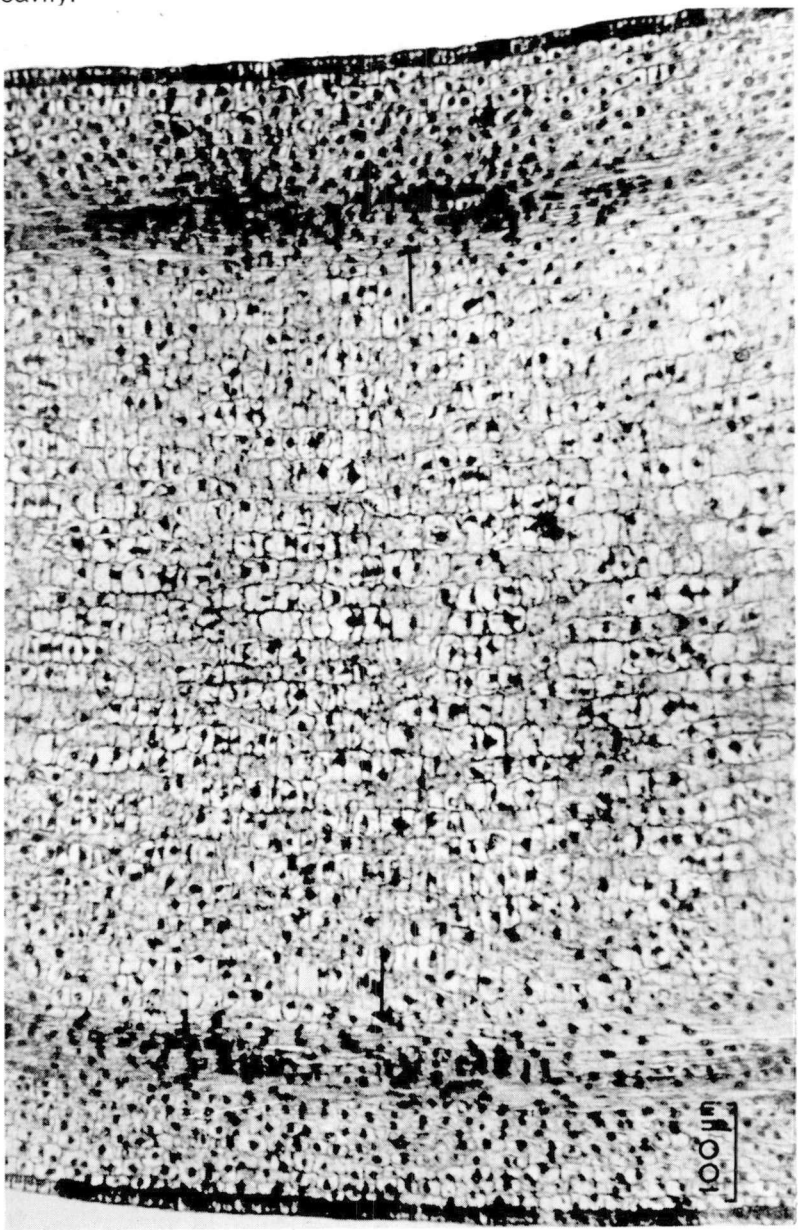

Figure 5. Longitudinal section of growing embryo showing promeristem. (arrows) × 125 (Ref. 19).

7. Primary vascularization in the seedling

The differentiation of the procambium into early vascular elements occurs as early as 24 hours after germination. At this stage, the radicle has only emerged a few millimeters outside the testa.

The procambial tissue at this stage is evident as densely staining thin walled rows of cells which have large nuclei, lesser cell inclusions and with little or no vacuoles. These procambial cells are longer than they are broad as seen in longitudinal sections. Cells measure approximately 30 × 3 × 4 mu.

The procambium cuts off cells towards the exterior which then differentiate to form phloem elements, and cells towards the interior to form xylem elements. Annular, annular-helical and helical (spiral) thickenings are observed in vessels at this stage. It appears that the differentiation of xylem proceeds from apex downwards as far as the hypocotyl is considered. There is therefore a basipetal development of xylem elements from the cotyledonary stalks downwards into the hypocotyl.

Longitudinal sections of the plumule at the four-day-old stage reveal that xylem vessel formation is evident in the plumule (*Figure 6*). The first fully differentiated spiral vessels are observed 500 μ below the junction of shoot apex with the leaf primordia. These vessels continue downwards for another 600 μ but no further vessels of similar age are found below. The proxylem elements in the vascular tissue below this region are definitely undergoing further differentiation. The promeristem in the shoot apex shows no differentiation. It is worthwhile to note that some proxylem elements have completed differentiation in some of the leaf primordia. The pattern of xylem development is therefore basipetal.

Sieve tubes appear to be much more well developed and numerous than xylem elements. In cross sections, more groups of phloem elements are found at different degrees of differentiation all along the exterior of the procambium. Longitudinal sections reveal sieve tubes at an older stage of development than xylem elements.

In serial cross sections from apex downwards it is evident that the promeristem is undifferentiated in the first few hundred microns of the apex, below the leaf primordia. Vessel formation is evident below this region in a basipetal pattern of development. The differentiation is not uniform around the whole stem. Cross sections reveal large and smaller groups of xylem. The number of groups vary, the distance between groups is not constant, thus revealing rather an irregular distribution of primary xylem.

On the whole, the vasculature can be described as an ectophloic siphonostele or a hollow cylinder of tissue with parenchymatous pith filling the inside and the cylinder itself consisting of phloem outside, xylem inside and the procambium sandwiched between them.

The xylem shows centrifugal development and is endarch, with protoxylem near the cambium. The phloem, as one would expect, is centrifugal in the stem.

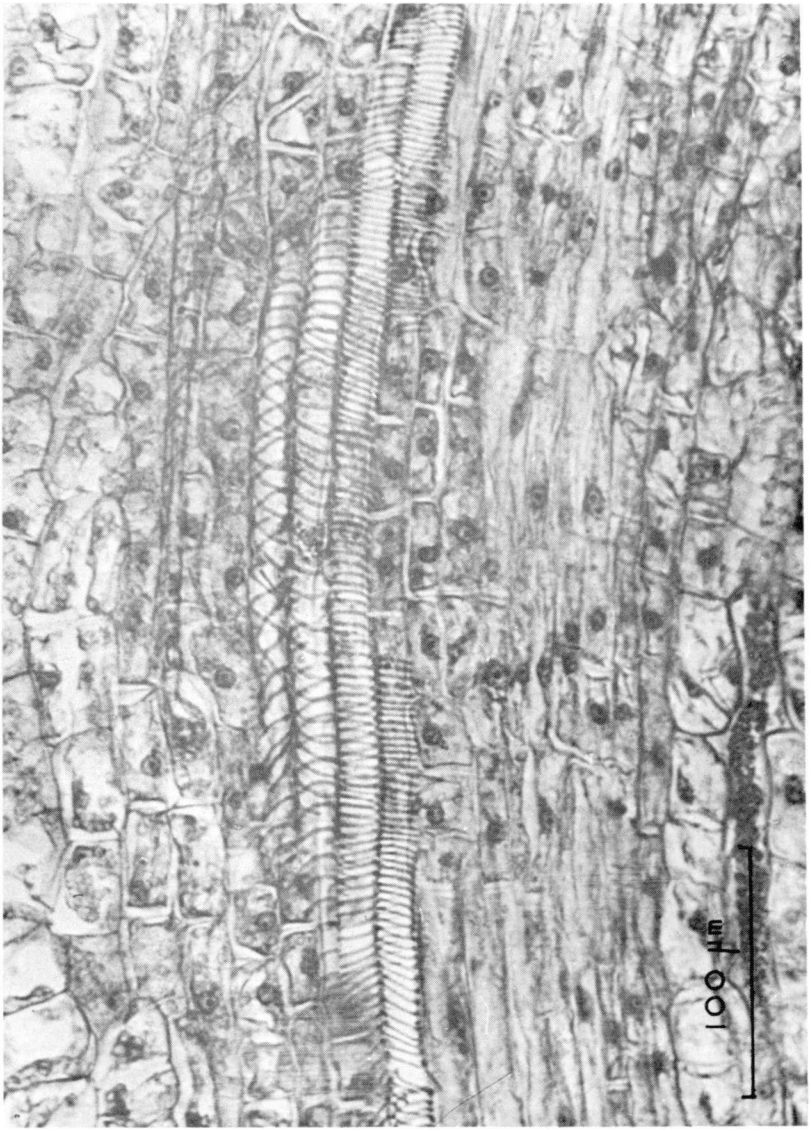

Figure 6. Longitudinal section of plumule showing xylem vessel formation. × 320 (Ref. 19).

8. The origin of prolaticifers and their transition to laticifers

Milanez[16-18] considered that the prolaticifers expel nuclear material during development. From longitudinal sections of terminal and axillary buds, he found that the primary laticiferous system is differentiated, beginning from the procambium in the vicinity of the phloem. Binucleate condition is one of the first indications of laticifer differentiation. Along the line of future vessels, he found cells which were already typically laticiferous, separated by cells only slightly differentiated (binucleate) and by still others in which there was no sign of any special evolution. There are unequivocal signs of nuclear interaction in multinucleate cells, one nucleus eventually increased in volume, became less stainable by progressive disappearance of the nucleoli and chromatin and finally became imprecise through the dissolution of the nuclear membrane itself. In some cells, the hypertrophy and chromatolysis of the nucleus is accompanied by special cytological phenomena: special affinity for some stains, appearance of elongated proteinaceous crystals, tendency of protoplasm to plasmolyse in some phases, *etc.* Various staining techniques reveal a high pectin content of the laticifer walls. The laticiferous elements of the embryo occupy a median position of the procambial cylinder.

There are several cells in the procambial region and external to the procambium which show specific stainability with safranin and other basic dyes[13]. These cells have probably an acidic cytoplasm and walls with pectin content. Some of these cells show transverse as well as longitudinal anastomoses with neighbouring cells. These cells are undoubtedly the prolaticifers (*Figure 7*). Tridimentionally viewing, these cells are distributed in a hollow cylinder in the external procambial tissue, maintaining a close association with phloem. The distribution extends from 2 - 3 cm below the apex in the four-day-old seedling. Laticifers are well formed and in different stages of maturity. Varying degrees of stainability of these cells indicate an underlying cytological complexity[19].

Calvert[7] has identified three systems of laticifers in the stem of *Hevea brasiliensis*. They are (1) hypodermal, (2) principal and (3) medullary. In the present writer's observations[13,19] no medullary and hypodermal systems were observed in the modern definition of these regions. The principal system, as observed in the procambial region belongs to the phloem proper.

9. Distribution of laticiferous tissue in the seed and seedling

In the seed, the laticifers are present only in the cotyledons. The first laticifers in the germinating embryo appear near the junction of the cotyledons with the axis. In the 24-hour stage, laticifers can be

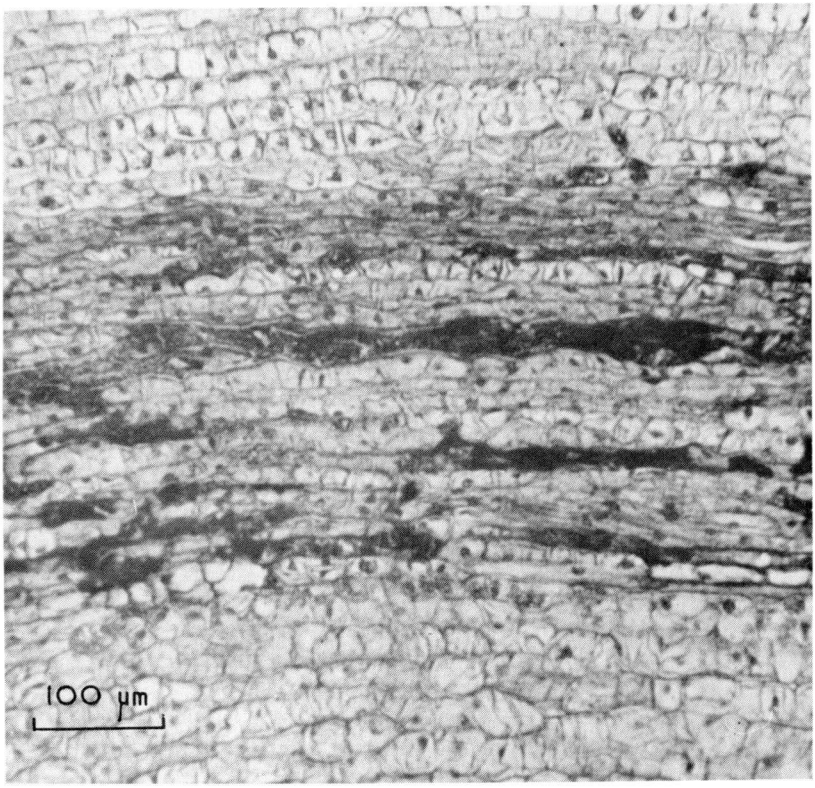

Figure 7. Longitudinal section of promeristem showing prolaticifers. × 160 (Ref. 19).

found in the hypocotyl, well below the point of attachment of cotyledons. When the seedling is two days old, the laticifers are present in the hypocotyl up to the region of lateral roots. A few were observed in the lateral roots, but none were found in the primary root. Even in the four-day-old seedling, no laticifer has been observed in the primary tap root. There are innumerable laticifers in the hypocotyl and in the plumule, nearly 3 cm below the apex. The prolaticifers are distributed mainly in the plumular region 2 - 3 cm below the apex. Prolaticifers, although present at the junction of primary and lateral roots, are absent in the primary root below the ring of laterals.

It appears that the laticifers in the phloem develop basipetally in the hypocotyl and in acropetal succession in the plumule.

10. Anatomical organisation of the virgin bark in the mature tree

As commercial interest in *Hevea* blossomed, the early researches of Scott[10,20,21] and Calvert[7] expanded in European circles and later on, in

the laboratories of the rubber plantations in South East Asia. Apart from problems of ontogeny, distribution and cytology, quantitative features of structural organisation under various hereditary and environmental conditions received much attention. There was also considerable attention paid to these features as they affect the exploitation and propagation of the plant.

The numerous publications of Arens, Arisz, Bobilioff, Bryce and Campbell, Frey-Wyssling, Gandrup, Heusser, Keuchenius, Maas, Meunier, Petch, La Rue, Sanderson and Sutcliffe, Scott, Schweizer, Taylor and Vischer and a number of other authors were ably reviewed by Bobilioff[5] and Van Iterson[22] so that these earlier authors would be cited in this review only when specifically required*.

By 1917, sufficient information was available for Bryce and Campbell[23] to summarise and supplement information on the structure of the mature bark of *Hevea*, the significant tissue in relation to exploitation.

After describing the spatial organisation of the laticiferous tissue in the bark of *Hevea*, they distinguished two zones, an inner soft zone and an outer hard zone, the hardness of which was attributed to the presence of the sclerified elements. These sclerified elements and the nature of their development received some attention in relation to ease of tapping. They noted the presence of copious tannin cells in the bark and by quantitative studies, demonstrated that latex vessel initiation from the cambium in mature trees was a rhythmic process and that there was a diminished latex vessel initiation during the wintering period. They found that the number of tangential latex vessel rows in the stem decreases with increasing height of sampling. They observed that the distance between rows of latex vessels was irregular. They also demonstrated a positive correlation coefficient between the number of latex vessel rows and the thickness of the bark.

The presence or absence of connections between rows of latex vessels also received much attention. The considerable interest shown in this problem is a practical manifestation of the philosophy of exploitation which prevailed at that time. Thus Vernet[24] observed rare connections between adjacent rows of latex vessels, an observation not verified by Arens[25], Meunier[26], Simon[27], Lock[28] *etc.* Arisz[29,30] claims to have seen 26 radial connections within a distance of 250 cm of bark in the base of the tree. Later workers, particularly Kaimal[31] could not confirm this view. It must be borne in mind when

*See ref. 114 for a recent review of the topic.

interpreting this observation that the earlier workers used acid fixatives which coagulated the latex and that they generally worked with sections of the order of 100 μ in thickness cut on hand microtomes. The present author's experience with such sections indicate that splashes of fixed latex, displaced from their original locations could lead to misinterpretations of anatomical organisation to the less specialised observer.

Work in Southeast Asia, was ably summarised by Bobilioff as mentioned earlier[5]. The problems investigated were, however, of a character similar to those reported above. Bobilioff established correlations of yield with anatomical characteristics.

A summary of the structural organisation from these researches and those of the present writers' would be sufficient for the purposes of this review. In a cross section of the bark, latex vessels are circular or somewhat irregular in shape with close apposition to the neighbouring parenchyma (*Figure 8*). They are arranged in regular rows almost parallel to the cambium. Considering the whole

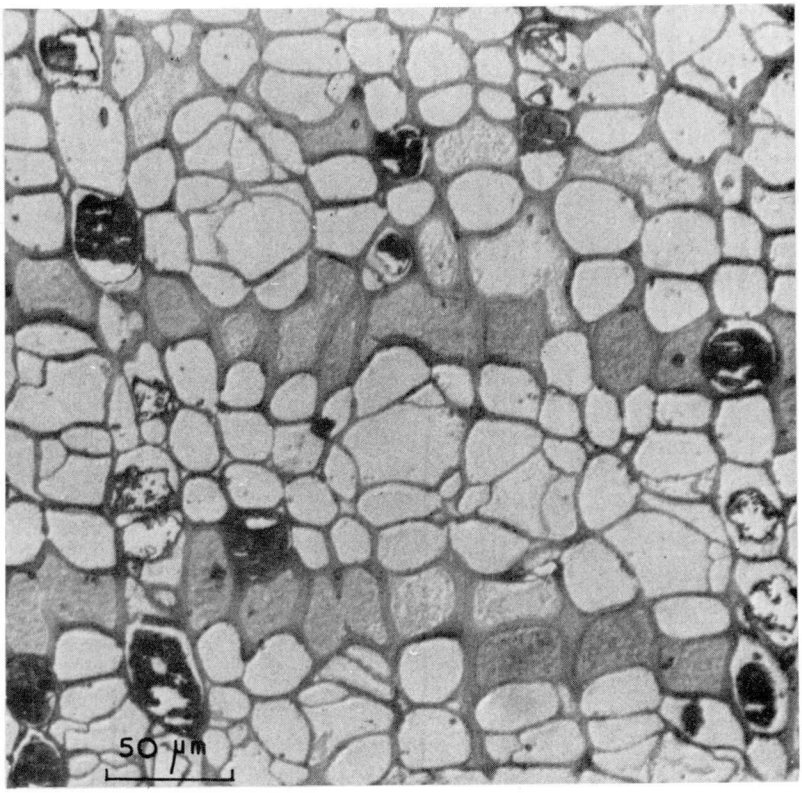

Figure 8. Cross section of bark. Latex vessel rows can be seen as grey cells. × 320.

tree, they are therefore in concentric rings as seen in cross sections of the tree. These rings or rows are separated by zones of sieve elements and phloem parenchyma cells. In radial longitudinal section, the vessels appear as almost straight tubes with occasional residual cross walls, which are annular and open (*Figure 9*). The vessels of the soft inner bark appear continuous in each row; but in the outer bark, they appear as discontinuous tubes. This appearance is due to the dilation of outer tissues and the centrifugal expansion since its inception in the primary bark. In tangential section, the latex vessel system resembles a meshwork of expanded metal. Thin tangential sections such as shown in *Figure 10* do not reveal such a pattern as each row is sliced through tangentially, but thicker sections specially prepared for this purpose bring out this pattern clearly as an anastomosing network of tubes (*Figure 11*). The meshes of the expanded-metal-work pattern are convex lens shaped in the inner soft bark, in outer bark, they are dilated convex lenses, irregular or ellipsoidal. All these planes of sections can be combined together to obtain a three-dimensional image of latex vessel

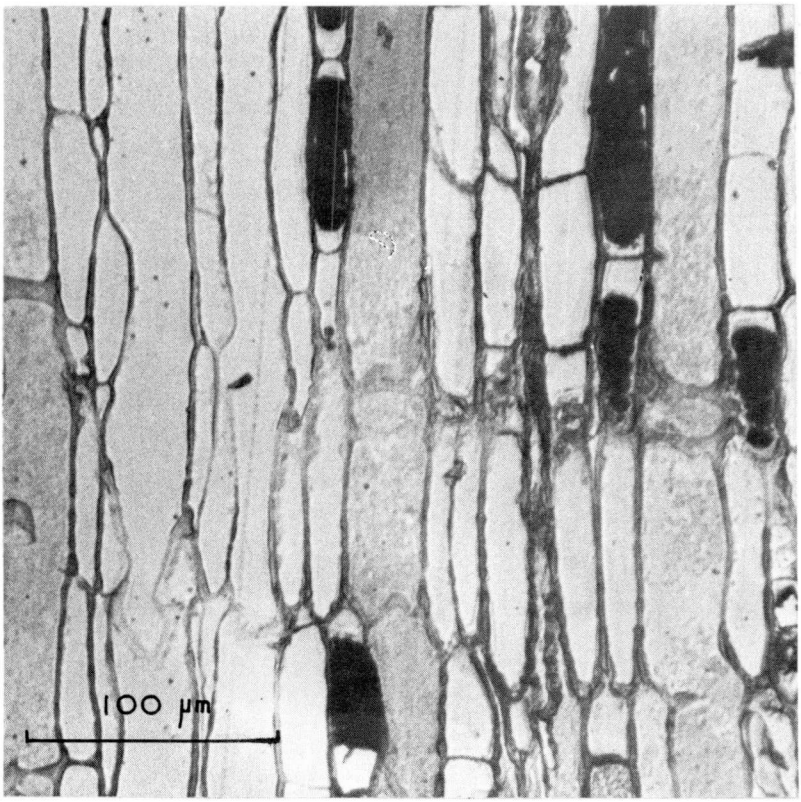

Figure 9. Radial longitudinal section of bark showing grey tubular latex vessels. × 320.

