Structural studies on Tension wood of *Hevea brasiliensis* (Para Rubber) with special reference to clonal variability

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BY

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Dedicated to
My Parents & Teachers

DECLARATION

I, FRANCIS MATHEW hereby declare that this thesis entitled **"Structural studies on Tension wood of** ***Hevea brasiliensis*** **(Para Rubber) with special reference to clonal variability",** is a bonafide record of the research work done by me at Rubber Research Institute of India, Kottayam-9, and that no part thereof has been presented earlier for any degree or diploma of any other University.

Kottayam
29.12.2003

FRANCIS MATHEW

CERTIFICATE

This is to certify that the thesis entitled "STRUCTURAL STUDIES ON TENSION WOOD OF HEVEA BRASILIENSIS (PARA RUBBER) WITH SPECIAL REFERENCE TO CLONAL VARIABILITY" is an authentic record of original research work carried out by FRANCIS MATHEW at the Rubber Research Institute of India, Kottayam, Kerala, under my supervision and guidance during the period – July 1997 to December 2003, for the award of the degree of Doctor of Philosophy in the Faculty of Science, Mahatma Gandhi University.

The work presented in this thesis has not been submitted for the award of any other degree or diploma earlier. It is also certified that FRANCIS MATHEW has fulfilled all the requirements and has passed the qualifying examination for Ph.D. of the Mahatma Gandhi University, Kottayam.

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ABBREVIATIONS USED

µm	:	micrometre
ANOVA	:	analysis of variance
C.S.	:	cross section
CES	:	Central Experiment Station
cm	:	centimetre
cm^2	:	square centimetre
df	:	degrees of freedom
DGCIS	:	Directorate General of Commercial Intelligence and Statistics
F	:	F- value
GA_3	:	Gibberellic acid
GF	:	gelatinous fibre
ha.	:	hectare
IAA	:	Indole-3-acetic acid
ITC	:	International Trade Centre
LH	:	lower half
LS	:	lower side
m^3	:	cubic metre
mm	:	millimetre
mm^2	:	squire millimetre
MRB	:	Malaysian Rubber Board
MS	:	mean sum of squares
MTIB	:	Malaysian Timber Industry Board
NF	:	normal fibre
NPS	:	not position specific
NS	:	non-significant
NW	:	normal wood
ppm	:	parts per million

R.L.S.	:	radial longitudinal section
RRII	:	Rubber Research Institute of India
RRIM	:	Rubber Research Institute of Malaysia
SS	:	sum of squares
t	:	t-value
T.L.S.	:	tangential longitudinal section
T.S.	:	transverse section
TIBA	:	2,3,5-Triiodo Benzoic acid
TW	:	tension wood
UH	:	upper half
US	:	upper side

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CHAPTER 1

INTRODUCTION

Of the ten species of the genus *Hevea*, *Hevea brasiliensis* (Willd. ex Adr.de Juss.) Muell. Arg., the para rubber, is the only species that is cultivated commercially for natural rubber production. The primary center of origin of *Hevea brasiliensis* is the Amazon basin and adjacent areas of Brazil. It has also flourished in certain other countries such as Bolivia, Peru, Ecuador, Columbia Guyana, Surinam and Venezuela.

History says that Sir Henry Wickham, the father of Natural Rubber, made a collection of rubber seeds from the confluence of River Tapajos and the Amazon (Schultes, 1977). Of the 7000 seeds he sent to Kew Garden, London in 1986, 2700 germinated. From these 1919 seeds were sent to Ceylon of which 90% survived and out of 18 seeds sent to Java only two survived (Dijikman, 1951). Another consignment of 22 seedlings was sent to Singapore in 1877 and all of them was reported to have survived. These initial planting materials together with other rubber trees grown in Ceylon were the foundation on which the Malaysian rubber industry is based (Barlow, 1978). The consensus on the history of the source of planting material to the South East Asian rubber plantation is that it had originated from the Wickham collections and from these, rubber cultivation spread to all other Asian countries (Schultes 1977; Simmonds, 1989).

In India, rubber cultivation was started in 1878, in Nilambur, Kerala State, as a forest crop, using the planting materials brought from the Royal Botanical Garden, Ceylon (Petch, 1914; Dean, 1987). However the first commercial rubber plantation of rubber was started in India by European planters in 1902 at Alwaye. The subsequent increase in area under rubber plantations is mainly attributable to the enterprise of a large number of Indian proprietary planters belonging to the former native states of Travancore and Cochin.

1.1 Rubber Tree – An eco-friendly potential source of timber

Rubber tree (*Hevea brasiliensis*) is a perennial hardwood species belonging to the family Euphorbiaceae, growing to a height of about 30 m. The tree has a straight trunk of 3 to 4 m height, attaining 70 – 110 cm diameter at breast height with profusely branched dense canopy (Reghu, 2002). The trees raised from seedling population show a higher girth compared to those raised from bud grafted planting materials. It has been estimated that at the age of 27 – 30 years, a seedling tree gives 1 m^3 and budded tree gives 0.57 m^3 timber at the time of clear felling, of which 60% is trunk wood and 40% is branch wood (Haridasan and Sreenivasan, 1985; George and Joseph, 2002). Over the time, bud grafted trees became common in all the major rubber producing countries as the primary objective was to obtain higher level of latex yield than timber. This development had serious implications on the yield of timber per tree compared to the availability during the early times, as the volume of the timber is directly proportional to the girth of the rubber tree.

The prevailing unilateral focus on latex production is at stake in view of the biological and agroclimatic constraints on enhancing productivity of natural rubber (NR) and the growing market uncertainties (George, 2002). In this regard, it will be contextual to examine the latex and timber yield potential of prominent clones developed in Malaysia as 'latex - timber' and 'timber - latex' clones so as to draw certain guidelines specific to the Indian context (Viswanathan and *et al.*, 2002). The reported higher timber yield potential of the latex - timber clones in 14 year old planting in Malaysia varied from 0.81 to 1.87 m^3 per tree (MTIB, 1998). The prominent clones identified for higher latex and timber production are from the PB 200 and PB 300 series and RRIM 900 and RRIM 2000 series (Lotfy *et al.*, 1995). Of the RRIM 900 series, 12 clones showed potential for timber production with an average timber volume of 1.09 m^3 per tree at the age of 21 years and in RRIM 2000 series, eight clones were identified having greater timber potentiality of 1.23 m^3 per tree at the age of 17 years (Ong *et al.*, 1995; MRB, 2003).

The decrease in the area of forests available for logging, shortage of other non-forest traditional timber species etc., led to the exploitation of the potentials of the easily available plantation timber like rubber wood. The distinct features of rubber wood compared to other alternative timber species are :

i. it is a by-product of rubber plantations

ii. it is inexhaustible in supply as rubber plantations are maintained on a sustained crop rotation of 25-30 years and

iii. its effect on reducing pressure on tropical forests enabling bio-diversity conservation, and the reported agronomic sustainability and carbon sequestering effect (George and Joseph, 1993; 2002; George, 2002).

Since rubber is grown as renewable plantations, the eco-friendly nature has become an advantage in promoting rubber wood products in major developed countries, where the "Green movement" is very strong. This led to the enhancement of rubber wood utilization and replacement of other non-renewable forest timber species to a great extent. The total production of rubber wood is sufficient to meet the global timber requirement to a certain extent. Good quality rubber wood products in the form of furniture, furniture components, treated and processed wood are being exported from major rubber growing countries, particularly from Malaysia to the developed countries like Japan, USA, UK etc.

1.2 Availability of rubber wood

Natural rubber cultivation assumes high socio-economic relevance in terms of the geographical concentration of area (87%) and production (78%) in Malaysia, Thailand, Indonesia, India and China (Viswanathan *et al.*, 2003). In India the current estimated average production of rubber wood per hectare is 150 and 180 m^3 in small holding and estate sector, respectively (George and Joseph, 2002). It has been estimated that 11 million m^3 of rubber wood logs are available worldwide annually (ITC, 1993). The current annual requirement of timber in India comes about 40 million m^3 for various industrial applications, whereas the current availability of timber has been estimated to be 29.25 million m^3. In India, the projected availability of rubber wood was 2.1 million m^3 during 2001-02, of which, sawn timber suitable for secondary processing constitutes about 21%. The potential contribution of rubber wood to the timber industry in India is around 2%. Moreover, rubber wood in India has the potential to conserve more than 20,000 hectares of natural rain forests on an annual basis (George and Joseph, 2002).

1.3 Commercial utilization of rubber wood

The current annual rate of industrial utilization of rubber wood comes about five million m^3, of which, Malaysia accounts for two million cubic meters, followed by

Thailand (one million m^3) and the rest was utilized by Indonesia, China, India etc. (Viswanathan *et al.*, 2003). In both these countries, rubber wood has become an important raw material for various wood-based industries. The industrial utilization of rubber wood in Malaysia is very efficient due to the adoption of modern technology and better management practices.

1.3.1 The Indian scenario

In India the industrial use of rubber wood was started only during 1950s when there was a shortage of species like *Mangifera indica* , *Polyalthia longifolia, Ailanthus malabaricus* etc., which were particularly used in match box and packing case industries. India's import of wood and wood products has increased from Rs.15720 million during 1997-98 to Rs. 19943.3 million during 1999-2000. Import of rough wood occupies major share (93%) in the total value of imports (DGCIS, 1998; 2000)

The major portion of rubber wood produced annually in India is not being utilized properly to meet the indigenous timber requirements. The current consumption pattern of rubber wood in India is dominated by packing case sector (56.5%), followed by plywood industry (26.5%). The secondary processing sector of rubber wood consumes only 14 per cent of the stem wood produced (George and Joseph, 2002). As compared to Malaysia and Thailand, in India the narrow range of product manufacture increases the recovery loss of rubber wood particularly in the field of value addition. The major factors which retards the development of rubber wood processing industry in India were identified as (i) absence of a statutory agency to monitor and promote the industry; (ii) absence of vertical integration; (iii) lower levels of capacity utilization and value addition; (iv) shrinking - supply of quality timber; (v) predominance of intermediaries and the resultant higher raw material procurement cost; (vi) working capital shortage; and (vii) market access issues (Viswanathan *et al.*, 2003).

1.4 Demerits of rubber wood

Rubber wood is a perishable timber and highly susceptible to biological deterioration. The high deposition of carbohydrates mainly in the form of soluble sugars and starch in the wood tissue makes rubber wood susceptible to fungal and insects attack soon after felling. This biological defect affecting the durability of rubber wood can be properly controlled by adopting appropriate preservative treatments.

Tension wood formation is the most serious natural defect adversely affecting the quality of rubber wood for specific end uses. It is a structural abnormality in wood formed by the development of unlignified or partially lignified specialized fibres called gelatinous fibres or G-fibres. The proportion of tension wood in *Hevea brasiliensis* may vary from tree to tree, and within the same tree, along the trunk and branches. The occurrence of tension wood restricts the versatile utilization of rubber wood for various applications. The structure, quantity and distribution of tension wood fibres reduce the physical, mechanical and strength properties of rubber wood to a great extent.

Hence to evaluate rubber tree as a potential source of timber for various end uses, the extent of tension wood formation and clonal variability has to be taken into account. As the impact of tension wood on various applications of rubber wood is unpredictable, a better understanding on the structural modifications taking place during tension wood formation as well as the causative factors responsible for tension wood formation in *Hevea brasiliensis* assumes significance. This would ultimately result in enhanced utilization of rubber wood by eliminating and / or minimizing the major demerits caused by tension wood, thus facilitating further value addition of rubber wood.

1.5 Relevance of the present study

With the rapid industrialization during the 21st century, the fragile earth is put to tremendous environmental pressure. In this context, protection of natural forest has become a necessity. In the name of conserving forest we can not substitute timber with any other materials. The best and eco-friendly alternative source of timber in place of the depleting natural timber resources is rubber plantations. But substituting rubber wood in place of the depleting quality timber resources necessitate improvement of its quality and durability. It has already been proved that the biological deterioration of rubber wood can be prevented by adopting appropriate wood preservations technologies. However, considerable attempts have not been made so far to ascertain the extent and mechanism of tension wood formation in *Hevea brasiliensis* and to control its negative impact in wood based industries.

In this context a detailed investigation on the formation and structure of tension wood in *Hevea brasiliensis* with special emphasis on clonal variability has been carried out. To understand the mechanism of tension wood formation in *Hevea*, various experiments were also conducted in the juvenile growth phase. The present investigation was carried out with the following objectives :

1. Extent of tension wood formation in *Hevea brasiliensis* with special emphasis on clonal variability.
2. Distribution pattern and directional effect of tension wood formation in rubber
3. Extent of tension wood formation in bud grafted plants and tissue culture plants

4. Tension wood formation and wind damage.
5. Distribution of tension wood in tapped and untapped zones.
6. Structural studies on tension wood.
7. Histochemical studies on tension wood
8. Identification and demarcation of tension wood zones in rubber wood through macroscopic staining.
9. Factors affecting tension wood formation in *Hevea brasiliensis*.

CHAPTER 2

REVIEW OF LITERATURE

2.1 Structural features of rubber wood

2.1.1 Gross structure

Rubber wood shows the general structure of hardwood with certain characteristic specific to the species. Bosshard (1966) classified rubber wood as light hardwood based on its density. Basic density and density of rubber wood at 12% moisture content vary even in mature trees of the same age and from same plantations . It may vary from 435 to 626 kg/m^3 (Bhat *et al.*, 1984) and this variation could be due to genetic or clonal differences.

The wood is diffuse porous, straight to slightly interlocked grained and medium course textured with a characteristic odor of rubber latex when freshly cut. Freshly sawn wood (green wood) is whitish yellow in colour and turns pale cream after drying. Growth rings are absent or ill-defined and the concentric marks which resemble growth rings in the cross sectional view are false rings formed by the distribution pattern of **tension wood** in association with banded apotracheal axial parenchyma (Reghu, 2002). The concentric rings combined with the large vessel elements give the timber an attractive appearance with clear figure on the longitudinal surface of the wood. Heartwood formation is virtually absent in rubber tree unlike in other durable hardwood species . Though reserve metabolites in the form of soluble sugars, starch etc. are abundant in the storage (parenchymatous) tissues, the conversion of these materials into pigmented extraneous heartwood substances does not takes place in rubber tree during the course of its short economic life span. Early and late wood differentiation is not possible in rubber wood even though significant seasonal growth variation has been reported. The long and continuous period of cambial activity associated with the fast growing nature of rubber trees restricts the formation of early and late wood (Reghu, 2002).

2.1.2 Anatomy of rubber wood

Rubber wood is composed of fibres (58%), vessel elements (8.5%), axial parenchyma (11.5%), and rays (22%) and are distributed in different patterns and proportions as in other typical hard wood species. Bhat *et al.* (1984) quantified the proportion of wood elements in rubber wood and concluded that the proportion of wood fibres is moderate in comparison to other fast growing timber species like *Gmelina arborea* and *Eucalyptus* species.

Fibers are non-septate, and belong to the medium group with a length of 0.8 – 1.8 mm (Anonymous, 1956; Bhat *et al.*, 1984; Reghu *et al*, 1989a). The width of fibres ranges from 19 – 27μm. (Silva, 1970; Reghu *et al.*, 1989a)

Vessel elements (pores) are evenly distributed as solitary or radial multiples of 2 - 4 or rarely more, with 3 - 5 pores per mm^2. The pores are moderately large to small and visible to the naked eye. The vessel lines are clearly visible in the longitudinal plane and are 154-798 μm. in length with a diameter ranging from 70-224 μm.. The lumen of the vessels are usually filled with tyloses (Reghu, 2002).

Axial and ray parenchyma are considered as soft tissues in rubber wood with the main function of storing the reserve metabolites. Axial parenchyma is appotracheal and banded with undulating lines. Scanty paratracheal parenchyma are also found in association with vessel elements. The high proportion of soft tissue (33%) comprising axial and ray parenchyma reflects the light hardwood nature of rubber wood.

Rays are heterogeneous, uni to penta-seriate. Both axial and ray cells have crystal deposits. Moreover unlike in other durable hardwood species the soft tissue in rubber wood are almost filled with reserve metabolites, especially in the form of soluble sugar and starch with out any protective quality. Hence rubber wood is highly susceptible to the attack of biological organisms leading to deterioration under natural conditions (Reghu, 2002). However, studies on the physical and mechanical properties of rubber wood conducted earlier proved that it could be efficiently used for a variety of items such as furniture, door and window shutters, packing cases, tool handles etc. (Kamala and Rao, 1993).

2.2 Major demerits of rubber wood

2.2.1 Susceptibility to biological deterioration

Rubber wood does not have any natural resistance to any biological organisms like fungi, insects and marine borers. It is highly perishable and does not contain phenolic compounds as extractives, an essential component to impart natural durability. Even though rubber wood has many desirable properties for different end uses, its commercial potentialities are limited unless it is properly impregnated with preservative chemicals to protect from biological deterioration (Gnanaharan, 2002). Various short term and long terms wood preservation techniques such as impregnation of preservatives through pressure and non-pressure methods are now widely adopted to protect rubber wood from biological deterioration. Extensive work has been done in the field of rubber wood preservation in India and abroad (Hong *et al.*, 1980; Gnanaharan and Mathew, 1982; Gnanaharan, 1983; Tam and Singh, 1987; Gnanaharan and Damodaran, 1993; Gnanaharan, 1996; Jose *et al.*, 1989; Hong and Liew, 1989; Janatan *et al.*, 1994; Kadarkutty, 1989).

2.2.2. Tension wood – a natural defect

Tension wood formation is a major natural defect in various hardwood species especially in *Hevea brasiliensis* resulting into various structural abnormalities. The degree of modification of wood structure associated with tension wood formation is extremely variable within and between tree species (Neccessany, 1958). The presence of tension wood influences and affects the chemico-physico-mechanical properties of wood which in turn affects the end use (Vijendra Rao and Hemavathi, 1990).

When a tree is brought out of its natural equilibrium state, in terms of space, it produces a special type of wood called **reaction wood** which restore the bent axes to its original position (Wardrop and Dadswell, 1948; Scurfield and Wardrop, 1963; Wardrop and Davis, 1964; Wardrop, 1964, Westing, 1968; Philipson *et al.*, 1971). Reaction wood in angiosperms, usually formed in the upper side of the leaning axes, is termed as **tension wood** and those formed in the lower side of gymnosperms is called **compression wood** (Wardrop and Dadswell, 1948; Scurfield and Wardrop, 1963; Wardrop and Davies, 1964; Wardrop, 1964; Westing, 1968, Philipson *et al.*, 1971). Tension wood formation has also been reported in upright trunk and branches of different species (Kaeiser, 1955; Wardrop, 1956; 1964; Hughes, 1965; Scurfield, 1973; Brown, 1974; Trenard and Gueneau, 1975; Cote, 1977; Fahn, 1982 and Reghu, 1983). It has also been reported that tension wood formation has an active part in normal architectural development of trees (Fisher and

Stevenson, 1981) and its formation has been related to the mechanism that allow the tree to respond with the environment where it grows (Jourez, 1997).

Tension wood has been classified into **compact tension** wood and **diffuse tension wood** based on its distribution pattern within the tree. In the former type, tension wood fibres are concentrated in a particular zone of the tree axis, in the form of compact arcs or bands, whereas in the latter type the fibres are scattered as discrete groups among the normal wood fibres (Reghu, 2002). The compact arcs of tension wood is clearly visible as white 'wooly' lustrous zone and diffuse tension wood could be identified only with the aid of microscope after specific staining reactions.

2.3 Structure of tension wood fibres

Structurally tension wood differs from normal wood in a number of ways and most of these differences are mainly associated with the structure and chemical composition of wood fibres. Generally tension wood fibres are designated as **gelatinous fibre or G-fibres**. Certain layers of the secondary wall of these fibres are unlignified or partially lignified and composed of crystalline cellulosic microfibrils which gives the characteristic gelatinous or sticky nature. The G-layer is variable in thickness, and normally replaces the innermost third layer of the secondary wall (S_3 layer). Nonetheless, it may also replace the secondary S_2 layer or may get incorporated with S_3 layer (Wardrop and Dadswell, 1955; Cote *et al.*, 1969; Scurfield, 1973).

In many tree species tension wood fibres are longer than normal wood fibres (Chow, 1946; Onaka, 1949; Kaeiser and Boyce, 1965). Jourez *et al.* (2001) reported more than 4.5% increase in length of G-fibres than normal wood fibres in poplar. Wardrop

(1964) reported that the G-fibres may be longer or shorter or equal to the length of normal fibres

Several workers have reported that the number and size of vessels are much lesser in tension wood than that of normal wood (Chow, 1946; Onaka, 1949; Kaeiser and Boyce, 1965; Cote *et al.*, 1969, Jourez *et al.*, 2001). However, Kucera and Philipson (1977) did not find any decrease in the frequency and diameter of vessels in tension wood in some primitive dicotyledonous species.

According to Cote and Day (1965) rays are unmodified in tension wood. Variation in morphology, distribution and dimensions of rays have been reported by Kucera and Neccessany (1970), Kucera and Bariska (1972); Kucera and Philipson (1977, 1978) and Rao, *et al.* (1982). In poplar (*Populus euramericana*) Jourez *et al.* (2001) reported a higher number of rays in tension wood than normal wood.

The chemical composition of tension wood and normal wood is complex as the woody tissue is composed of many chemical constituents which are not distributed uniformly. Histochemical investigations helps to obtain some insight into the chemical composition of these tissues (Stevenson, 1975). Jaccard (1938) and Hillis *et al.* (1962) reported the occurrence of reduced starch reserves in tension wood. It has already been proved by various researchers that the lignin content is reduced in tension wood fibres (Marra, 1942; Wardrop and Dadswell, 1948; 1955a; 1955b; Schwerin, 1958; Norberg and Meir, 1966; Timell, 1969; Furuya *et al.*, 1970; Scurfield, 1972 and Cote, 1977). The studies conducted by Scurfield (1972) on the histochemical changes associated with tension wood formation concluded that tension wood fibres are histochemically heterogeneous.

2.4 . Mechanism of tension wood formation

Experimental studies to understand the mechanism of tension wood formation dates back to the beginning of the last century and various theories and hypothesis have been put forth to elucidate the cause/s of tension wood formation and its function in trees. Extensive experiments were conducted to prove mechanical stress as the causative factor responsible for reaction wood formation (Metzger, 1908; Munch, 1938; Sinnot, 1952; Scurfield and Wardrop, 1962). However, Ewart and Mason (1906); Jaccard (1919, 1938); Onaka (1949); Hartmann (1949); and Robards (1965, 1966) opined that gravitational response was the major cause of reaction wood formation in both angiosperms and gymnosperms. Bending experiments conducted by Berlyn, (1961), Argenbright and Bensend, (1968), Fisher, (1978), Tomlinson, (1978) and Fisher and Stevenson (1981) proved that tension wood formation was positively correlated with the angle of leaning from vertical. The review of Boyd (1977) on the mechanism of reaction wood formation suggested that the initial internal stress results in reaction wood formation. According to Wilson and Archer (1977), the change in the equilibrium position of stem and branches effected by gravitational stimulus may be the actual cause of reaction wood formation.

The uneven distribution of auxins in the upper and lower parts of the leaning stems and branches was also reported to be responsible for reaction wood formation (Wershing and Bailey, 1942; Onaka, 1949; Fraser, 1952; Balch, 1952; Wardrop, 1956; Neccessany, 1958; Casperson, 1963; 1965; Cronshaw and Morey, 1965; Kennedy and Farrar, 1965; Morey and Cronshaw, 1968a; 1968b; Smolinski, *et al.*, 1974). Induction and inhibition of tension wood in stem axis through the external application of various growth regulators *viz.* Indol - 3 Acetic Acid (IAA), Gibberlic Acid (GA_3) , 2-3-5 - Tri-Iodo

Benzoic Acid (TIBA) and Morphactins had been experimentally demonstrated earlier (Wardrop, 1956; Kennedy and Farrar, 1965; Smolinki *et al.*, 1974; Casperson, 1963; 1965; Koto, 1956; Reghu, 1983). Application of IAA inhibited tension wood formation (Neccessany, 1958; Casperson, 1963; 1965; Kennedy and Farrar, 1965; Cronshaw and Morey, 1968; Morey and Cronshaw 1966; 1968a; 1968b; 1968c; Robnett and Morey 1973; Reghu, 1983). The lateral application of IAA on erect epicotyls induced tension wood on the side opposite to the side of application (Casperson, 1963; 1965; Blum, 1971). Cronshaw and Morey (1965) and Kennedy and Farrar (1965) induced tension wood by the application of TIBA on the upper half of inclined shoots. GA_3 was reported to have no direct effect on tension wood formation (Blum, 1971). GA_3 and TIBA together induced tension wood formation, whereas the combinations of IAA, GA_3 and TIBA inhibited tension wood formation (Morey and Cronshaw, 1968a; 1968b). Application of morphactin suppressed tension wood formation in hardwoods (Smolinski *et al.*, 1974) and induced compression wood formation in softwoods (Phelps *et al.*, 1977).

Based on the extensive studies on the causative factors responsible for tension wood formation in three hardwood species *viz. Azadirachta indica, Mangifera indica* and *Polyalthia longifolia,* Reghu (1983) concluded that there must be a sequential occurrence of multiple factors leading to tension wood formation in hardwood species.

2.5 Tension wood formation in *Hevea brasiliensis*

Tension wood formation is a common phenomenon in rubber. The distribution pattern, structure and properties of tension wood in rubber wood has been reported by several workers (Bobilioff, 1923; Edgar, 1958; Dijikman, 1951;

Tisseverasinghe, 1970; Panikkar, 1971; Sharma and Kukreti, 1981; Vijendra Rao *et al.*,1983; Lim, 1985; Reghu *et al.*, 1989b; Reghu, 2002).

Panikkar (1971) observed the presence of tension wood in one-year-old seedlings and mature twigs of *Hevea brasiliensis*. Sharma and Kukreti (1981) reported that the proportion of tension wood in *Hevea* may vary in different specimens from the same tree (15 - 65%) or even in different trees. The proportion of tension wood in the rubber tree varies at different height levels within a tree as well as between trees (Vijendra Rao *et al.*, 1983), depending on the influence of environmental factors where it grows. Vijendra Rao *et al.* (1983) made an extensive study on the nature and distribution of tension wood in the rubber wood.

Reghu *et al.* (1989a) studied the proportion of tension wood at different height levels, in the clone PB 86 and observed an increase in the percentage of tension wood from the base to top of the tree trunk. Maximum percentage of tension wood (36%) was recorded at a height of 360 cm while at 60 cm height, the tension wood was the minimum (8–11.5%). In all the height levels the tension wood fibres were significantly shorter and broader than normal wood fibres. Sulaiman and Lim (1992) studied the proportion of tension wood in two clones of *Hevea brasiliensis* (RRIM 600 and PB 260) at different ages and reported 30% to 40% tension wood. Moreover in PB 260, the percentage of tension wood increased with a concomitant increase in tree height whereas in RRIM 600 the trend was just the reverse.

2.6 Tension wood – wood working problems

Tension wood differs from normal wood in many respects especially in its physical, chemical and anatomical properties (Sharma and Kukreti, 1981; Vijendra Rao *et al.*, 1983; Viju *et al.*, 1987; Joseph and Mathew, 1989; Reghu *et al.*, 1989b; Rao and Hemavathi, 1990; Sulaiman and Lim, 1992; Choo and Hasim, 1994). As tension wood is generally weaker than normal wood, its occurrence creates various problems in the utilization of rubber wood for various wood based industries (Panshin *et al.*, 1964; Hughes, 1965). The presence of the unlignified cellulosic G-layer of tension wood fibres makes the wood surface lustrous, wooly and rough causing various wood working and finishing problems (Lim and Sulaiman, 1994; Hughes, 1965). Some of the practical disadvantages of tension wood during primary wood processing, machining and finishing of end products are listed below:

(i) The saws and cutters get blunted and sawing and peeling green wood often produce rough and wooly surface.

(ii) The unlignified G-layer of tension wood fibres tend to be pulled out during cutting and stick to the saw blade preventing the further free movement of the saw (Lim and Sulaiman, 1994; Reghu, 2002).

(iii) As the G-layer is rich in moisture content and lacks lignin, longitudinal shrinkage of tension wood is very severe during seasoning resulting into uncontrollable distortion and warping in the form of tension twisting, spring, bow and cup etc. (Anonyms, 1972).

(iv) Rubber wood is liable to collapse especially where compact tension wood is pronounced (Hughes, 1965).

CHAPTER 3

MATERIALS AND METHODS

3.1 Distribution pattern, proportion and structure of tension wood in mature trees

3.1.1 Materials

Mature trees of four clones of *Hevea brasiliensis* (Willd. ex Adr. de Juss.) Muell. Arg. were selected from the Central Experimental Station of Rubber Research Institute of India at Chethackal, Ranni, Kerala, to study the distribution pattern and structure of tension wood in mature trees. The general features of the clones selected and the age of trees are furnished below : -

Clone	Age of trees (years)	General features
Tjir 1	29	A primary clone of Indonesian origin. Good vigour and heavy crown liable to wind damage.
GT 1	23	A primary clone of Indonesian origin. Upright stem with variable branching habit. Crown is narrow and open with globular shape. (RRIM, 1970 a).
RRIM 600	28	A hybrid clone evolved by the Rubber Research Institute of Malaysia (parentage : Tjir 1 X PB 86). Tall tree with straight trunk, moderately to fairly heavy branching. The crown is narrow and broom shaped (RRIM, 1970 b).
RRII 105	23	A hybrid clone evolved by the Rubber Research Institute of India (parentage - Tjir 1 X Gl 1). Tall trees with straight trunk, good branching and dense canopy (Nair *et al.*, 1975).

3.1.2 Methodology

3.1.2.1 Collection of wood discs

Four trees of each clone, from the experimental field were clear felled. The leaning direction of the trees were recorded prior to felling using inclinometer as per Bhat *et al.* (1981). Wood discs having 7.5 cm thickness were cut from the main trunk at three height levels *viz.* 60 cm , 210 cm and 300 cm, from the ground level, hereafter designated as disc A, disc B and disc C, respectively (Fig. 1a). Wood discs were selected from both tapped and untapped regions of the trees. Disc A of all clones were prepared from the region where normal tapping was done. Disc B of Tjir 1 and RRIM 600 were selected from tapped regions and those of GT 1 and RRII 105 were cut from the untapped region with virgin bark. Disc C of all clones were collected from the untapped region.

From each height level, two wood discs were prepared of which one was used for quantification of tension wood and the other was sampled for structural and histochemical studies.

Immediately after cutting, the surfaces of wood discs used for the quantification of tension wood were sprayed with 0.5% aqueous solution of the fungicide, Sodium Penta- Chloro Phenate (NaPCP) to protect from sap stain (blue stain) fungus infection.

3.1.2.2. Preparation of samples

Cubic blocks of wood having 2 x 2 x 2 cm size were prepared from the disc along the entire diameter excluding pith for structural and histochemical investigations. Ten samples were prepared from the disc, comprising five samples each from both radii. Of the five samples, one sample represented the zone contiguous to the pith and another from the extreme periphery. Three more samples were taken from the zone in between these samples at equal distance. The blocks prepared from one side of the disc were labeled as B1, B2, B3, B4 and B5 from pith to periphery, and the blocks from the corresponding positions in the opposite side were labeled as b1, b2, b3, b4 and b5, respectively (Fig. 1b).

Wood samples thus prepared were fixed in Formalin–Acetic–Alcohol (FAA) for structural and histochemical investigations. Samples fixed in 4% formaldehyde were used for histochemical localization of lipids.

The samples fixed in FAA were subjected to microtomy using Reichert-Jung sledge microtome. Sections at 30 μm thickness were taken at transverse (TS), tangential longitudinal (TLS) and radial longitudinal (RLS) planes and stained with toludine blue 'O' for light microscopy. Measurements were taken using Leitz Aristoplan research microscope attached to Leica Q5000IW Image analysis system.

As the samples from each radius were from identical positions, in terms of growth, the data recorded from the corresponding samples on either side of the disc were pooled together to compute the sample mean as shown below:

Sample 1 – Mean of B1 + b1

Sample 2 – Mean of B2 + b2

Sample 3 – Mean of B3 + b3

Sample 4 – Mean of B4 + b4

Sample 5 – Mean of B5 + b5

The disc mean was computed from the average values of 1st, 2nd, 3rd, 4th and 5th samples. Likewise the tree mean was calculated from the disc mean and the clone mean was computed from the tree mean values.

3.1.2.3 Quantification of tension wood

The cross sectional surface of the wood disc were scanned in the macro-viewer (fitted with JVC 280 k CCD colour video camera) of Leica Q5000IA image analysis system and the image was acquired. The total surface area of the disc and the area occupied by compact tension wood were measured from the acquired image using Leica QWin V.2.1 image analysis software.

3.2. Effect of leaning angle on tension wood formation in mature trees

To study the effect of leaning direction on tension wood formation, parameters such as leaning angle of the trunk, percentage of growth eccentricity of wood disc at different heights and the proportion of tension wood were considered. Growth eccentricity, in terms of percentage pith eccentricity (PPE) was calculated using the formula suggested by Akachuka *et al.* (1997).

$$\text{Percentage pith eccentricity (PPE)} = (D / G) \times 100$$

where

D = Distance between the geometric center and actual position of pith in the wood disc

G = Geometric center of the wood disc (based on the mean radius of the disc)

3.3 Distribution pattern and proportion of tension wood formation in immature plants

Bud grafted poly bag plants of 10 clones were selected to observe the extent of TW formation in the immature growth phase as described below.

Treatments	:	10 clones Tjir 1, Gl 1, GT1, PB 5/51, PB 217, PB 235, RRIM 600, RRIM 623, RRIM 703 & RRII 105
Design	:	Completely Randomized Design (CRD)
Replications	:	4
Plants / plot	:	3
Spacing	:	30 cm X 60 cm
Location	:	Rubber Research Institute of India, Kottayam.

At the age of 10 months, samples were collected from the stem, at 5 cm height from the bud union and fixed in FAA. Microtome sections at cross sectional plane were prepared at 30μm thickness and stained in toludine blue 'O' (O'Brien *et al.*, 1964). The quantification of TW was done using Leica Q5000IA image analysis system attached to Leitz Aristoplan research microscope.

3.4 Tension wood formation in bud grafted and non-bud-grafted (tissue culture) plants

A comparative study on the extent of TW formation between bud- grafted plants (Fig. 2a) and tissue culture plants (Fig. 2b), developed through somatic embryogenesis, of the clone RRII 105 at the age of 8 months, was carried out (Fig. 2 a & b). Wood samples were collected from. 3 cm, 21 cm and 30 cm from the ground and fixed in

FAA. Sections at cross sectional plane were prepared and stained with toludine blue 'O'. The proportion of tension wood in each samples was ascertained through image analysis technique.

3.5 Tension wood formation in tapped and untapped zones of the trunk

To compare the extent of tension wood formation between tapped and untapped regions within trees, the proportion of tension wood in tapped (disc A) and untapped zones (disc C) were recorded and the data was subjected to statistical analysis.

3.6 Tension wood formation and wind damage

Four mature trees of the clone RRII 105, affected by wind damage (trunk snap) were selected from the field trial at CES, Chethackal to study the role of tension wood formation on wind damage. Wood discs were collected from three positions such as lower part of the break (disc A), point of break (disc B) and upper part of the break (disc C). The proportion of tension wood in each positions was quantified from the disc using image analysis system.

3.7. Structural studies on tension wood

3.7..1 Dimension of fibres and vessel elements

Wood tissue prepared from sampled blocks was macerated in Jeffrey's fluid (Berlyn and Mikshsche, 1976), stained with toludine blue 'O' and mounted in 10% glycerin. The length and width of normal wood fibres (NF), tension wood fibres (GF), and vessel elements were measured using Leitz Aristoplan research microscope under bright field. For each parameter, 100 readings per sample were considered for computing the mean values.

3.7.2. Fibre wall thickness

Wood sections at cross sectional plane were used for measuring the fibre wall thickness. The total thickness of primary and secondary walls in both normal and gelatinous fibres were recorded using image analysis system.

3.7.3 Analysis of pores

Wood sections at cross sectional plane were used to determine the parameters such as total number and area occupied by pores per unit C.S. area in both tension wood and normal wood zones. The total number and area occupied by pores per cm^2 cross sectional area of wood were measured as suggested by Reghu (1983). Measurements were taken from 10 microscopic fields at random. The average area of pores was calculated by dividing the total C.S. area of pores per cm^2 with the number of pores per cm^2.

3.7.4. Analysis of rays

The population and dimension of rays in tension wood and normal wood zones were recorded from tangential longitudinal sections of wood using image analysis system. The population of rays was determined by counting the number of rays passing through an unit tangential line (1 mm) in tangential longitudinal sections (Reghu, 1983) The mean height and width of rays were measured at random from 10 microscopic fields per sample.

3.8 Histochemical studies

Histochemical studies were conducted only in the clone RRII 105. The following staining methods and histochemical tests were employed using sledge microtome sections at 30 µm thickness.

1. Starch : Iodine - Potassium Iodide (I_2- KI) (Johanson, 1940)
2. Lipids : Sudan Black B (Gomari, 1952)
3. Cellulose : I_2 - KI - Sulphuric acid (Berlyn and Mikshe, 1976).
4. Total proteins : Mercuric Bromophenol blue (Mazia *et al.*, 1953)
5. Lignin : Phloroglucinol - HCl (Purvis *et al.*, 1964).

3.9 Visual identification of tension wood in rubber wood logs

The macroscopic staining procedure using Zinc – Chloro- Iodide (Grzeskowiak *et al.*, 1996), a combination of Zinc Chloride, Potassium Iodide and Iodine was tried for the visual identification and demarcation of tension wood zones in rubber wood. This macroscopic stain was directly applied on the cut surface of green as well as dried logs and observed the colour specificity for tension wood and normal wood zones.

3.10 Factors affecting tension wood formation

3.10.1 Angle of leaning

To study the effect of angle of leaning on tension wood formation, four month old seedling plants raised in poly bags were used. The plants were bent artificially at three different angles from vertical i.e. 45^0, (Fig. 3 a & b) 90^0 (Fig. 3 c & d) and 135^0 (Fig. 4 a & b) using an inclinometer (Bhat, *et al.*, 1981). After one month, samples were collected from three positions; *viz.* (i) basal portion below the bent, (ii) bent portion, and (iii) the portion above the bent, hereafter referred to as sample A, B and C, respectively. Wood samples collected from seedlings grown vertical were used as control (Fig. 4 c & d).

3.10.2 Angle of leaning with defoliation

To study the effect of defoliation - cum - angle of leaning on tension wood formation, four months old seedling plants grown vertical were defoliated and subjected to artificial bending at 45^0, (Fig. 5a & b) 90^0 (Fig. 5c & d) and 135^0 (Fig. 6a & b). The plants were allowed to grow for one month and samples were collected from three positions *viz.* (i) basal portion below the bent, (ii) bent portion, and (iii) the portion above the bent, hereafter referred to as sample A, B and C, respectively. Defoliated seedlings grown vertical were used as control (Fig. 6c & d). Wood samples collected from respective experiments were fixed in FAA, sectioned and stained with toludine blue O. Observations on total area of wood and the area occupied by tension wood were taken using image analysis system.

3.10.3 Effect of gravity on tension wood formation

Seedlings grown vertical were artificially looped in vertical plane and allowed to grow for one month as shown in Fig. 7a & b. . The looped portion was divided into three sectors such as upper part of the loop (UPL), lower part of the loop (LPL) and lateral part of the loop (LtPL) for analysis. Wood samples were also collected from the basal upright portion of the plant (SBL) for analysis.

Wood samples collected from respective positions were fixed in FAA, sectioned and stained with toludine blue O. Parameters such as total area of wood and the area occupied by tension wood were measured using image analysis system.

3.10.4 Effect of growth regulators on tension wood formation

3.10.4.1 Apical application of IAA, TIBA and GA_3 on artificially bent plants

Vertically grown bud-grafted poly-bag plants of the clone RRII 105 at the age of eight months were used for this study. The shoot apex was removed by cross cutting and the plants were inclined artificially at 90^0 angle. A slit along the vertical axis of the stem, approximately 0.5 cm deep, was made at the terminal cut, and a cover glass was inserted in it. It divided the stem axis into upper half (UH) and lower half (LH) (Fig. 8. a & b). Growth substances such as Indole-3- Acetic acid (IAA), Gibberellic acid (GA_3) and 2,3,5 Triiodobenzoic acid (TIBA) at 500 ppm concentration in lanolin were applied on the upper and lower halves and lanolin alone as control. The treatment schedule is shown below:

Growth substances	Expt.	Position	Applications
IAA	1	UH	IAA - 500 ppm
		LH	Lanolin
	2	UH	Lanolin
		LH	IAA - 500 ppm
GA3	1	UH	GA - 500 ppm
		LH	Lanolin
	2	UH	Lanolin
		LH	GA - 500 ppm
TIBA	1	UH	TIBA - 500 ppm
		LH	Lanolin
	2	UH	Lanolin
		LH	TIBA - 500 ppm
Control		UH	Lanolin
		LH	Lanolin
UH – upper half, LH – lower half			

The growth regulators were applied in every alternate days for a period of one month. After discarding 1 mm cut surface from the extreme tip, the stem axis (applied portion) was collected and fixed in FAA. Microtomes sections were prepared from the fixed samples and stained in toludine blue 'O'. The stained sections were observed under Leitz Aristoplan research microscope.

3.10.4.2. Lateral application of IAA, GA_3 and TIBA on plants grown vertical

Bud-grafted polybag plants of the clone RRII 105, at the age of eight months, were used for this study. External application of growth substances such as IAA, GA3 and TIBA at 500 ppm concentration in lanolin and lanolin alone (as control) was done. The growth regulators were applied on the bark, in the form of a band, covering the entire circumference of the stem (Fig. 8 c & d). The application of growth substances was continued every alternate days for a period of one month. Samples were collected from three zones as follows : (i) Sample A – lower portion of the applied zone (ii) Sample B – portion of the applied zone and (iii) Sample C – upper portion of the applied zone

Samples collected from each experiments were fixed in FAA, sectioned and stained with toludine blue O. Parameters like total area of wood and the area occupied by tension wood were ascertained using image analysis system.

3.10.4.3 Lateral application of IAA on plants grown vertical through incision of bark

The bark of vertically grown shoots was incised on one side and IAA in lanolin at 500 ppm concentration was applied on the incised portion (Fig. 9a & b arrows).

Wood samples were collected from the lower portion of the applied zone (sample A), portion of the applied zone (sample B) and upper portion of the applied zone (sample C) and quantified the tension wood formed.

3.10.4.4 Lateral application of IAA and TIBA on plants under artificial bending

Vertically grown bud-grafted poly bag plants of the clone RRII 105, at the age of 8 months were artificially bent at 45^0 and allowed to grow for one month (Fig. 9c & d). The inclined portion was treated with external application of IAA and TIBA at 500 ppm in lanolin. Samples were collected from three positions, A, B, and C, respectively as shown in Fig. 9c & d.

3.11 Statistical analysis

Analysis of variance (ANOVA) was done to estimate the variation in TW formation at different height levels and between clones in both mature and immature phases. ANOVA was also used to ascertain the variability in characters such as length and width of fibres and frequency of pores etc. in NW and TW zones with respect to tree height as well as between clones. The data from four clones were considered together to ascertain the variation between different height levels. Paired t-test was done to compare the characters in normal and tension wood zones. In rest of the cases, population mean was considered for comparison.

3.11 Photography

Photomicrographs (for structural and histochemical studies) and photo macrographs (for experimental studies) were taken in Leitz Aristoplan Research microscope and Wild M8 stereo zoom microscope, respectively attached to Wild MPS 46 Photo Automat. Kodak Gold 35 mm colour film was used for photography.

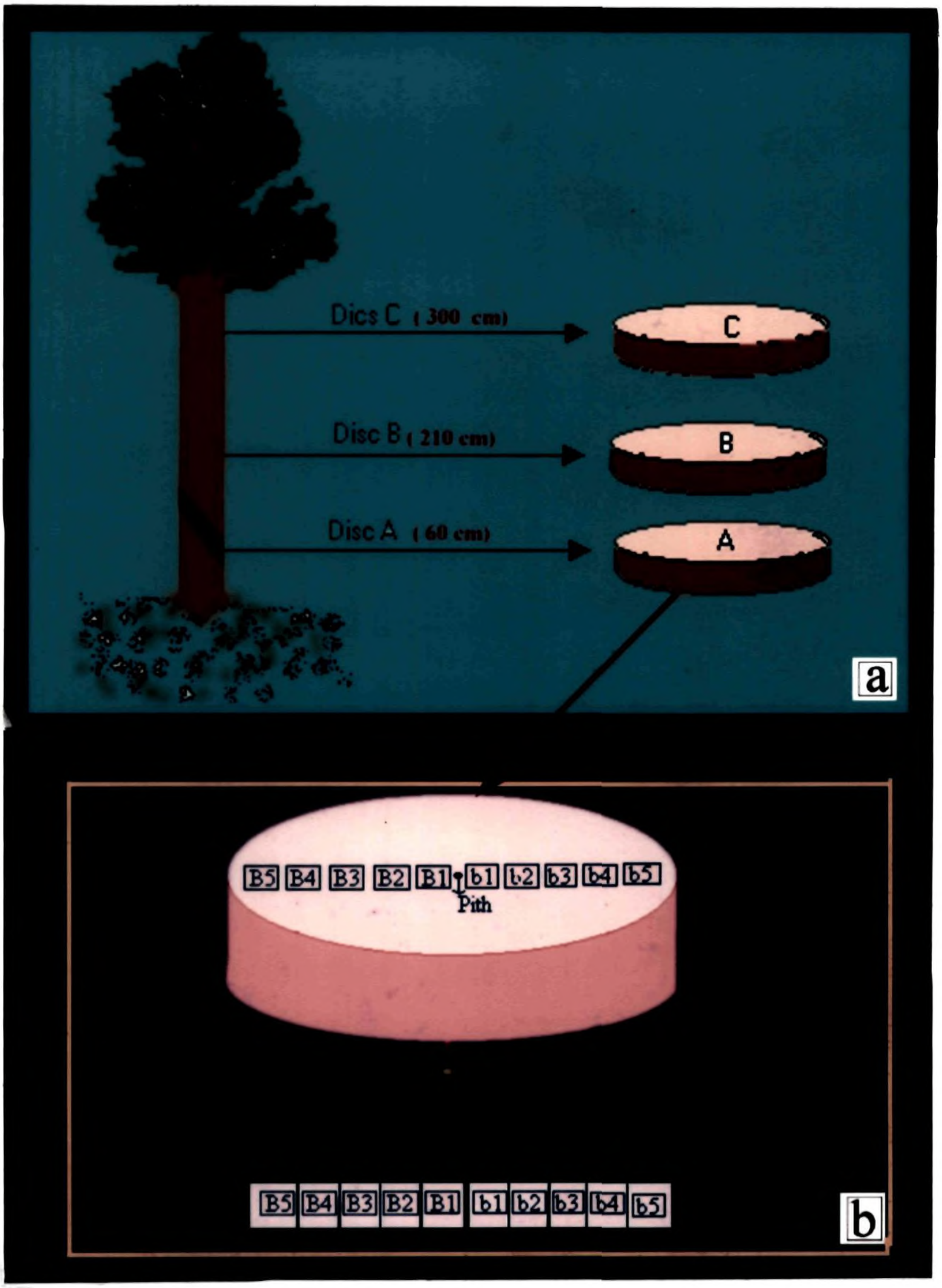


Fig. 1. Diagrammatic representation of collection of wood discs from tree and preparation of samples

a. collection of wood discs from three height levels;

b. preparation of sample blocks from wood disc

(B1, B2, B3, B4, B5; b1, b2, b3, b4 & b5 - sample blocks from both radii

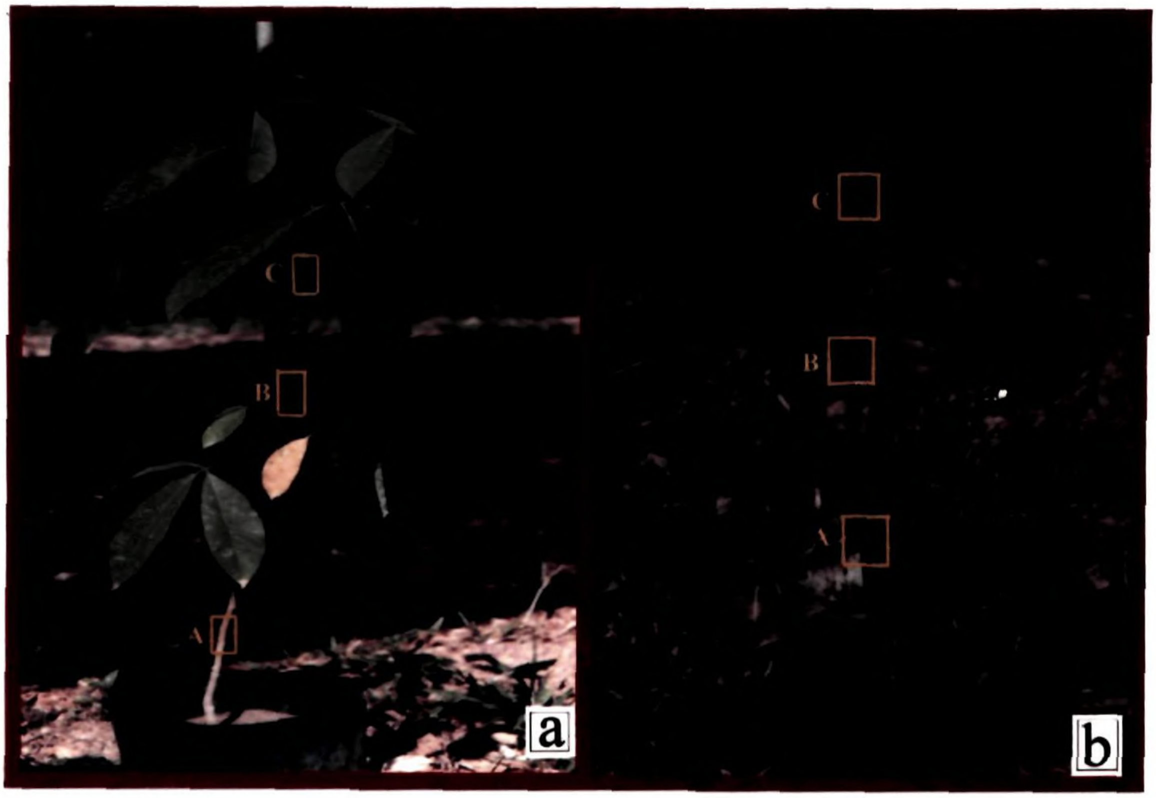


Fig. 2. Tissue culture plant and budgrafted plant at the age of 8 months (Clone RRII 105)
a. tissue culture plant; b. budgrafted plant
(A, B , C - sample positions)

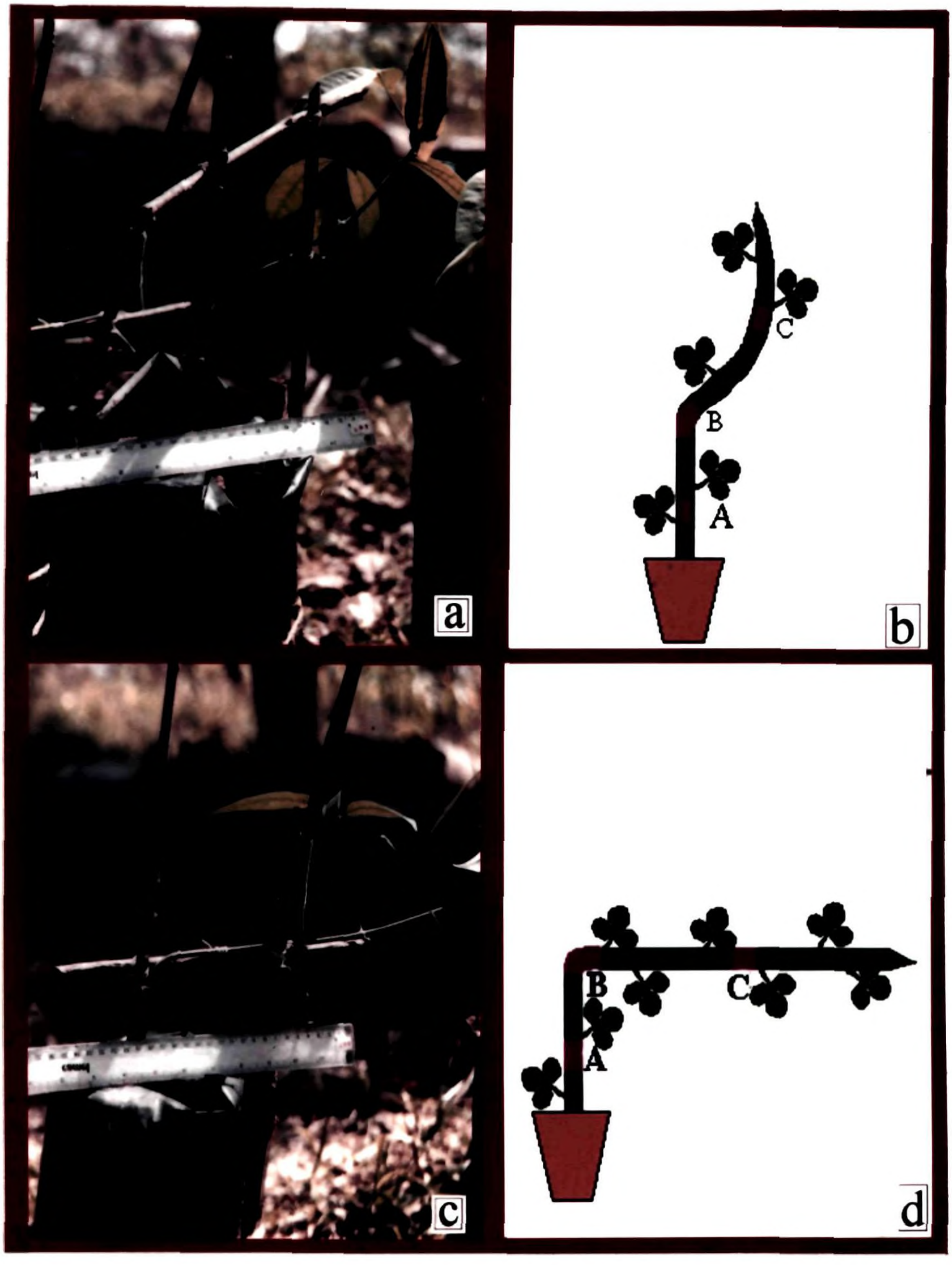


Fig. 3 Angle of leaning : seedlings bent at 45° and 90°
a. seedling bent at 45°; b. diagrammatic representation of sample collection
c. seedling bent at 90°; d. diagrammatic representation of sample collection
(A, B, C - sample positions)

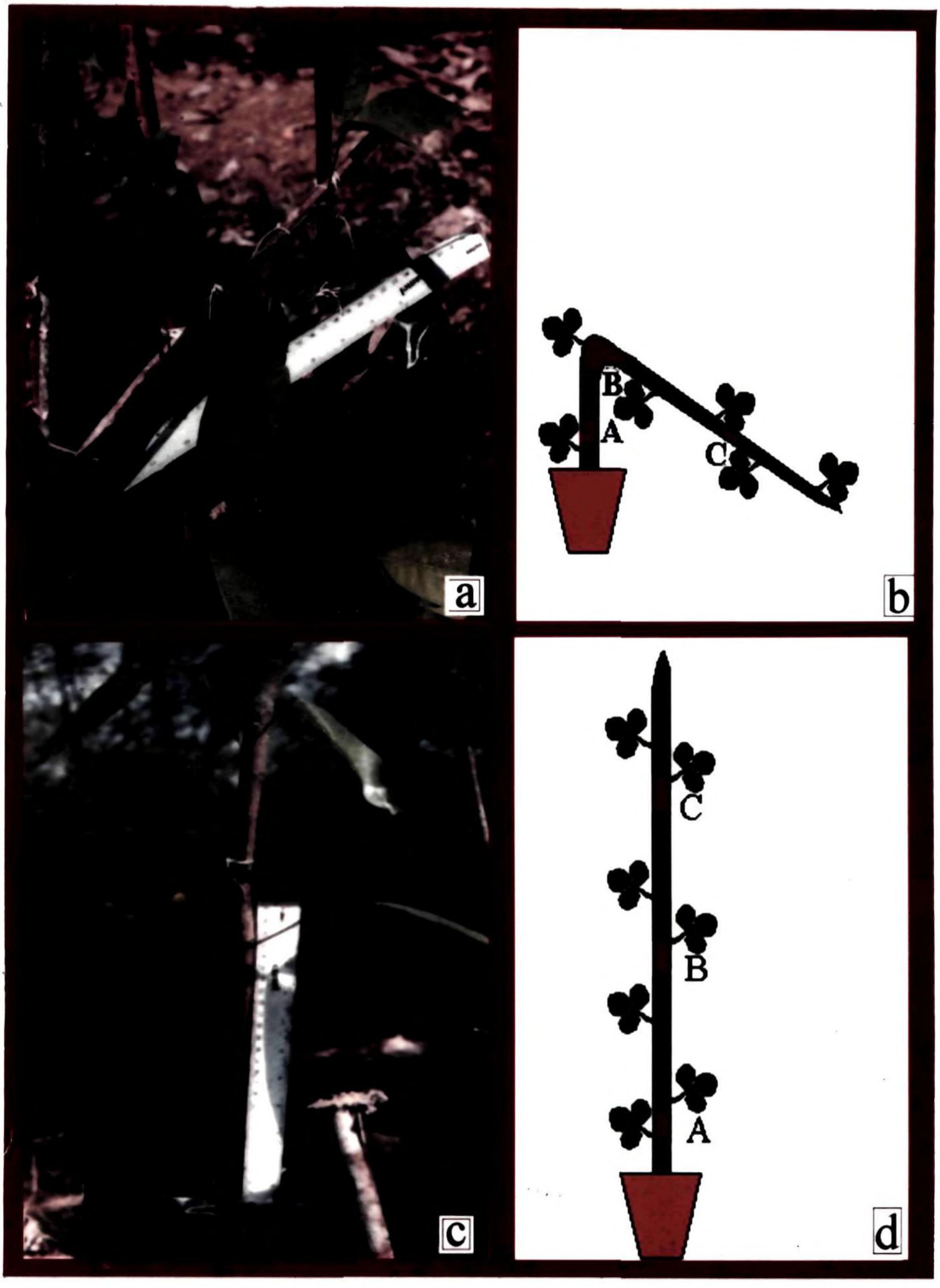


Fig. 4. Angle of leaning : seedlings bent at 135°
a. seedling bent at 135°; b. diagrammatic representation of sample collection
c. seedling grown vertical (control); d. diagrammatic representation of sample collection. (A, B , C - sampling positions)