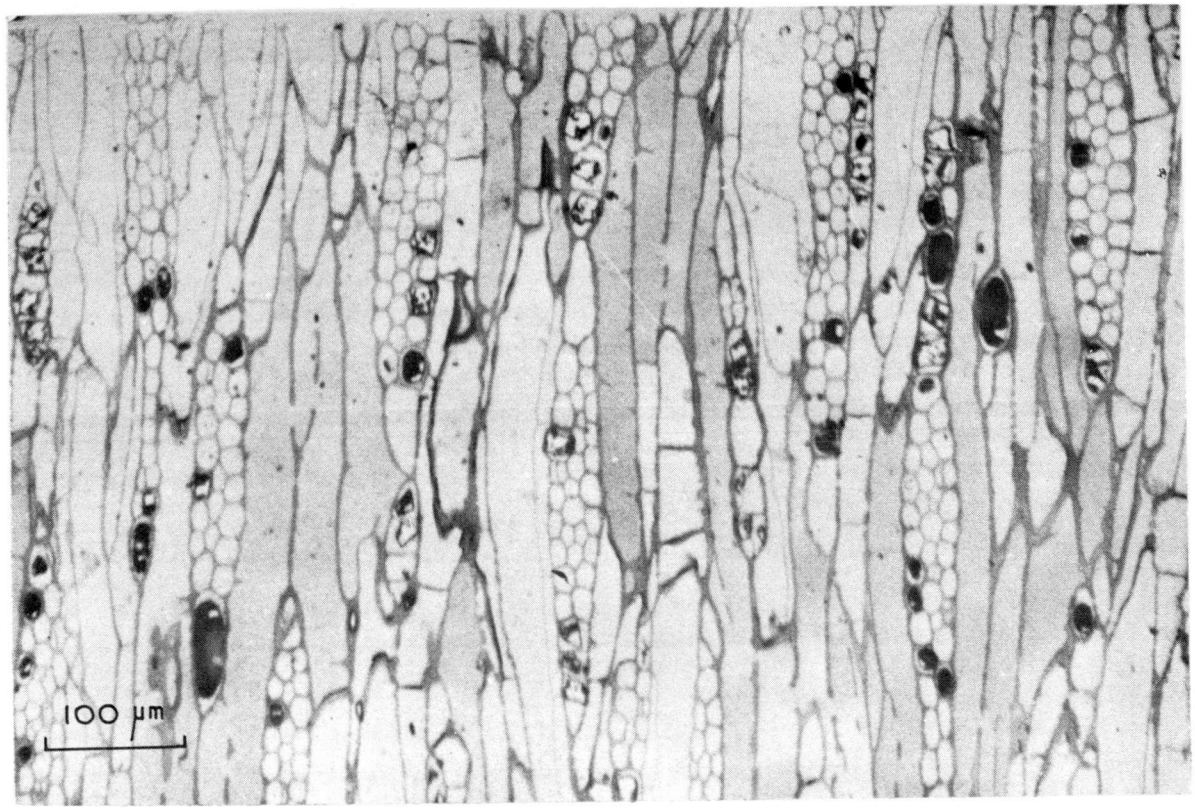

Figure 10. Tangential section of bark showing anastomosing grey tubes of latex vessels. × 175

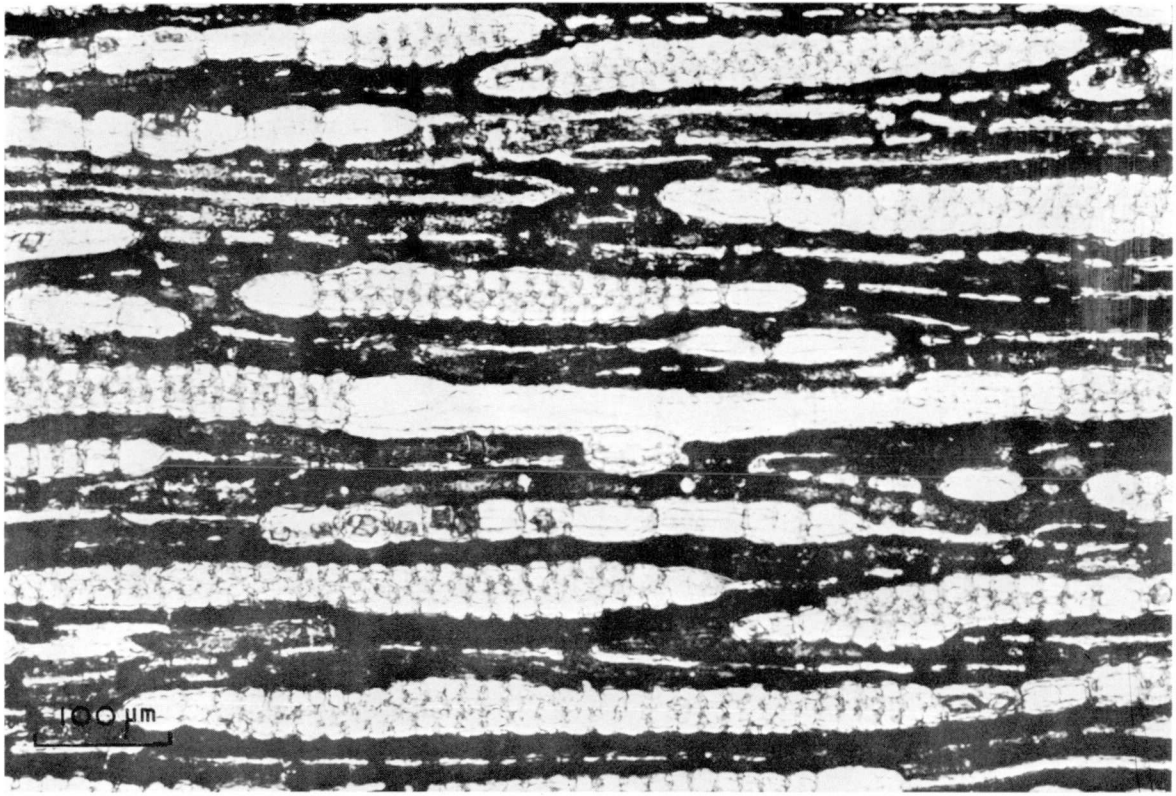

Figure 11. Thick tangential section of bark. Note the dark network of latex vessels. × 180

distribution in the bark of *Hevea*. *Figure 12* shows such a concept, modified from Bobilioff[5] adapted from Riches and Gooding[32] and Gomez *et al*[33]. Latex vessels (shown in green) are placed in vertical rows which weave round the medullary rays. There are many anastomoses within rings, but few or none between rings. A considerable proportion of the peripheral parenchyma undergoes sclerification to form stone cells. The layers of latex vessel rings near the cambium are sandwiched by active sieve tubes and parenchyma. This is typical of the structure of 'virgin bark'. In the renewed bark, the structure of the hard bark differs. The peripheral tissues, being generated by accelerated activity of the phellogen, appear to be in a lesser state of senescence; there is the characteristic absence of the sclerenchyma ring, the endodermal equivalent. The number of latex vessel rings are dependent, however, on the activity of the vascular cambium in initiation of latex vessels.

Three dimensionally, latex vessels are thus long interconnected tubes forming concentric cylindrical mantles, extra cambially situated with successive mantles sandwiched between layers of other phloem tissue. These mantles extend the length of the tree. As the tree ages, mantles successively produced by cambium are gradually pushed outwards. As the mantles are required to increase their circumference due to increase in girth of the tree, they do so by accomodation in the tissue by lateral dilation than by growth[34]. This obviously brings disruption to the external latex vessels.

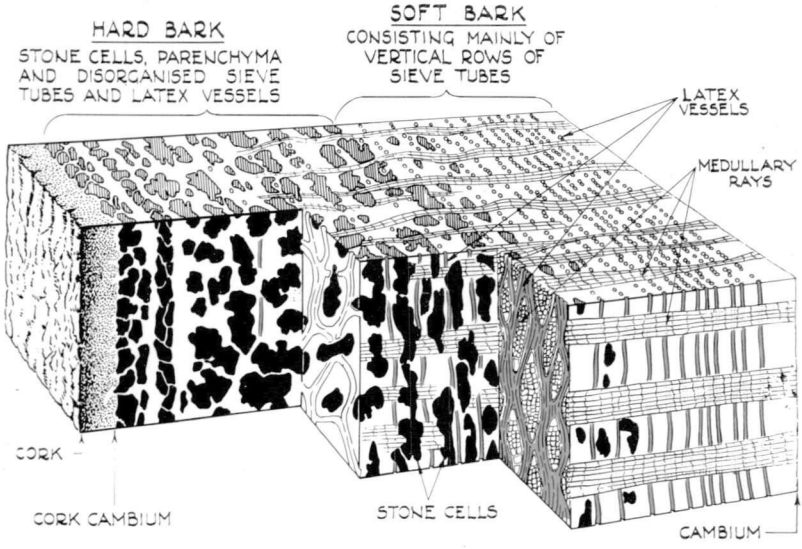

Figure 12. Three-dimensional diagram of bark. × 10. (Ref. 33).

In an early development stage of the virgin bark, the stone cell ring is represented by phloem fibre cells just inside the starch sheath of the pericycle[35]. These bundles later coalesce to form a continuous ring. The cell walls become thicker by secondary growth, become lignified and are converted to stone cells in the stone cell ring (*Figure 13*)..

Distributed in the outer bark are groups of lignified parenchyma cells which are called stone cells. The hardness of the bark depends on the quantity of stone cells present. Bobilioff[36] recognised five different types of bark based on the stone cell distribution.

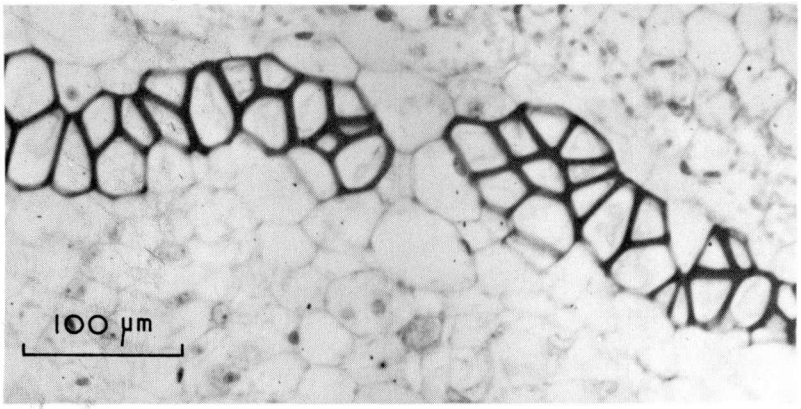

Figure 13. Stone cell ring. The gap between stone cell groups is a feature in young stems. × 200.

Tannin cells are distributed throughout the bark tissue[37]. All tissues with the exception of perisperm may contain tannin; the quantity of which depends on the age and position of cells. Tannin cells (*Figure 14*) are particularly abundant in the bark and are principally situated on both sides of latex vessels. There is also tannin in stone cells. Especially remarkable is the strong accumulation of tannin in the renewed bark and underlying woody parts, in callus tissue, in primordia of buds, in the neighbourhood of branching of roots and shoots and at the base of leafstalks. In any tissue an accumulation of tannin corresponds to an increased metabolism.

11. Bark regeneration and cork formation

The bark reacts to the injury induced by tapping by the formation of wound tissue[38]. The wound tissue (*Figure 15*) consists of cork on the outside and cork parenchyma or phelloderm in the inside. The vascular cambium is also activated to produce new tissue at an accelerated rate. Bobilioff[39] observed that in six months of renewal a

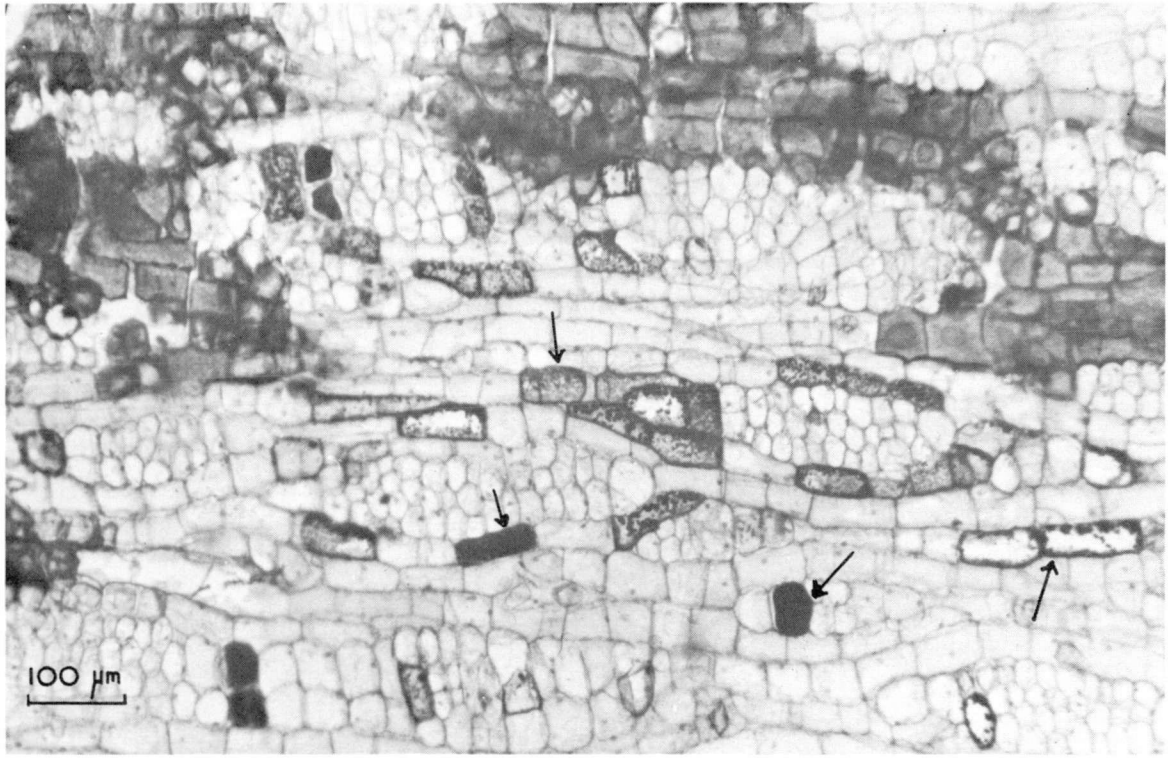

Figure 14. Tannin cells. (arrow) × 120.

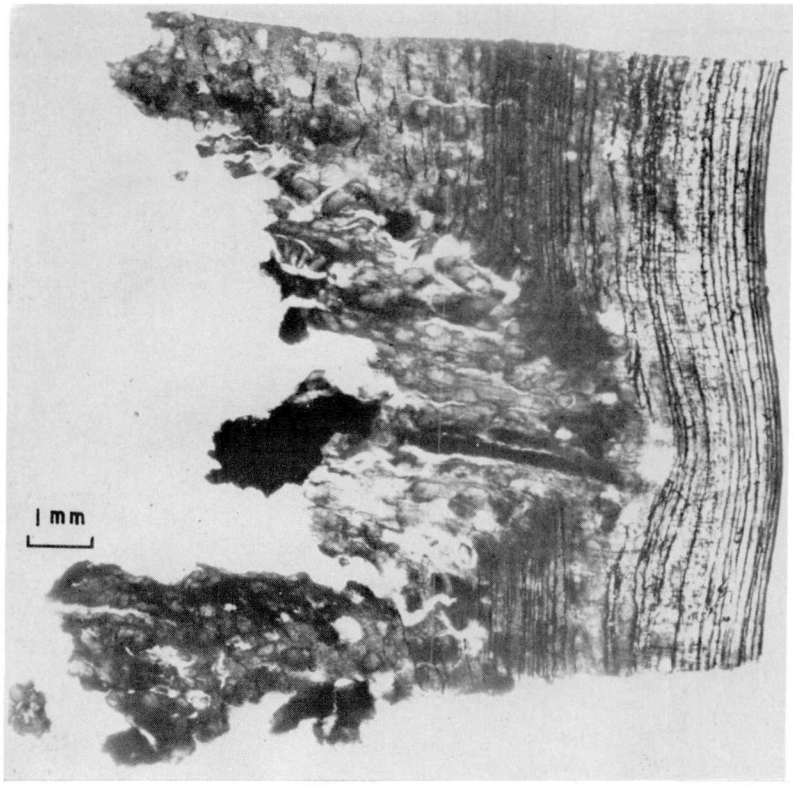

Figure 15. Wound tissue (regeneration of bark). × 8.

significant increase in the number of latex vessel rows can be found. After one year the number of latex vessel rows reaches the original level in the virgin bark. In the renewed bark the proportion of the soft bark is greater than that in the original bark. As the bark becomes older, stone cells are formed which increases with age of the cortex.

In a comparative study on four Malaysian buddings[40] it was found that the renewal was very rapid at first and slowed down later so that six months later, the growth of renewed bark was not much faster than that of the normal growth of virgin bark.

Vischer[41] and Gandrup[42,43] considered bark renewal and cork formation and came to the conclusion that after the initiation of normal cork cambium, the activity of it results in periderm formation and sloughing off of cork cells from external regions. There were multiple cork layers in some circumstances of bark renewal. Other workers who considered the effects of tar on renewal of bark[44,45]

came to the observation that an increase in thickness of bark was detected after application of tar on the bark, but the increase was only due to accelerated phellogen activity and that there was no increase in laticiferous tissue in the treated bark.

An increased thickness of bark as a result of application of several vegetable and mineral oils[46] was a consequence of the activation of cork cambium. No increase of laticiferous tissue was observed. The oils were applied with or without the addition of 2,4-D. All treatments however had a beneficial effect on bark renewal, but highly significant effects were observed only in treatments containing 2,4-D.

12. Quantitative considerations on laticiferous tissue

(*a*) *The number of latex vessel rings.* The number of latex vessel rings is a clonal characteristic[46-48], but it is also influenced by the rate of growth of the tree: the more rapid the growth, the greater the frequency with which latex vessel rings are initiated and hence the larger their number. The growth relationship differs between clones, for there are slow growing clones with large numbers of latex vessel rings and fast growing clones with small numbers of rings.

(*b*) *Effect of age of tree on the number of latex vessel rings.* One important determinant of the number of latex vessel rings is the age of the planting material[23,33]. *Figure 16* shows the relationship between the number of latex vessel rings and the age of the trees for clones RRIM 501 and RRIM 623, taken from a number of trials in the R.R.I.M. Experiment Station at Sungei Buloh[33]. The relationship is linear up to about fifteen years of age, but thereafter there is a suggestion that in RRIM 501 there is a reduction in the rate of production of latex vessel rings. The linear relationship between latex vessel ring number and the age of the tree for the two clones does not differ significantly.

(*c*) *Effect of height of sampling on number of latex vessel rings.* It is generally held that in seedling trees the number of latex vessel rings declines with increasing height of sampling[23, 33, 48, 49, 50]. As the number of latex vessel rings bears a relation to the bark thickness, and as bark thickness decreases with height in conical stems, the decrease in number of latex vessel rings may be considered to be related to the conicity of the stem[50, 51]. The effect of the height of sampling on the number of latex vessel rings was studied on 32-year-old untapped trees of nine clones by Gomez *et al*[33]. They showed that the number of latex vessel rings at three different heights of sampling, did not differ significantly with the height of sampling with only one exception.

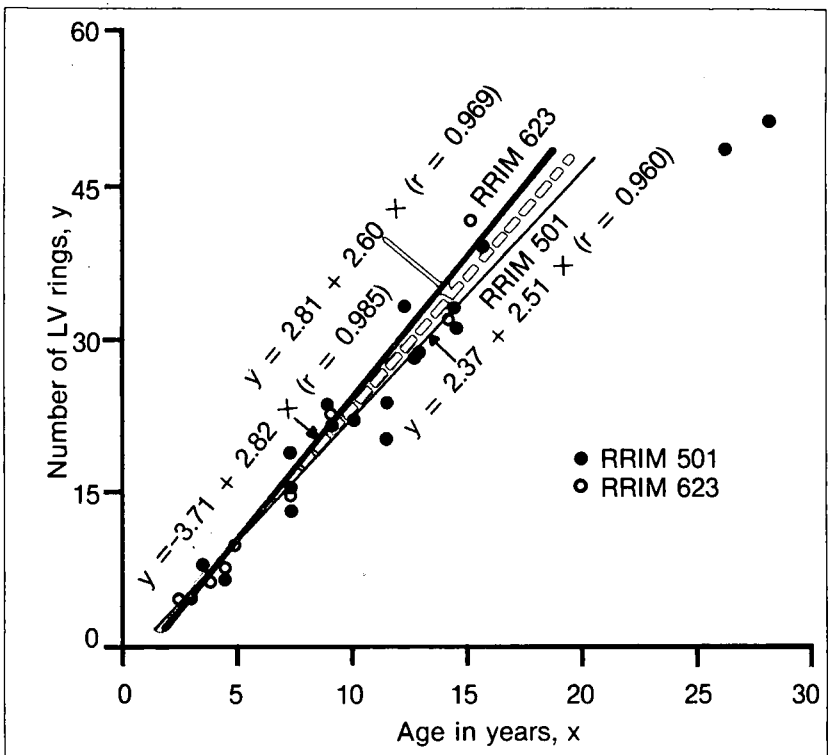

Figure 16. Relation between number of latex vessel rings and age of trees. (Ref. 33).

(*d*) *Distribution of latex vessel rings.* Bobilioff[52] studied the distribution of latex vessel rings in four groups of unselected seedlings and obtained frequency polygons with near-normal distributions. The mean number of latex vessel rings lay between 8.63 and 11.28. Bryce and Gadd[53] reported a mean number of 11.25 rings at 61 cm height for 161 ten-year-old illegitimate seedlings, and Sanderson and Sutcliffe[48], a mean of 13.1 rings at 51 cm height for 599 eight-year-old unselected seedlings.

Gomez *et al*[33] studied ten trees (aged eight-and-a-half years from budding) from each of 112 clones which gave a frequency histogram with a much higher mean value of 25.6 rings. These three sets of data are expressed as cumulative frequency curves, and give an indication of the increase in the number of rings that has been achieved in the forty years (1924-64) due to breeding and selection (*Figure 17*). The maximum number of rings in unselected seedlings was about 27, which is close to the mean ring number of modern clones. This emphasises the fact that over the years, selection based on yield has resulted in a corresponding increase in the number of latex vessel rings. This is to be expected from the high correlation of yield with latex vessel ring[54-56].

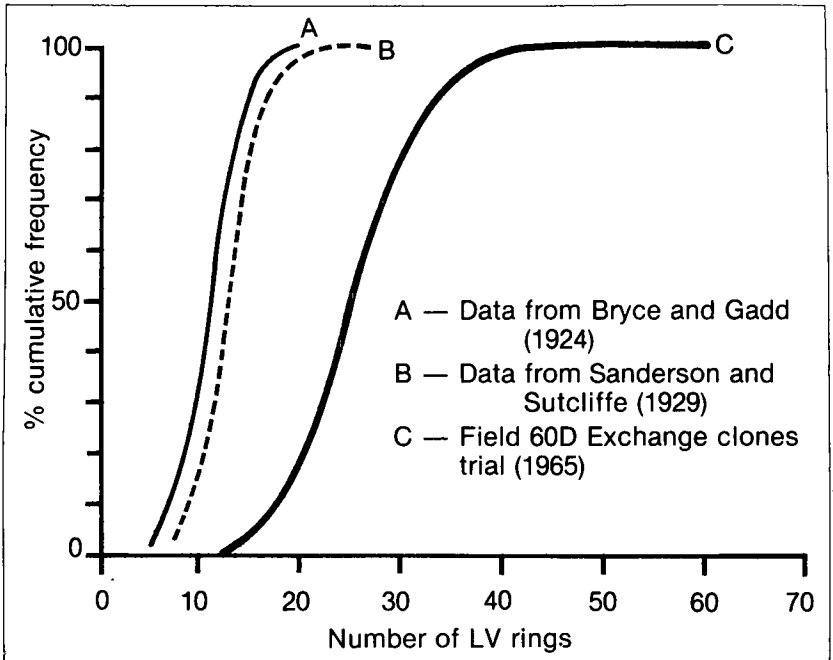

Figure 17. Effect of breeding on cumulative frequency of latex vessel rings (Ref. 33).

(*e*) *Density of latex vessel rings in the bark.* The latex vessel rings are initiated from cambial cells. As successive rings are formed they are pushed outwards in the course of growth. Further measurements on the 112 clones already mentioned[33] showed nearly 40% of the rings to be within 1 mm of the cambium, and that the number of rings diminished to zero over a distance of 5–8 millimetres (*Figure 18*).

The concentration of latex vessel rings in the bark differs markedly between clones. Of the 112 clones studied, the proportion of latex vessel rings within 1 mm of the cambium was up to 55% in one clone, up to 50% in five clones and 30–45% in ninety-eight clones. Among all the clones, 20–55% of the latex vessel rings were in the first millimetre from the cambium, 10–35% in the second millimetre and 10–30 per cent in the third millimetre.

(*f*) *Distance between latex vessel rings.* The variation in the average distance (in μ) between any two consecutive rings with increasing distance from the cambium is shown in *Figure 19.* Clonal differences become prominent beyond the third millimetre from the cambium.

(*g*) *Effect of age on the density of latex vessel rings.* That the distribution of latex vessel rings in virgin bark changes markedly

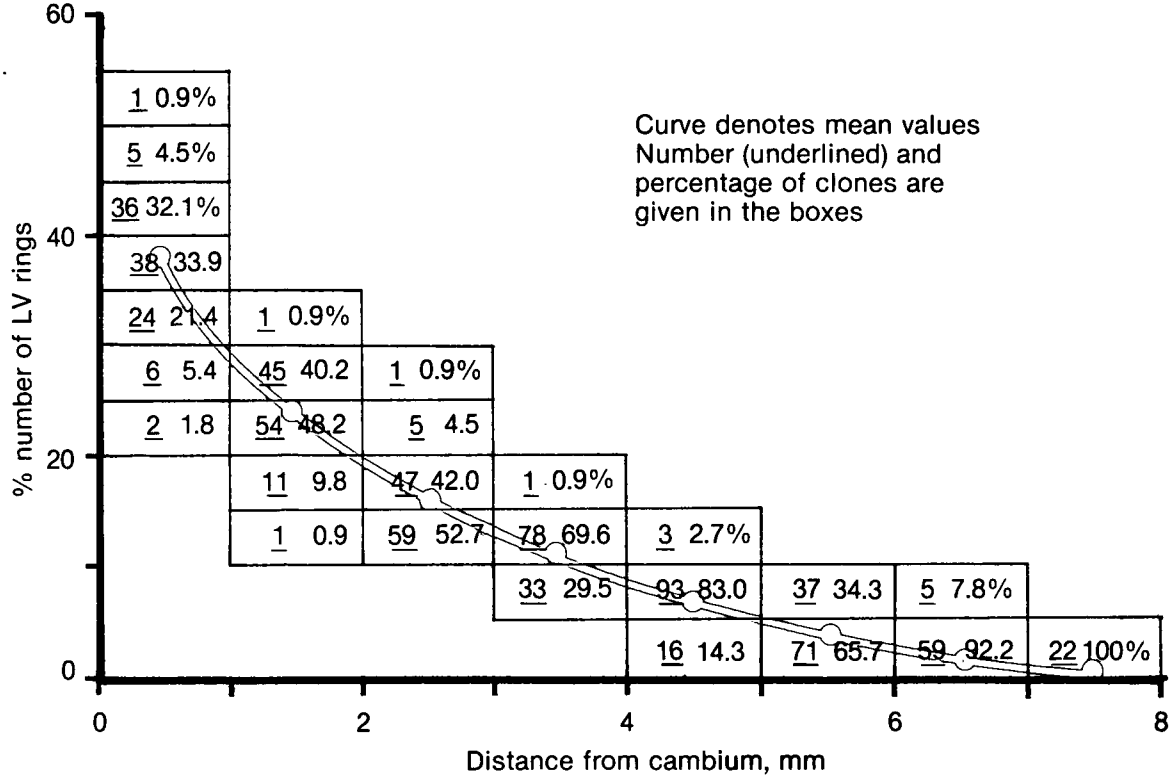

Figure 18. Distribution of latex vessel rings. (Ref. 33).

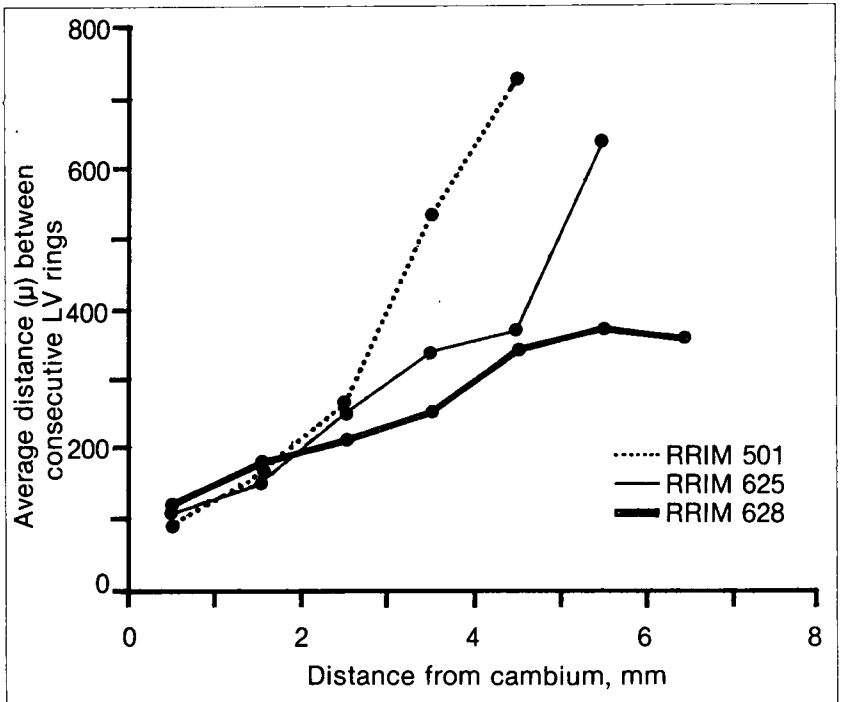

Figure 19. Distance between latex vessel rings (Ref. 33).

with age can be seen in *Figure 20.* In trees below five years of age the rings are concentrated in the first 4–5 mm, 40% being in the second millimetre. Over the following five years a pattern emerges of a high concentration near the cambium, tailing away to zero within 8 mm of the cambium. This is followed over the years by a progressive broadening of the zone of high concentration near the cambium to the point where, by the twenty-fifth year, some 75% of the latex vessel rings are rather uniformly distributed through the innermost 5 millimetre of bark[33].

The tailing away in latex vessel concentration near the cambium in 32-year-old untapped trees (*Figure 21*) reflects the fall-off in latex vessel ring production that occurs in older trees.

(*h*) *Density of latex vessels within rings.* The quantity of laticiferous tissue produced by a tree depends not only on the number of its latex vessel rings but also on the number of latex vessels in each ring. *Figure 22* gives the density of latex vessels per millimetre of ring (in rings close to the cambium and in those in the productive bark) for different girth classes for three clones. Differences are significant between the two positions, and clonal

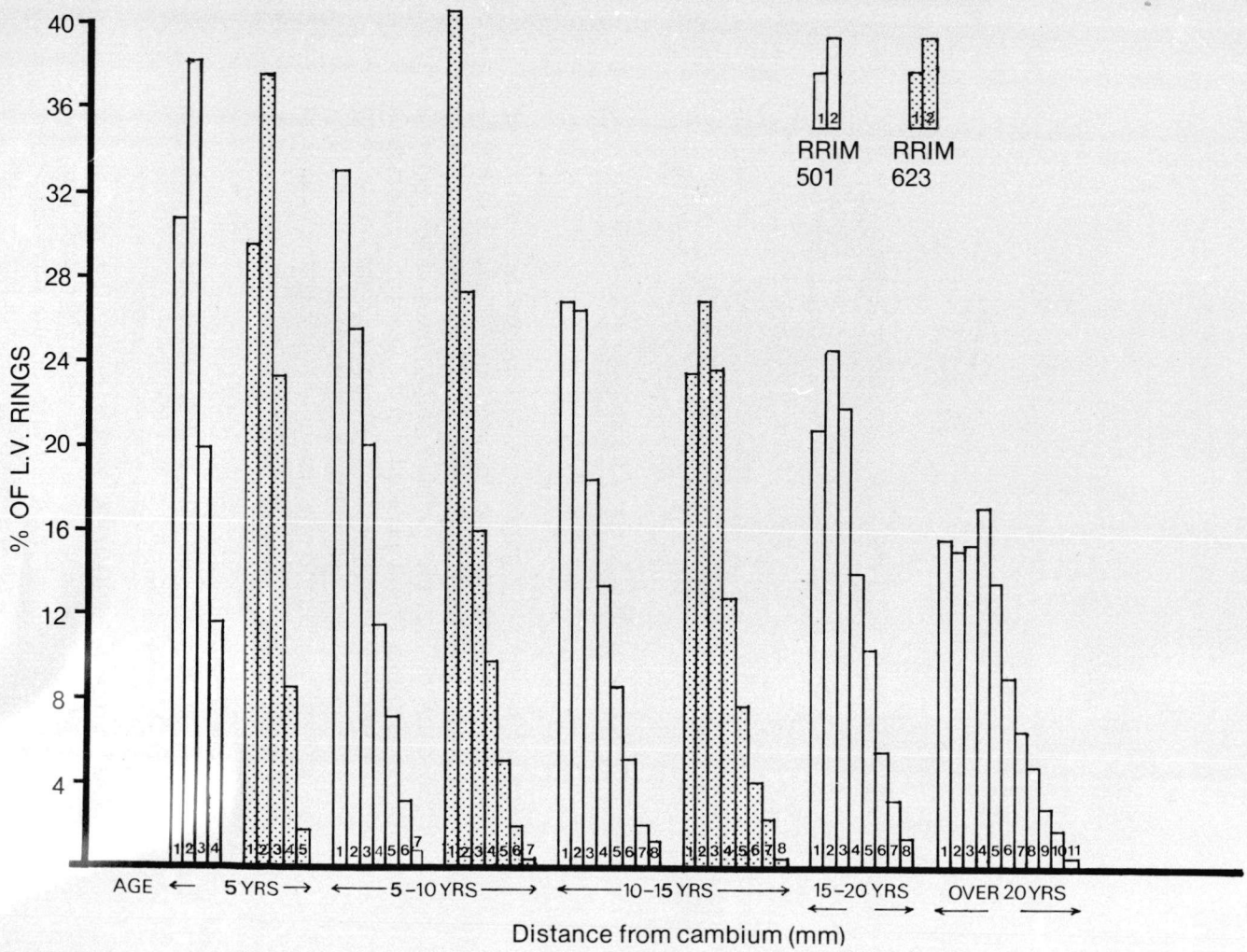

Figure 20. Effect of age on density of latex vessel rings (Ref. 87).

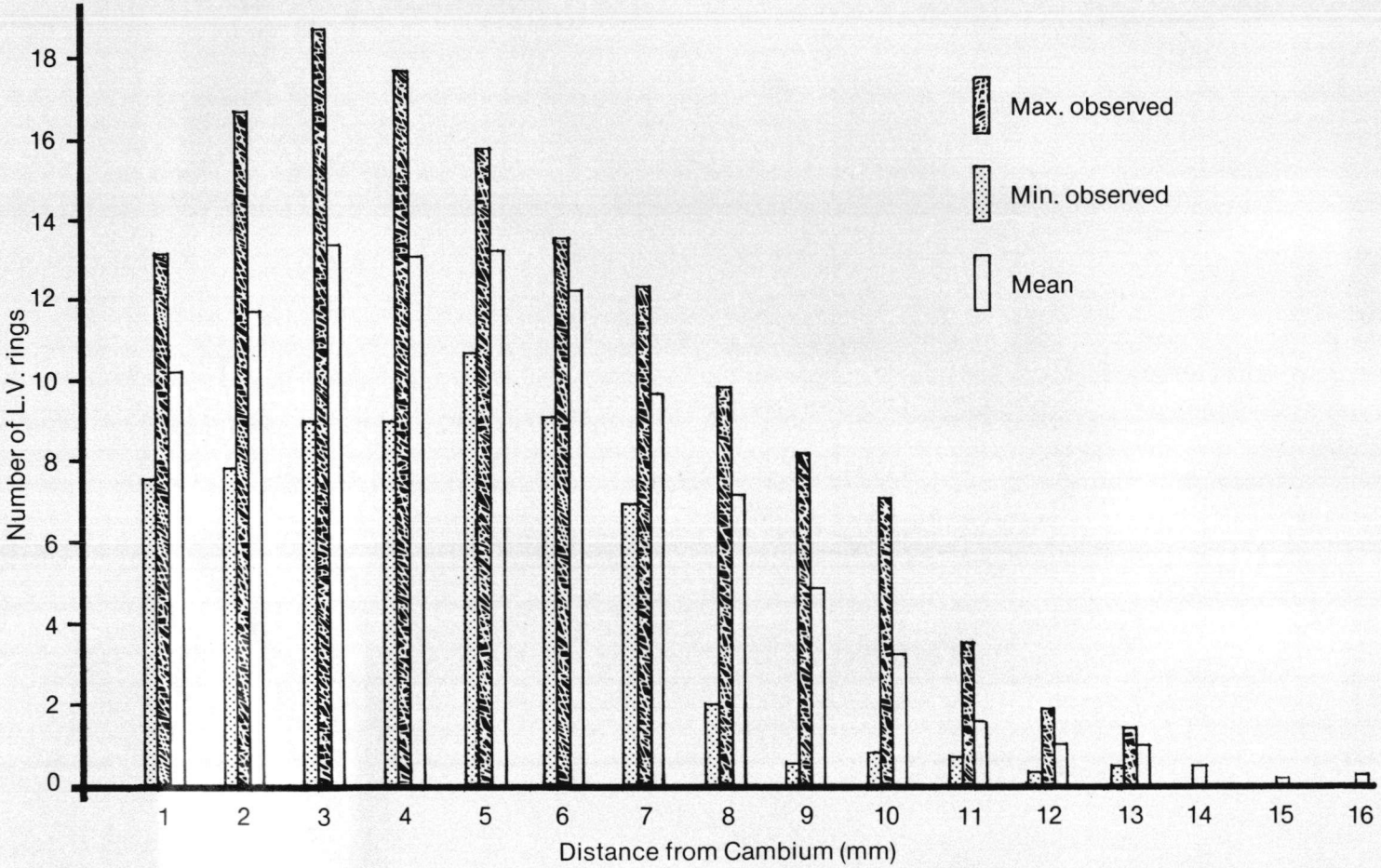

Figure 21. Distribution of latex vessel rings in 32-year-old trees. (Ref. 87).