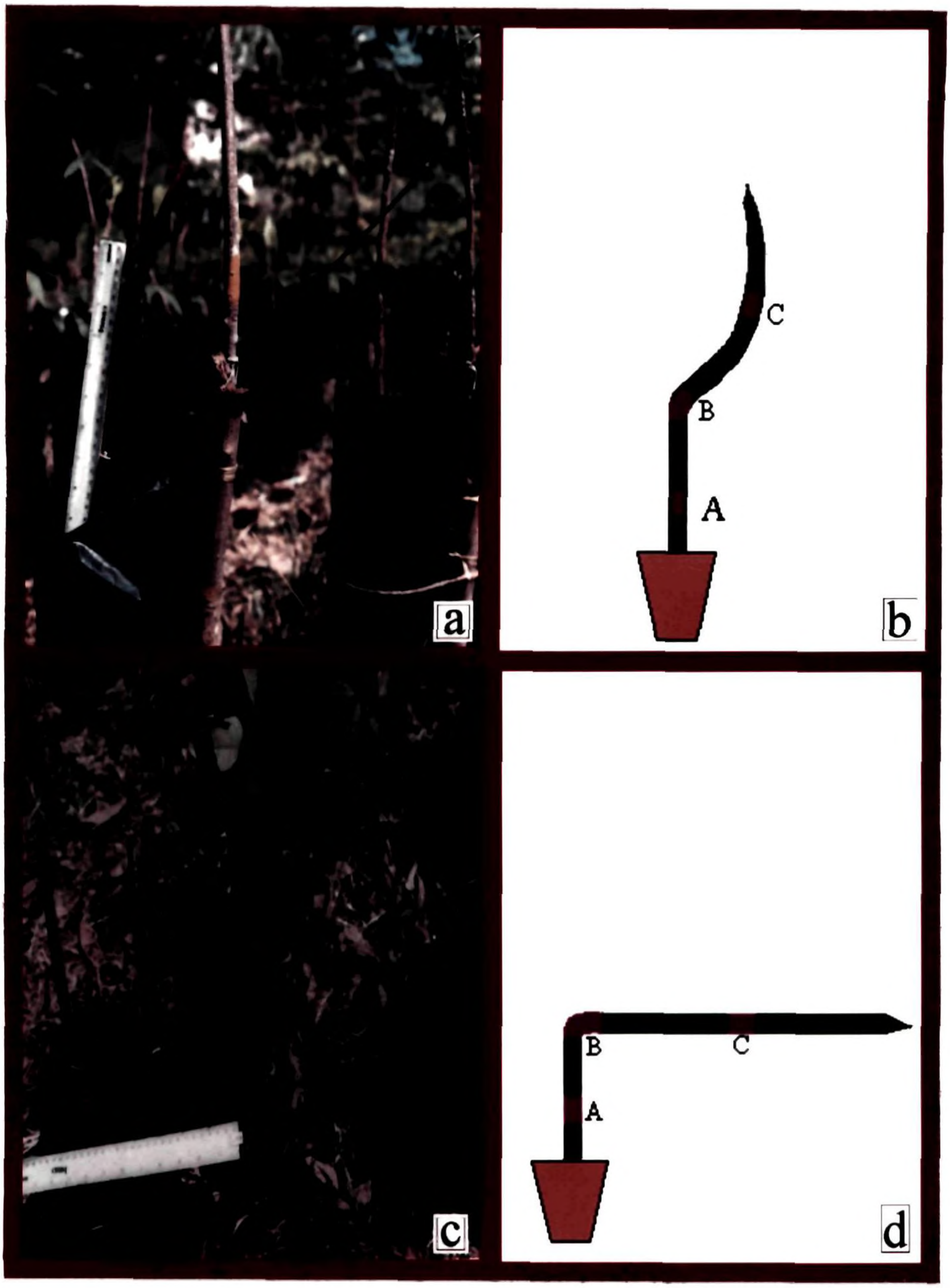


Fig. 5. Angle of leaning with defoliation : defoliated seedlings bent at 45° and 90°
a. seedling bent at 45°; b. diagrammatic representation of sample collection
c. seedling bent at 90°; d. diagrammatic representation of sample collection
(A, B, C - sample positions)

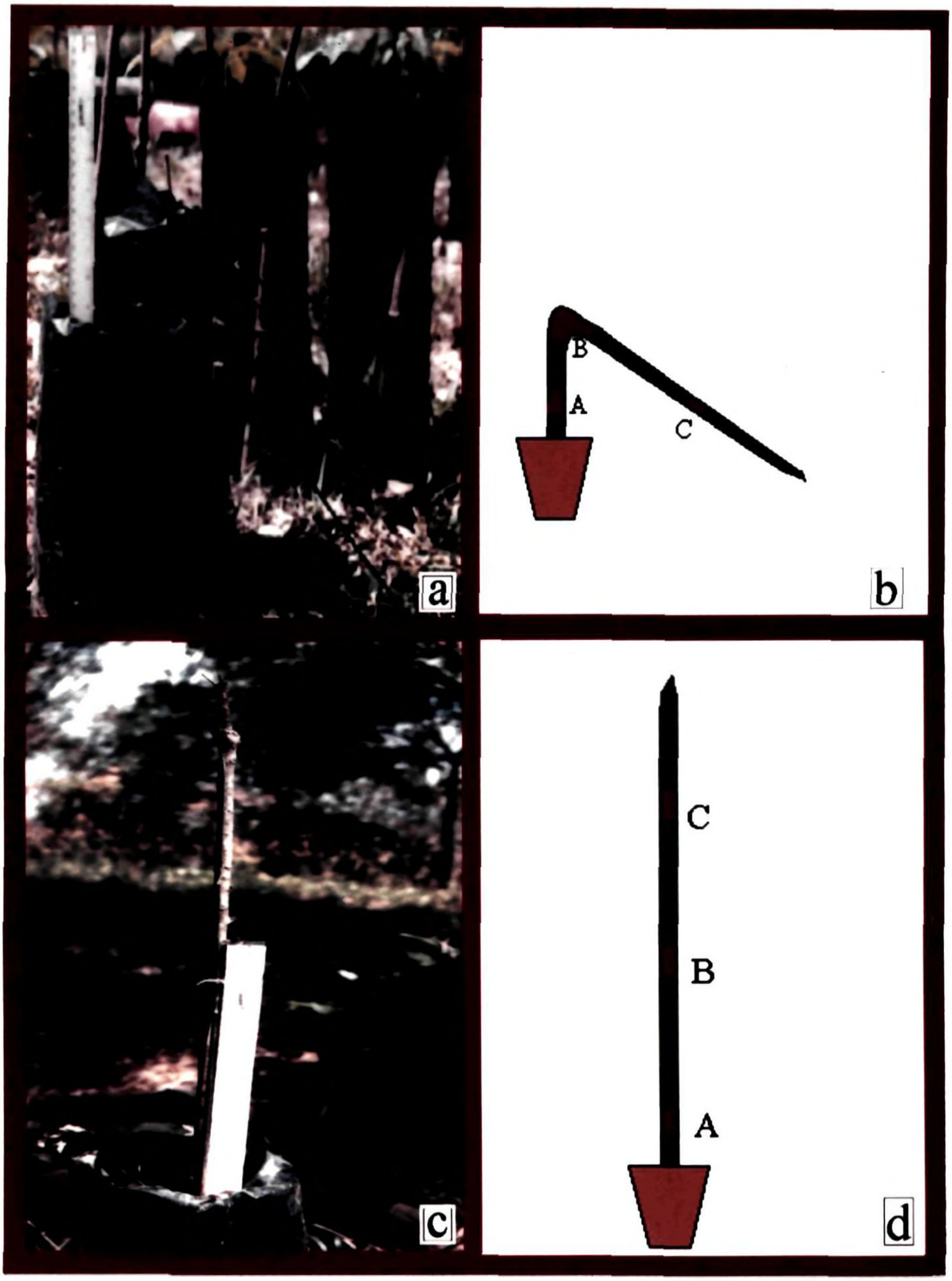
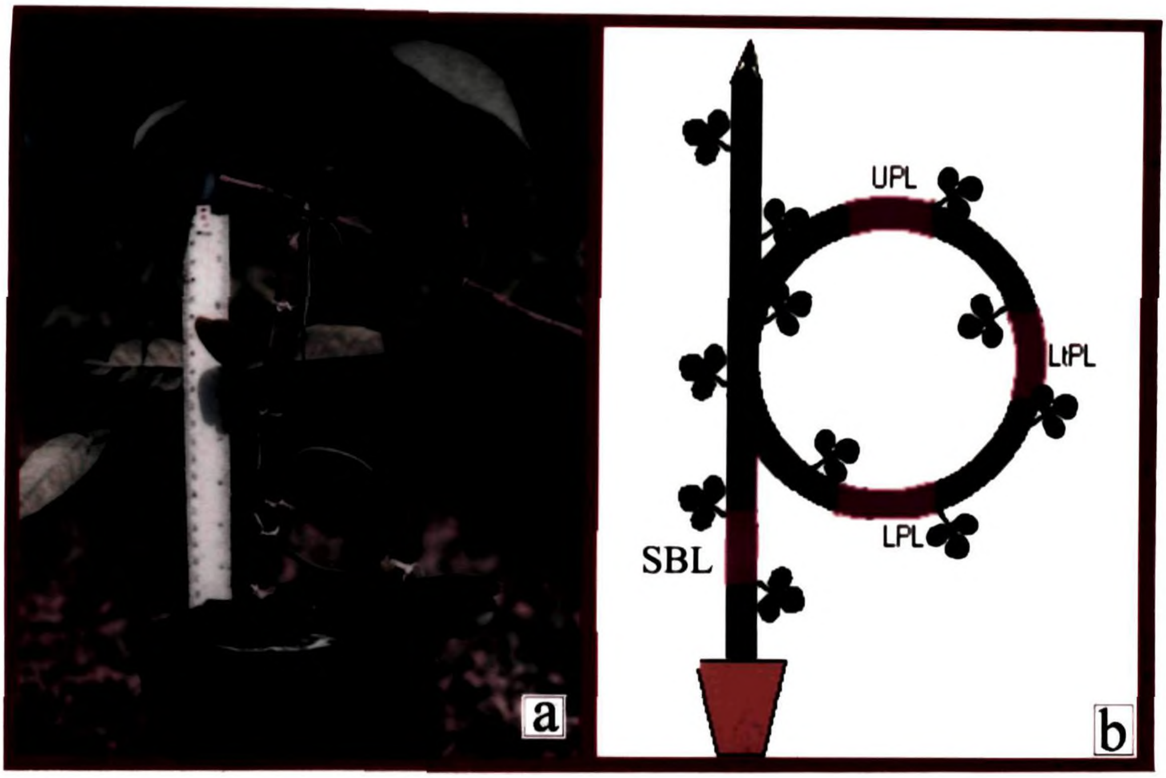


Fig. 6. Angle of leaning with defoliation : defoliated seedling bent at 135° .
a. defoliated seedling bent at 135°; . b. diagrammatic representation of sample collection; c. defoliated seedling grown vertical (control); d. diagrammatic representation of sample collection. (A, B, C - sample positions)



g. 7. Loop Experiment

a. seedling set as loop ; b. diagrammatic representation of sample collection;
UPL.: upper part of the loop; LPL : lower part of the loop;
LtPL : lateral part of the loop; SBL : sample before looping

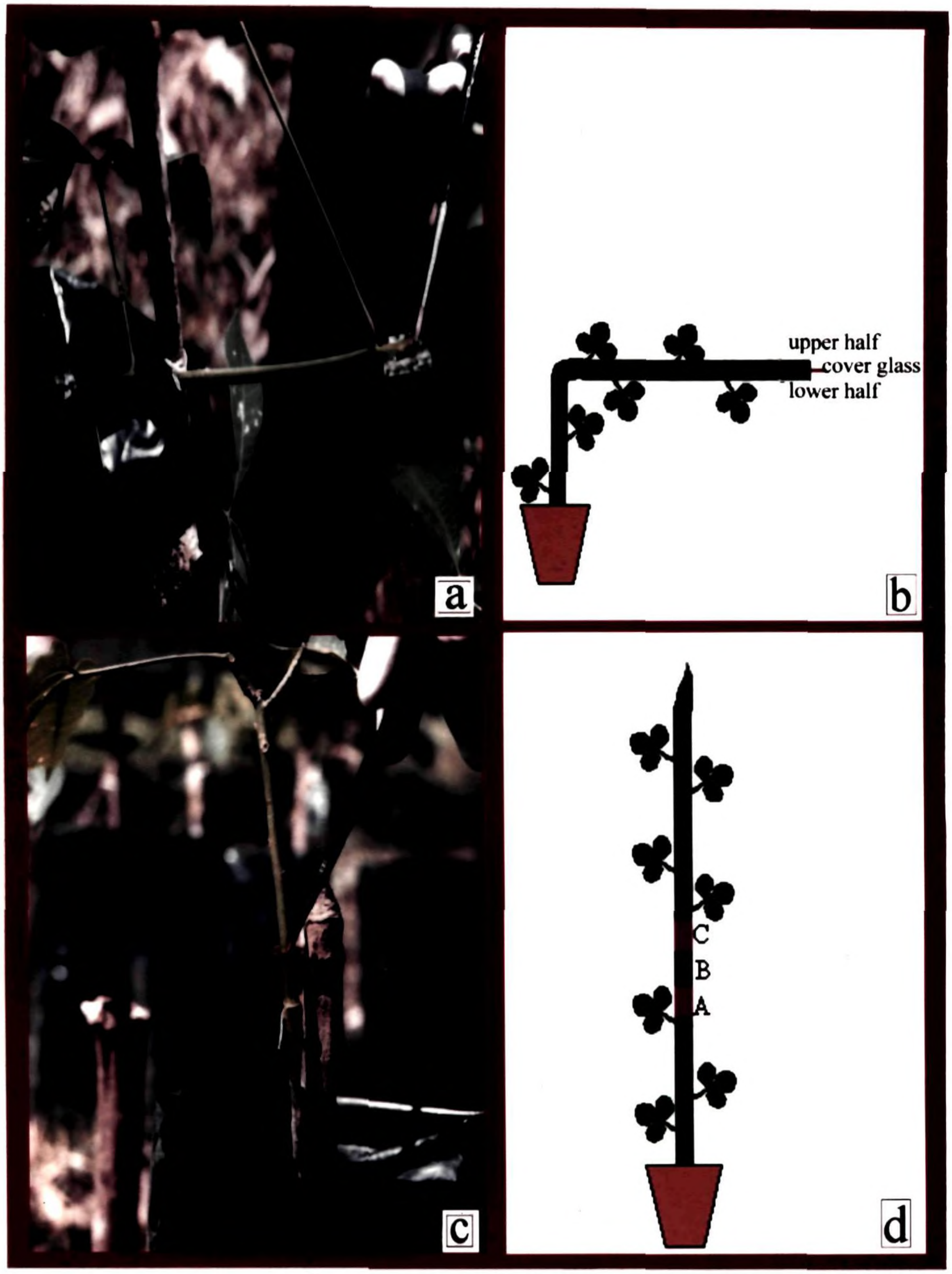


Fig. 8. Method of application of growth regulators on bent and vertically growing plants

a. apical application of IAA, GA_3 and TIBA on decapitated plant bent at 90°;

b. diagrammatic sketch showing method of application

c. lateral application of IAA, GA_3 and TIBA on vertically growing plant;

d. diagrammatic representation of sample collection (A, B, C - sample positions)

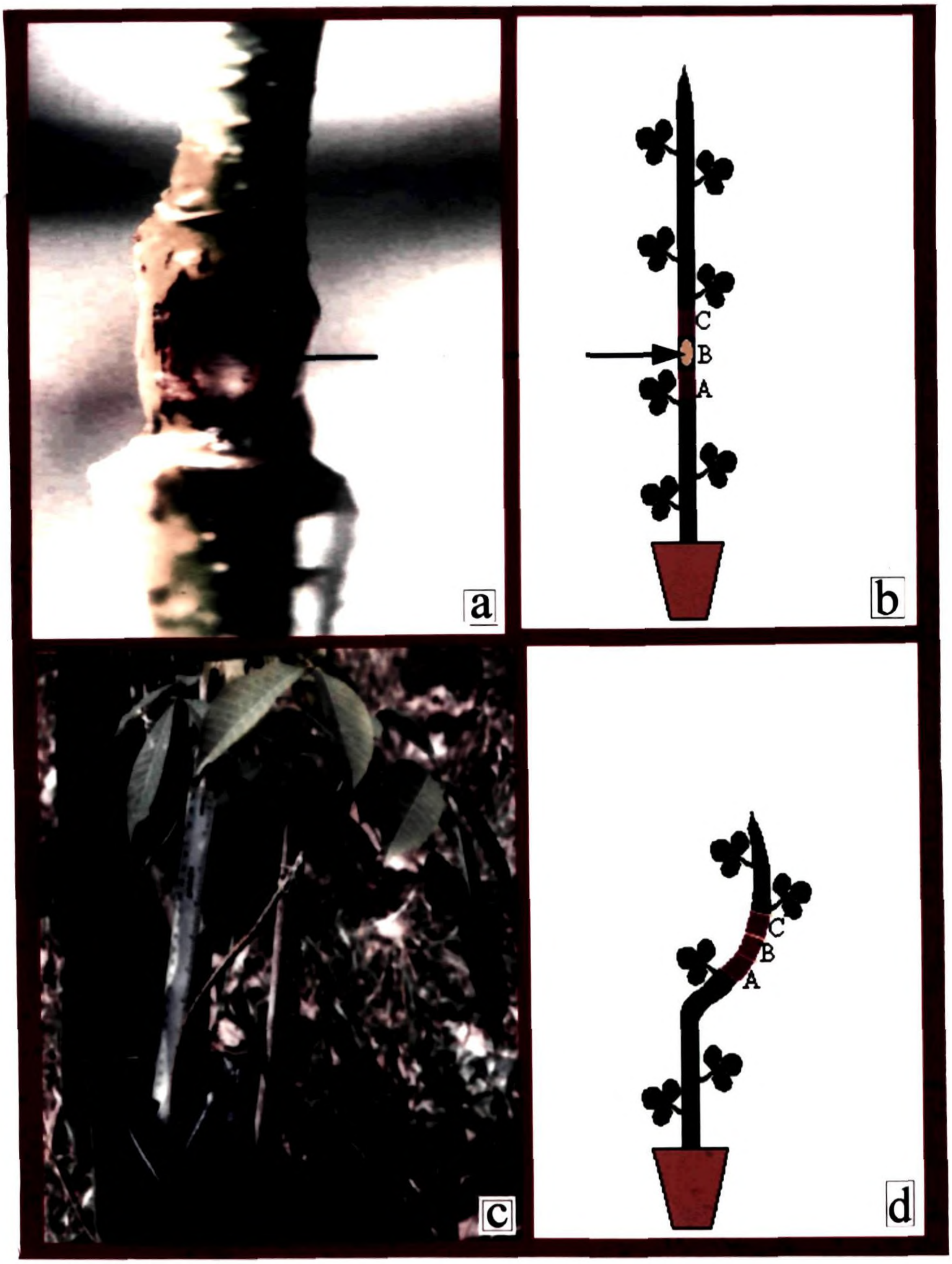


Fig. 9. Method of application of growth regulators on bent and vertically growing plants
a. application of IAA on vertically growing plant through bark incision;
b. diagrammatic representation of sample collection;
c. lateral application of IAA and TIBA on plant bent at 45°; d. diagrammatic representation of sample collection (A, B, C - sample positions)

CHAPTER 4

RESULTS

4.1 Distribution pattern and proportion of tension wood in mature trees

The distribution pattern of tension wood (TW) in *Hevea brasiliensis* varies from tree to tree, clone to clone and even within the same tree along the length of the trunk. In Tjir 1, the compact arcs of TW were visible as silvery lustrous patches in the wood disc at cross sectional plane (Fig. 10a - arrows). Tension wood arcs were mainly concentrated around the pith region and extended further towards the periphery as narrow bands. Microscopic examination revealed that the compact bands (Fig. 12a - arrow) and discrete groups (Fig. 12a - arrow head) of tension wood fibres were densely stained in toludine blue O. Normal fibres were stained deep blue (Fig. 12 b & d) whereas the gelatinous layer of tension wood fibres stained purplish red (Fig. 12c & e) and detached from the adjacent walls forming convoluted mass in the fibre lumen (Fig. 12c - arrows).

In the clone GT 1, TW zones appeared as white 'wooly' lustrous arcs or bands located in the central and peripheral region (Fig. 10b - arrows). The compact arcs of TW were very broad (Fig. 13a - arrow) with well developed G-fibres (Fig. 13 c & e). Discrete groups of G-fibres occur in the matrix of normal fibres (Fig. 13a – arrow heads).

Normal wood fibres (Fig. 13b & d) and tension wood fibres were clearly distinct through differential stainability.

In RRIM 600, broad bands of TW were observed in the peripheral and middle portion of the wood disc, especially in the wider zone of the eccentric disc. (Fig. 11a- arrows). Tension wood bands were closely packed and arranged one above the other separated by banded axial parenchyma (Fig. 14a - arrows). The G-layer of tension wood fibres stained purplish red (Fig. 14c & e) and were always detached from the adjacent walls as convoluted rings (Fig. 14c). Normal wood (NW) fibres stained bluish colour in toludine blue O (Fig. 14 b & d).

In RRII 105, the TW bands were narrow and concentrated mainly in the periphery and pith regions (Fig. 11b - arrows). Unlike in other three clones, the white wooly lustrous nature of TW was less prominent in RRII 105. Both compact and diffuse type of TW showed intense stainability differentiating normal and tension wood fibres (Fig. 15a - arrows). The walls of normal wood fibre stained deep blue (Fig. 15b & d) and the G-layer of TW fibres were stained purple red (Fig. 15c & e) with total or partial detachment from the adjacent walls (Fig. 15c).

In all the clones studied, the percentage of TW showed a gradual increase from base to top of the tree trunk except in GT 1, where it was maximum in Disc B (Fig 16a).

In comparison between clones, the proportion of TW (clone average) was maximum in RRII 105 (28.31%) followed by RRIM 600 (26.49%) and Tjir 1 (18.79%) and the minimum value (16.75%) was observed in GT 1 (Fig. 16b). Analysis of variance (Table 1) indicated that the clonal difference irrespective of height levels was not statistically significant. The difference in the proportion of TW at different height levels for the clones Tjir 1, GT 1 and RRII 105 was not statistically significant but in RRIM 600 it was significant at 5% level.

Table 1. ANOVA for proportion of tension wood in mature trees of four clones

Character	Clones	Source	MS	df	SS	F
Variation between height levels within clones	Tjir 1	Treatment	105.88	2	52.94	0.61 NS
		Error	774.46	9	85.82	
	GT 1	Treatment	264.26	2	132.13	2.64 NS
		Error	449.36	9	49	
	RRIM 600	Treatment	516.67	2	258.33	7.53 *
		Error	308.53	9	34.28	
	RRII 105	Treatment	129.13	2	64.56	0.84 NS
		Error	690.67	9	76.74	
Variation between clones (irrespective of height levels)		Treatment	385.78	3	128.59	3.37 NS
		Error	457.15	12	38.09	

* significant at 5 % level, NS : non-significant

4.2 Distribution pattern and proportion of tension wood in immature plants

Bud grafted poly bag plants of 10 clones at the age of 10 months were used to observe the distribution pattern and proportion of tension wood in the immature growth phase.

In Tjir 1, compact TW was formed in the form of a peripheral band with well developed G-fibres (Fig. 17a – arrows). G-fibres were also distributed among the normal fibres. Broad bands of compact TW were observed in the clone RRIM 703 (Fig. 17b - arrows). In PB 5/51, TW was formed as a continuous ring encircling the pith as well as in the periphery (Fig, 17e - arrows). Discrete groups of G-fibres were also distributed among the normal fibres (Fig. 17c - arrow head). Tension wood fibres were distributed uniformly in all the wood zones of RRIM 623 with feeble stainability (Fig. 17d - arrows). In the case of remaining clones such as GT 1 (Fig. 18a - arrows), RRIM 600 (Fig. 18b - arrows), PB 217 (Fig. 18c - arrows), PB 235 (Fig. 19d - arrows), RRII 105, (Fig. 19a -

arrows) and Gl 1 (Fig. 19b - arrows) tension wood were formed as compact arcs surrounding the pith and periphery.

The proportion of TW in the immature growth phase of 10 clones are given in Table 2. The formation of TW was maximum in Tjir 1 (49.97%) and minimum in Gl 1 (14.32%). In RRII 105, the percentage of TW was 18.28%. Analysis of variance (Table 3) indicated highly significant clonal variability.

Table 2. Proportion of tension wood in the immature plants of ten clones

Clone	Proportion of TW (%)
Tjir 1	49.97
RRIM 703	37.59
PB 5/51	34.91
RRIM 623	34.71
GT 1	30.28
RRIM 600	28.98
PB 217	25.14
PB 235	18.82
RRII 105	18.28
Gl 1	14.32

Table 3. ANOVA for proportion of tension wood in the immature plants

Source	SS	df	MS	F
Treatment	3657.98	9	406.44	3.95 * *
Error	3079.84	30	102.66	
Total	6737.83	39		

* * significant at 1 % level

4.3 Tension wood formation in bud-grafted and non bud-grafted (tissue culture) plants

The extent of TW formation in bud grafted plants and tissue culture plants of the clone RRII 105, of the same age was observed. In general, the proportion of TW was maximum in the basal portion and minimum in the upper portion of both bud-grafted and tissue culture plants. The proportion of TW was higher in tissue culture plants irrespective of sample positions. In the case of bud-grafted plants, the proportion of TW at different height levels ranged from 0.14 – 37.81% with the mean value of 12.75%, whereas tissue culture plants had wider range of 7.33 – 46.98% with the mean value 27.49% (Table 4).

Table 4. Proportion of tension wood in budgrafted and tissue culture plants

Sample position	Proportion of TW (%)			
	Bud-grafted plants		Tissue culture plants	
	Sample mean	Plant average	Sample mean	Plant average
A	37.81	**12.75**	46.98	**27.49**
B	0.14		28.46	
C	0.32		7.33	

4.4 Effect of leaning angle on tension wood formation in mature trees

The leaning angle of the trees from vertical and the rate of growth eccentricity in wood disc were considered to understand the directional effect of tree leaning on TW formation. The leaning angle, growth eccentricity and percentage of TW in four clones at three height positions are given in Table 5.