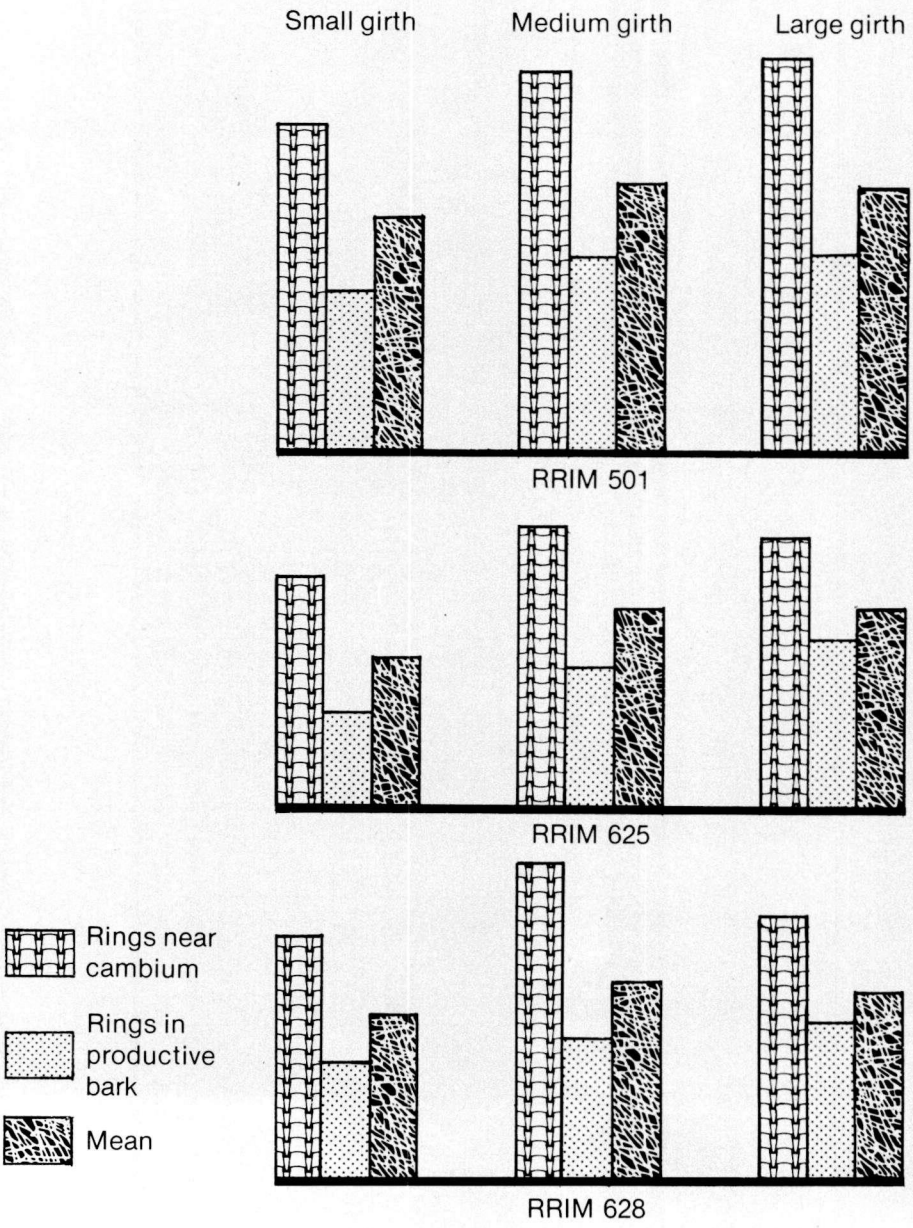

Figure 22. Number of latex vessels/mm of latex vessel ring. (Ref. 87).

differences are also apparent. Latex vessel density is higher in rings near the cambium than in those in the outer bark.

(*i*) *Diameter of latex vessels.* The studies of Frey-Wyssling[57] and Riches and Gooding[32] relate the influence of the diameter of the latex vessels on the rate of flow of latex to Poiseuille's equation for viscous flow in a capillary, where it is shown that the volume of flow is proportional to the fourth power of the radius of the capillary.

Table 1 shows the mean diameter of latex vessels of eight clones. The figures relate only to the first five rings near the cambium. The mean diameter ranges from 21.6–29.7 μ corresponding to a potential difference in flow of more than three times between the smallest and largest vessels. Significant clonal differences are evident.

Ashplant[58-61] was of the strong opinion that there was a good correlation coefficient between diameter of latex vessels and yield (+ 0.76). He also found that average cortex cell diameter and latex yield are correlated properties. While this information has been of substantial interest to selectionists, no real confirmation of these effects have been recorded in literature to date.

TABLE 1. MEAN DIAMETER OF LATEX VESSELS OF DIFFERENT CLONES (after ref. 33)

Clone	Mean (μ)
RRIM 608	29.7
RRIM 601	28.9
RRIM 501	28.1
RRIM 600	27.1
RRIM 604	23.4
RRIM 609	23.1
RRIM 613	21.9
RRIM 605	21.6
Grand Mean	25.6
S.E. of clone mean	± 0.97

The vertical lines link values which do not differ significantly (P = 0.05).

13. Considerations Pertaining to the Efficiency of Tapping

During tapping, the horizontal depth of tapping is controlled to avoid wounding the tree. In practice the tapper is guided by his experience of how deep he can safely cut, and of how much latex flow

he can expect. This does not mean that the latex vessel system is efficiently exploited; for efficient exploitation the maximum number of latex vessel rings should be opened for a given length of the tapping cut[33].

The approximate total number of latex vessels at a given cross-section of the bark may be taken as nfG, where n is the number of latex vessel rings, f is the mean density/millimetre of latex vessels in a ring and G is the girth of the tree.

The total cross-sectional area of latex vessels would be nfG (πr^2) where r is the radius of the latex vessel.

As there is little or no connection between adjacent latex vessel rings, yield increases as more rings are cut. (The actual contribution to yield by each ring of latex vessels depends on other physical factors and may not be constant for successive rings). A consideration of the proportion of latex vessel rings left uncut during tapping is therefore an essential requirement for assessing whether maximum productivity is being obtained. It is usually assumed that 1 mm of bark near the cambium is left untapped. A number of samples from tapping cuts from a mixed population of trees of different clones were therefore examined.

Figure 23 shows a section through the tapping cut from one of the trees.

About 20% of the bark was found to have been left untapped, in fact about 50% of the latex vessel rings were not cut (*Table 2*). The various linear correlations of bark characteristics in *Table 3* show that there is a significant relation between the total bark thickness and the thickness of untapped bark for the samples studied. No significant correlation was evident between the thickness of untapped bark and the number of latex vessel rings in the untapped bark. However, when expressed as percentage a significant correlation was obtained because of the correlation which exists between the total number of latex vessel rings and the total bark thickness.

In *Figure 24* the percentage of latex vessel rings which are likely to be left untapped is compared at various depths of tapping. Since the thickness of untapped bark is 1.3 mm with a standard deviation of 0.5 mm (*Table 2*), the percentage of uncut latex vessel rings for 0.5, 1.0, 1.5 and 2.0 mm thickness of untapped bark from cambium has been plotted.

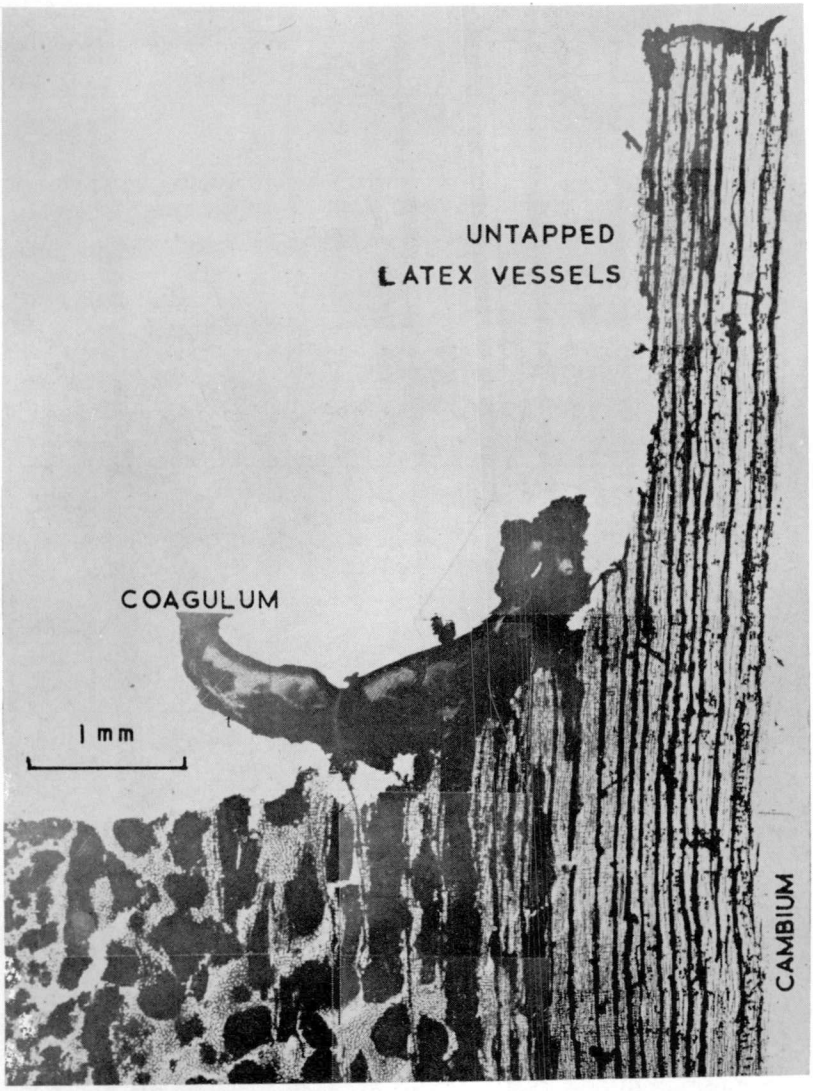

Figure 23. Section through a tapping cut. × 20.

It is to be noted that in 50% of the clones, if the depth of tapping comes no closer than 2 mm from the cambium, no more than 38% of the latex vessel rings are exploited. Tapping 0.5 mm deeper cuts another 10% of the rings, and tapping to within 1 mm of the cambium achieves 62% exploitation. Tapping deeper still, to leave 0.5 mm of bark near the cambium, uses 80% of the vessel rings.

Figure 25 shows the percentage cumulative distribution of the number of latex vessel rings in 32-year-old untapped clonal material (at a height of 150 cm from the graft union), and *Figure 26* shows the

TABLE 2. MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION OF BARK THICKNESS AND NUMBER OF LATEX VESSEL RINGS CUT DURING TAPPING (after ref. 33)

Variable	No. of trees	Mean	S.D.	C.V. (%)
Total bark thickness (mm)	32	6.01	0.93	15.5
Thickness of untapped bark (mm)	32	1.31	0.52	39.7
Untapped bark (%)	32	21.6	7.1	32.9
Total number of LV rings	32	20.0	5.1	25.5
Number of LV rings in untapped bark	32	10.0	3.1	31.0
Number of LV rings in untapped bark (%)	32	50.8	11.3	22.2

TABLE 3. LINEAR CORRELATION BETWEEN BARK THICKNESS AND LATEX VESSEL RINGS (after ref. 33)

Correlation	No. of trees	Correlation coefficient (r)
Total bark thickness and thickness of untapped bark	32	0.594***
Total number of LV rings and total bark thickness	32	0.447*
Number of LV rings in untapped bark and thickness of untapped bark	32	0.256N.S.
LV rings in untapped bark (%) and untapped bark (%)	32	0.410*

*$P < 0.05$ ***$P < 0.001$ N.S. - Not significant

distribution in three modern clones. It is clear that as the tree ages, the distribution of latex vessel rings undergoes a gradual shift away from the cambium. The effect of deeper tapping would therefore result in a progressively smaller response as the tree grows older. Clonal differences appear to be more important in the younger age groups. From *Figure 25* it is apparent that for the 32-year-old trees the loss involved in uncut latex vessel rings in the 1 mm segment of bark nearest the cambium is of the order of 8–13% for the clones studied, whereas from *Figure 26* it would appear that with younger trees 30–45 per cent can be missed.

As an average of 40% of the latex vessel rings are untapped, n should be corrected to 0.6 n. For a half-circumference tapping cut,

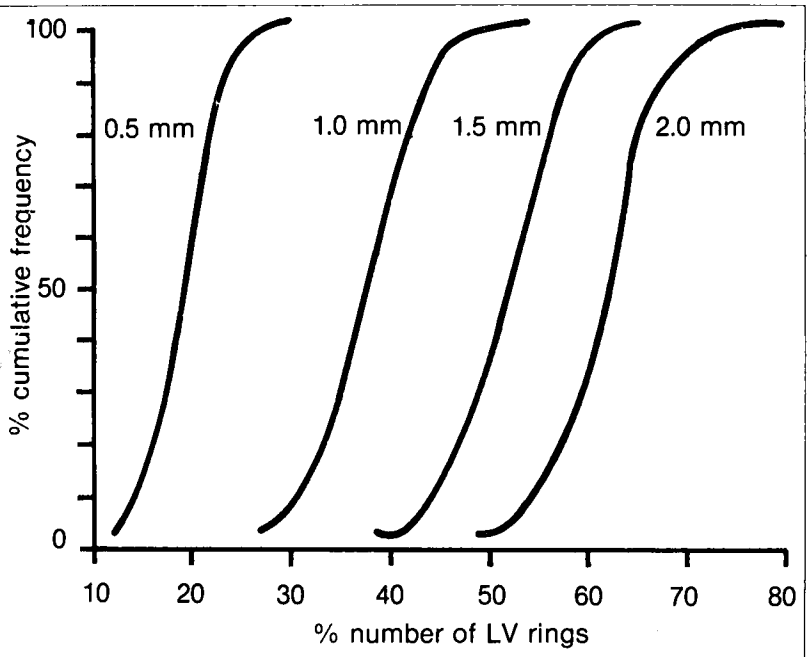

Figure 24. Percentage cumulative frequency distribution of percentage number of latex vessel rings for intervals of 0.5 mm from cambium. (Ref. 33).

the approximate number of latex vessels cut per tapping for practical purposes is 0.3 nfG, and the cross-sectional area is 0.3 nfG πr^2.

Deep tapping, through increasing the number of latex vessel rings exploited, increases yield by an amount that depends in part on the spatial distribution of the latex vessel rings in the bark: the greater the proportion of rings near the cambium, the more effective will deep tapping be in increasing yield[62-64]. However, Southorn and Gomez[65] have shown that the physiology of latex flow is influenced by the length of the tapping cut, in that the shorter the length of cut the higher is the degree of latex vessel plugging and the greater the rate of flow of latex. Interactions such as these and the long-term effects on the physiology of the tree due to possible wounding of the cambium by deep tapping can only be realised by field experiments.

14. Alignment of tissue in the stem

Petch[66]examined twenty-five trees after peeling off the bark and found that in 18 of them the wood elements inclined slightly to the right. A later investigation by De Jong[67, 68] on 93 trees revealed an average of 3.7° inclination to the right. He calculated that if the slope of the tapping cut was from upper left to lower right instead of upper right to lower left an extra yield was obtainable, which ranged from

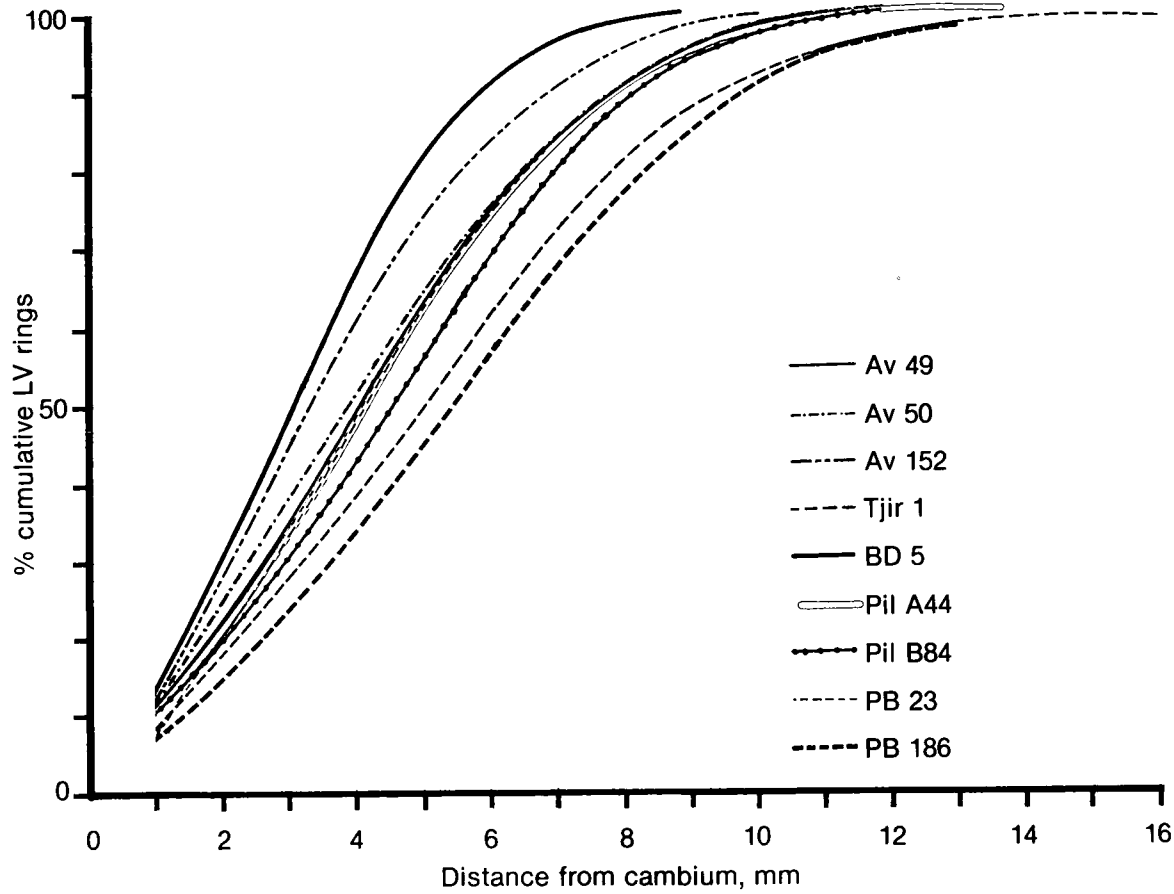

Figure 25. Percentage cumulative distribution of the number of latex vessel rings at intervals of 1 mm from cambium. (Ref. 33).

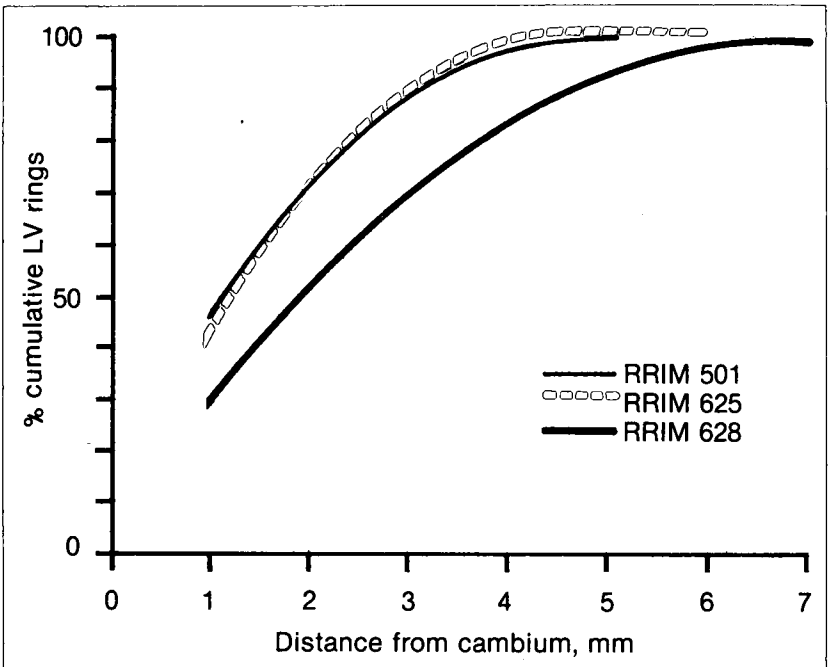

Figure 26. Percentage cumulative distribution of the number of latex vessel rings at intervals of 1 mm from cambium. (Ref. 33).

six per cent for 27 degrees slope and 14 per cent for a 45 degrees slope. Experiments by Maas[69] on seedlings and Rubber Research Institute of Malaya[70] on buddings of Pil B 95 revealed that an extra yield of 8.6% (25° slope) to 15.4% (45° slope) was obtainable for seedlings and 13.1% (30° slope) for Pil B 85. In the RRIM experiment, the extra yield varied from 4.5% to 25.4% in proportion to the heights of the tapping cut above the union.

Gomez and Chen[71] investigated the relationship in the orientation of bark tissues and the exposed surface of wood after removing a piece of bark and found that there is a very high correlation between the inclination of both these tissues to the vertical axis of the tree. As there were no significant difference between the angles of tissue orientation between inner bark and outer wood, and as the measurement on outer wood elements was simple and practicable, they measured the inclination of the wood elements. They investigated further the effects of age on the inclination. Thirty-three-year-old untapped budded trees of eight clones were investigated at two different heights. Although significant differences between clones could be demonstrated, they found that the differences between heights was only significant for one clone investigated. Although no correlation was found between girth and angle of

deviation for five of the clones examined, three others showed a tendency towards positive correlations on plots between girth and angle of deviation. In one clone, the effect of age on the angle of inclination was compared between 12-year-old buddings and twenty-five-year old buddings, but no differences were found.

From a survey of twenty-seven clones it was found that the angle of deviation from the vertical need not always be positive (to the right). In clones BD 5, RRIM 600 and 618 a proportion of the trees showed a deviation to the left but clones were generally deviated to the right. Thus mean angles of deviation varied from 2.1° to 7.1° to the right and in cases of left orientations, the angles varied from 3.2 degrees to 3.8 degrees.

15. Slope of tapping cut and tissue alignment

If the inclination of the latex vessels is to the right upward as usual (dotted lines in *Figure 27*), a tapping cut sloping in the opposite direction (*i.e* to the left upward) will cut more vessels for a given proportion of the stem's circumference (*e.g.* a half spiral, compare lengths of lines RS and SP in *Figure 27*). The usual inclination of a half spiral to the left is also considered to be positive. Assuming the circumference of the tree to be constant and that the density of the latex vessels in the bark does not vary, the number of vessels cut by a sloping half spiral cut compared with a horizontal half spiral is in the ratio:

$$1 + (\tan S. \tan D) : 1$$

where S is the angle the tapping cut makes with the horizontal and D the angle of deviation of the latex vessels from the vertical.

If the inclination of the latex vessels is to the left, the angle is considered to be negative. Removing the negative sign (s) outside the product of tangent's term, which is indicated by P, the following values are obtained for the number of vessels cut by a sloping half-spiral, compared with a horizontal half spiral cut:

Slope of cut	*Inclination of latex vessels*	
	Right	*Left*
Left upward	1 + P : 1	1 − P : 1
Right upward	1 − P : 1	1 + P : 1

The relative yield from a cut applied in the wrong direction, (*i.e.* right upward for normal trees or the usual slope to the left on exceptional trees with negative inclination), to the cuts correctly applied may be estimated as:

$$\frac{1 - P}{1 + P} = R$$

The advantage of steepening the slope of a correctly orientated cut from the recommended 30° for buddings to 45° in the modal range of vessel inclination of 3-4° is only about 2-3%, whereas the length of cut to be tapped is increased by 22%. The small increase in yield for this extra labour and greater spillage risks is scarcely profitable[71]. Moreover if the thickness of bark shaved off at each tapping as measured along the axis of the latex vessels is kept constant at the optimum for reopening the cut, then the steeper the angle or slope the greater will be the rate of bark consumption as measured vertically on the tree. This increase is trivially small because for unit

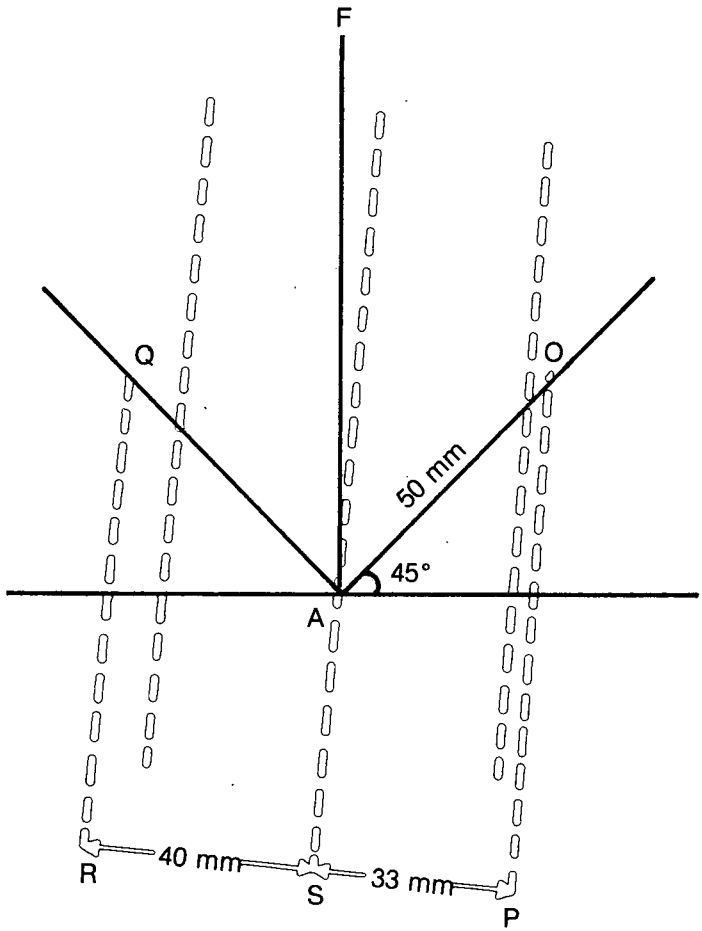

Figure 27. Effect of left or right cuts on the number of latex vessels cut. (Ref. 71).

bark consumption along the axis of the vessels, the vertical consumption is:

$$\text{unit } (\cos D + \sin D. \tan S)$$

i.e. unit $(1 + P) \cos D$.

where the cosine of the deviation of the vessels is the largest term for all values normally encountered.

Mass[69] demonstrated the converse that when the vertical bark consumption was kept constant, *i.e.* the shavings from the steeper cuts were slightly thinner, perpendicular to the cut or along the vessels, the yield was 19% more from cuts at 25° than those at 45°. The greatest disadvantage of steeper cuts is that the length of the panel is reduced, because the height of opening must be somewhat lower to enable the tapper to reach the upper end of the cut and more bark must be left untapped when the lower end of the cut reaches the union or the ground. The difference in length of half spiral panels for cuts sloping at angles of S_1 and S_2 respectively is:

$$\text{girth of the tree } (\tan S_1 - \tan S_2)$$

For example, if S_1 and S_2 are 45° and 30°, the difference in their tangents is 0.42 so that the steeper angle may consume more bark — equal to about one year's tapping on each virgin bark panel on the S/2.d/2 100% system (compare △ ABG and △ ACG in *Figure 28*).

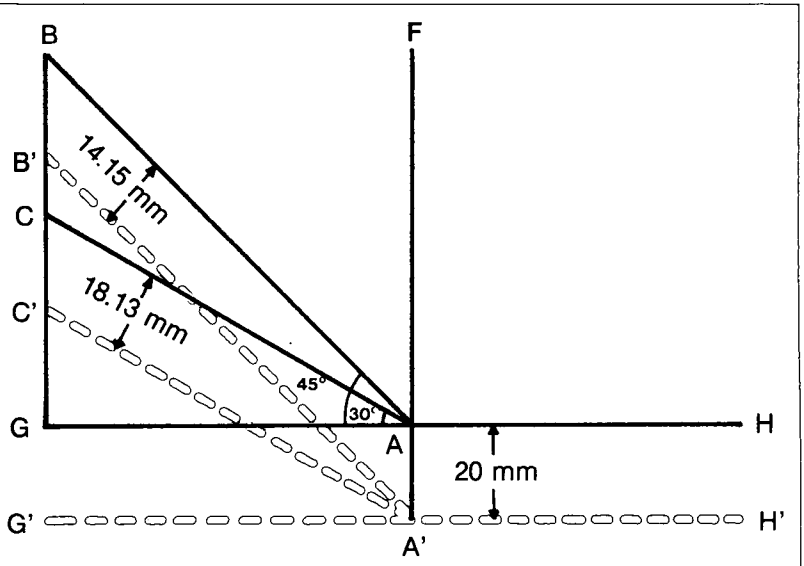

Figure 28. Effect of varying angles of slope of tapping cut on bark consumption. (Ref. 71).

In the case of seedlings, whose modal range of vessel inclination is 4 - 5°, steepening the tapping cut from the recommended

twenty-five degrees to forty-five degrees might result in a 4 - 5% increase in yield. However, in seedling trees there is a more pronounced taper in stem diameter and the number of latex vessels declines with height more rapidly than in buddings[51]. Thus steepening the tapping cut might not cut as many more latex vessels as the theoretical model suggests. Higher bark consumption and the serious disadvantage of shorter panels apply to seedlings as well as buddings so also do greater labour input and increased spillage risks. Therefore the determination of tapping cut slope should continue to rest on practical considerations.

16. Relationship between structural properties and yield

Several workers in the past have studied the relationship between various structural factors and the yield of the tree. Significant contributions of the past are recorded in *Table 4.*

Most workers were interested in arriving at simple correlations between any one structural property and yield. For these purposes, the number of latex vessel rings is an adequate property, Gomez *et al*[33] have considered in detail the factors affecting the quantitative

TABLE 4. CORRELATION BETWEEN STRUCTURAL PROPERTIES AND YIELD

Planting Material	Structural Property	Correlation Coefficient	Reference
3 clones	No. of latex vessel rings	0.86***	77
21 clones	do	0.78***	78
100 clones	do	0.70***	79
80 clones (nursery) 33 months	do	0.55***	80
seedlings	do	0.55***	52
seedlings	do	0.57***	81
seedlings	do	0.51***	82
97 clones	do	0.35***	56
80 clones (nursery) 33 months	do	0.60***	72
	Distance between latex vessel rings	0.27*	72
do	Diameter of latex vessels	−0.01 N.S.	72
do	Diameter of sieve tubes	−0.12 N.S	72
do	Bark thickness	0.49***	72

*** P = <0.001 * P = < 0.05

determination of laticiferous tissue. Apart from the number of latex vessel rings, the density of latex vessels/ring, the diameter of latex vessels, the circumference of the ring, the distance between rings *etc* were identified as properties partially determining the quantity of the laticiferous system. Narayanan *et al*[56, 72] and Narayanan and Ho[37] and Ho *et al*[74]have studied simple, partial and multiple correlations with these characters and yield. The number of latex vessel rings continues to be the most important single property highly related to yield.

Gunnery[75] proposed a relationship between sieve tube diameter and yield. He found high yielding trees with larger sieve tubes. Fernando and Tambiah[76] have followed up this hypothesis and found a similar qualitative relationship. The only extensive study is that of Narayanan *et al*[72] who found a poor relationship between sieve tube diameter and yield on 80 clones growing in the nursery 33 months after budding.

17. Factors determining yield in nursery plants

For selection purposes it is useful to relate nursery characters with yield of mature trees. There are few attempts in literature relating nursery characters with future yield of mature trees[72, 78, 79, 83]. Narayanan *et al*[72, 73] studied the relationship between yield of clones 33 months after budding, with yield obtained 56 months after budding and related these to structural properties such as girth, bark thickness, number of latex vessel rings, distance between latex vessel rings, density of latex vessels, diameter of latex vessels, diameter of sieve tubes, plugging index and other latex properties. Of the correlations observed, girth and number of latex vessel rings were two structural properties important in determining yield of young plants grown in the nursery. The average distance between consecutive latex vessel rings and latex drc have varying associations with young nursery buddings. The major constituents (N, P, K) of dry latex are related to yield through dry rubber content.

Partial correlations studied indicated that girth, number of latex vessel rings and plugging index are not correlated with each other and contribute towards yield of young buddings independently.

18. Effect of yield stimulation on bark anatomy

De Jonge[84, 85] reported briefly on the effect of yield stimulants containing 2,4-Dichlorophenoxy acetic acid (2,4-D) and 2,4,5-Trichlorophenoxy acetic acid (2,4,5-T) on renewing bark. Significant increases in bark thickness were recorded for stimulated bark. No significant difference could be established in the number of latex vessel rows in the treated bark.

A further study was conducted by Gomez[86] on the effects of 2,4-D formulation on the laticiferous system of renewing bark, and on general bark anatomy. He found that renewal starts primarily by the formation of a secondary cork cambium (phellogen) from peripheral exposed cells of the approximately one millimetre of phloem tissue left untapped during the tapping operation. The cork cambial cells divide, forming phelloderm tissue on the interior, and phellum (cork) on the exterior (*Figure 29*). Thus, the activity of the

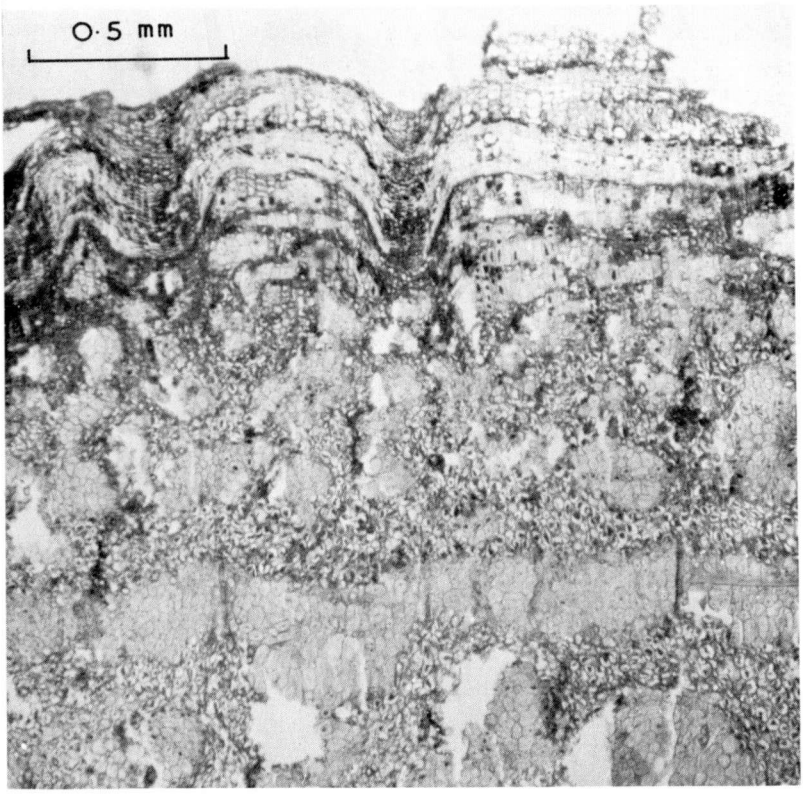

Figure 29. Section through renewing bark showing periderm and cork. × 50.

phellogen creates a tissue called 'periderm' which comprises the phellum, phellogen and phelloderm. Meanwhile, the vascular cambium divides, forming the phloem of the renewing inner bark – a normal activity associated with secondary thickening, in this instance, accelerated by the wound reaction due to tapping. The formation of the phellogen and subsequent formation of periderm occurs within a few days in bark exposed after tapping, as evidenced by the presence of chlorenchyma which is observed in renewing bark of one to two week's growth.

Young laticifers have their origin in renewing bark from tissue produced by the vascular cambium. They originate from initials situated close to the cambium. No initiation of laticifers or dedifferentiation occurs in the more mature parts of the phloem. Latex vessels retained in the untapped part of the bark are gradually displaced outwards as new phloem tissue is produced from the vascular cambium.

In the control trees and stimulated trees examined, there was a zone of tissue near the vascular cambium termed 'new phloem tissue' which represented a growth of about eight months. A zone of deep coloration due to anthocyanin was located outside the new phloem tissue. This together with the inner new phloem tissue was termed 'normal tissue'. The tissues outside normal tissue exhibited some structural disorganisation and hence was called 'disturbed tissue'. It was found in this study[86] that the disturbed tissue consisted of meristematic cells of the periderm. The outer periderm in the stimulated bark consisted of deeply fissured, thick, hard, corky tissue which showed microscopic malformations. From a comparative study it was evident that there was a significant increase in total bark thickness in bark treated with stimulants. The thickness of 'new phloem tissue' and 'normal tissue' remained unchanged by stimulant application. The thickness of disturbed tissue was increased 97% in one treatment (stimulex) and 210% in palm oil/petrolatum based treatment. The total number of latex vessels was significantly less for the palm oil/petrolatum based treatment. This was due to the lowering of latex vessel rings in the new phloem tissue which indicates that this type of stimulation of renewed bark affects the initiation of latex vessels by the vascular cambium. Corky tissues in the stimulated trees were 200 - 500 per cent of that of the control.

More recently studies were conducted on bark stimulated with ethrel[87]. No characteristic new effects were observed. The usual increase of periderm tissue due to stimulant application was however apparent.

19. Effect of mineral deficiencies on bark anatomy

Keuchenius[88] studied the relative importance of soil type on annual increment of latex vessel rings and found that latex vessel increments on good soil was 3.14 rings/year, on average soil was 2.42 rings/year and on poor soil was 1.74 rings/year. The increases in latex vessel rings correlated closely with that of girth increase. Maas[89] also observed that the rate of formation of latex vessels was influenced by differences in the soil and is accelerated by the application of various minerals.

Samsidar Hamzah *et al*[90] studied in detail the effect of mineral deficiencies on the bark anatomy of *Hevea* seedlings (Tjir 1) grown for one year in sand culture. They found that the various treatments induced profound changes in the bark anatomy in quantitative fashion.

Figure 30, 31 and *Table 5* show the summary of their results.

Nitrogen deficiency reduces the size of the plant and consequently, stem diameter, bark thickness, phloem thickness, cell size *etc* are reduced. The latex vessel size, latex vessel number and the latex vessel index are considerably reduced.

The other major elements, phosphorus, potassium and magnesium have also major effects. Although phosphorus deficiency reduces stem diameter, bark thickness and phloem thickness, the cell size is not considerably reduced. Although latex vessel number is reduced, size is not reduced. However, the latex vessel index is considerably affected.