Table 5. Angle of leaning , pith eccentricity and proportion of tension wood in mature trees

Clone	Disc	Leaning angle (^{0} from vertical)	Growth eccentricity (%)	Proportion of TW (%)
Tjir 1	A	4	11.70	15.76
	B	12.25	24.77	17.79
	C	20	22.03	22.82
	Clone Average	12.08	19.50	18.79
GT 1	A	5.25	14.65	11.69
	B	14.25	13.56	23.18
	C	22.25	32.12	17.63
	Clone Average	13.92	20.11	16.75
RRIM 600	A	6	28.59	17.30
	B	15.75	17.34	29.99
	C	26	18.32	32.19
	Clone Average	15.92	21.42	26.49
RRII 105	A	5.75	10.20	24.31
	B	18	24.96	28.28
	C	25.5	14.54	32.35
	Clone Average	16.42	16.57	28.31

In all the clones studied, the leaning angle was lower in disc A and higher in disc C indicating that the angle of inclination of tree trunk increased from base to top. The average leaning angle from vertical was maximum in clone RRII 105 (16.42^0) and minimum for Tjir 1 (12.08^0). For clone GT 1 and RRIM 600, it was 13.92^0 and 15.92^0 respectively.

The percentage of growth eccentricity did not show any consistent pattern with respect to tree height. In Tjir 1 and RRII 105 the percentage of growth eccentricity was higher in disc B and lower in disc A. In GT 1, it was higher in disc C and lower in disc A. In the case of RRIM 600, disc A showed maximum growth eccentricity and minimum in disc B.

Proportion of TW was maximum in RRII 105 (28.31%) and minimum in GT 1 (17.50). For RRIM 600 and Tjir 1 it was 26.50% and 18.79%, respectively. In RRII 105, both the leaning angle and proportion of TW was highest.

Table 6 showed the correlation between angle of leaning, growth eccentricity and proportion of TW. The correlation between tree height and angle of leaning was highly significant in all the clones. Tree height and proportion of TW showed a highly significant correlation coefficient in RRIM 600. Angle of leaning and growth eccentricity was significantly correlated in GT 1.

Table 6. Correlation between tree height, angle of leaning, pith eccentricity and proportion of tension wood in mature trees

Clone	Source	Tree height	Angle of leaning	Growth eccentricity	Proportion of TW
Tjir 1	Tree height	1.00	0.961 * *	0.363	0.337
	Angle of leaning		1.00	0.468	0.411
	Growth eccentricity			1.00	0.065
	Proportion of TW				1.00
GT 1	Tree height	1.00	0.932 * *	0.545	0.315
	Angle of leaning		1.00	0.617 *	0.435
	Growth eccentricity			1.00	0.234
	Proportion of TW				1.00
RRIM 600	Tree height	1.00	0.887 * *	-0.249	0.733 * *
	Angle of leaning		1.00	-0.227	0.528
	Growth eccentricity			1.00	-0.373
	Proportion of TW				1.00
RRII 105	Tree height	1.00	0.930 * *	0.162	0.397
	Angle of leaning		1.00	0.247	0.417
	Growth eccentricity			1.00	-.317
	Proportion of TW				1.00
* significant at 5% level; * * significant at 1% level					

4.5 Tension wood formation in tapped and untapped zones of the trunk

The proportion of TW in tapped and untapped zones in mature trees of four clones is presented in Table 7. The percentage of TW was higher in the untapped zone than the tapped zone in Tjir 1, RRIM 600 and RRII 105, whereas in GT 1 the percentage of TW was identical in both regions. Analysis of the data using t-test revealed that the variation in the proportion of TW between tapped and untapped zones was found to be significant when the clones were considered together. (t = -4.13 at 15 df).

Table 7. Proportion of tension wood in tapped and untapped zones within trees

Clones	Proportion of TW (%)	
	Tapped zone	Untapped zone
Tjir 1	15.76	22.82
GT 1	17.69	17.63
RRIM 600	17.30	32.19
RRII 105	24.31	32.35

4.6 Tension wood formation and wind damage

Wind damage is a common phenomenon in rubber plantations, mainly in the form of trunk snap (Fig. 21 a & b). Four trees affected by trunk snap were selected and quantified the proportion of TW in three positions (Table 8). It was observed that the proportion of TW was maximum (26 %) in the wood disc collected from the point of break (disc B) and minimum (18.75 %) in disc below the point of break (disc A). Statistical analysis indicated that the difference in the proportion of TW in disc B was statistically significant over disc A and C (Table 9). The compact mass of TW was mainly concentrated on the opposite side of the point of break (Fig. 21c - arrow).

Table 8. Proportion of tension wood in trunk snapped trees

Tree No.	Proportion of TW (%)		
	Disc from below the point of break (Disc A)	Disc from the point of break (Disc B)	Disc from above the point of break (Disc C)
1	16	21	18
2	24	32	28
3	13	20	17
4	22	31	27
Mean	**18.75**	**26**	**22.5**

Table 9 t- test for proportion of tension wood in trunk snapped trees

Source	df	t
Variation between Disc A & B	3	-8.49 * *
Variation between Disc C & B	3	-12.42 * *

* * significant at 1% level

t values with –ve sign : the proportion of TW was higher in disc B

4.7. Visual identification of tension wood in rubber wood logs

Zinc – Chloro – Iodide reagent was directly applied on the cut surface of the fresh as well as dried wood discs and the staining pattern was observed. The compact bands of TW stained brownish pink in freshly cut wood discs (Fig. 22b) whereas the normal wood zone retained its original colour similar to that in unstained control samples (Fig. 22a). The staining reaction on dried and fungus infected wood discs was negative as revealed by its non-stainability indicating that this macroscopic staining procedure is applicable only in freshly sawn green wood containing high moisture content.

4.8. Structural studies on tension wood

4.8.1 Fibres

In rubber wood, fibres are libriform, non-septate and long with numerous simple pits on the wall. Fibers are of two types based on its structure and composition *viz.* normal wood fibres (Fig. 23a & b) and tension wood fibres or gelatinous fibres (Fig. 23d & e) designated as NF and GF respectively. NF stained blue and GF stained purplish red with toludine blue 'O'.

4.8.1.1 Length of fibres

Variation in the length of NF and GF at different positions within the disc is presented in Fig. 24. In all the clones, the length of NF and GF varied from pith to periphery. However, in majority of the discs the fibre length was maximum in the peripheral zone and minimum near the pith zone.

The length of NF and GF at three height levels are given in Table 10. In all the clones, the average length of NF was higher than that of GF. The average length of NF and GF was 1248.90 μm and 1058.56 μm in RRII 105, 1205.70 μm and 994.83 μm in

RRIM 600, 1268.89 μm and 1102.63 μm in GT 1 and 1192.92 μm and 1066.59 μm in Tjir 1. ANOVA carried out for the length of NF and GF was found to have no significant variation with respect to different clones and also between different height levels among the clones (Table 11). However, the variation in length between NF and GF was statistically significant in all the four clones (Table 12).

Table 10. Length of normal and gelatinous fibres at three height levels

Clone	Disc	Fibre length (μ m)			
		NF		GF	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	1245.95	**1248.90**	1046.75	**1058.56**
	B	1236.63		1059.45	
	C	1264.12		1069.45	
RRIM 600	A	1169.68	**1205.74**	962.05	**994.83**
	B	1203.25		989.03	
	C	1244.30		1033.40	
GT 1	A	1248.82	**1268.89**	1082.84	**1102.60**
	B	1260.82		1123.47	
	C	1297.05		1101.50	
Tjir 1	A	1169.53	**1192.92**	1076.60	**1066.59**
	B	1168.35		1074.95	
	C	1240.88		1048.23	

Table 11. ANOVA for length of normal and gelatinous fibres

Character	Source	SS	df	SS	F
Variation between height levels (irrespective of clones)	Treatment	5043.66	2	2521.83	1.17 NS
	Error	19266.28	9	2140.69	
Variation between clones (irrespective of height levels)	Treatment	14551.60	3	4850.53	2.56 NS
	Error	22705.64	12	1892.13	

NS : non-significant

Table 12 . t- test for length of normal and gelatinous fibres

Clone	df	t
RRII 105	11	18.38 * *
RRIM 600	11	23.60 * *
GT 1	11	10.48 * *
Tjir 1	11	3.68* *

* * significant at 1% level

4.8 1.2. Width of fibres

Fig. 25 explained the variation in the width of NF and GF at different sample positions within wood discs. The width of NF and GF of all the clones showed slight variability from pith to periphery. However, in majority of cases the width was maximum in sample near the periphery and minimum near the pith zone.

In all the clones studied, the mean width of NF was lower than that of GF. The width of NF ranged from 19.7 μm to 20.88 μm whereas the mean width of GF ranged from 21.03 μm to 23.56 μm (Table 13).

Table 13. Width of normal and gelatinous fibres at three height levels

Clone	Disc	Width of fibres (μ m)			
		NF		GF	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	20.12	**20.27**	23.22	**22.57**
	B	20.66		22.47	
	C	20.04		22.01	
RRIM 600	A	20.03	**20.25**	22.18	**22.25**
	B	20.23		22.27	
	C	20.40		22.31	
GT 1	A	19.38	**19.70**	20.96	**21.03**
	B	20.05		21.09	
	C	19.67		21.03	
Tjir 1	A	20.95	**20.88**	23.93	**23.56**
	B	20.72		23.14	
	C	20.95		23.62	

The width of NF was more or less the same in all the clones studied whereas the width of GF was higher in Tjir 1 (23.56 μm)than rest of the clones. The width of NF and GF was found to have statistically significant variation with respect to different clones and also between the different height levels among the clones (Table 15). The difference in the width between NF and GF was highly significant in all the clones (Table 14).

Table 14. ANOVA for width of normal and gelatinous fibres

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	8.98	2	4.49	5.16 *
	Error	16.53	9	0.87	
Variation between clones (irrespective of height levels)	Treatment	13.17	3	4.39	6.55 *
	Error	8.04	12	0.67	

* significant at 5% level

Table 15. t-test for width of normal and gelatinous fibres

Clone	df	t
RRII 105	11	-7.40 * *
RRIM 600	11	-10.64 * *
GT 1	11	- 8.68 * *
Tjir 1	11	- 9.00 * *

* * significant at 1% level
t value with –ve sign : the value was high for G -fibres

4.8.1.3. Fiber wall thickness

Table 16 depicts the average fibre wall thickness of NF and GF at different height levels. The average wall thickness of NF was comparable in all the clones. Similar trend was also observed in the case of GF.

Table 16. Wall thickness of normal and gelatinous fibres

Clone	Disc	Wall thickness (μm)			
		NF		GF	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	3.36	3.39	4.26	4.14
	B	3.45		4.12	
	C	3.35		4.04	
RRIM 600	A	3.34	3.38	4.07	4.05
	B	3.40		4.08	
	C	3.41		4.09	
GT 1	A	3.24	3.29	4.39	4.32
	B	3.35		4.24	
	C	3.29		4.33	
Tjir 1	A	3.50	3.49	4.39	4.32
	B	3.46		4.24	
	C	3.52		4.33	

ANOVA (Table 17) carried out for the wall thickness of NF and GF indicated that the variation in the fibre wall thickness between clones and between height levels was not statistically significant. In comparison between NF and GF the average wall thickness was higher in GF than NF in all the clones and the difference was statistically significant (Table 18).

Table 17. ANOVA for wall thickness of normal and gelatinous fibres

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	7.21	2	3.60	2.23 NS
	Error	13.60	9	1.51	
Variation between clones (irrespective of height levels)	Treatment	10.82	3	3.60	2.88 NS
	Error	15.08	12	1.25	

NS : non-significant

Table 18. t- test for wall thickness of normal and gelatinous fibres

Clone	df	t
RRII 105	11	-13.85 * *
RRIM 600	11	-25.37 * *
GT 1	11	-15.83 * *
Tjir 1	11	-26.07 * *

* * significant at 1% level
t value with –ve sign : the value was higher for G-fibres

4.8.2. Vessel elements

The vessels (pores) were oval to round in cross sectional view and are distributed in solitary or in radial multiples. The vessels present in the central zone of the disc usually had narrow lumen and arranged in groups of two or more, while those present in the peripheral zone were solitary with wide lumen.

4.8.2.1 Length of vessel elements

The length of vessel elements in different samples from pith to periphery within wood discs is given in Fig. 26. In all the clones the vessel length was higher near the pith region and lower in peripheral zone.

Table 19 represents the mean length of vessel elements which was maximum in GT 1 (652.05 μm) followed by RRII 105 (617.61 μm), RRIM 600 (607.83 μm) and minimum in Tjir 1 (576.18 μm). Analysis of variance indicated that the variation in length of vessel elements with respect to tree height was not significant in all clones. However, between clones, the variation in the length of vessel elements was significant at 5% level (Table 20).

Table 19. Length of vessel elements

Clone	Disc	Length (μm)	
		Disc average	Clone average
RRII 105	A	593.14	**617.61**
	B	618.44	
	C	641.26	
RRIM 600	A	575.06	**607.83**
	B	589.33	
	C	659.11	
GT 1	A	646.54	**652.05**
	B	646.11	
	C	663.51	
Tjir 1	A	566.28	**576.18**
	B	575.34	
	C	586.91	

Table 20. ANOVA for length of vessel elements

Character	Clones	Source	MS	df	SS	F
Variation between height levels within clones	Tjir 1	Treatment	855.39	2	427.69	0.26 NS
		Error	14580.86	9	1620.09	
	GT 1	Treatment	787.77	2	393.88	0.28 NS
		Error	12460.75	9	1384.52	
	RRIM 600	Treatment	16184.36	2	8092.17	3.01 NS
		Error	24126.17	9	2680.68	
	RRII 105	Treatment	4636.15	2	2318.07	1.23 NS
		Error	16920.94	9	1880.10	
Variation between clones (irrespective of height levels)		Treatment	11713.42	3	3904.47	4.97 *
		Error	9413.14	12	784.43	

* significant at 5% level, NS : non-significant

4.8.2.2 Width of vessel elements

Fig. 27 showed the width of vessel elements at different radial positions within the wood disc. In GT 1 and Tjir 1 the width of vessel elements was lowest near the pith zone and highest in the peripheral zone. In RRII 105 and RRIM 600 the vessel width showed a fluctuating trend from the pith outwards especially in the intermediate zone.

Among the four clones investigated, RRII 105 had the maximum vessel width (217.68 µm) followed by GT 1 (202.30 µm), Tjir 1 (198.77 µm) and minimum (197.99 µm) in RRIM 600 (Table 21). Variation in the width of vessel elements between different height levels and between clones was not statistically significant (Table 22).

Table 21. Width of vessel elements

Clone	Disc	Width (µm)	
		Disc average	Clone average
RRII 105	A	219.32	**217.68**
	B	214.70	
	C	219.02	
RRIM 600	A	192.46	**197.99**
	B	195.33	
	C	206.18	
GT 1	A	198.64	**202.30**
	B	208.78	
	C	199.47	
Tjir 1	A	190.08	**198.77**
	B	197.96	
	C	208.27	

Table 22. ANOVA for width of vessel elements

Character	Clones	Source	MS	df	SS	F
Variation between height levels within clones	Tjir 1	Treatment	665.52	2	332.75	2.80 NS
		Error	1067.57	9	118.62	
	GT 1	Treatment	253.78	2	126.89	0.55 NS
		Error	2078.56	9	230.95	
	RRIM 600	Treatment	418.76	2	209.38	0.59 NS
		Error	3193.91	9	354.87	
	RRII 105	Treatment	53.43	2	26.71	0.04 NS
		Error	5670.87	9	630.10	
Variation between clones (irrespective of height levels)		Treatment	1133.92	3	377.97	2.49 NS
		Error	1820.84	12	151.73	

NS : non-significant

4.8.3 Analysis of pores

4.8.3.1 Number of pores

The mean number of pores (per cm^2 C.S. area of wood) in normal and tension wood zones at three height levels is presented in Table 23.

Table 23. Number of pores (per cm^2 C.S of wood) in normal and tension wood zones

Clone	Disc	Frequency of pores			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	384.48	**414.10**	280.40	**321.23**
	B	446.83		314.18	
	C	413.10		369.13	
RRIM 600	A	529.91	**535.94**	423.66	**474.74**
	B	540.07		452.37	
	C	537.85		548.20	
GT 1	A	464.69	**506.02**	479.42	**523.89**
	B	557.42		566.88	
	C	495.93		525.36	
Tjir 1	A	477.39	**500.63**	523.28	**516**
	B	486.10		478.02	
	C	538.40		547.68	

The number of pores per cm^2 in both NW and TW zones was lowest in RRII 105 (414.10 and 321.23 respectively). Of the four clones studied, the higher pore number per

cm^2 in the NW zone was observed in RRIM 600 (535.94) and that in TW zone was observed in GT 1(523.89).

ANOVA indicated that the number of pores in NW and TW zones was not statistically significant with respect to clones and also between different height levels (Table 24).

Comparing the NW and TW zones, the number of pores per cm^2 was highly reduced in the TW zone of RRII 105 (321.23) and RRIM 600 (474.74), whereas in GT 1 (523.89) and Tjir 1 (516) it was vice versa. However, the variation between the zones was statistically significant only in RRII 105 (Table 25).

Table 24. ANOVA for number of pores in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	17821.32	2	8910.66	0.77 NS
	Error	104136.59	9	11570.73	
Variation between clones (irrespective of ht. Levels)	Treatment	32538.06	3	10846.02	2.03 NS
	Error	64052.83	12	5337.73	

NS non-significant

Table 25. t-test for number of pores in normal and tension wood zones

Clone	df	t
RRII 105	11	3.20 * *
RRIM 600	11	0.96
GT 1	11	-0.74
Tjir 1	11	-1.52

* * significant at 1% level
t value with –ve mark : the value was higher in TW zone

4.8.3.2 Total area occupied by pores

The total area occupied by pores per cm^2 C.S. area of wood in normal and tension wood zones at three height levels is presented in Table 26.

The total area occupied by pores in both NW and TW zone was maximum in RRII 105 (11.40 mm^2 and 10.28 mm^2 respectively) and minimum in Tjir 1 (10.08 mm^2

and 9.40 mm^2 respectively). ANOVA did not show any statistically significant difference for this character among the clones as well as between height levels (Table 27). The difference in the pore area between NW and TW in each of the clones was statistically significant only in GT 1 (Table 28).

Table 26. Total area occupied by pores in normal and tension wood zones

Clone	Disc	Total area occupied by pores (mm^2 / cm^2 C.S. area)			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	9.44	**11.40**	8.85	**10.28**
	B	12.26		10.61	
	C	12.49		11.40	
RRIM 600	A	9.27	**10.99**	9.27	**10.08**
	B	11.45		10.34	
	C	12.25		10.66	
GT 1	A	10.04	**11.24**	8.91	**9.79**
	B	11.74		10.23	
	C	11.96		10.24	
Tjir 1	A	8.86	**10.08**	8.49	**9.40**
	B	10.34		10.01	
	C	11.04		9.70	

Table 27 ANOVA for total area occupied by pores in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	19.10	2	9.55	2.74 NS
	Error	31.27	9	3.47	
Variation between clones (irrespective of height levels)	Treatment	4.16	3	1.38	1.28 NS
	Error	13.01	12	1.08	

NS : non-significant

Table 28. t- test for total area occupied by pores in normal and tension wood zones

Clone	df	t
RRII 105	11	1.80
RRIM 600	11	1.60
GT	11	5.47 * *
1Tjir 1	11	2.07

* * significant at 1% level

4.8.3.3 Average area of pores

The average cross sectional area of pores in NW and TW zones at three height levels is given in Table 29.

Table 29. Average cross sectional area of pores in normal and tension wood zones

Clone	Disc	Average area of pores (mm^2)			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	0.029	**0.033**	0.037	**0.037**
	B	0.032		0.038	
	C	0.036		0.036	
RRIM 600	A	0.021	**0.025**	0.028	**0.027**
	B	0.025		0.026	
	C	0.031		0.026	
GT 1	A	0.024	**0.026**	0.021	**0.021**
	B	0.026		0.022	
	C	0.028		0.020	
Tjir 1	A	0.021	**0.024**	0.019	**0.021**
	B	0.024		0.024	
	C	0.026		0.020	

Of the four clones studied, the average pore area in NW zone and TW zone was the highest in RRII 105 (0.033 mm^2 and 0.037 mm^2 respectively) and the lowest in Tjir 1 (0.024 mm^2 and 0.021 mm^2 respectively). ANOVA indicated that the variation in average pore area in NW and TW was not statistically significant with respect to different clones and also between height levels (Table 30).

The average pore area was comparatively higher in NW zone than TW zone in the case of two clones *viz.* GT 1 and Tjir 1, whereas the trend was just the reverse in the case of RRII 105 and RRIM 600. However the difference in the pore area between NW and TW was statistically significant only in clones RRII 105 and GT 1 (Table 31).

Table 30. ANOVA for average cross sectional area of pores in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	0.186	2	0.093	2.51 NS
	Error	0.33	9	0.037	
Variation between clones (irrespective of ht. Levels)	Treatment	0.194	3	0.064	2.66 NS
	Error	0.291	12	0.024	

NS : non-significant

Table 31. t- test for average cross sectional area of pores in normal and tension wood zones

Clone	df	t
RRII 105	11	-2.44 *
RRIM 600	11	-0.05
GT 1	11	3.30 * *
Tjir 1	11	1.435

* significant at 5% level
* * significant at 1% level
t value with –ve sign : the values were higher in TW zone

4.8.4 Analysis of rays

Rays are heterogeneous and uni to multi-seriate in rubber wood. The distribution, morphology and dimension of rays showed considerable variation between NW and TW zones in *Hevea* clones.

4.8.4.1 Frequency of rays

The frequency of rays was determined by counting the number of rays passing through an unit tangential length (1 mm) in longitudinal section of NW and TW zones separately and the results were presented in Table 32.

The range in frequency of rays was almost identical in NW (8.75 - 10.51) and TW (8.79 - 10.51) in all the clones studied. ANOVA carried out for frequency of rays in NW and TW zones indicated that the variation was not statistically significant with respect to different clones as well as at different height levels (Table 33). The difference in the ray frequency between NW and TW zones in individual clones was also not significant (Table 34).

Table 32. Frequency of rays in normal and tension wood zones

Clone	Disc	Frequency of rays (no. of rays passing through 1 mm tangential length)			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	10.17	**9.98**	10.38	**10.12**
	B	10.02		10.20	
	C	9.75		9.80	
RRIM 600	A	8.66	**8.75**	8.77	**8.79**
	B	8.96		8.90	
	C	8.64		8.70	
GT 1	A	10.69	**10.38**	9.97	**9.87**
	B	10.27		9.96	
	C	10.18		9.67	
Tjir 1	A	10.76	**10.51**	10.44	**10.51**
	B	10.45		10.79	
	C	10.32		10.31	

Table 33. ANOVA for frequency of rays in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	0.50	2	0.25	0.45
	Error	4.95	9	0.55	
Variation between clones (irrespective of ht. levels)	Treatment	7.71	3	2.57	2.45
	Error	12.60	12	1.05	

NS : non-significant

Table 34. t- test for frequency of rays in normal and tension wood zones

Clone	df	t
RRII 105	11	-1.08
RRIM 600	11	-0.74
GT 1	11	1.931
Tjir 1	11	-0.57

t value with -ve sign : the values were higher in TW zone

4.8.4.2 Height of rays

Table 35 depicts the height of rays in NW and TW zones at three height levels.

The ray height in NW and TW was highest in GT 1 (376.55 µm. and 384.09 µm respectively) and lowest in RRIM 600 (321.44 µm and 332.66 µm, respectively). Analysis of variance revealed that the variation in height of rays in NW and TW zones was not statistically significant between clones as well as height levels (Table 36) .

In comparison between NW and TW, the height of rays was higher in TW zone than NW zone in all the clones studied even though the variation between them was not statistically significant in the case of individual clones (Table 37).

Table 35. Height of rays in normal and tension wood zones

Clone	Disc	Height of rays (µm)			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	281.48	**344.08**	364.14	**382.48**
	B	372.49		399.69	
	C	378.29		383.62	
RRIM 600	A	315.98	**321.45**	325.14	**332.66**
	B	320.74		339.68	
	C	327.63		333.15	
GT 1	A	374.80	**376.55**	369.28	**384.10**
	B	383.37		375.55	
	C	371.49		407.47	
Tjir 1	A	343.81	**345.95**	353.35	**353.03**
	B	355.23		363.97	
	C	338.82		341.78	

Table 36 ANOVA for height of rays in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	565.91	2	282.95	0.68 NS
	Error	3706.72	9	411.85	
Variation between clones (irrespective of height levels)	Treatment	7378.26	3	2459.42	2.83 NS
	Error	10422.72	12	868.56	

NS : non-significant

Table 37. t-test for height of rays in normal and tension wood zones

Clone	df	t
RRII 105	11	-0.57
RRIM 600	11	-1.32
GT 1	11	-0.98
Tjir 1	11	- 0.91

t value with –ve sign : the values were higher in TW zone

4.8.4.3 Width of rays

The width of rays (Table 38) in both NW and TW zones was highest in RRIM 600 (41.24 μm and 39.40 μm respectively) and the lowest in GT 1 (34.50 μm and 34.26 μm respectively).

Table 38. Width of rays in normal and tension wood zones

Clone	Disc	Width of rays (μm)			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	39.41	**38.34**	36.59	**34.76**
	B	37.86		34.33	
	C	37.76		33.36	
RRIM 600	A	43.73	**41.24**	40.00	**39.40**
	B	39.92		39.44	
	C	40.05		38.77	
GT 1	A	36.14	**34.50**	31.82	**33.03**
	B	33.54		32.23	
	C	33.82		35.06	
Tjir 1	A	38.71	**37.44**	39.05	**35.83**
	B	36.34		33.83	
	C	36.68		34.60	

Among the four clones, RRIM 600 had maximum ray width in NW (41.24 μm) and TW (39.4 μm) followed by RRII 105 (38.34 μm and 34.76 μm respectively), Tjir 1 (37.44 μm and 35.83 μm respectively) and the minimum in GT 1 (34.5 μm and 33.03μm respectively) (Table 38). ANOVA (Table 39) carried out for width of rays in NW and TW zones did not show any significant difference in ray width between clones and also between different height levels.

In comparison between NW and TW, in the individual clones, the width of rays was lower in TW zone than NW zone and the variation was significant in all the clones except Tjir 1 (Table 40).

Table 39 ANOVA for width of rays in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	37.04	2	18.52	2.86 NS
	Error	58.28	9	6.47	
Variation between clones (irrespective of height levels)	Treatment	68.94	3	22.98	2.96 NS
	Error	93.06	12	7.75	

NS : non-significant

Table 40. t- test for width of rays in normal and tension wood zones

Clone	df	t
RRII 105	11	6.89 * *
RRIM 600	11	3.12 * *
GT 1	11	2.54 *
Tjir 1	11	1.41

* Significant at 5% level

** significant at 1% level

4.8.4.4 Height / width ratio of rays

.Height / width ratio of rays in NW and TW zones at three height levels were computed and presented in Table 41.

Table 41. Height / width ratio of rays in normal and tension wood zones

Clone	Disc	Height / width ratio of rays			
		NW zone		TW zone	
		Disc average	Clone average	Disc average	Clone average
RRII 105	A	9.99	**10.37**	10.21	**11.44**
	B	10.42		12.37	
	C	10.70		11.74	
RRIM 600	A	7.52	**7.98**	8.42	**8.60**
	B	8.14		8.70	
	C	8.27		8.69	
GT 1	A	10.46	**10.98**	11.38	**11.68**
	B	11.47		12.12	
	C	11.01		11.54	
Tjir 1	A	9.09	**9.49**	9.06	**10.17**
	B	9.96		11.28	
	C	9.43		10.16	

In both NW and TW, the height / width ratio of rays was the highest in GT 1 (10.98 and 11.68 respectively) followed by RRII 105, Tjir 1 and the lowest in RRIM 600 (7.98 and 8.60 respectively). ANOVA indicated that the difference in the height / width ratio in NW and TW was not statistically significant with respect to clones as well as at different height levels (Table 42).

The ratio was significantly higher in TW zone than NW zone in all the clones except Tjir 1 where the difference was only numerical (Table 43).

Table 42 ANOVA for height width ratio of rays in normal and tension wood zones

Character	Source	SS	df	MS	F
Variation between height levels (irrespective of clones)	Treatment	1.54	2	0.77	0.40 NS
	Error	17.12	9	1.90	
Variation between clones (irrespective of height levels)	Treatment	20.82	3	6.94	3.23 NS
	Error	25.08	12	2.15	

NS : non-significant

Table 43. t- test for height width ratio of rays in normal and tension wood zones

Clone	df	t
RRII 105	11	-2.92 *
RRIM 600	11	-2.75 *
GT 1	11	-3.02 *
Tjir 1	11	-1.49

* Significant at 5% level

t value with –ve sign : the values were higher in TW zone

4.9 Histochemical Studies

4.9.1 Starch.

Starch grains stained bluish black with I_2-KI reagent and were localized in the axial (Fig. 28a & b – arrows) and ray parenchyma cells (Fig. 28 a & b – arrow heads). The frequency of starch bearing cells and the number of grains per cell varied considerably in NW and TW zones. The total number and area occupied by starch grains per cm^2 C.S. area and average area of grains in NW and TW zones are presented in Table 44.