Calcium deficiency reduces stem diameter, cell size, latex vessel number and latex vessel size. The latex vessel index is also affected markedly. Sulphur deficiency does not affect stem diameter and bark thickness, but phloem thickness is reduced. Although cell size and latex vessel size is not affected, cell number and latex vessel number are affected. Latex vessel index is however, reduced. Manganese, a minor element, shows major effects in reducing stem diameter, bark thickness, phloem thickness, cell

TABLE 5. STRUCTURAL CHANGES DUE TO MINERAL DEFICIENCIES : VALUES EXPRESSED AS % OF CONTROL (after ref. 90)

Property	C.P.	-N	-P	-K	-Mg	-Ca	-S	-Mn	-Fe	-B	-Zn	-C
Mean diameter of stem	100	30	48	49	46	67	85	53	84	104	90	78
Bark thickness	100	38	64	57	53	87	89	54	88	92	73	83
Phloem thickness	100	28	53	54	45	85	87	48	88	91	67	83
No. of cells in phloem	100	54	59	94	80	110	87	82	111	99	95	121
Average cell size	100	51	87	57	55	75	99	58	80	90	69	67
Latex vessel no.	100	60	67	51	61	83	60	94	159	114	57	153
Latex vessel size	100	74	85	78	89	75	105	80	80	115	141	89
Latex vessel index*	100	14	27	22	25	42	53	40	106	135	73	106

*Product of latex vessel number, size and diameter of plants, C.P. = Control Plant. Values underlined are significantly different from control.

size, latex vessel number, latex vessel size and latex vessel index. Iron has minior effects on these parameters although there is a reduction in latex vessel size and an increase in latex vessel number. Boron deficiency appears to increase stem diameter, and latex vessel index. The effects of boron were however discounted due to a probable experimental error. Zinc deficiency has effects on cell size and latex vessel number and size and consequently it reduces latex vessel index. Although copper deficiency reduces latex vessel size, it increases latex vessel number.

These studies clearly show the magnitude of effects of mineral deficiencies on tissue growth and plant performance. Whether

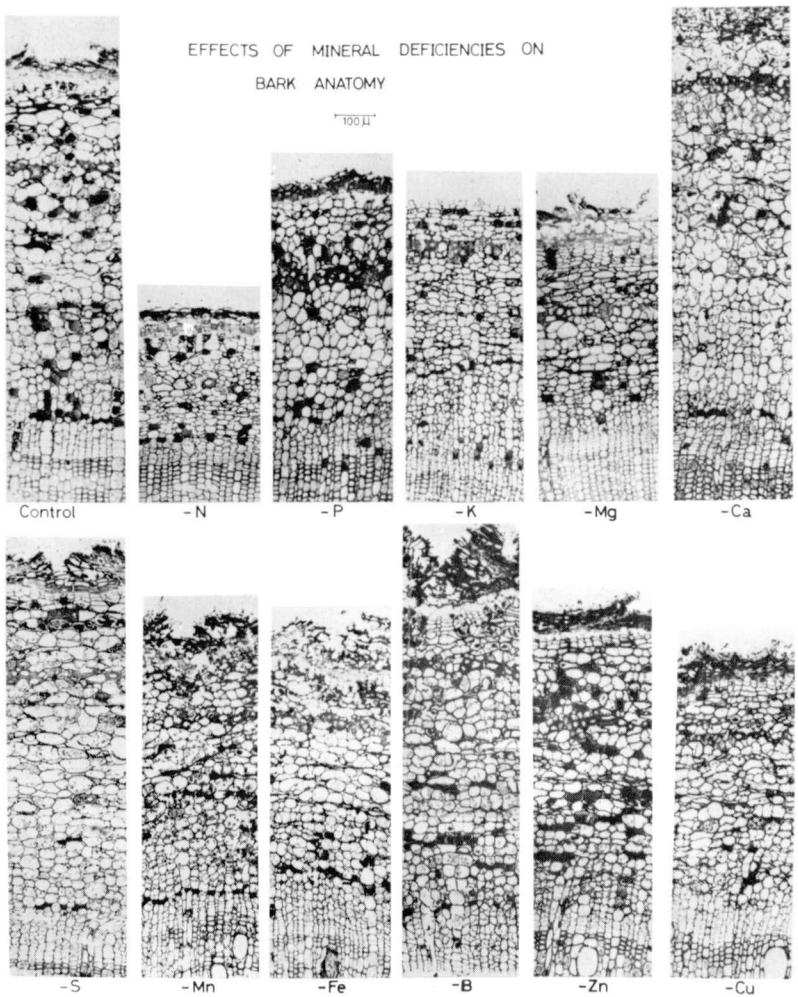

Figure 30. Cross sections of bark from plants with mineral deficiencies. × 50 (Ref. 90).

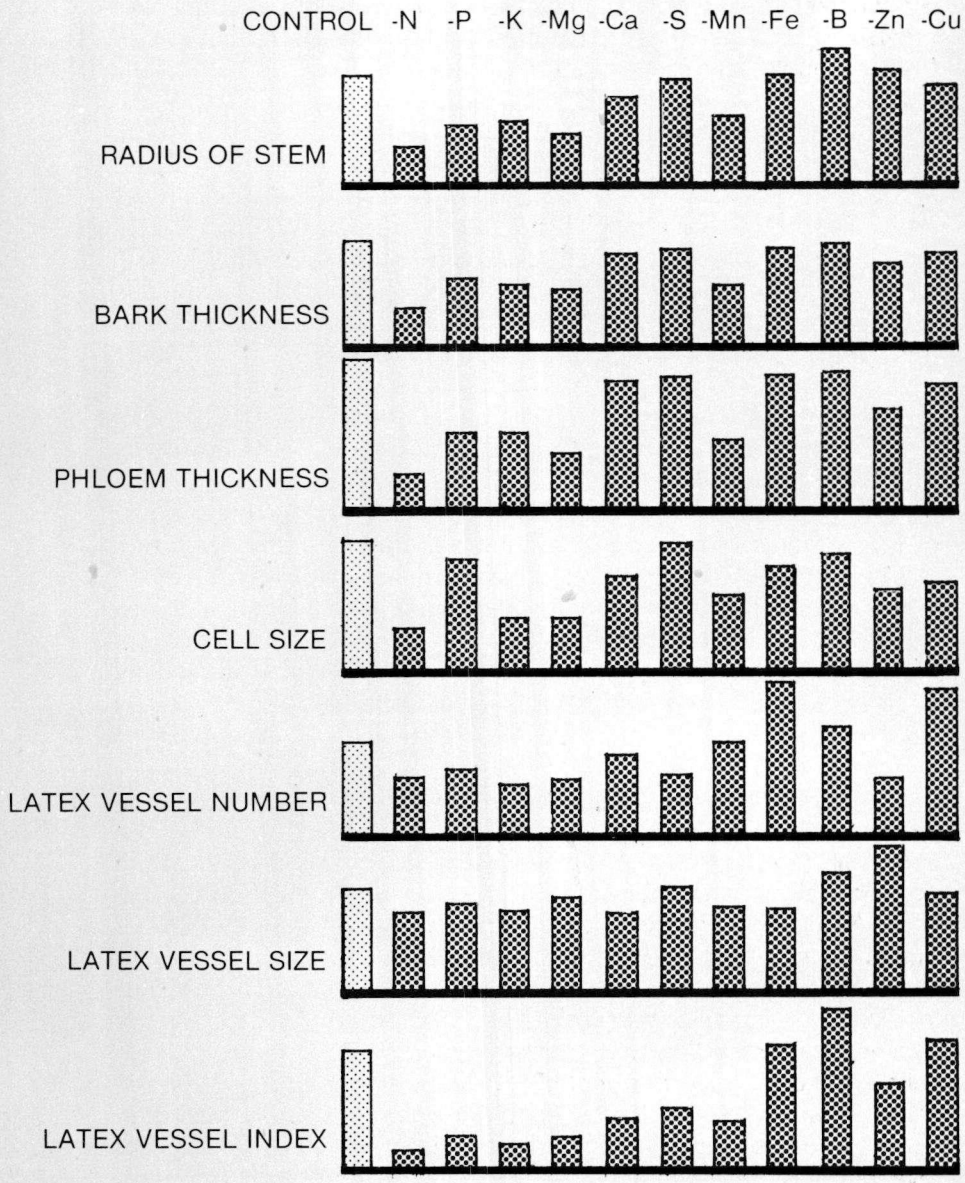

Figure 31. Effects of mineral deficiencies on bark anatomy. (Ref. 90).

these deleterious effects can be compensated by corrective treatment is yet to be shown.

20. Morbid anatomy of the bark

'Brown bast' is a typical disease of *Hevea* which produces cancerous growths in the bark tissue, resulting in unusual malformations of the tree trunk. Many investigators in the past have worked on the anatomy of the bark affected by brown bast. Notable among these are Rands[91-94], Sanderson and Sutcliffe[95] and Rhodes[96]. These investigators recognised the histological symptoms leading to abnormal tissue growth in bark from brown bast affected trees. They found a depletion of starch in tissue affected by the disease. Oil globules are frequently present. A brown substance similar to tannin is abundant, many of the cells being entirely filled with this substance. Some cell walls are also discoloured probably due to this substance[97].

Many cells in the bark become meristematic, especially those in the vicinity of latex vessels (*Figure 32*). Such meristems contribute to the partial displacement and disorganisation of latex vessels. The latex in such vessels is likely to be coagulated. Some of these meristematic zones reveal a dedifferentiation and further redifferentiation of latex vessels. Many cells in the meristematic region soon accumulate tannin, and examination of such tissue reveal varying degrees of lignification. Ultimately stone cells are formed. There are instances where latex vessels display stone cells (*Figures 33, 34*). Frequently these cells contain calcium oxalate crystals.

The formation of sclereids frequently occurs in brown bast affected bark to an extraordinary degree. Sometimes almost the whole of the affected zone is bounded on its inner and outer edges by practically continuous lines of sclereids which may form a network. At a later stage cleavage often occurs along the outer line of this stone cell zone and the outer bark peels off as a scale leaving the sclereids exposed. In such instances burr formation does not take place. In cases of burr formation, an affected zone is enclosed by a newly differentiated cambium which cuts off xylem and phloem cells and surrounds the affected zone now consisting of damaged cells. A burr is thus formed (*Figure 35*) which ultimately results in occluded xylem in the phloem. To external appearance the bark may reveal several protuberances, but deep inside small balls of woody tissue are occluded.

Rands[91-94] and Rhodes[96] observed wound gum formation in affected tissue. They found that this wound gum is insoluble and

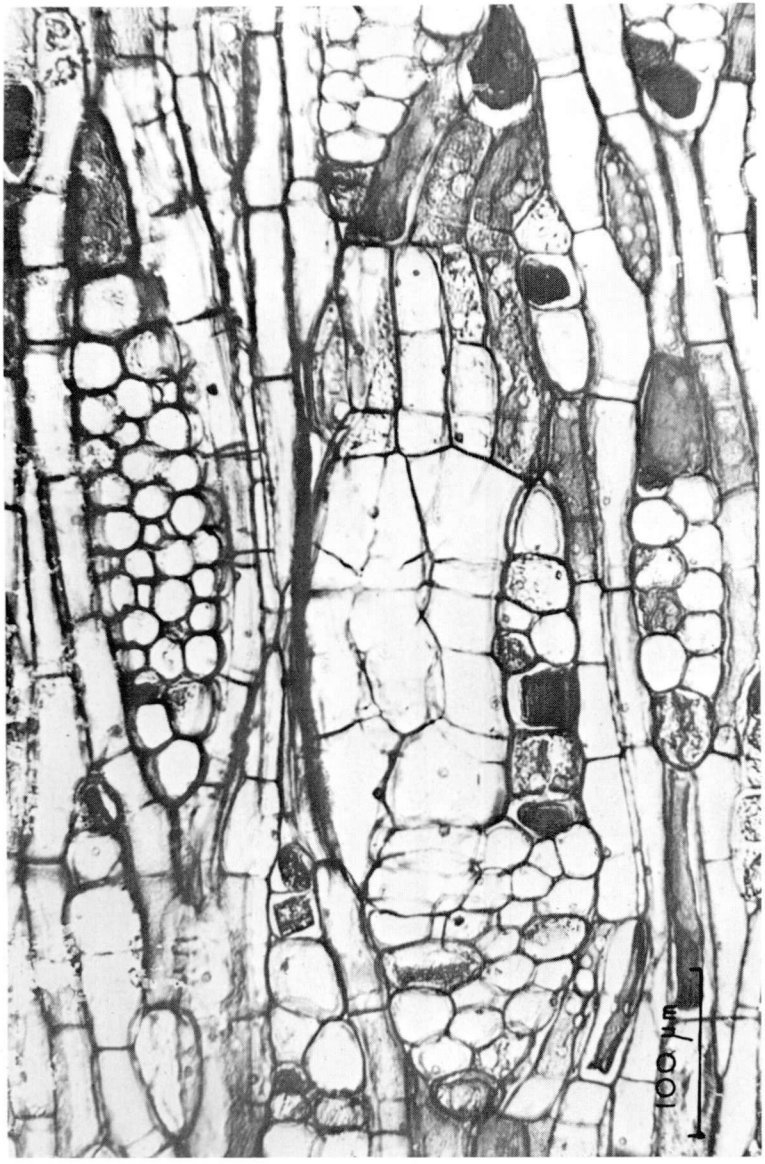

Figure 32. Tangential section of brown bast affected bark showing meristematic activity. × 210.

resistant. After various microchemical tests they came to the conclusion that this substance is resistant to acids and alkalis and gives reactions for tannins and later for lignin.

Unpublished observations by the author indicate tylose formation in latex vessels in brown bast affected tissue. The tyloses later

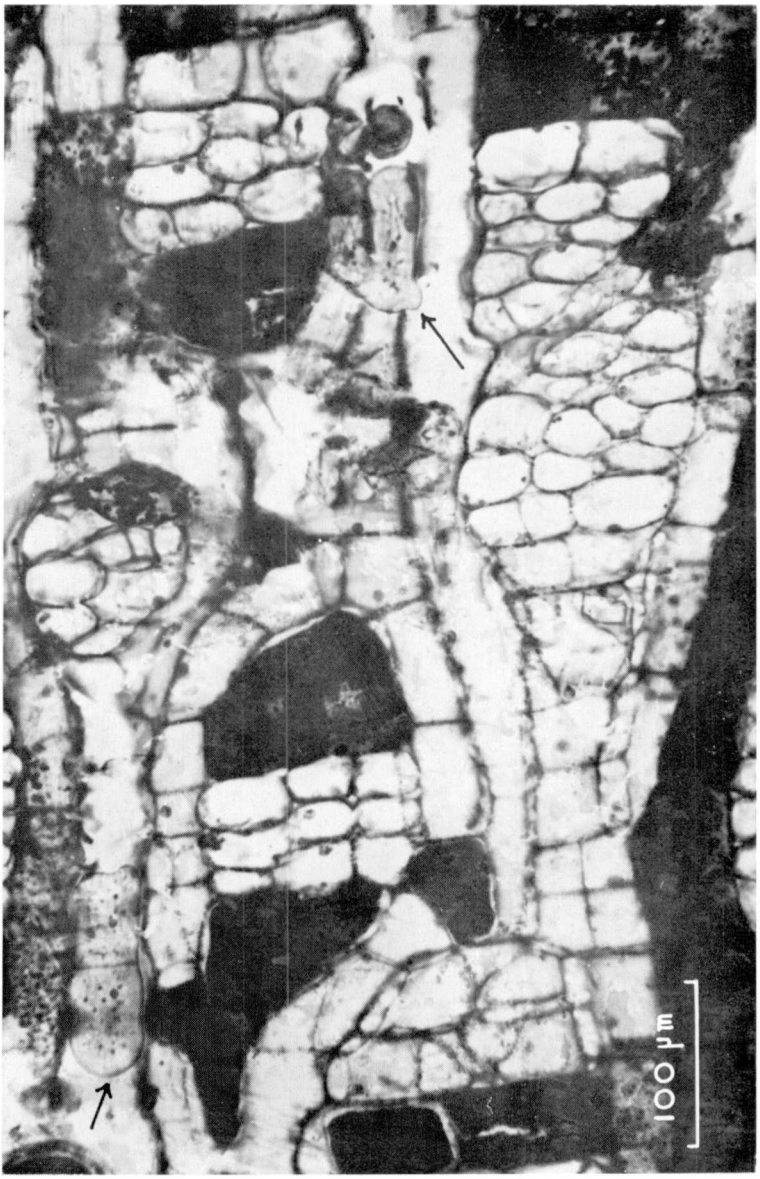

Figure 33. Tangential section of brown bast affected bark showing stone cells in latex vessels. (arrows) × 210.

become filled with tannins and lignification of the tylose wall is a secondary phenomenon. These tyloses may be occasional as seen in *Figure 36* or they may be more numerous. Physical blockage of latex vessels may result from the occurrence of tyloses in them before the onset of other secondary symptoms. Such partially blocked vessels may not contribute to the yield of normal trees

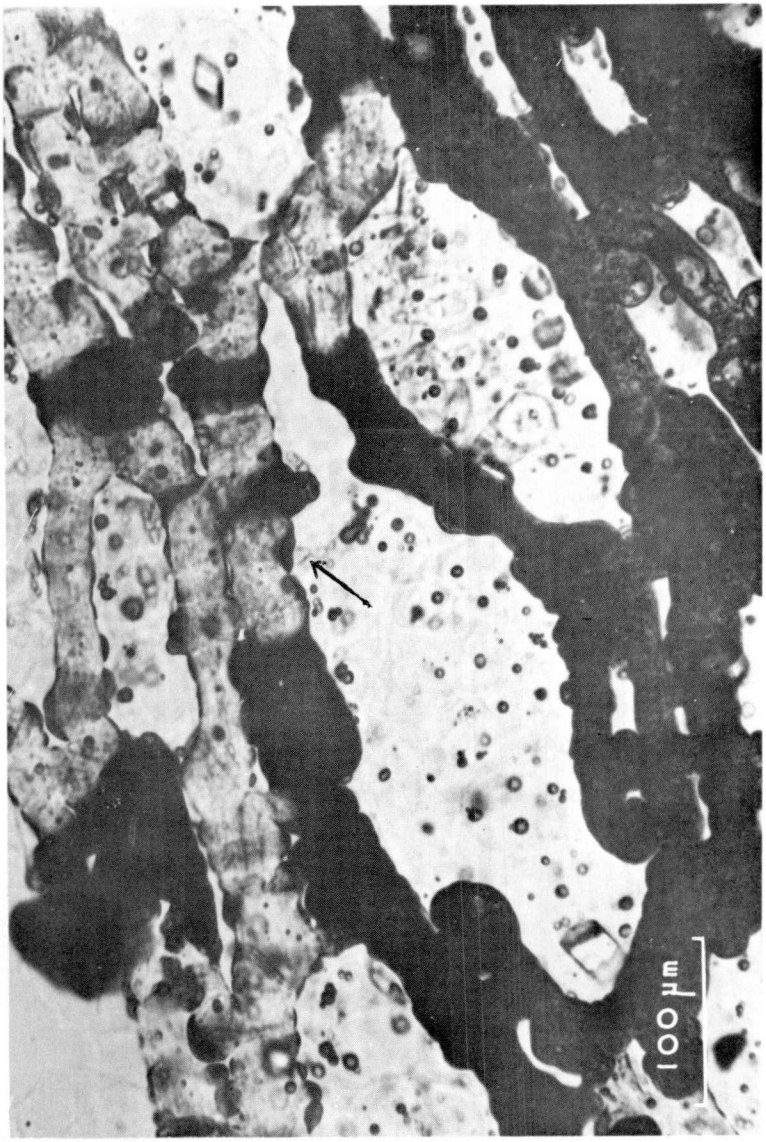

Figure 34. Tangential section of brown bast affected bark showing stone cells in latex vessels. (arrow) × 210.

which are in the process of developing early symptoms of dryness. A recent independently published article has confirmed some of these findings[112].