The total number of starch grains per cm^2 area was low in the TW zone to the extent of 45% compared to the NW zone. Similarly the total area occupied by starch grains per cm^2 C.S. area was 26% less in the TW zone than the NW zone. In the case of average grain area, the trend was just the reverse where it was 26.5% high in TW zone.

Table 44 Number and area occupied by starch grains per cm^2 C.S. area and average area of grains in normal and tension wood zone (clone RRII 105)

Character	NW zone	TW zone
No. of starch grains	2.3×10^5	1.23×10^5
Total area occupied by starch grains	0.34 cm^2	0.25 cm^2
Average area of starch grain	0.15 mm^2	0.21 mm^2

4.9.2 Cellulose

The G-layer of the TW fibres showed swelling due to the reaction with I_2KI - Sulphuric acid reagent and attained pale violet colouration (Fig. 28d - arrows) indicating that this specialized layer is cellulosic and devoid of lignin. Nevertheless, the lignified walls of both NW and TW fibres did not show such swelling and positive colour reaction. (Fig 28c & d - arrow heads).

4.9.3 Lignin

Normal wood fibres showed purplish red stainability with Phloroglucinol - HCl reaction indicating the presence of lignin (Fig. 29b & d). The G-layer of TW fibres did not show such stainability (Fig. 29a & c - arrows) indicating that this layer is totally unlignified. However, the fibre walls except G-layer of TW fibres showed low level of lignification (Fig. 29a - arrow head) as revealed by its feeble stainability.

4.9.4 Lipids

Lipids stained bluish black with Sudan black 'B' (Fig. 30a & b - arrows). Localization of lipid was observed only in few ray and axial parenchyma cells in both NW and TW zones. Traces of lipid globules were also localized in few cells of both wood types. Even though the number of cells showing lipid localization was very limited, it was more or less uniform in both NW and TW zones.

4.9.5 Total proteins

Total proteins stained blue with Mercuric Bromophenol blue. Localization of proteins was mainly concentrated in ray cells (Figs. 30c & d – arrows). The lumen of few fibres and axial parenchyma cells showed feeble stainability indicating the presence of traces of proteins. The cells containing total protein were found to be very few in both NW and TW zones.

4.10 Factors affecting tension wood formation in *Hevea*

4.10.1 Angle of leaning

4.10.1.1 Plants with foliage

The formation of TW in four month old young rubber seedlings was observed after artificial bending of the shoots at different angles from vertical. Plants inclined at 45^0 and 90^0 angle from vertical showed a gradual increase in the proportion of TW from base to top of the plant, whereas plants inclined at 135^0 angle showed maximum TW formation in position B (middle portion) and minimum in position A (basal portion) (Figs 31a, b, c). In all experiments, irrespective of different angles, the formation of TW was not confined to a particular zone in position A. However, in position B and C of two experiments (90^0 & 135^0), the distribution of TW was confined mainly in the upper side of the bent axis (Figs. 31b, c - arrows). Where as in the case of 45^0 inclination TW formation was more prominent in the lower side as broad band as well as narrow bands encircling the pith (Fig. 31a - arrows). The peripheral zone of vertical stem of the control plants also showed narrow bands and distinct groups of gelatinous fibres (Fig. 31d - arrow) . The distribution of TW in different positions and its proportion are presented in Table 45.

In general, the formation of TW was maximum (39.6%) in plants bent at 90^0 and the minimum (23.75%) at 45^0. Plants bent at 135^0 occupied second position (28.15%) in the proportion of TW. Tension wood formation was also observed in vertically grown control plants but its proportion (3.66%) was negligible.

Table 45. Distribution and proportion of tension wood in plants after artificial bending

Leaning angle (degrees from vertical)	Sample Position	Position of TW formed	Proportion of TW (%)	
			Sample mean	Plant mean
45	A	NPS	9.86	**23.75**
	B	US	28.11	
	C	LS	33.29	
90	A	NPS	29.31	**39.60**
	B	US	43.43	
	C	US	46.06	
135	A	NPS	21.57	**28.15**
	B	US	36.80	
	C	US	26.08	
Vertical (control)	A	NPS	5.64	**3.66**
	B	NPS	3.96	
	C	NPS	1.40	

LS - lower side of the bent axis
US - upper side of the bent axis
NPS - not position specific

4.10.1.2 Plants without foliage

Defoliated seedlings bent at 45^0, 90^0 and 135^0 angles from vertical also showed TW formation as narrow bands in both central and peripheral zones (Fig. 32a, b , c -

arrows), whereas in control plants its formation was restricted only in the extreme periphery in the form of a narrow ring (Fig. 32d - arrow).

Table 46. Distribution and proportion of tension wood in defoliated plants after artificial bending

Leaning angle (degrees from vertical)	Sample Position	Position of TW formed	Proportion of TW (%)	
			Sample mean	Plant mean
45	A	NPS	4.84	**9.49**
	B	US	7.92	
	C	LS	15.72	
90	A	NPS	16.85	**17.14**
	B	US	19.47	
	C	US	15.10	
135	A	NPS	3.59	**10.83**
	B	US	17.02	
	C	US	11.89	
Vertical (control)	A	NPS	0.44	**0.15**
	B	NPS	0.00	
	C	NPS	0.00	

LS – Lower side of the bent axis
US – Upper side of the bent axis
NPS – Not position specific

With regard to the proportion of TW (Table 46) the plants inclined at angle 90^0 showed the highest (17.14 %) proportion followed by 135 ^{0} (10.83%) and the lowest in 45^0 inclination (9.49 %), similar to the experiments conducted in plants with foliage. The quantity of TW formed was negligible (0.15 %) in control plants.

4.10.2 Effect of gravity on tension wood formation

To examine the gravitational response on tension wood formation, plants were looped in vertical plane and observed the extent of TW formation in four different positions of the loop. All portions of the loop exhibited TW formation at different intensities. The formation of TW was not position specific in those samples collected from the basal portion before the loop (SBL) where its formation was in the form of a narrow ring (Fig. 33a - arrow). TW formation was maximum in upper part of the loop (UPL), mainly confined to the upper side as compact mass and extending further towards the lower side (Fig 32b - arrows). The distribution pattern of TW in the lower part of the loop (LPL) was also mainly on the upper side as thick mass and extended further towards the lower side (Fig. 33c - arrows). The outer half of lateral part of the loop (LtPL) showed broad band of TW which extends further as a narrow band on the opposite side (Fig. 33d - arrow). Prominent growth eccentricity was observed in all the segments of the loop.

The proportion of TW formed in each segments of the loop were also recorded and presented in Table 47. The maximum proportion TW was recorded in UPL (44.08%) followed by LPL (42.26%), LtPL (33.1%) and minimum in SBL (25.3%).

Table 47. Distribution and proportion of tension wood in different segments of the loop

Sample position	Proportion of TW formed (%)	Position of TW formed
UPL	44.08	upper side
LPL	42.26	upper side
LtPL	33.10	outer side
SBL	25.30	not position specific

4.10.3 Effect of growth regulators on tension wood formation

4.10.3.1 Apical application of IAA, GA_3 and TIBA on artificially bent plants

Indole-3-Acetic acid (IAA), Gibberellic acid (GA_3) and 2-3-5-Triiodo Benzoic acid (TIBA) (500 ppm in lanolin) and lanolin alone (as control) were applied on the upper and lower halves of decapitated plants bent at 90^0 angle. For brevity of description, the upper and the lower halves of the bent axes were referred to as UH and LH, respectively. The results of these experiments are described under separate heads as growth regulator

/ lanolin *i.e.* UH with growth regulator and LH with lanolin or lanolin / growth regulator *i.e.* UH with lanolin and LH with growth regulator.

4.10.3.1.1 Application of IAA

(a) IAA / lanolin : Tension wood formation was absent in both upper (Fig. 34a) and lower halves (Fig. 34b). The differentiation of wood elements was slightly decreased in the IAA treated upper half than that of the lanolin treated lower half.

(b) Lanolin / IAA : Tension wood formation was virtually absent in both UH (Fig. 34c) and LH (Fig. 34d). A decrease in wood differentiation associated with an increase in the differentiation of phloem tissue (bark) was noticed in the UH. The number and size of pores was also highly reduced in the newly differentiated xylem tissue in UH.

4.10.3.1.2 Application of GA_3

(a) GA_3 / lanolin : A narrow band of tension wood was formed in UH treated with GA_3 (Fig. 34e - arrow) whereas it was absent in LH (Fig. 34f). Formation of wood and bark tissue was more or less uniform in both halves.

(b) Lanolin / GA_3 : A narrow band of TW was formed in LH treated with GA_3 (Fig. 33h - arrow) whereas its formation was absent in UH (Fig. 34g). In both halves, the development of wood tissue was relatively high.

4.10.3.1.3 Application of TIBA

(a) TIBA / lanolin : Tension wood formation was absent in both the upper (Fig. 35a) and lower halves (Fig. 35b). Wood and bark formation was more or less uniform in both halves.

(b) Lanolin / TIBA : Tension wood formation was absent in both the upper (Fig. 34c) and lower halves (Fig. 34 d). The number and size of vessels was higher in UH than that of LH.

4.10.3.1.4 Lanolin / Lanolin (control) : Tension wood formation was absent in both upper (Fig. 35e) and lower halves (Fig. 35f).

The results of the apical application of different growth regulators on artificially bent seedlings are consolidated in Table 48. The data revealed that the exogenous application of IAA and TIBA inhibited TW formation while GA_3 application induced TW formation. It was also observed that the application of IAA and TIBA restricts the differentiation of wood elements and enhances the differentiation of bark tissue.

Table 48 .Effect of application of growth regulators on plants bent artificially at 90°

Growth regulator	Expt.	Position	Treatment	Response		
				Bark formation	Wood formation	TW formation
IAA	1	UH	IAA	High	Highly reduced	Absent
		LH	Lanolin	Normal	Normal	Absent
	2	UH	Lanolin	High	Highly reduced	Absent
		LH	IAA	High	Limited	Absent
GA_3	1	UH	GA	Normal	Normal	Present
		LH	Lanolin	Normal	Normal	Absent
	2	UH	Lanolin	High	Highly reduced	Absent
		LH	GA	Normal	Slightly reduced	Present
TIBA	1	UH	TIBA	Normal	Normal	Absent
		LH	Lanolin	High	Highly reduced	Absent
	2	UH	Lanolin	Normal	Normal	Absent
		LH	TIBA	High	Normal	Absent
Control (Lanolin)	1	UH	Lanolin	Normal	Reduced	Absent
		LH	Lanolin	High	Highly reduced	Absent

4.10.3.2 Lateral application of IAA, GA_3 and TIBA on vertically grown plants

IAA, TIBA, GA_3 and lanolin (control) were applied laterally on vertical stem axis of bud grafted plants of the clone RRII 105. The stem samples from the site of application, below and above the zone of applied site were used to assess TW formation.

4.10.3.2.1 IAA

Tension wood bands were observed in the peripheral wood zone in those samples below the position of application. (Fig 36a - arrow). Differentiation of bark tissue was relatively high at the site of IAA application (Fig. 36b). The proportion of TW was maximum in position A (6.23%) followed by position C (1.52%). and the minimum (0.83%) in position B (Table 49). On an average, the formation of TW was considerably reduced (5.34%) in plants treated with IAA .

4.10.3.2.2 GA_3

Tension wood formation was very prominent as compact arcs covering the major portion of the wood zone (Fig. 36c - arrow). The proportion of TW was maximum in position A (41.49 %), followed by position B (28.91 %) and the minimum in position C (16.02 %) with an average value of 28.80 % (Table 49) indicating that the lateral application of GA_3 induced TW formation.

4.10.3.2.3 TIBA

Lateral application of TIBA also induced TW formation as well developed continuous bands mainly in the peripheral wood zone (Fig. 36d - arrow) The proportion of TW was maximum in position A (31.12 %) followed by position C (12.25 %) and minimum in position C (8.34 %) with an average value of 17.23% (Table 49).

4.10.3.2.4 Lanolin (control)

Tension wood formation was also noticed in lanolin applied control plants as broad bands (Fig. 37a - arrows). Its formation was maximum in position A (41.27%) and minimum in position C (8.36%) with an average proportion of 23.22% (Table 49).

Table 49. Proportion of TW in vertical plants treated with lateral application of growth regulators

Sample Position	Proportion of TW (%)			
	IAA	GA_3	TIBA	Lanolin
A	6.23	41.49	31.12	41.27
B	0.83	28.91	8.34	20.02
C	8.96	16.02	12.25	8.36
Plant Average	5.34	28.80	17.23	23.22

4.10.3.3 Lateral application of IAA on plants grown vertical through incision of bark

IAA was applied laterally on vertical stem axis of bud grafted plants of the clone RRII 105, through bark incision. The samples from the site of application, below and above the zone of applied site were considered for ascertaining TW formation.

Tension wood formation was observed in all the sample positions (Fig. 37b). The proportion of TW was higher in position A (10.48%) than in position B (8.59%) and C (8.96%) with an average value of 9.34% (Table 50).

Table 50. Proportion of tension wood in vertical plants treated with lateral application of IAA through bark incision.

Sample position	Proportion of TW (%)
A	10.48
B	8.59
C	8.96
Plant average	9.34

4.10.3.4 Lateral application of IAA and TIBA on artificially bent stem axis at 45°

IAA and TIBA were applied laterally on bud grafted plants of the clone RRII 105 after artificial bending. The samples from the site of application, below and above the zones of the applied site were observed for TW formation.

4.10.3.4.1 IAA

Tension wood formation was observed in the peripheral wood zone (Fig. 37c - arrow). The proportion of TW was maximum in position A (17.19%) followed by position C (14.05%) and the minimum in position B (6.04%) with an average proportion of 12.42% (Table 51).

4.10.3.4.2 TIBA

The formation of TW was highly reduced irrespective of samples at different positions (Fig. 37d). Position C was observed with maximum proportion (13.06%) followed by position A (11.16%) and the minimum in position B (9.26%) with an average value of 11.16% (Table 51).

Table 51. Proportion of tension wood in plants bent at 45^0 treated with lateral application of IAA and TIBA

Sample position	Proportion of TW (%)	
	IAA	TIBA
A	17.19	11.16
B	6.04	9.26
C	14.05	13.06
Plant average	12.42	11.16

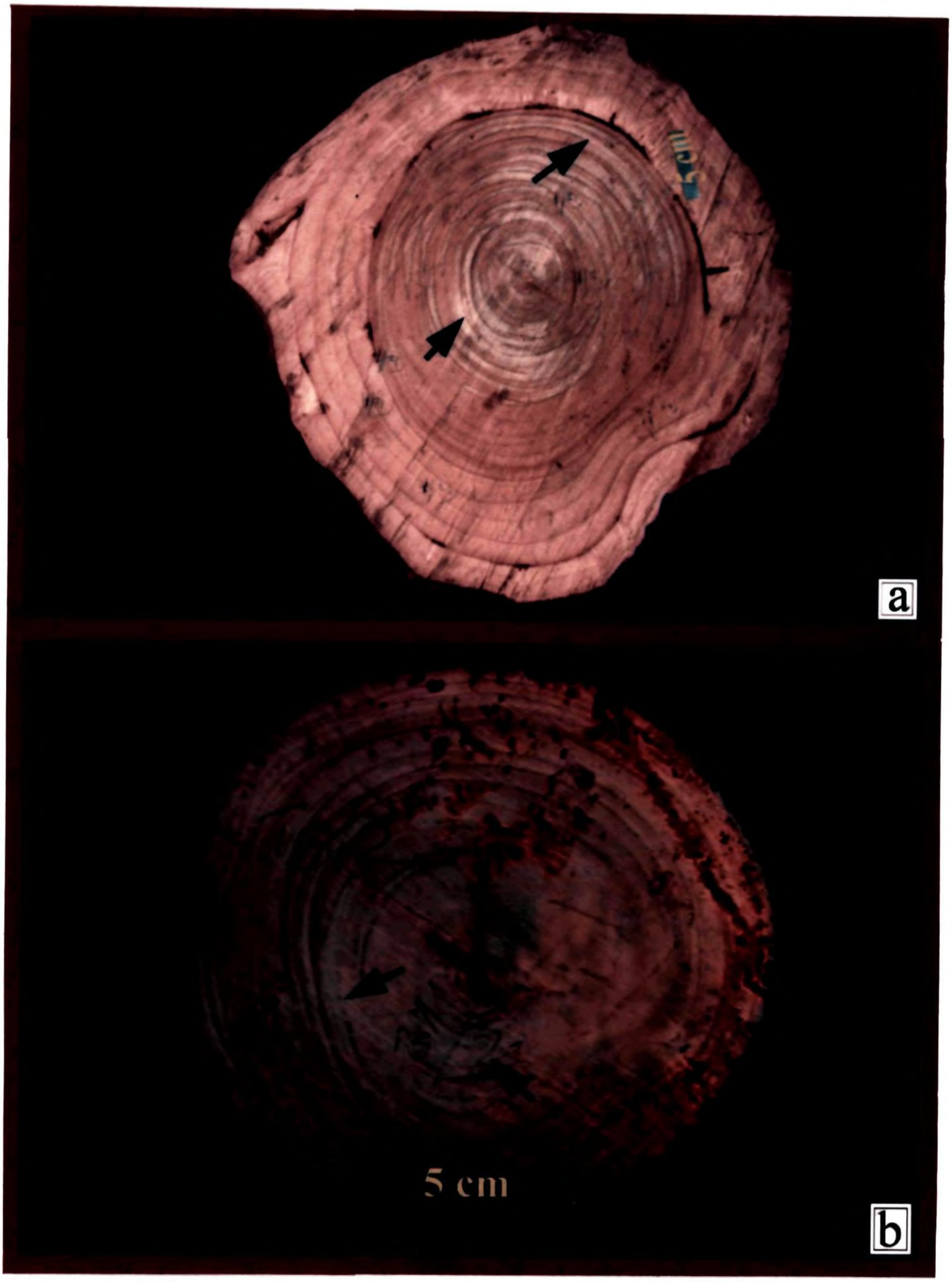


Fig.10. Cross-sawn discs of rubber wood showing white wooly arcs of compact tension wood (arrows)
a. Clone Tjir 1; b. Clone GT 1

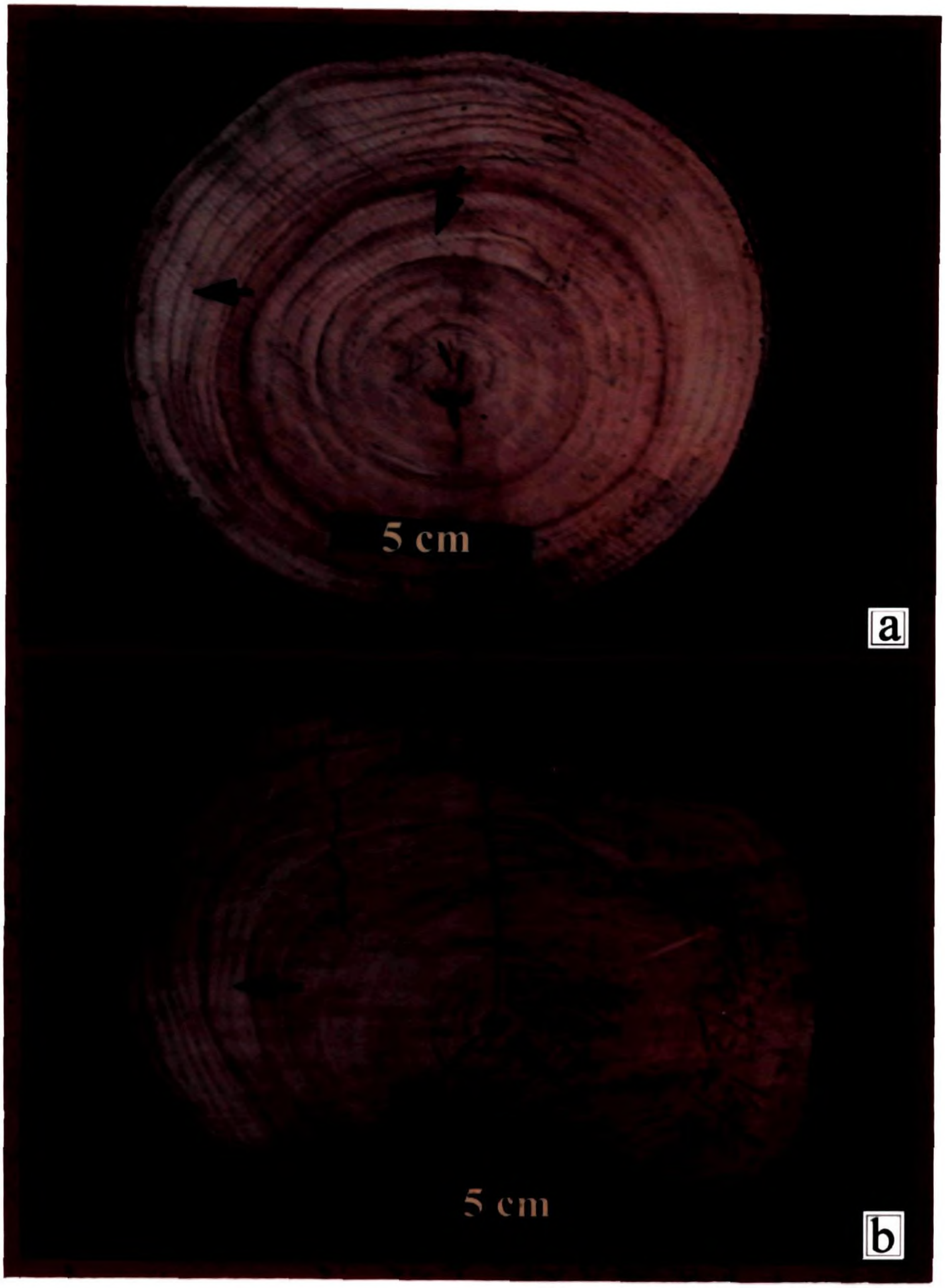
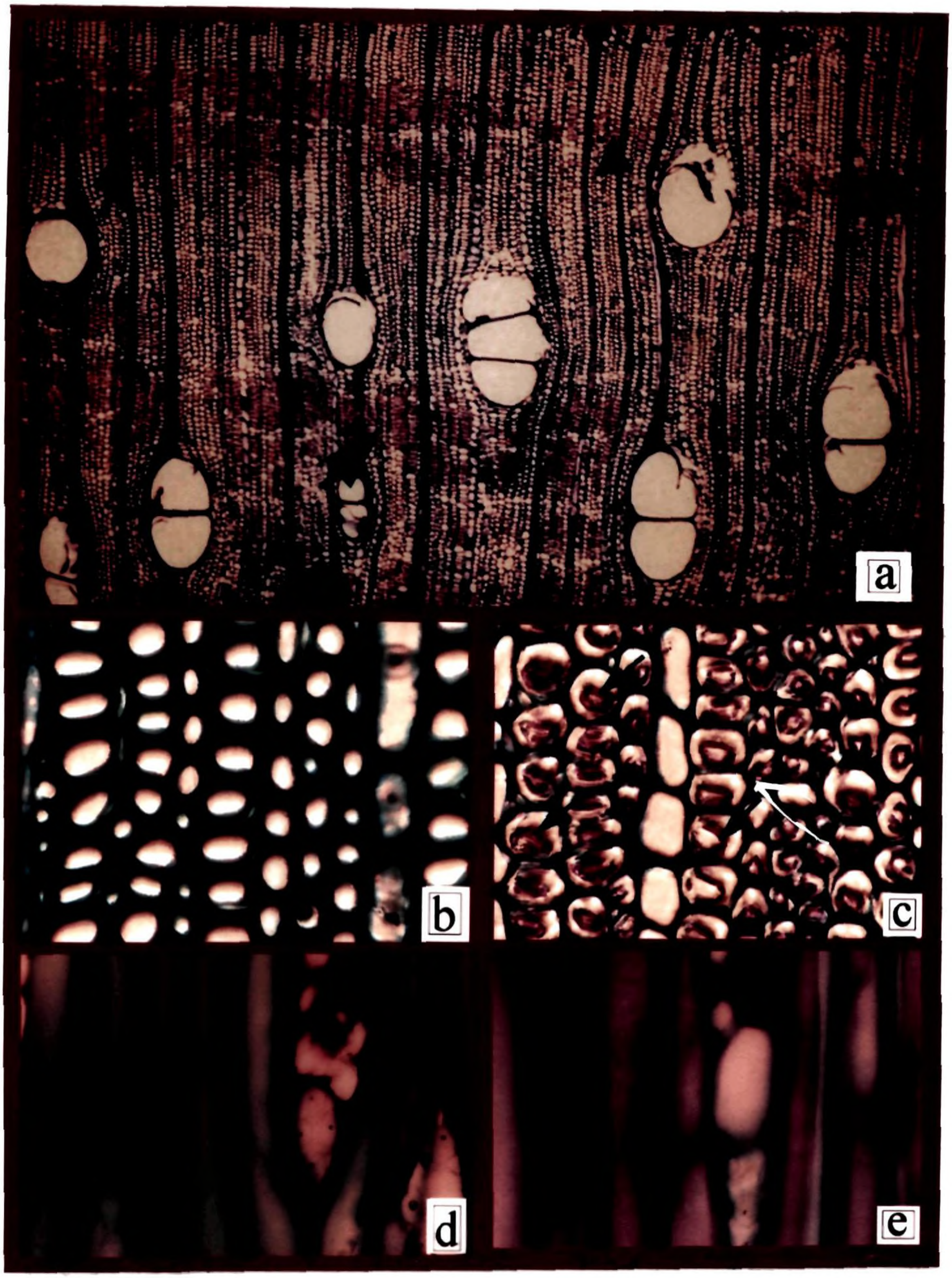


Fig.11. Cross-sawn discs of rubber wood showing white wooly arcs of compact tension wood (arrows)
a. Clone RRIM 600; b. Clone RRII 105



ɜ.12. Distribution pattern and structure of tension wood and normal wood (clone Tjir 1)

a. C.S. of wood showing compact arcs of tension wood (arrows) and discrete groups of tension wood fibres (arrow head). X34; b. C.S. of normal wood fibres. X500;

c. C.S. of tension wood fibres showing detachment of G-layer (arrow). X500;

d. T.L.S. of normal wood fibres. X210; e. T.L.S. of tension wood fibres. X235

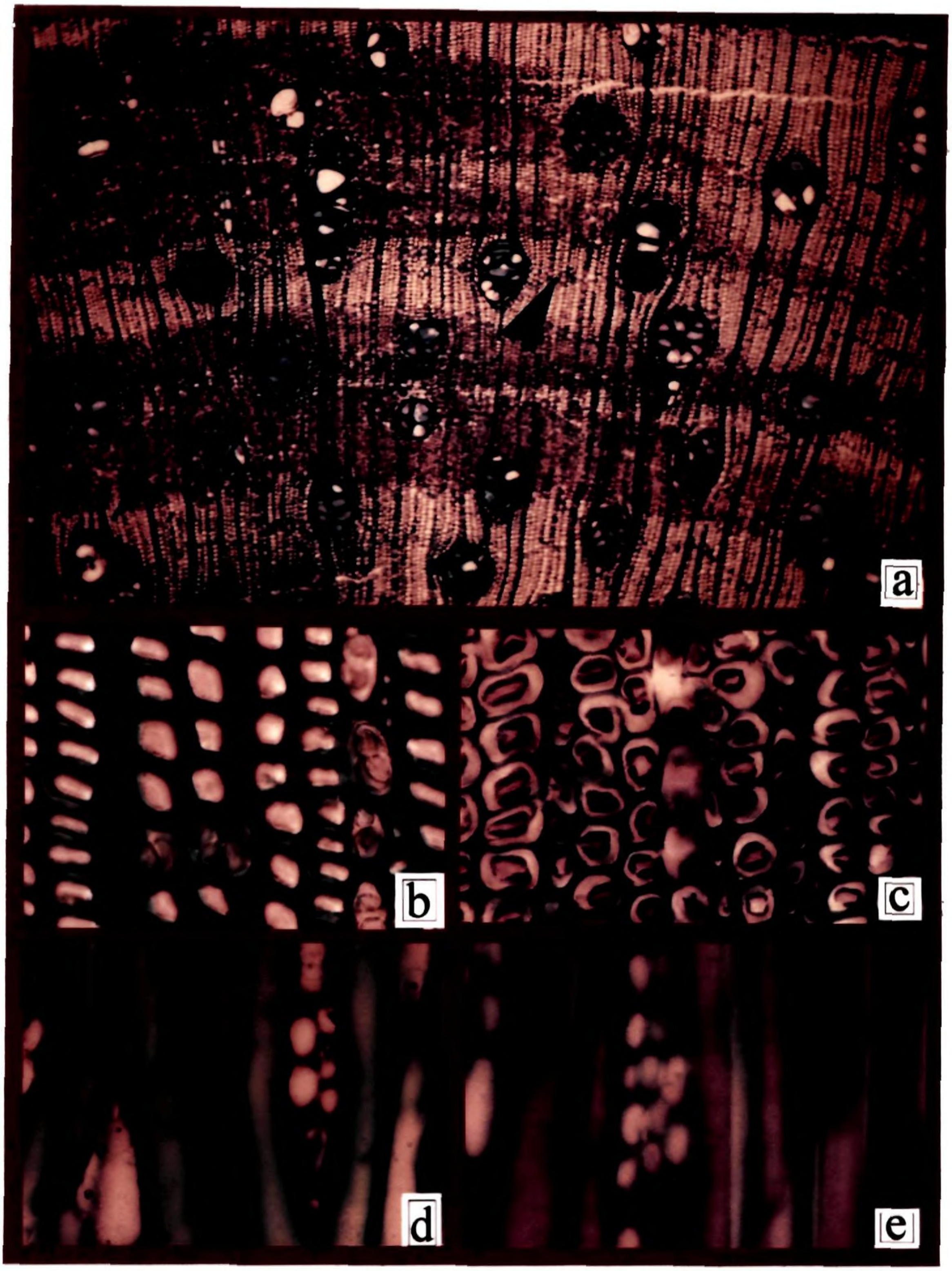


Fig.13. Distribution pattern and structure of tension wood and normal wood (clone GT 1)
a. C.S. of wood showing broad bands of compact tension wood (arrows) and normal wood (arrow heads). X34; b. C.S. of normal wood fibres. X500;
c. C.S. of tension wood fibres showing detachment of G-layer from adjacent wall. X500;
d. T.L.S. of normal wood fibres. X210; e. T.L.S.. of tension wood fibres. X235.

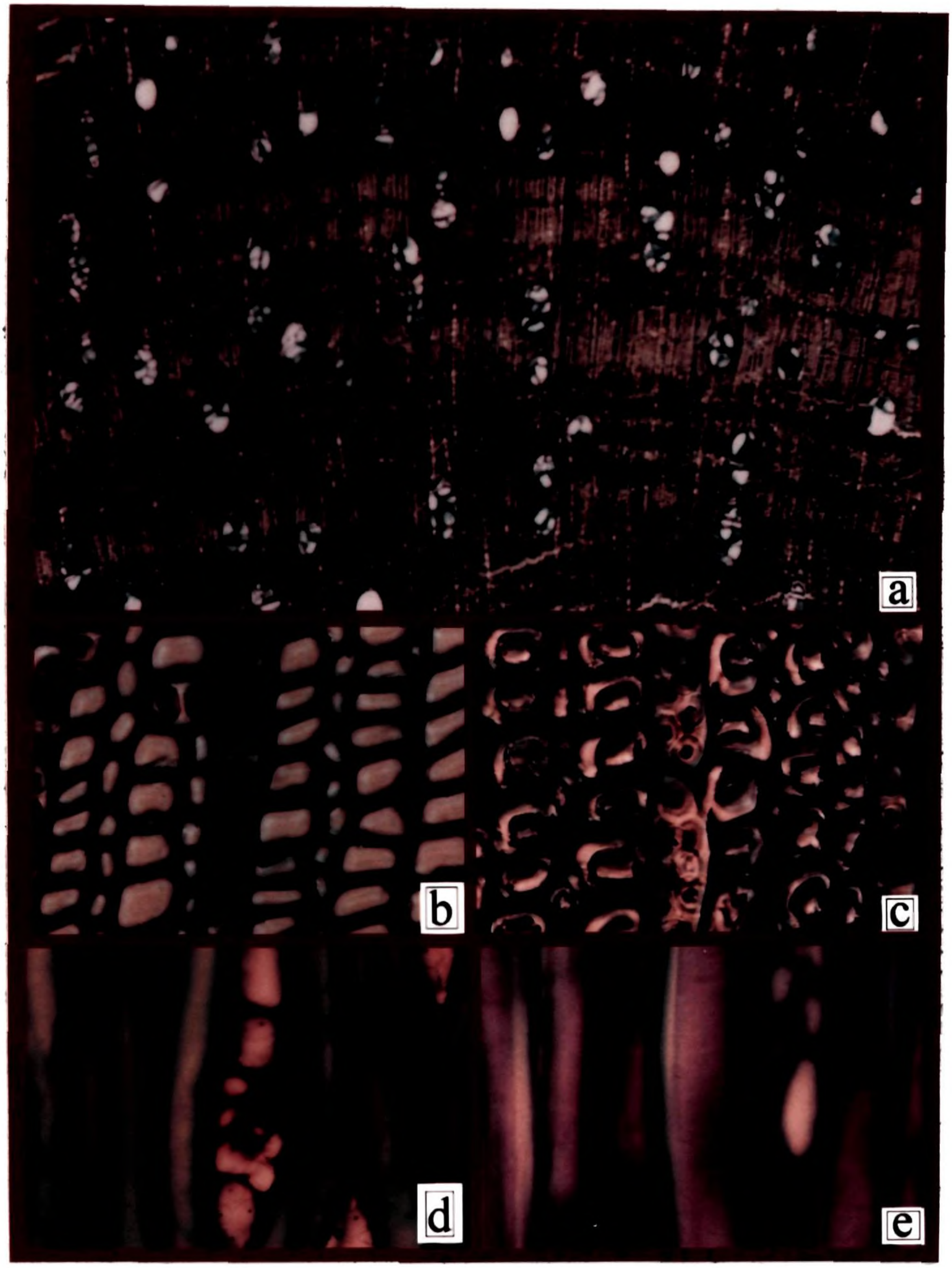


Fig. 14. Distribution pattern and structure of tension wood and normal wood (clone RRIM 600)
a. C.S. of wood showing compact arcs of tension wood. X34;
b. C.S. of normal wood fibres. X500; c. C.S. of tension wood fibres showing thick G-layer detached from adjacent walls. X500;
d. T.L.S. of normal wood fibres. X210; e. T.L.S. of tension wood fibres. X235.

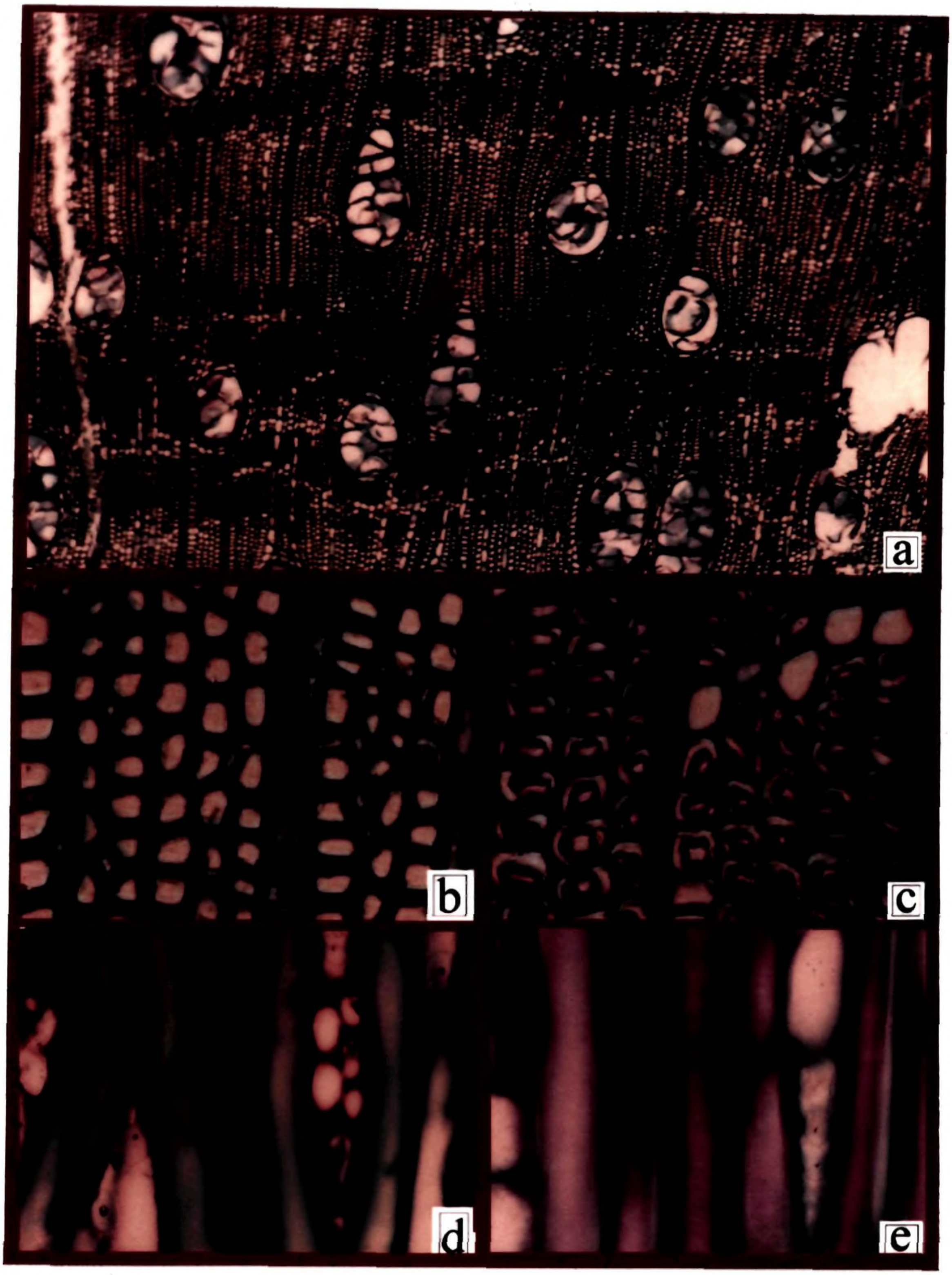
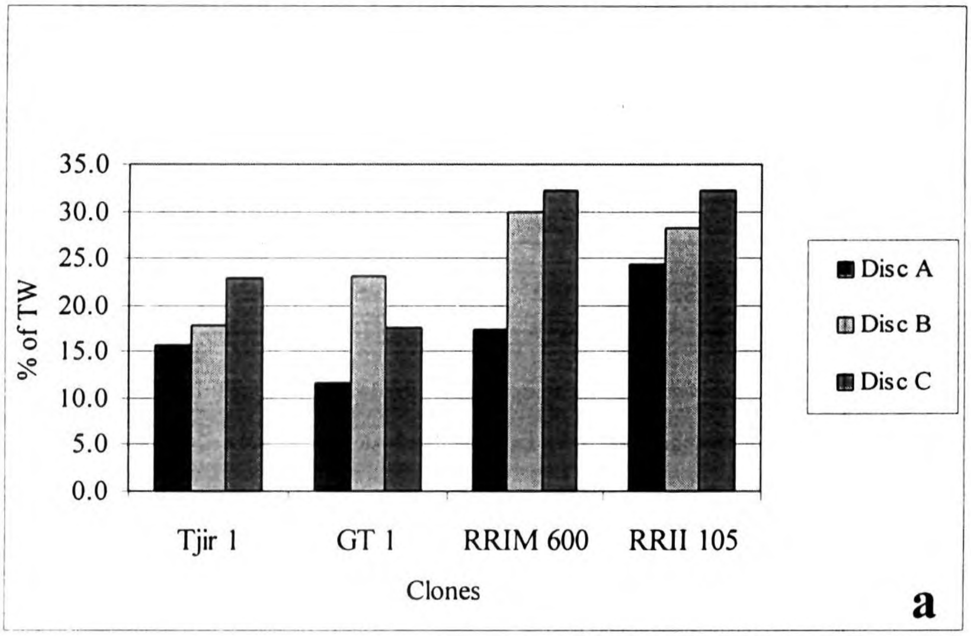


Fig. 15. Distribution pattern and structure of tension wood and normal wood (clone RRII 105)
a. C.S. of wood showing compact mass of tension wood (arrows). X34;
c. C.S. of normal wood fibres. X500; c. C.S. of tension wood fibres showing convoluted G-layer. X500; d. T.L.S. of normal wood zone showing normal wood fibres. X210; e. T.L.S. of tension wood fibres. X235.



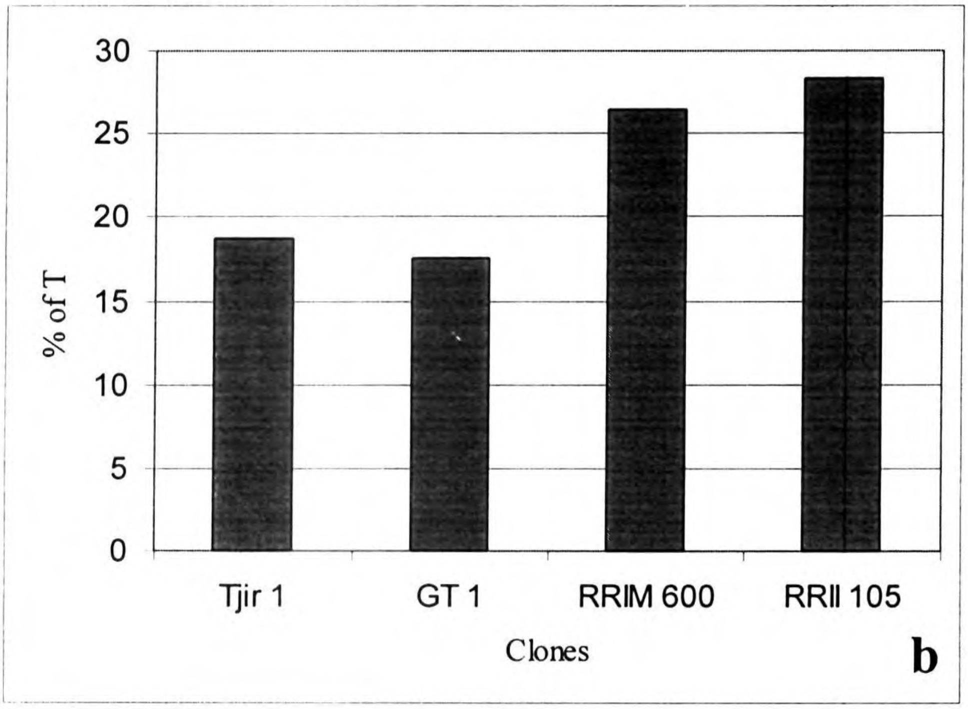


Fig. 16. Proportion of tension wood in mature trees

a. proportion of tension wood within clones at three height levels;

b. proportion of tension wood in different clones (clone average)

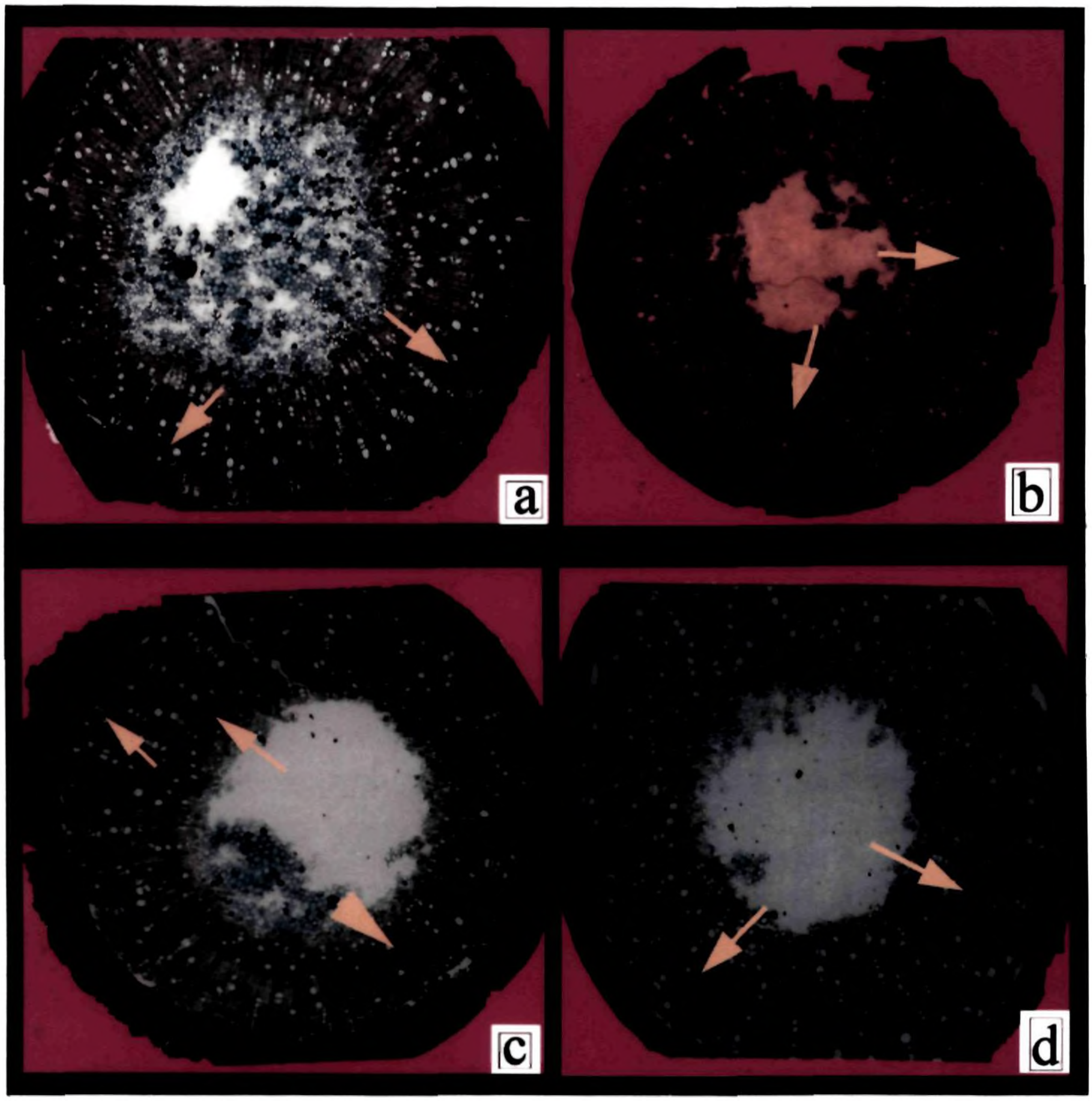
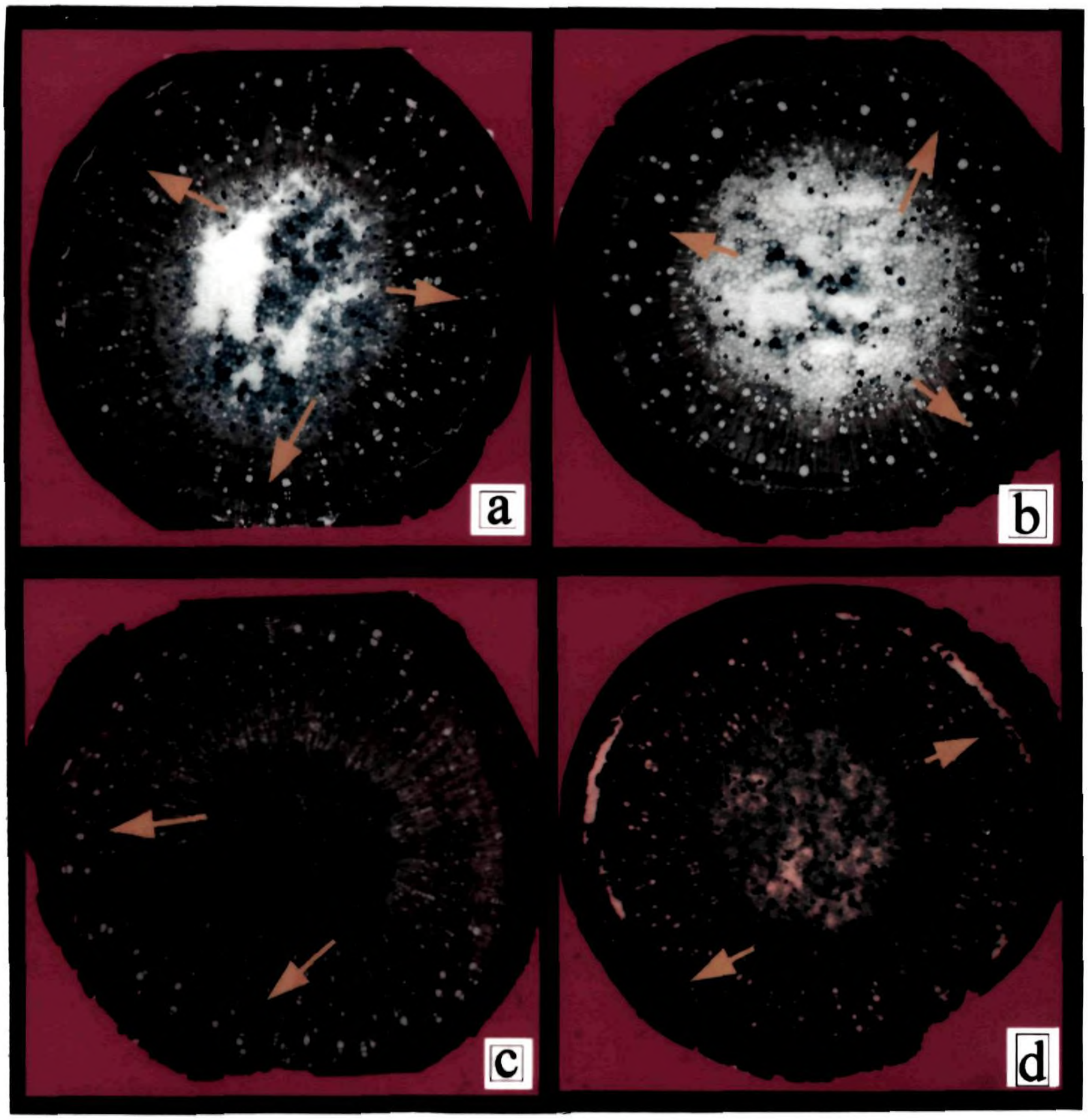


Fig. 17. Cross section of wood showing distribution of tension wood (arrows) in ten month old budgrafted plants of different clones
a. Tjir 1. X9; b. RRIM 703. X11; c. PB 5 / 51. X10; d. RRIM 623. X9.



'ig. 18. Cross section of wood showing distribution of tension wood (arrows) in ten month old budgrafted plants of different clones

a. GT 1. X11; b. RRIM 600. X10; c. PB 217. X12; d. PB 235. X12.

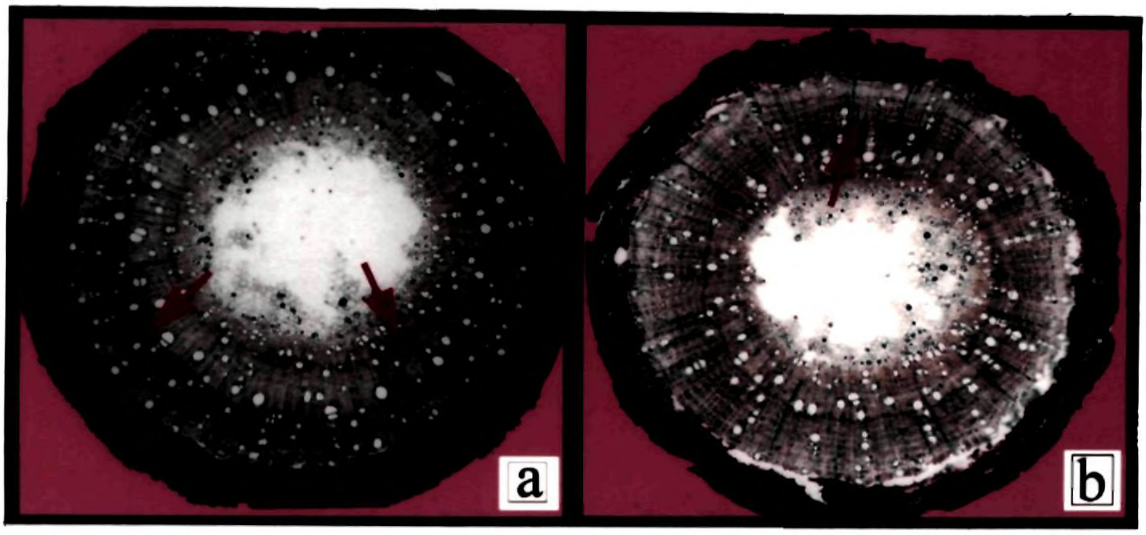


Fig. 19. Cross section of wood showing distribution of tension wood (arrows) in ten month old budgrafted plants of different clones
a. RRII 105. X11; b. Gl 1. X13.

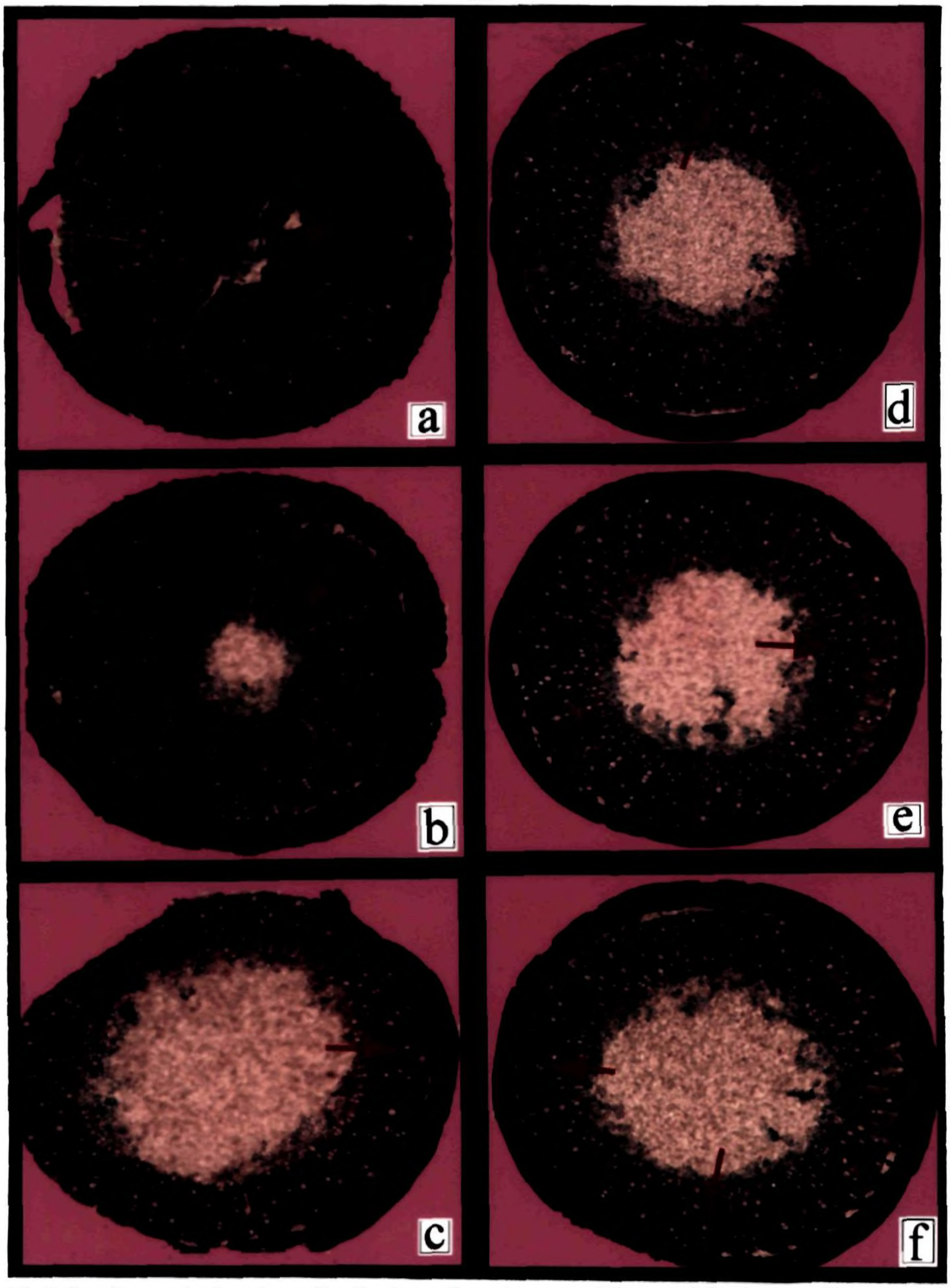


Fig. 20.C.S. of wood showing distribution of tension wood (arrows) in tissue culture plant and bud grafted plant

a - c. Tissue culture plant : a. basal portion. X10; b. middle portion. X10; c. upper portion. X10.

d - f. Bud-grafted plant : d. basal portion. X8; e. middle portion. X8; f. upper portion. X10.