It has been shown by several authors notably by Bealing and Chua[98] that intensive tapping leads to increased incidence of dryness. They showed that tapping results in diminished

Figure 35. Cross section of Hevea bark showing occluded xylem. (arrow) × 5.

permeability of the latex vessels and that there is *in situ* coagulation of latex as a result of a critical reduction in the permeability of the vessel walls. Perhaps the histological symptoms described above

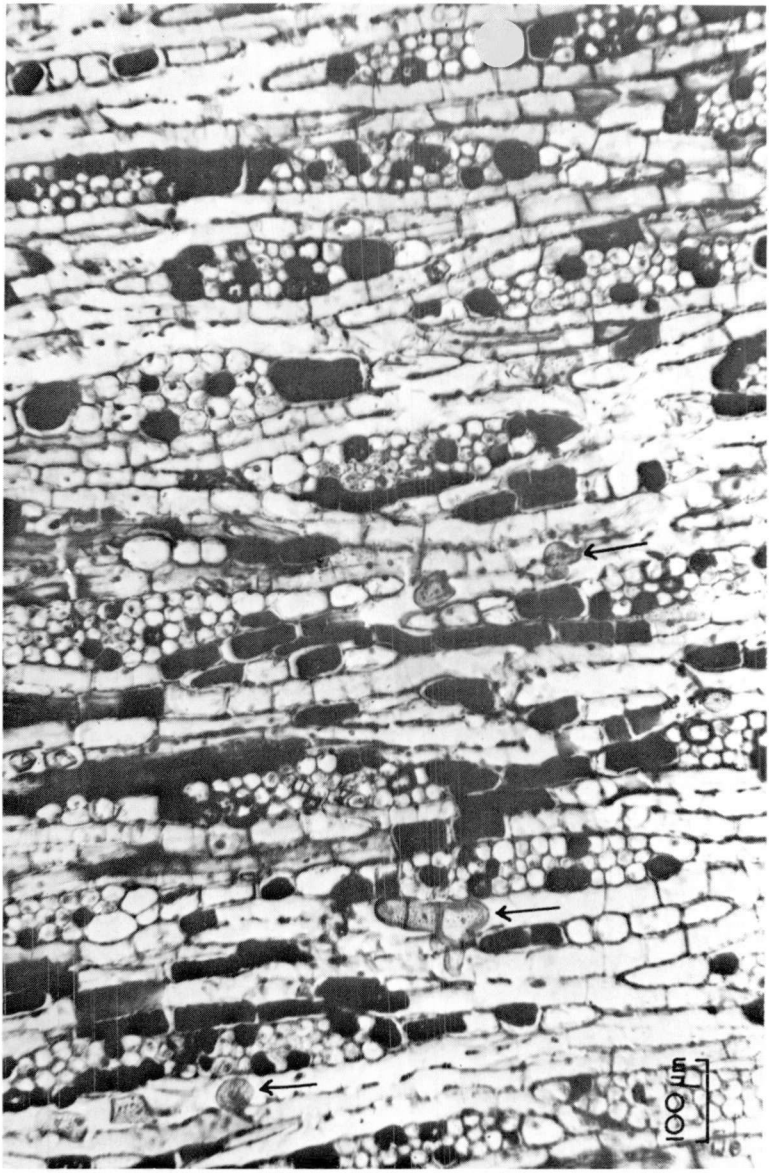

Figure 36. Tangential section of latex vessels with tyloses. (arrows) × 100.

are secondary to the primary causative mechanism leading to decrease in permeability of latex vessels.

21. Leaf anatomy

Leaf is the most important appendage of the shoot. Although its function in the life of the plant is so important, comparatively little is

known about the anatomy of the *Hevea* leaf particularly of different phenotypes and under different types of husbandry.

Bobilioff[5] has briefly described the anatomy of the leaf. Scott[99] has reported on the distribution of laticiferous tissue in the leaf. *Hevea* leaf consists of three leaflets. The leaf blade is dorsiventral in type and the upper surface is shiny and darker than the lower surface which is dull and of a lighter colour. *Figure 37* shows the sur-

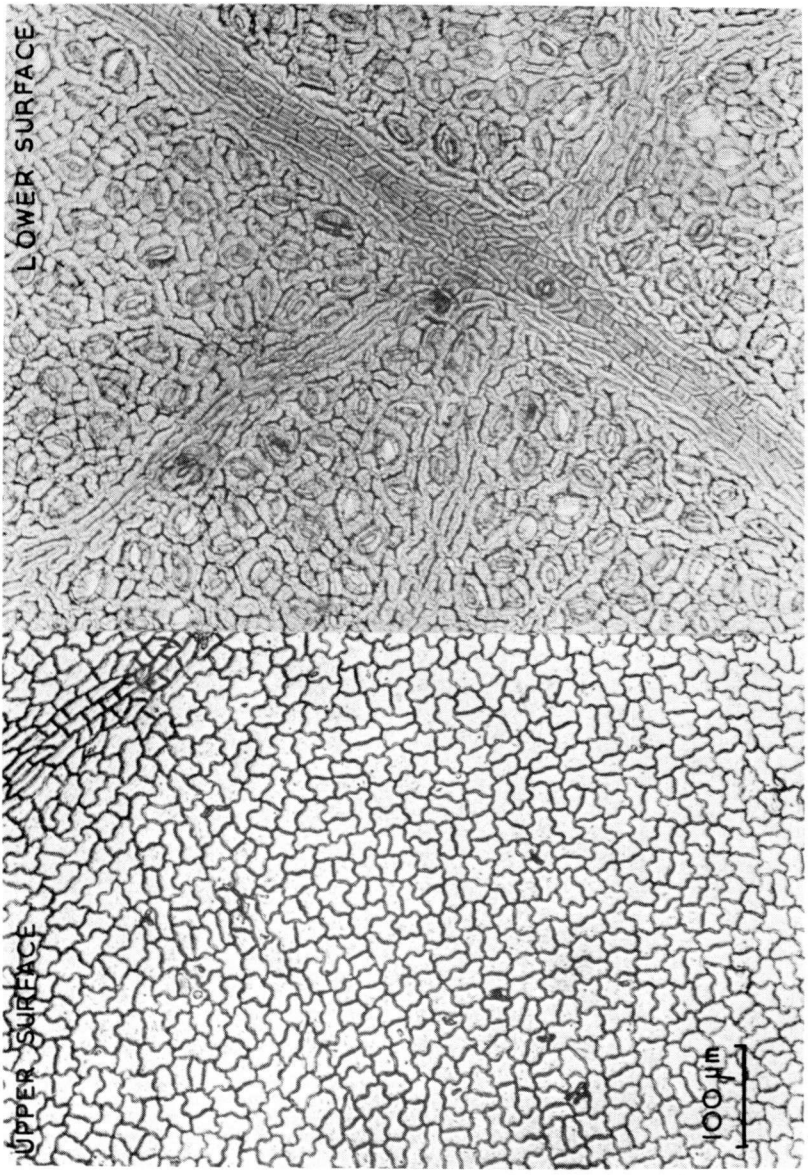

Figure 37. Micrographs of upper and lower surface of leaf. × 125.

face patterns of the upper epidermis and lower epidermis respectively. Stomata are present only in the lower epidermis. The number of stomata per unit area of leaf has been investigated by Senanayake[100] and Senanayake and Samaranayake[101]. They found that different species of *Hevea* could be distinguished by abaxial foliar characteristics such as outline of epidermal walls, appearance of epidermal cells, stomatal guard cells and the presence of epidermal hairs. The transmission of dominant species specific characters to interspecific hybrids suggested that the characters may be useful for recognising hybrids early and also for identifying parents in artificial and natural hybridizations. In an examination of 25 cultivars of *Hevea brasiliensis* they showed a wide range of stomatal density per unit leaf area. However there was no recognisable relationship between stomatal density and the known yielding ability of the experimental plants. They found that further research into variation of this character under different agro-climatic conditions was necessary before using this as an additional criterion for identifying cultivars of *Hevea brasiliensis*.

The waxy pattern on the surface of the leaves studied by electron microscopy (*Figure 38, 39*) also show clonal differences, but quantification of this property is difficult and hence its use for identification purposes is qualitative.

An examination of the leaf anatomy shows that the upper epidermis is a monolayer. Palisade cells immediately below the upper epidermis are also present as a monolayer. Spongy parenchyma forms a multilayer with one row of cells close to the lower epidermis and a few cell layers with plenty of gas space (*Figure 40*). The lower epidermis has many ridgelike appendages.

There have been some reports regarding the connection between leaves and rubber productivity of *Hevea* trees. One such observation belongs to Bobilioff[102] who investigated Parkin's hypothesis that when a leaf is severed at the base of its petiole, no latex exudes from the injured surface. Microscopic investigation revealed the presence of an abscission layer at the base of the petiole as the cause of interruption of latex flow. Nevertheless he extrapolated these findings to interpret that laticiferous tubes do not conduct organic matter and that the latex from the trunk does not originate from the leaves. He further concluded that there is no relationship between anatomical structure of leaves and the petioles and yield of a given tree and that there is no correlation between the size of leaves and latex production, a view in opposition to that of Aggelen-Bot[103].

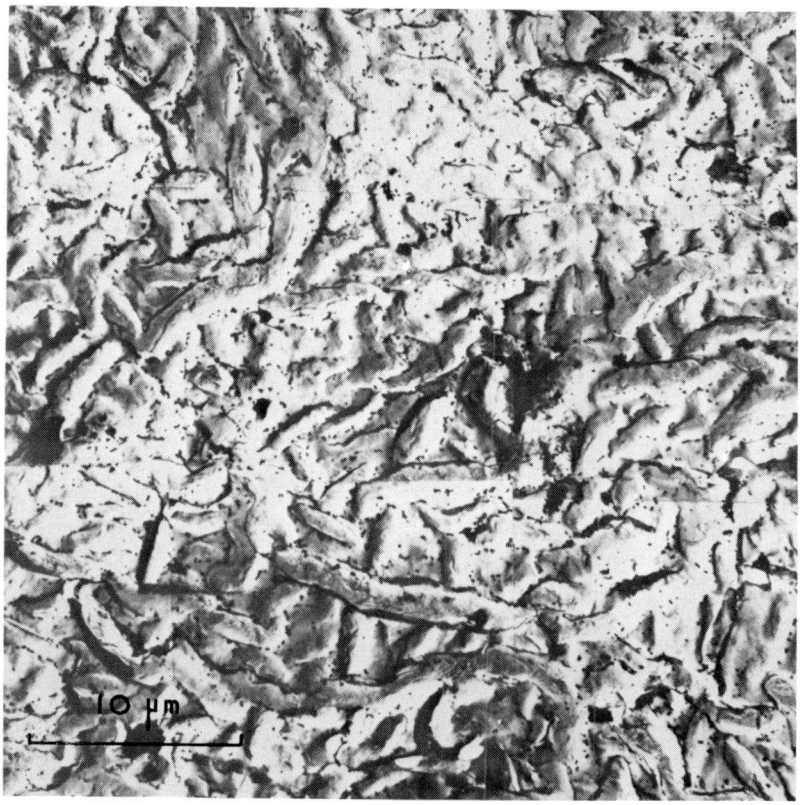

Figure 38. Electron micrograph of waxy pattern on upper leaf epidermis. × 2700.

A reticulate cuticle has been reported for the lower epidermis[104]. On each cell there is a thick ridge of cuticle, median in position and oriented parallel to the long axis of the cell. From this central ridge, several arms originate with gradual tapering ends. Some of these extend to neighbouring cells and establish connection with the main ridge and arms thereof, forming a loose reticulum. Leaves from all over the Malaysian peninsular showed the reticular pattern and hence it was concluded that this is not affected by environmental factors.

Gomez[105] studied various leaf characteristics of 11 clones. He made observations on leaf thickness, palisade thickness, spongy layer thickness, number of palisade cells in unit leaf section, the number of spongy cells in unit leaf section and the number of stomata in the lower epidermis. *Tables 6 - 15* give the relevant information.

The surface area of leaflets are not significantly different for the clones. The number of stomata in the lower epidermis of the

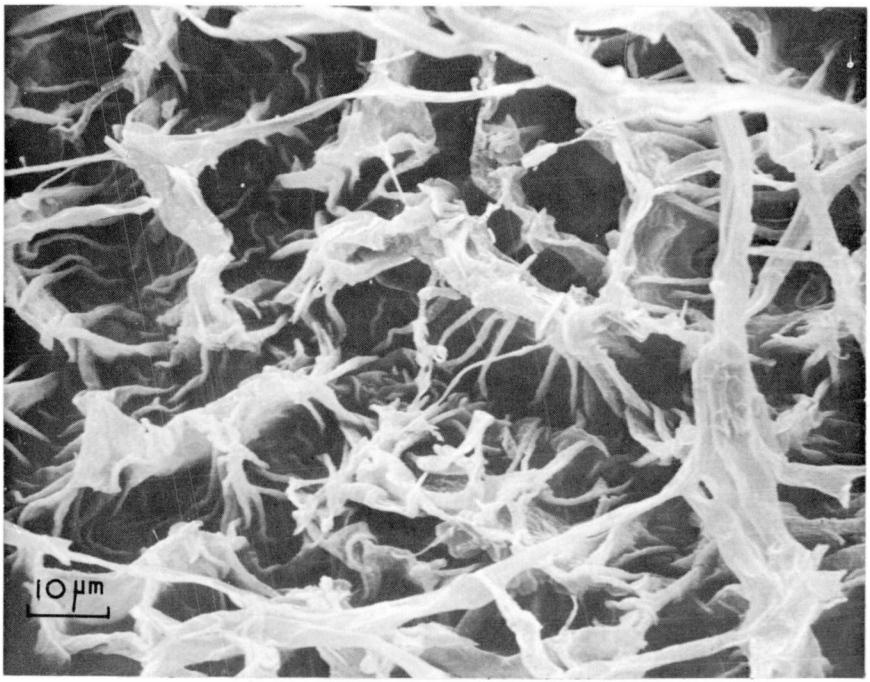

Figure 39. Scanning electron micrograph of waxy pattern on upper leaf surface. × 1000.

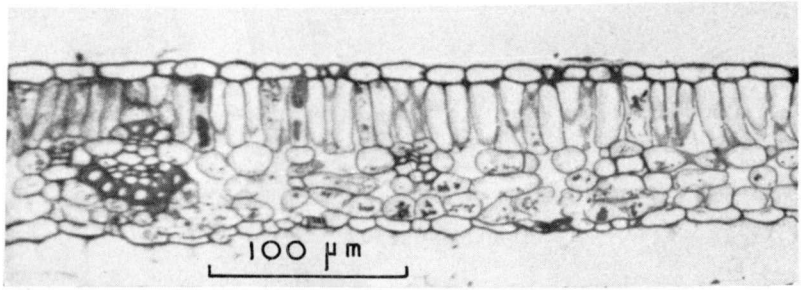

Figure 40. Cross section through Hevea leaf. × 250.

clones are significantly different. The same order of difference between clones is detected for a number of properties such as 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. In the thickness of spongy tissue, the order of clonal differences was significant only at $P = 0.01$ level.

TABLE 6. SURFACE AREA OF LEAFLETS (IN SQ. CM)

Clone	Surface area (sq. cms)
PR 255	120.53
ES 7	103.53
SS 2	97.13
RRIM 614	93.60
IRCI 10	91.60
RRIC 3	91.27
RRIM 605	86.87
RRIM 600	81.60
RRIM 501	77.73
PB 86	75.40
ES 4	74.27

Mean = 90.32
s.e. = 10.177
l.s.d. = 29.09

TABLE 7. NUMBER OF STOMATA IN LOWER EPIDERMIS (PER SQ. MM)

Clone	No. of stomata (per sq. mm)
IRCI 10	369.29
RRIM 600	350.37
RRIC 3	337.20
RRIM 614	316.19
ES 4	299.31
RRIM 501	294.93
PB 86	293.59
SS 2	292.83
PR 255	292.20
ES 7	286.51
RRIM 605	277.93

Mean = 310.03
s.e. = 9.375
l.s.d. = 26.25

TABLE 8. NUMBER OF UPPER EPIDERMAL CELLS (PER SQ. MM)

Clone	No. of cells (per sq. mm)
RRIM 501	1794.73
RRIM 605	1775.53
ES 7	1686.47
IRCI 10	1604.40
PR 255	1589.40
PB 86	1588.47
RRIC 3	1558.93
RRIM 600	1492.93
RRIM 614	1429.27
ES 4	1315.40
SS 2	1133.47

Mean = 1542.64
s.e. = 103.536
l.s.d. = 295.92

TABLE 9. LEAF THICKNESS (μ)

Clone	Leaf thickness (μ)
SS 2	143.37
RRIM 614	132.25
RRIM 600	119.63
ES 4	118.47
PB 86	112.93
RRIM 501	111.89
RRIM 605	110.87
RRIC 3	107.60
PR 255	107.43
ES 7	103.56
IRCI 10	100.11

Mean = 115.28
s.e. = 5.85
l.s.d. = 16.708

TABLE 10. THICKNESS OF PALISADE TISSUE (μ)

Clone	Palisade thickness (μ)
SS 2	70.19
RRIM 614	61.47
RRIM 501	54.04
RRIM 605	52.01
RRIM 600	51.23
RRIC 3	49.21
PB 86	48.23
ES 7	44.15
PR 255	43.90
IRCI 10	42.83

Mean = 51.59
s.e. = 2.62
l.s.d. = 7.488

TABLE 11. THICKNESS OF SPONGY TISSUE (μ)

Clone	Spongy layer thickness (μ)
SS 2	55.08
RRIM 614	51.35
RRIM 600	49.44
ES 4	48.22
PB 86	46.03
ES 7	43.89
PR 255	43.85
RRIC 3	43.20
RRIM 605	42.23
RRIM 501	41.31
IRCI 10	40.27

Mean = 45.90
s.e. = 2.75
l.s.d. = 7.86

TABLE 12. MEAN NUMBER OF CELLS IN UNIT LENGTH OF PALISADE LAYER

Clone	Cell no./0.2 mm length of palisade tissue
RRIM 614	38.80
IRCI 10	35.93
RRIM 600	35.90
RRIC 3	33.17
PB 86	32.57
PR 255	31.27
RRIM 501	31.13
ES 7	29.70
SS 2	29.13
RRIM 605	27.57
ES 4	25.20

Mean = 31.85
s.e. = 2.173
l.s.d. = 60.8

TABLE 13. MEAN NUMBER OF CELLS IN UNIT LENGTH OF SPONGY LAYER

Clone	Cell no./0.2 mm length of spongy tissue
RRIM 614	52.53
IRCI 10	51.97
RRIM 600	51.40
RRIC 3	48.57
PB 86	46.83
ES 7	46.37
PR 255	45.60
RRIM 501	45.50
ES 4	41.53
RRIM 605	41.33
SS 2	39.17

Mean = 46.44
s.e. = 1.731
l.s.d. = 4.85

TABLE 14. MEAN NUMBER OF STOMATA PER LEAFLET

Clone	Number
PR 255	3 521 887
IRCI 10	3 382 696
RRIC 3	3 077 624
ES 7	2 966 238
RRIM 614	2 959 538
RRIM 600	2 859 019
SS 2	2 844 258
RRIM 605	2 414 378
RRIM 501	2 292 491
ES 4	2 222 975
PB 86	2 213 669

Mean = 2 795 889
s.e. = 455 970
c.v. (%) = 16.31

TABLE 15. CELL NUMBER PER 0.2 MM STRIP OF LEAF SECTION

Clone	Number
RRIM 614	91.33
IRCI 10	87.90
RRIM 600	87.30
RRIC 3	81.74
PB 86	79.40
PR 255	76.87
RRIM 501	76.63
ES 7	76.07
RRIM 605	68.90
SS 2	68.20
ES 4	66.73

Mean = 78.27
s.d. = 8.30
c.v. (%) = 10.60

Amand[106] worked on the relationship between leaf angle and productivity of *Hevea*. He observed that the angle of attachment of leaf varied from 51° 51' to 65° 45' and that there is a negative correlation with the yield of trees. No other workers have however confirmed or taken such a correlation seriously.

22. Effect of mineral deficiencies on leaf anatomy

Hevea plants growing under minerally deficient conditions exhibit a variety of morphological symptoms on their leaves[107]. Their anatomy also show considerable differences[87]. *Figure 41* summarises the findings of a recent investigation.