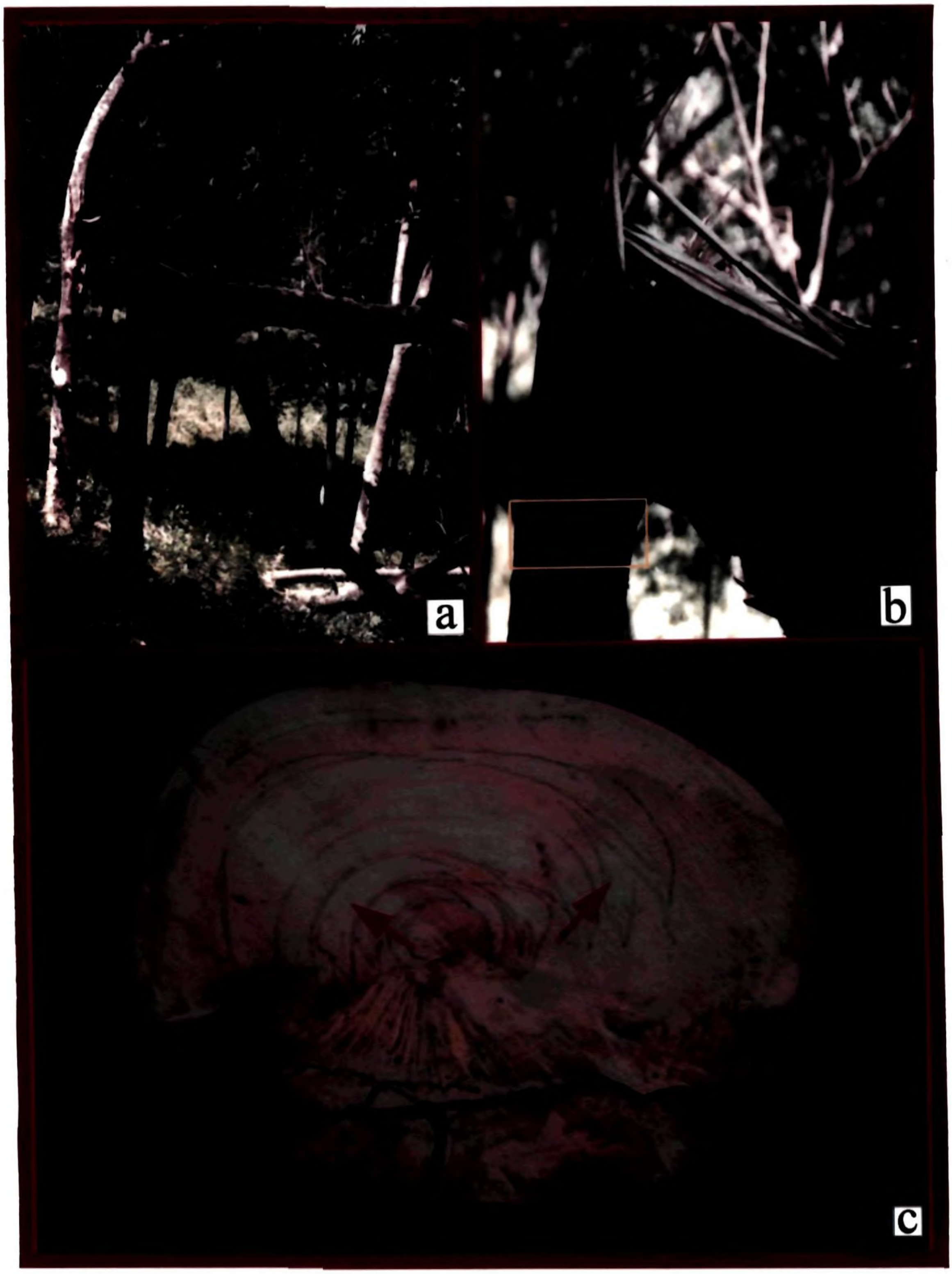


Fig. 21. Tension wood formation and wind damage
a. field view of rubber trees showing trunk snap;
b. position of trunk snap;
c. C.S. of wood disc from broken portion showing compact arcs of tension wood (arrows).

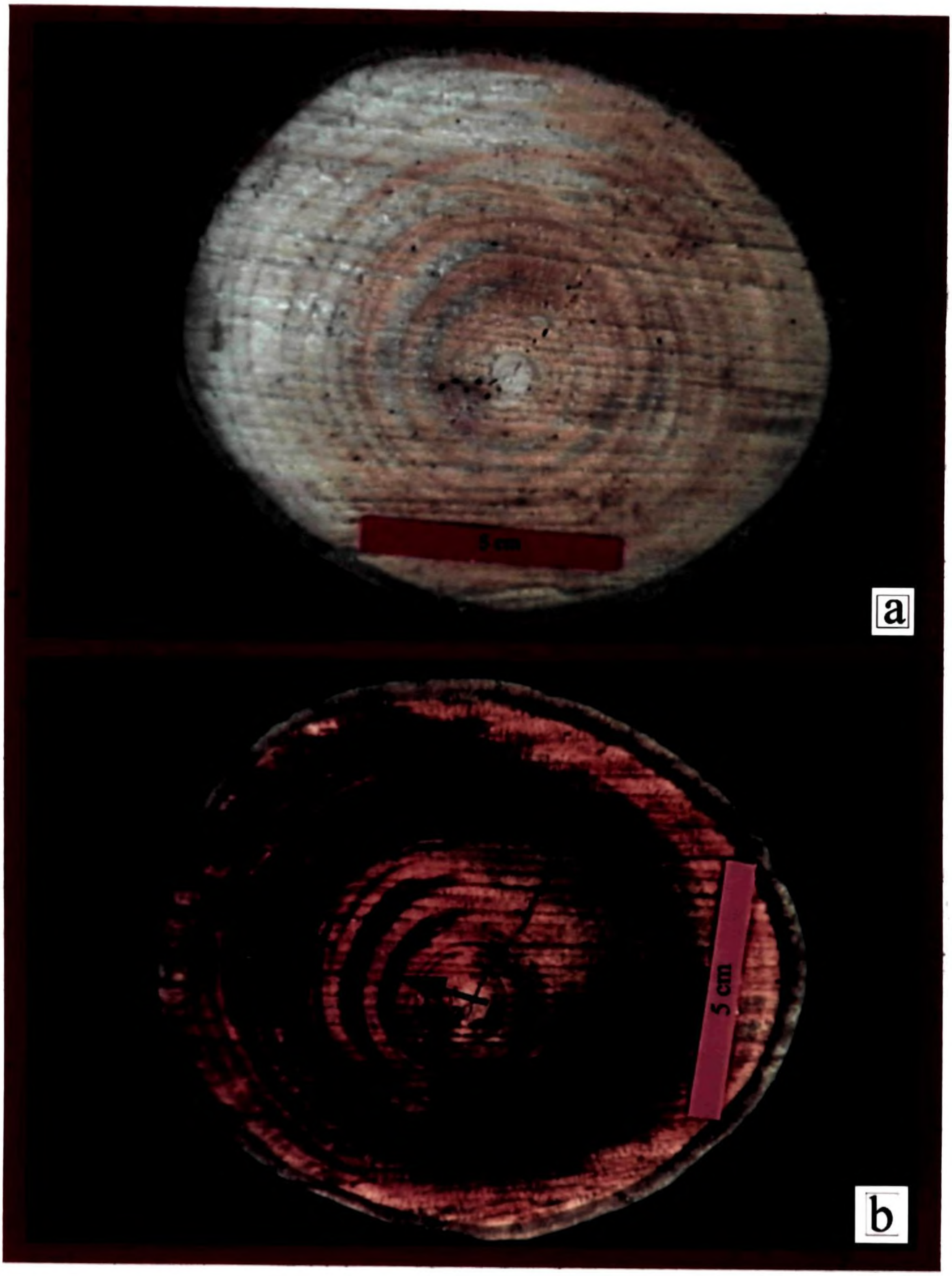


Fig. 22. Macroscopic staining of tension wood

a. C.S. of wood disc before the application of the stain;

b. C.S. of wood showing brownish pink stainability of tension wood zones with Zinc-chloro-iodide (arrows).

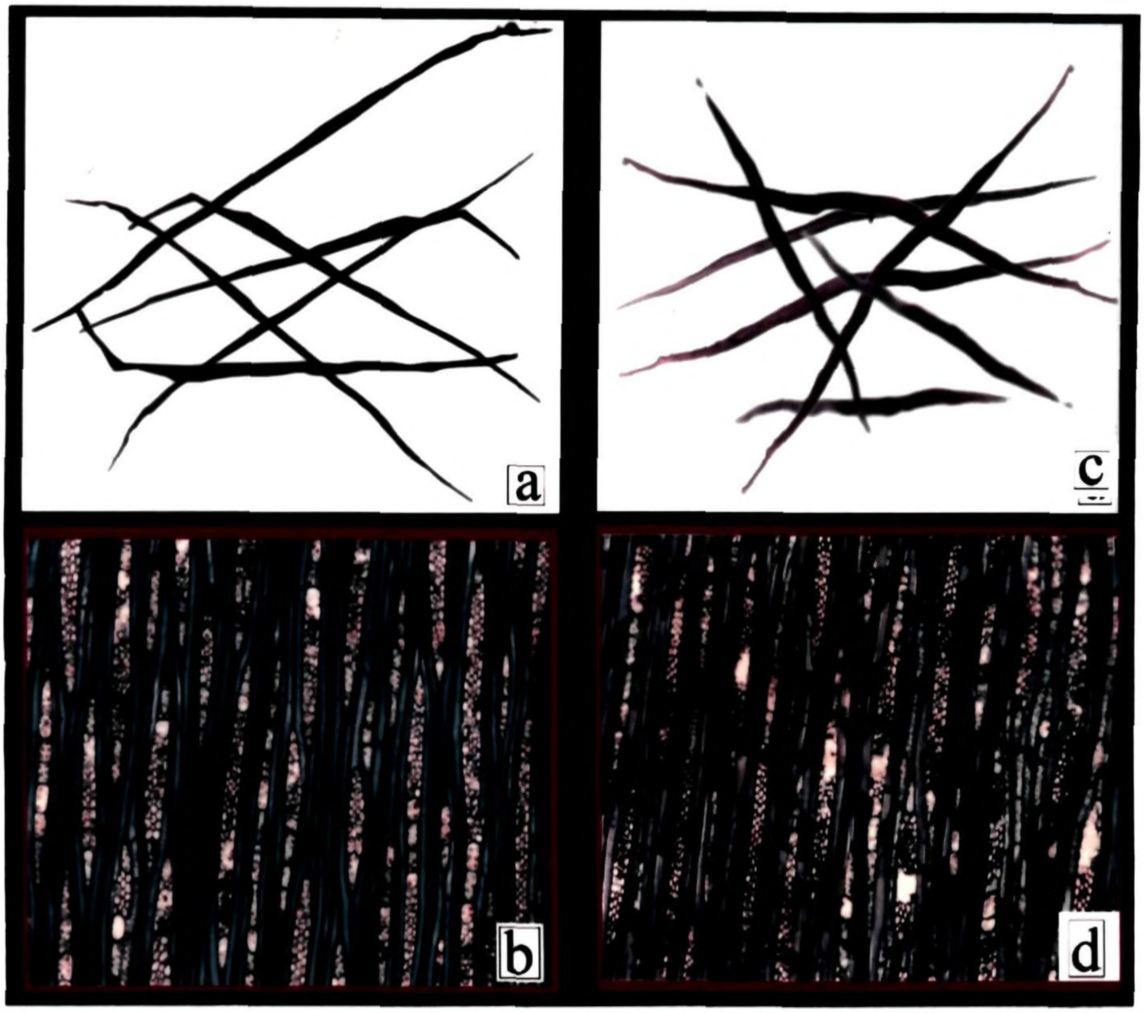


Fig. 23. Morphology of normal and tension wood fibres (after staining with toludine blue O)
a. Macerated normal wood fibres. X55; b. T.L.S. of normal wood fibres. X72;
c. Macerated tension wood fibres. X55; d. T.L.S. of tension wood fibres. X58.

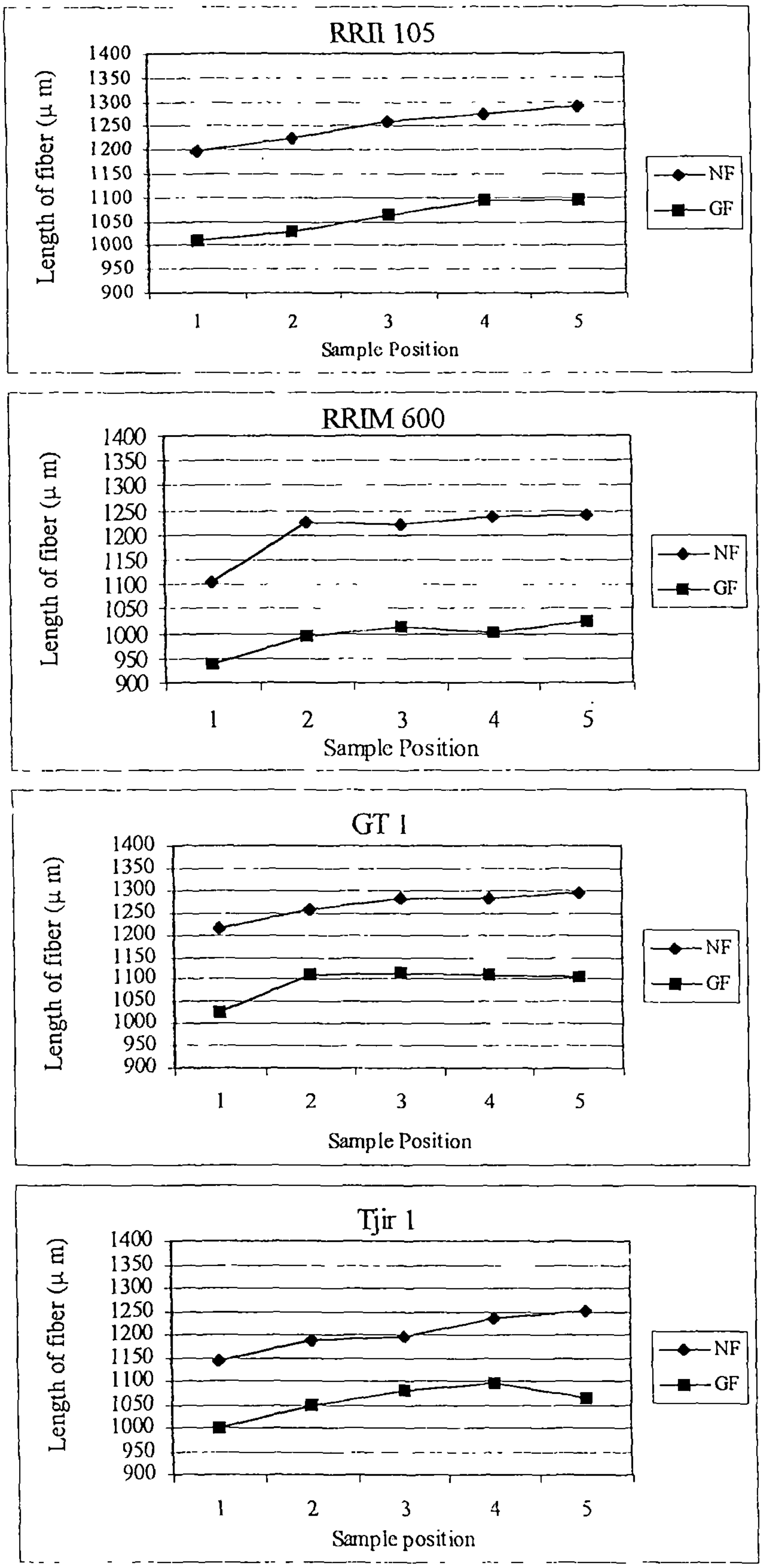


Fig. 24. Length of normal and tension wood fibers from pith to periphery (NF ; normal wood fibres, GF : tension wood fibres)

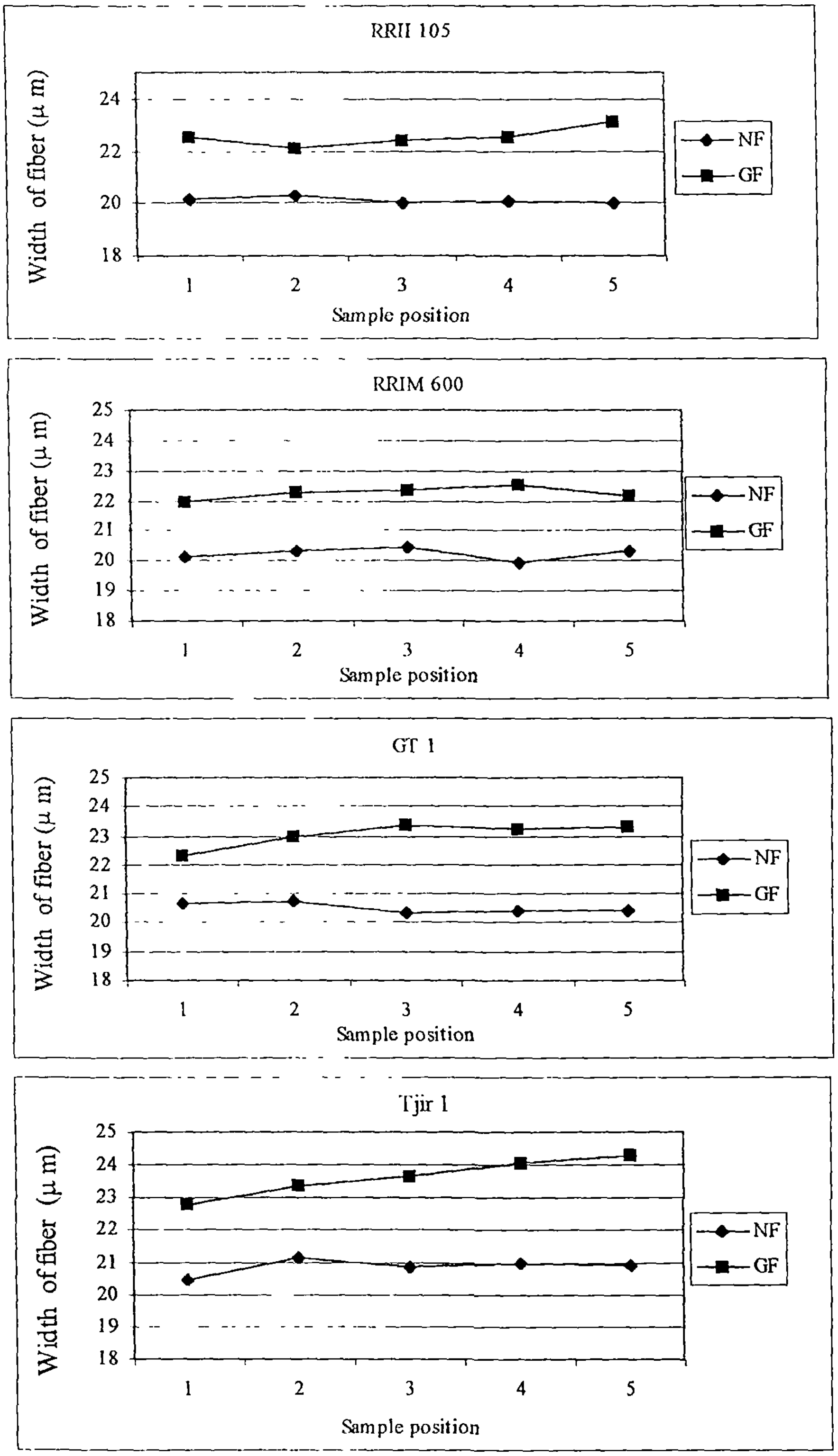
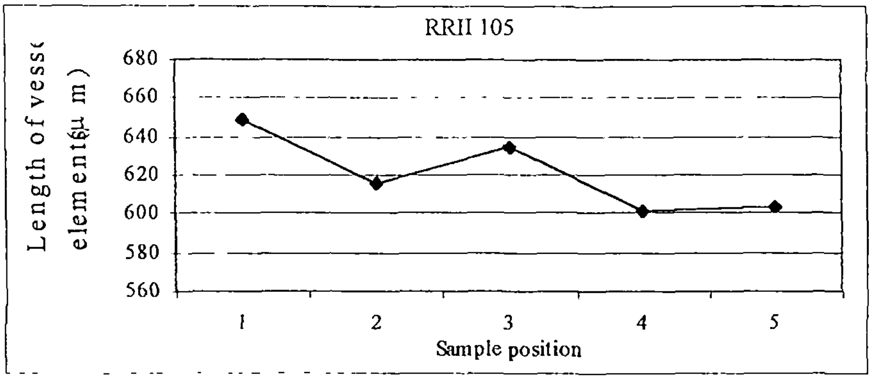
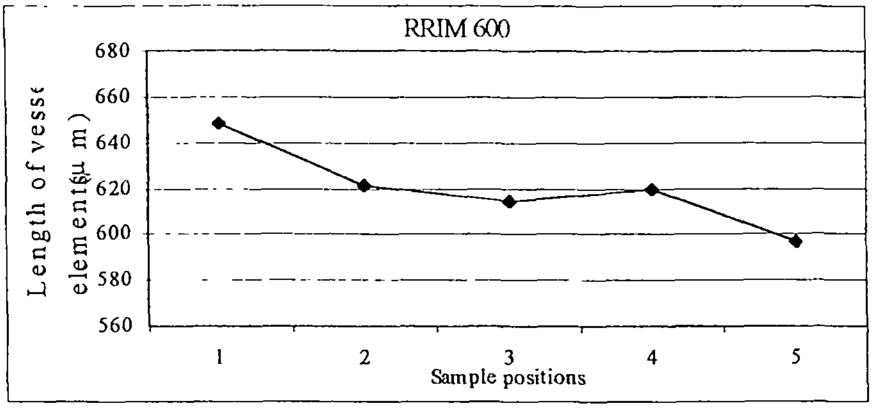
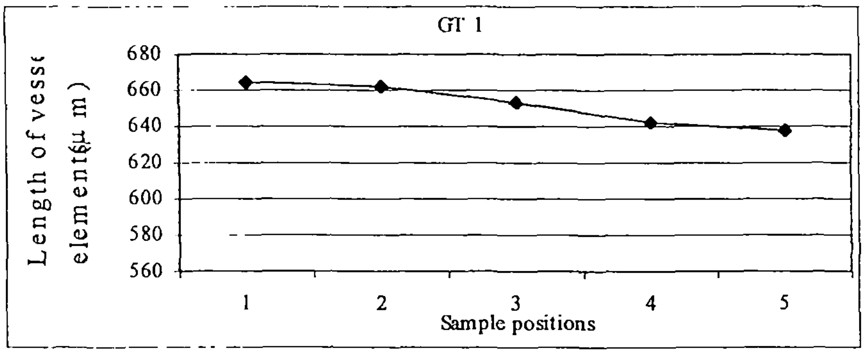


Fig. 25. Width of normal wood and tension wood fibers from pith to periphery
(NF ; normal wood fibres, GF : tension wood fibres)







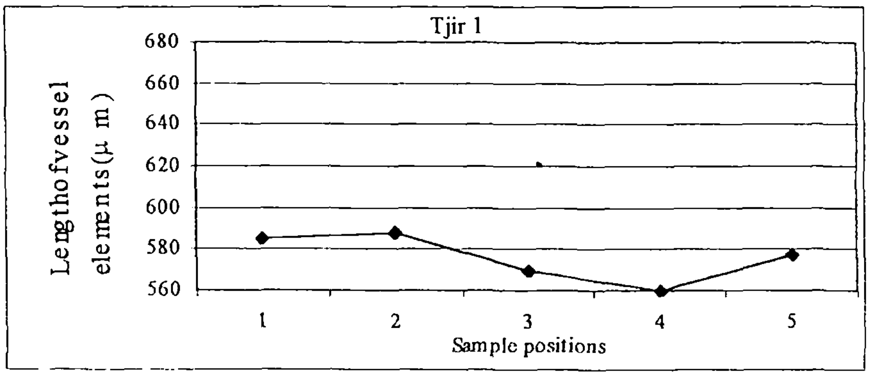


Fig. 26. Length of vessel elements from pith to periphery

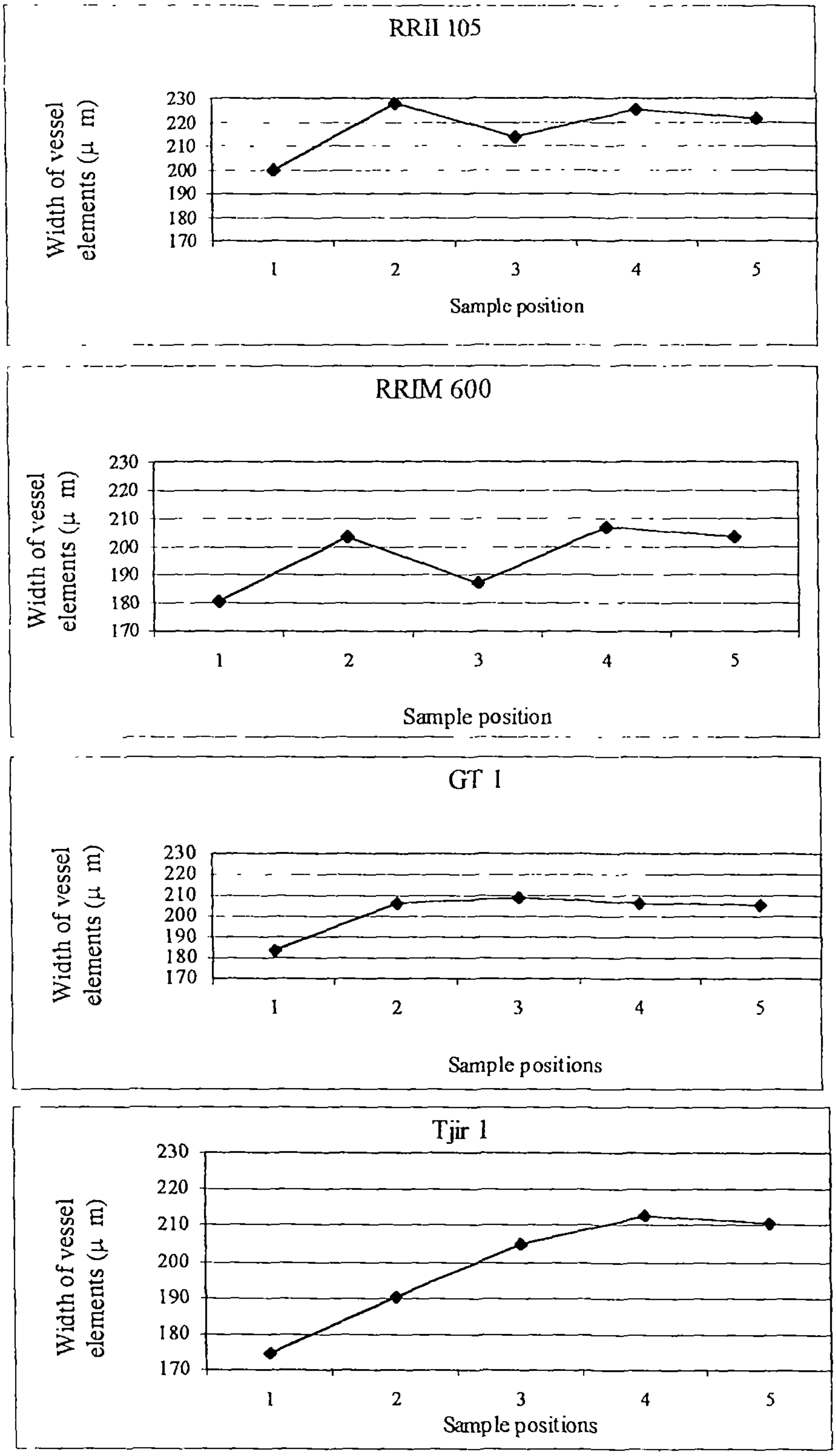


Fig. 27. Width vessel elements from pith to periphery

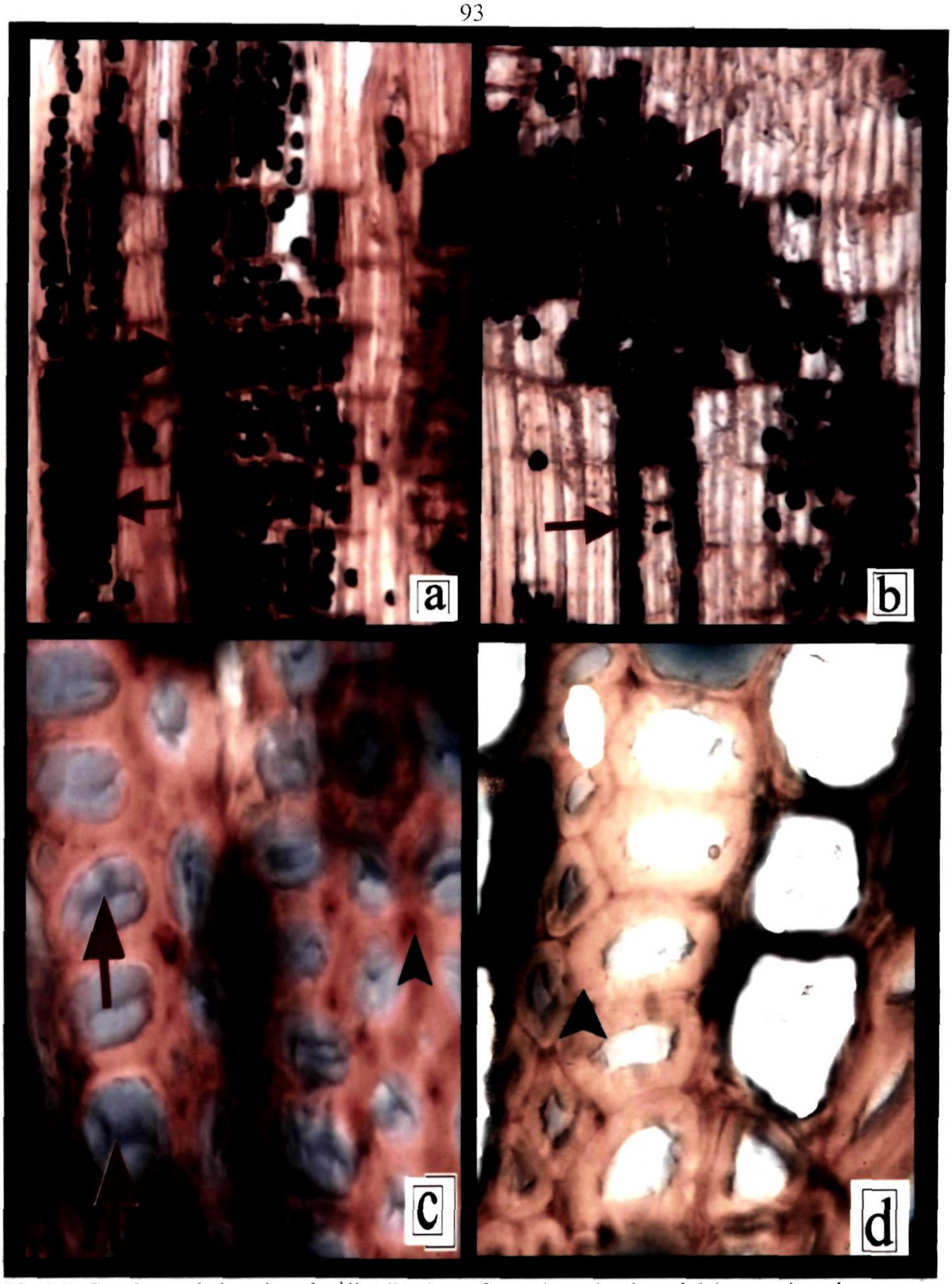


Fig. 28. R.L.S. of wood showing the distribution of starch grains in axial (arrows) and ray (arrow heads) parenchyma cells

a. tension wood zone. X265; b. normal wood zone. X223.

c & d. Localization of cellulose

c. C.S. of tension wood fibres showing cellulosic G-layer (arrows). X843;

d. normal wood fibres. X1016.