Leaf thickness is increased in calcium and sulphur deficiencies while it is reduced in zinc, copper and manganese deficiencies. Upper epidermal thickness is highest under iron deficiency and lowest under calcium. Lower epidermis values are highest for zinc and lowest for calcium. Number of palisade cells are increased in potassium deficiency and iron deficiency, but the percentage area covered by palisade cells in section is increased for phosphorus and calcium deficiencies and reduced under boron deficiency. Number of spongy parenchyma cells are increased under iron deficiency, but the percentage area covered by spongy cells in leaf

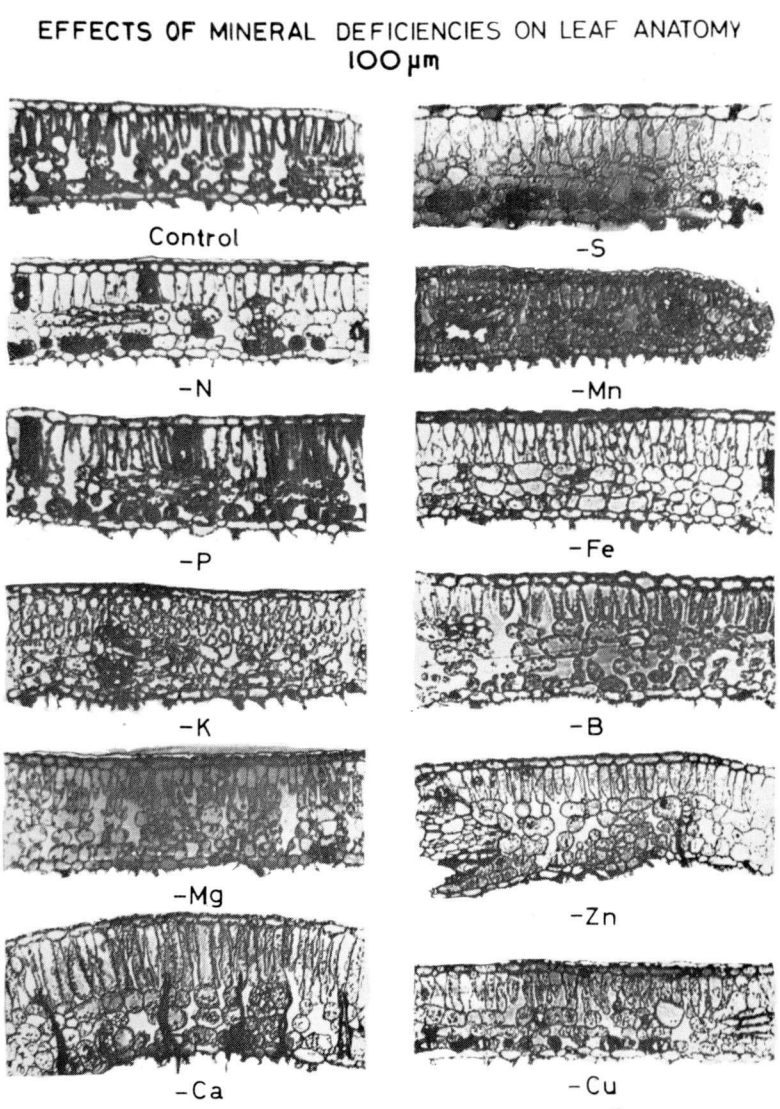

Figure 41. Cross sections through leaves of plants with mlneral deficiencies. × 140.

cross section is increased by boron deficiency. Cell sizes are altered considerably in many instances, but a systematic quantitative study is lacking.

23. Wood Anatomy

The principal water conducting tissue of the vascular system is the xylem. The xylem is a complex tissue consisting of many different types of cells, living and non-living. The most characteristic are the

tracheary elements, which conduct water. Some of the tracheary elements combine the function of conduction with that of support. The xylem also commonly contains specialised supporting elements, the fibres. Another type of basic cell type in the xylem is the living parenchyma cells.

Two fundamental types of tracheary elements occur in the xylem: the tracheids and vessel members. In the mature state, both are more or less elongated cells with lignified secondary walls and devoid of protoplasts. They differ among themselves in their perforations. Tracheids have pit pairs on their common walls whereas vessel members are perforated in certain areas of contact with other vessel members. They thus form fused long continuous tubes, the vessels. Sap moving through these structures passes freely from element to element through perforations, whereas in tracheids, it traverses the walls.

Figure 42 shows a cross section through the xylem of a young stem and *Figure 43* through sapwood of a mature tree. *Figure 44* shows a tangential section. The large cells are obviously vessel elements and numerous tracheids, fibres and parenchyma cells can be seen in the ground tissue. Starch, when stored, occurs in the parenchyma cells. The medullary rays which maintain a communication system with the bark can also be seen.

A complete cross section of the stem of *Hevea* would reveal that wood tissue makes up the bulk of the cross section with the bark forming only a small percentage of the radius of the stem. The strength of *Hevea* wood is of paramount economic importance as weak stems collapse in windstorms. In recent years it has been found that wood strength is related to wind damage susceptibility[108]. A systematic study is lacking on the relationship between wood strength and fibre characteristics.

Tylose formation in xylem vessels have been reported by Vischer[109]. This occurs as a reaction to wounding. Tapping being a wounding process stimulates the parenchyma cells near wood vessels to form tyloses which intrude into wood vessels and occasionally block them. *Figure 45* shows a young vessel member showing tyloses formed due to inflicted injury.

24. Postscript on puncture tapping

In conventional tapping, the bark is excised up to a depth of 1 mm from the cambium. The exposed cells are immediately sealed by fatty substances and the meristematic activity of the cork cambium gives rise to peridermal tissue in the renewing bark. The vascular

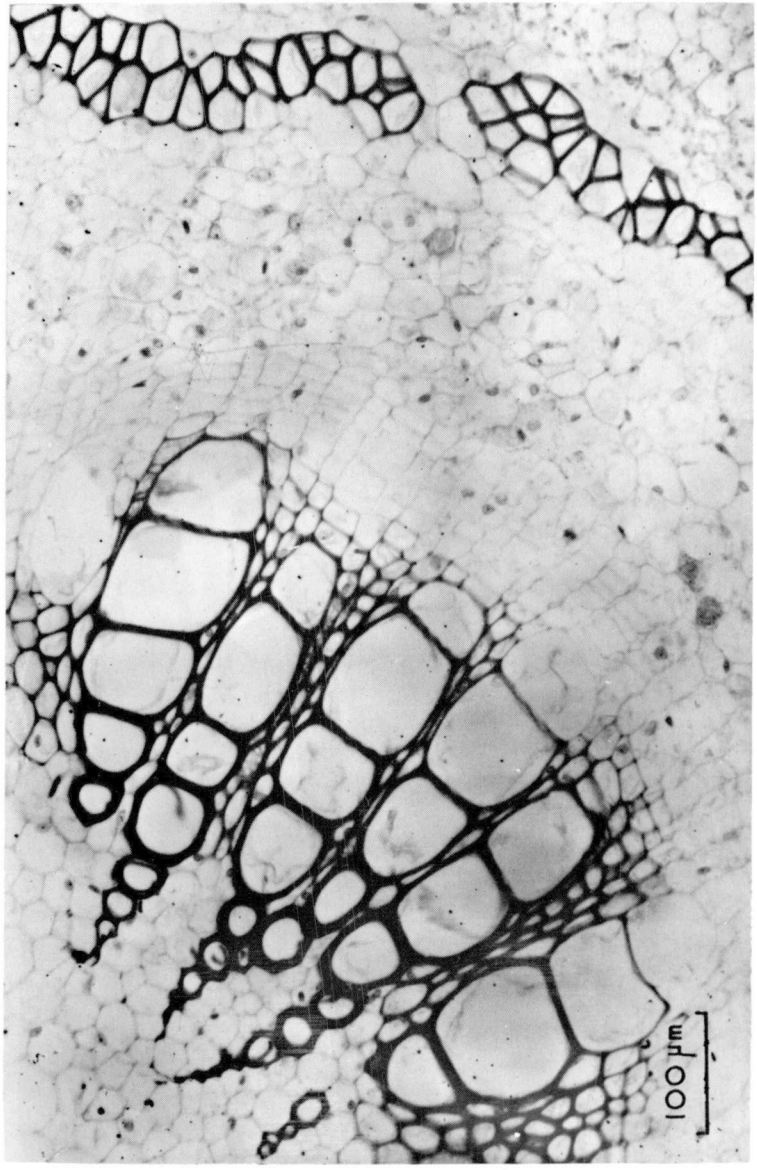

Figure 42. Cross section through xylem of young Hevea stem. × 150.

cambium also regenerates latex vessels in the inner phloem continuously generated by secondary growth.

In recent times, there has been considerable interest on puncture tapping and hence the anatomy of bark renewal in puncture tapped trees was recently considered by Samsidar Hamzah anc

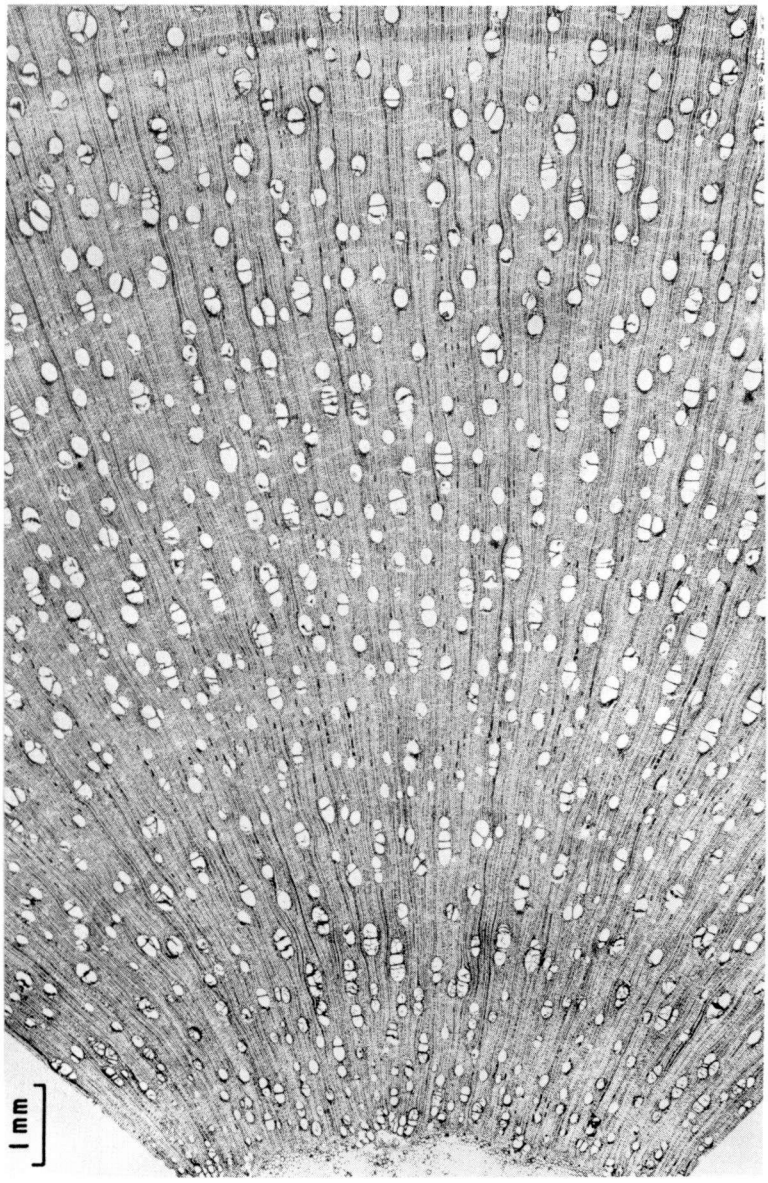

Figure 43. Cross section through sapwood of mature tree. × 10.

Gomez[110]. As the bark is punctured, the wound is closed by a plug of latex which probably has a protective function. The cells adjacent to the puncture too seem to be affected as shown by a characteristic discoloration which is more intense along the periphery of the wound (*Figure 46*). In sections which are previously bleached prior

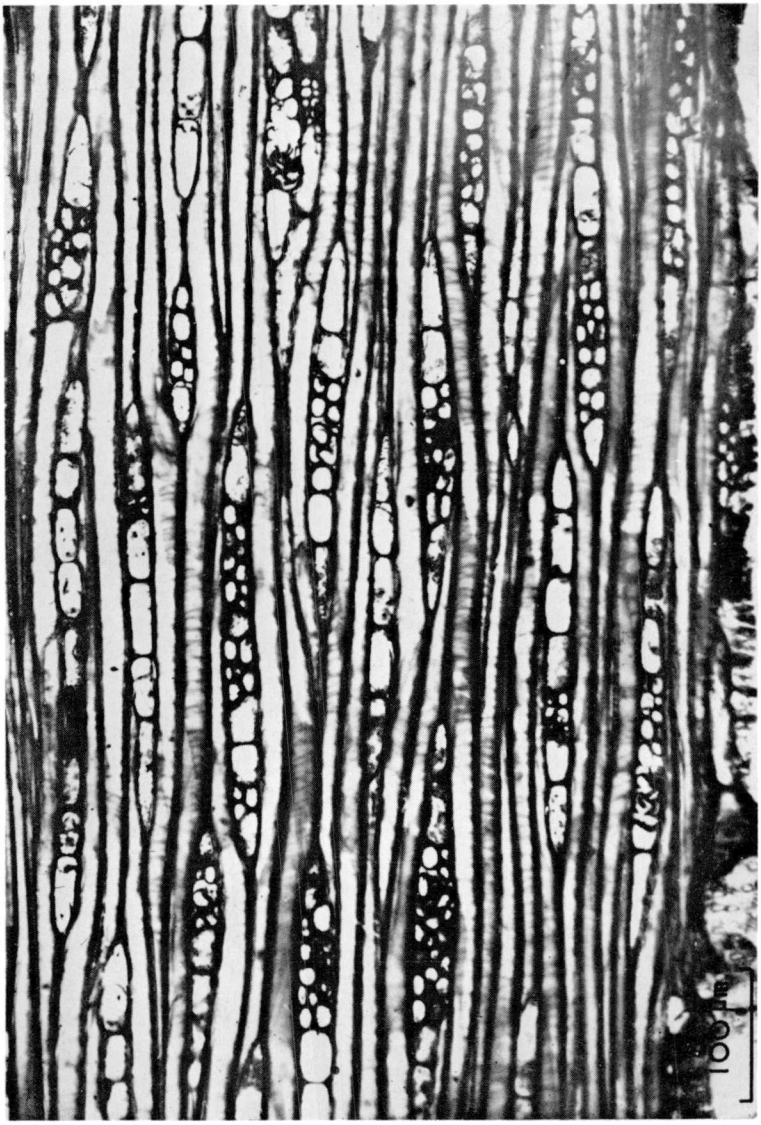

Figure 44. Tangential section through sapwood of a mature tree. × 170.

to staining, the discoloration is removed except in the more intensely discolored zone. This indicates that the 'wounded zone' is still a part of the living bark and that the discoloration is due to the presence of substances protecting the protoplasts against decay or desiccation. The more intensely discolored zone has been found to be made up of lignified/suberised cells. Tonnelier *et al*[111] identified these groups of cells as tannin cells.

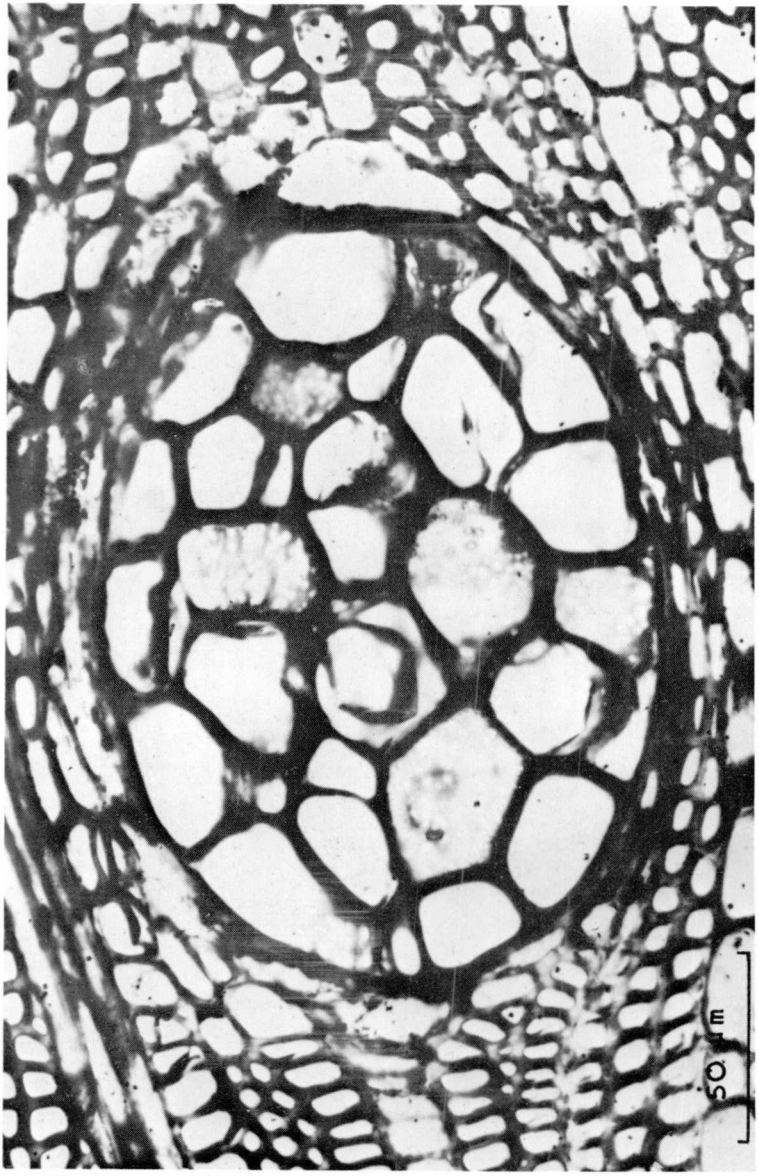

Figure 45. Cross section of a young xylem vessel with tyloses. × 480.

Cork cambium is presumably developed from the peripheral cells of the 'wounded zone'. The peridermal tissue is formed, of which the phelloderm later develops into stone cells. In samples examined three years after puncturing, stone cells completely surrounded the 'wounded zone'. The scar tissue or scabs seen on the surface of the bark when the flaky external bark is removed is actually made up of the wounded zone plus the peridermal tissues.

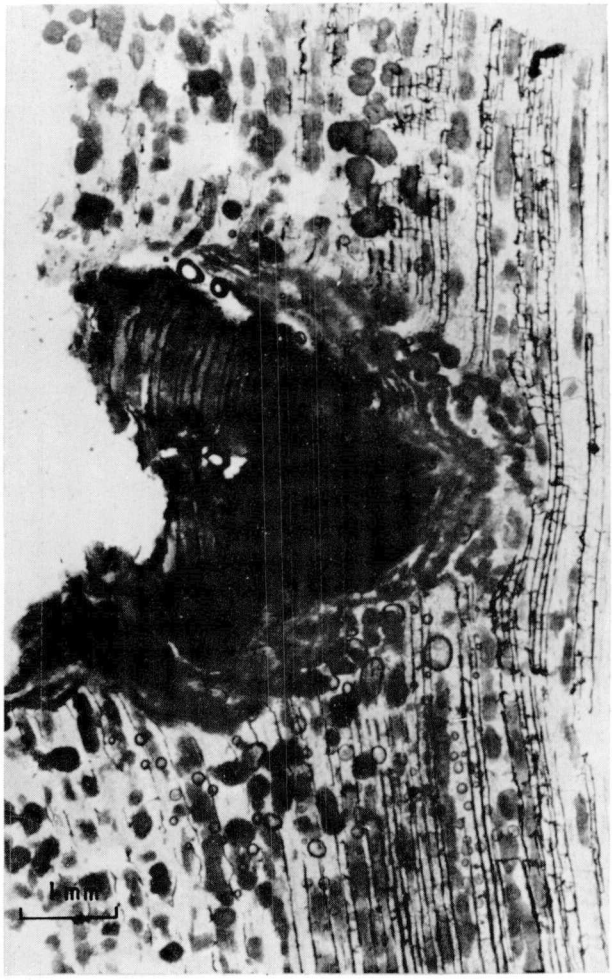

Figure 46. Section through a puncture hole showing wound repair. × 12.

The continuity of the vascular cambium in the meantime is not affected permanently by the puncture, and bark renewal proceeds in the normal fashion. Latex vessel formation in the newly formed phloem seems to be delayed at first and is seen as a gap between the first two latex vessels near the cambium.

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