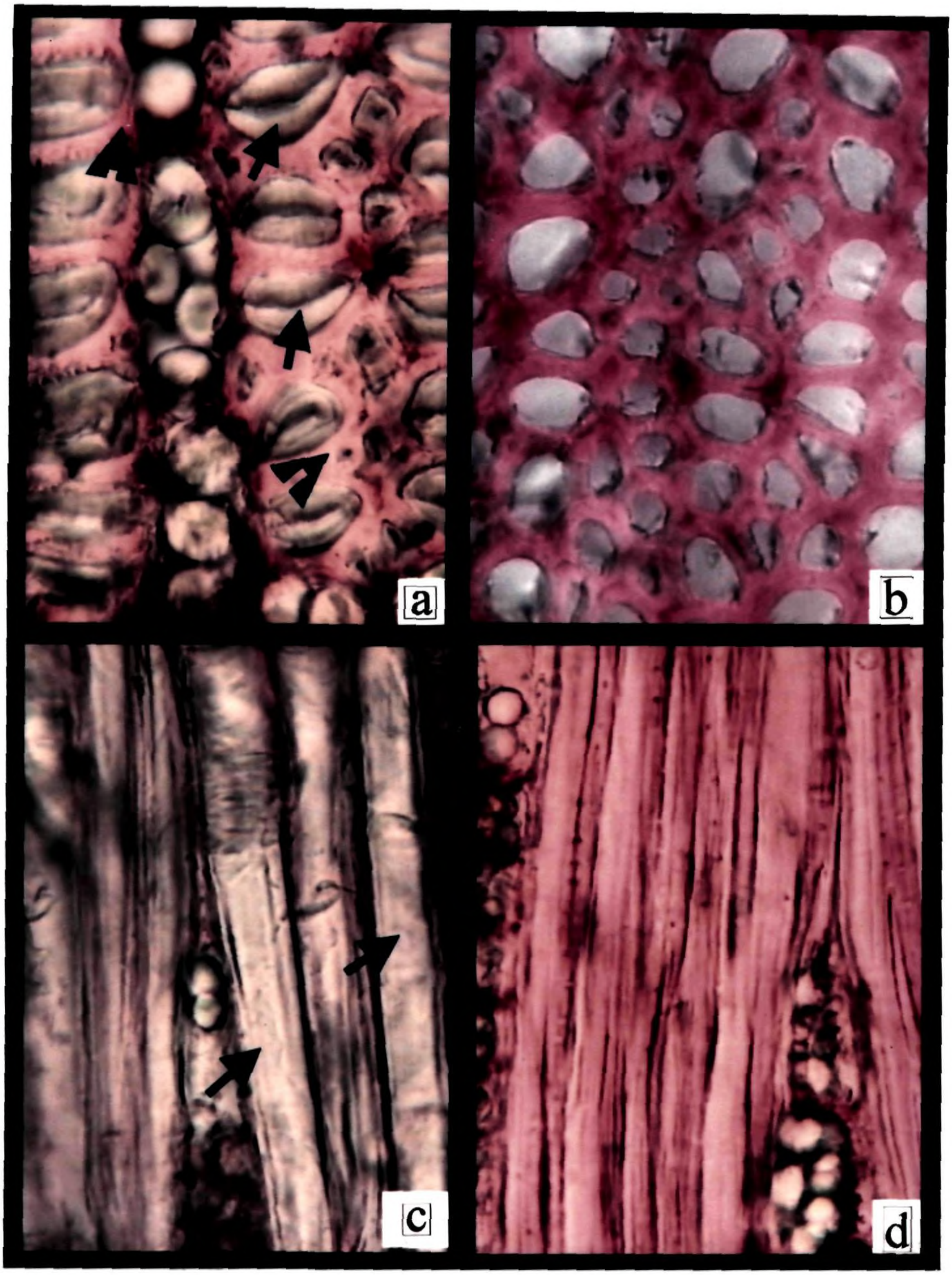


Fig. 29. Localization of lignin in tension wood and normal wood fibres

a. C.S. of tension wood fibres showing unlignified G-layer (arrow). X831;
b. C.S. of normal wood fibres showing lignified wall (arrow head). X476;
c. T.L.S. of tension wood fibres showing unlignified G-layer. X903;
d. T.L.S. of normal wood fibres showing lignified walls. X503.

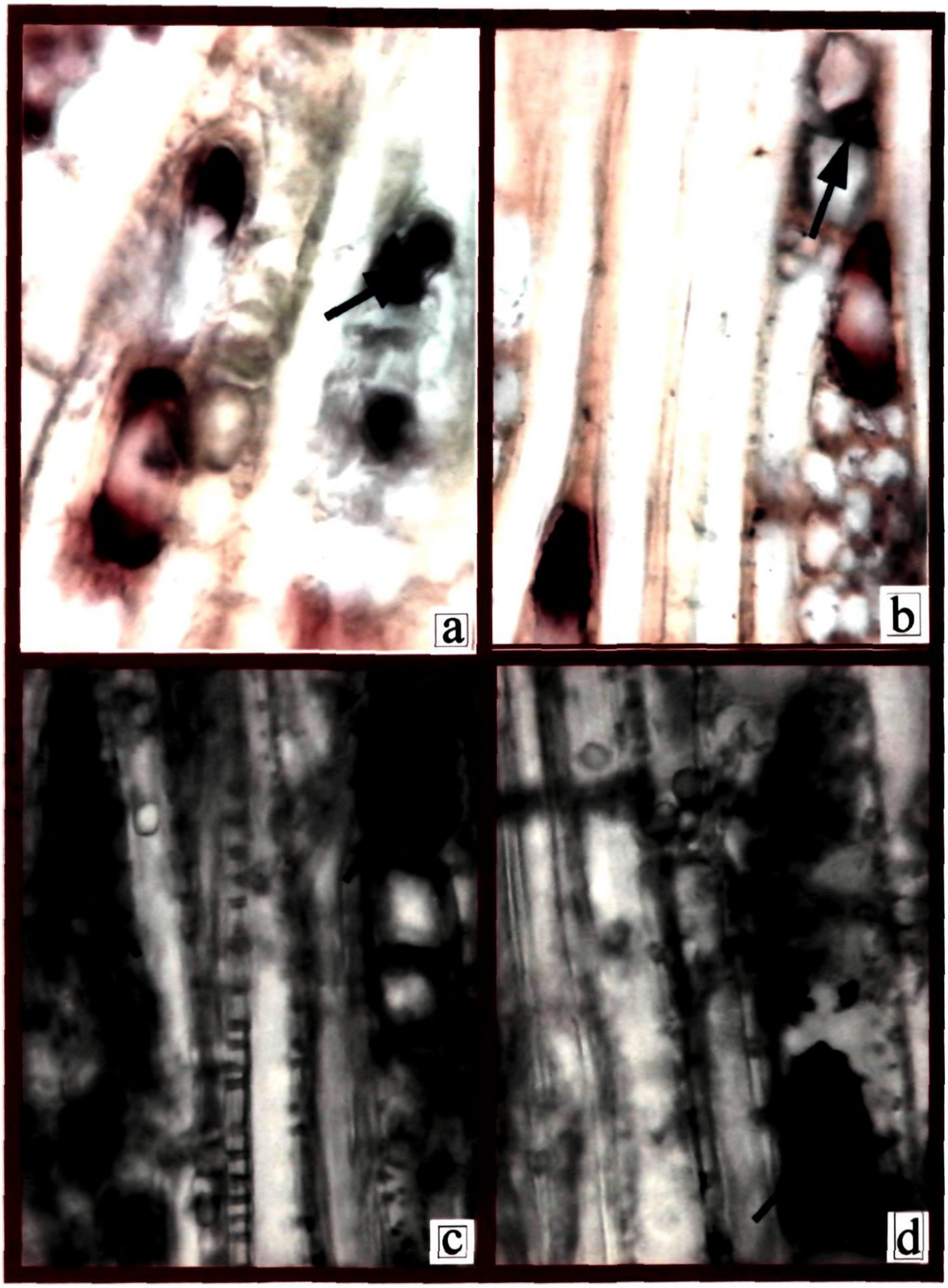


Fig. 30. a&b. T.L.S. of wood showing localization of lipids (arrows)
a. tension wood zone. X506; b. normal wood zone. X451.
c&d. T.L.S. of wood showing localization of total proteins
c. tension wood zone. X660; d. normal wood zone. X864.

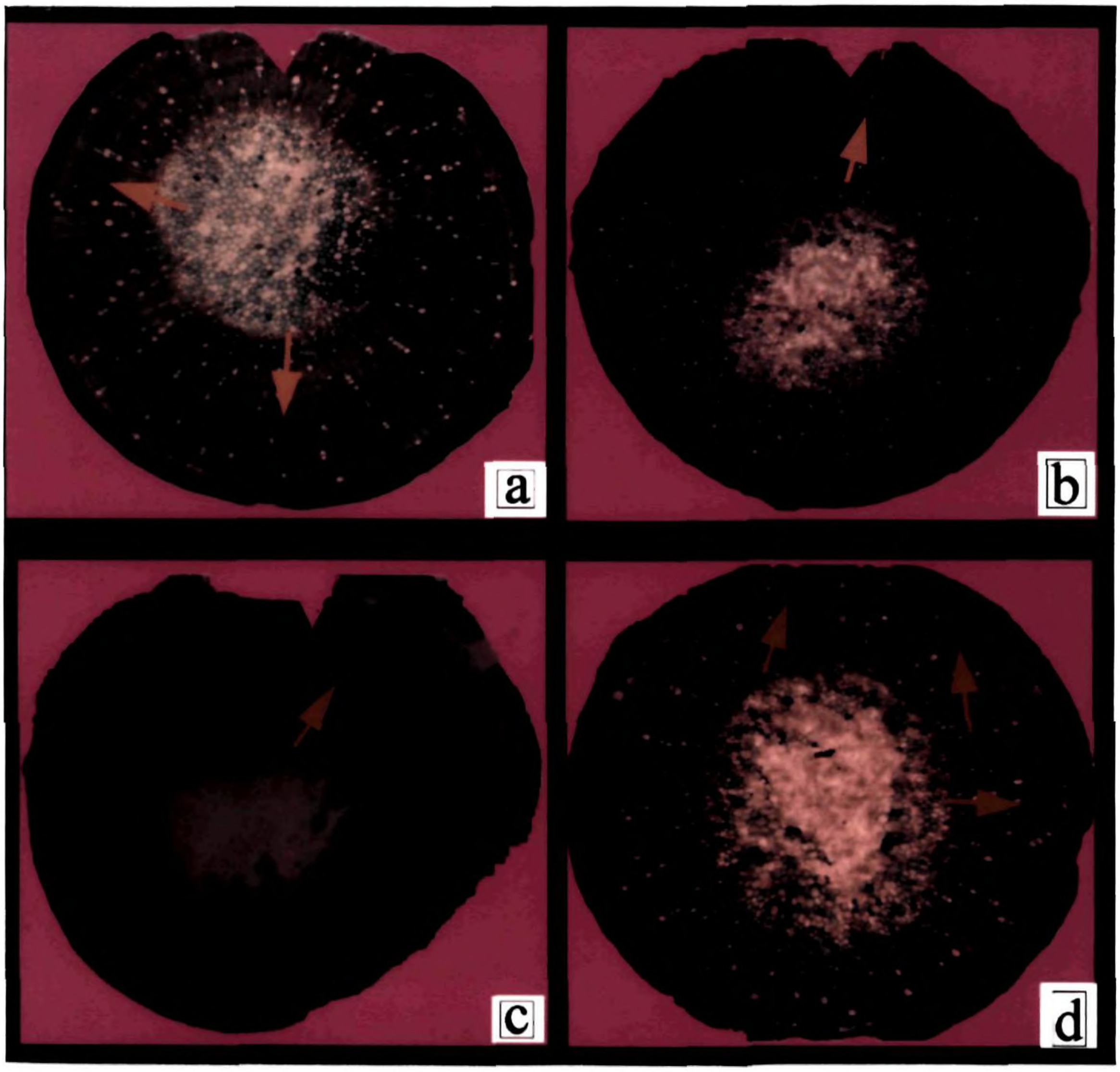
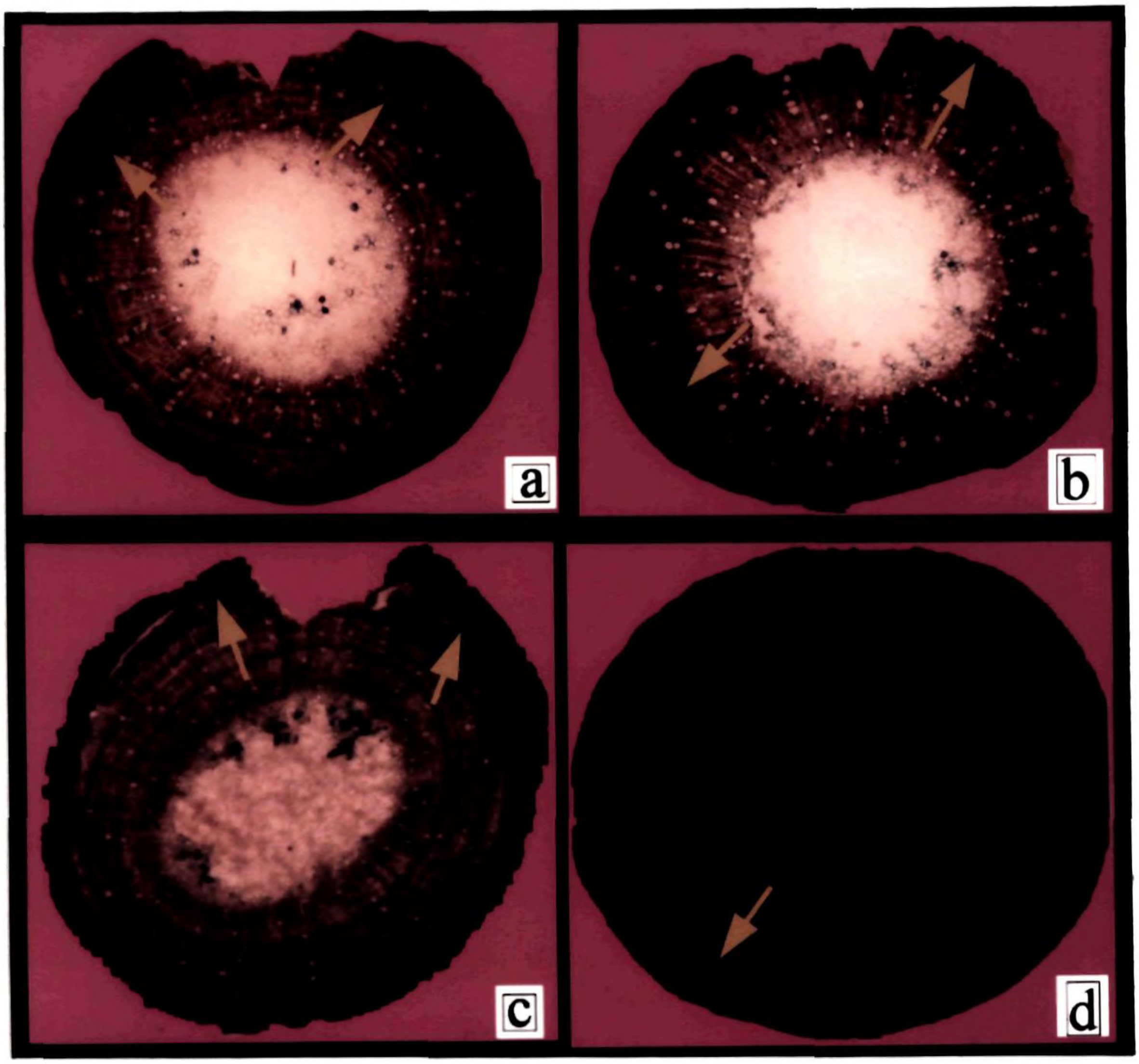


Fig. 31.C.S. of wood showing distribution of tension wood (arrows) in four month old inclined and vertical seedlings (notches indicates the upper side of the bent axis) a. seedling bent at 45^0. X16; b - seedling bent at 90^0. X14; c. seedling bent at 135^0. X15; d. Seedling grown vertical. X20.



. 32. C.S. of wood showing distribution of tension wood (arrows) in four month old defoliated, inclined and vertical seedlings (notches indicates the upper side of the bent axis)

a. seedling bent at 45^0 . X16; b. seedling bent at 90^0. X18;
c. seedling bent at 135^0. X16; d. seedling grown vertical. X18.

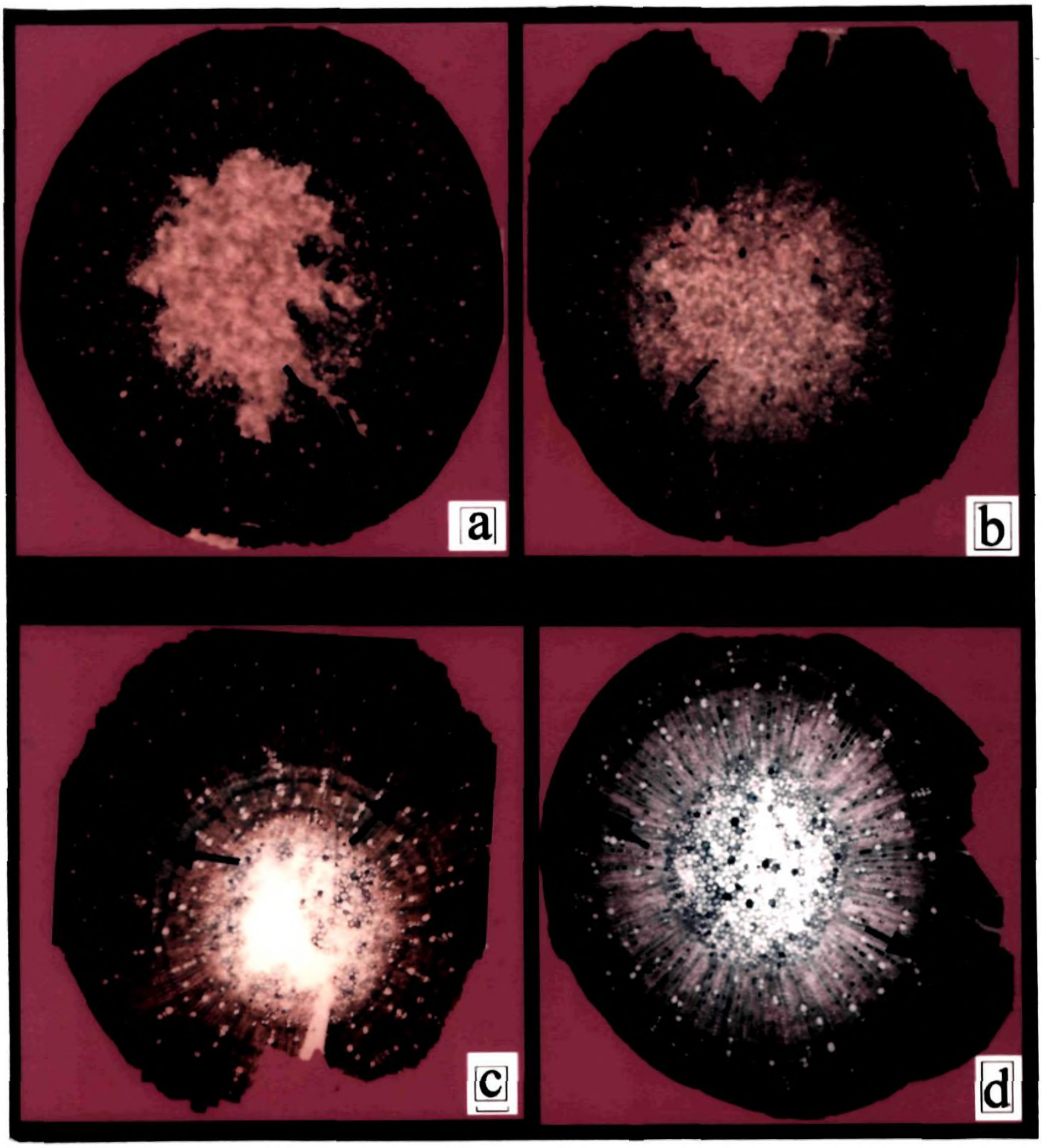


Fig. 33. C.S. of wood showing distribution of tension wood in different segments of the loop (arrows)

a. sample portion before looping (SBL). X17; b. upper part of the loop (UPL). X14;
c. lower par of the loop (LPL). X18; d. lateral part of the loop (LtPL). X18.

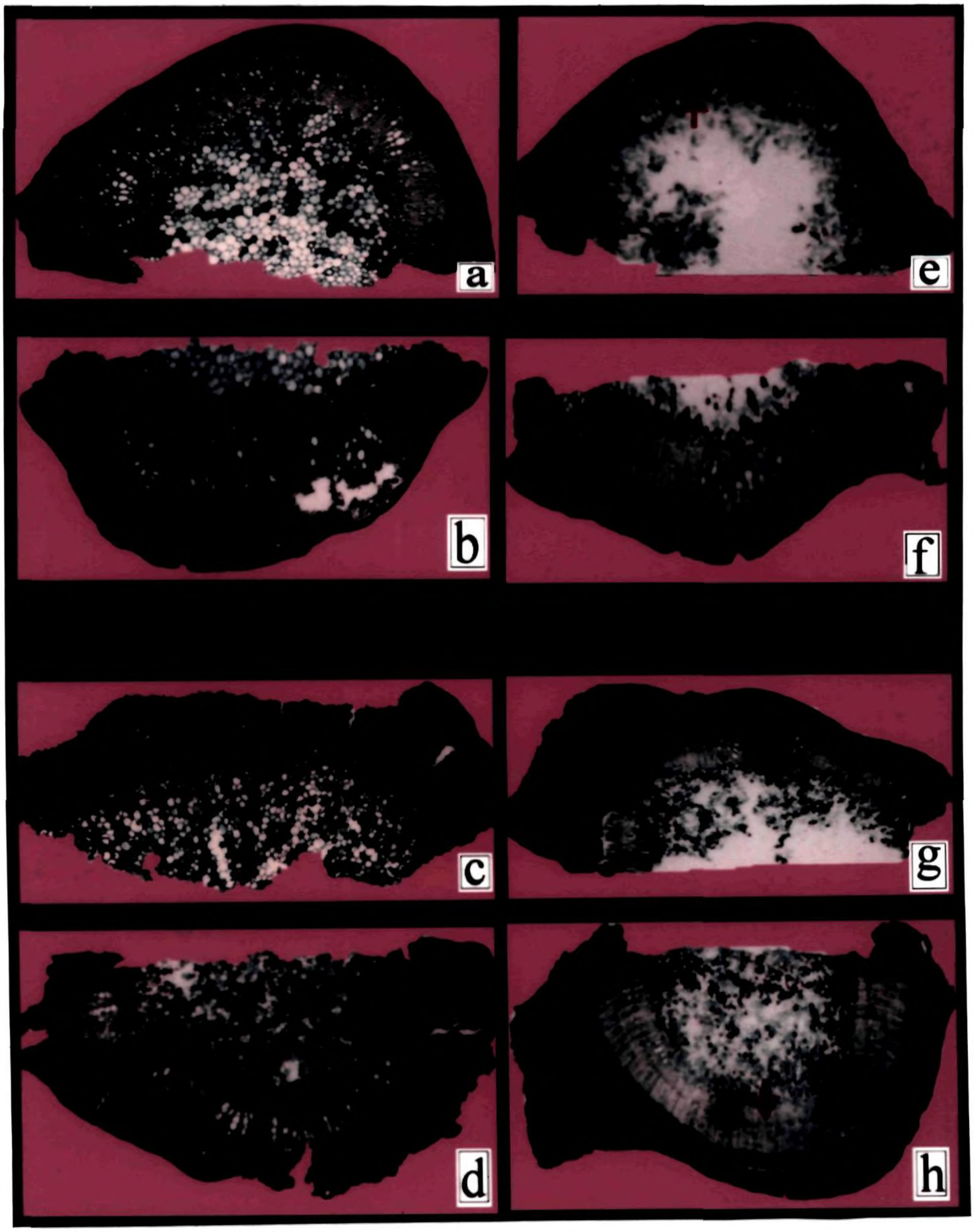


Fig. 34. C.S. of wood from upper and lower halves of the bent axis treated with IAA and GA_3
a-d : IAA a. upper half treated with IAA. X26; b. lower half treated with lanolin. X32 ;
c. upper half treated with lanolin. X35; d – lower half treated with IAA. X24;
e - h : GA_3 e. upper half treated with GA_3 showing tension wood formation (arrow). X35;
f. lower half treated with lanolin. X21; g. upper half treated with lanolin. X13;
h. lower half treated with GA_3 showing tension wood formation (arrow). X14.

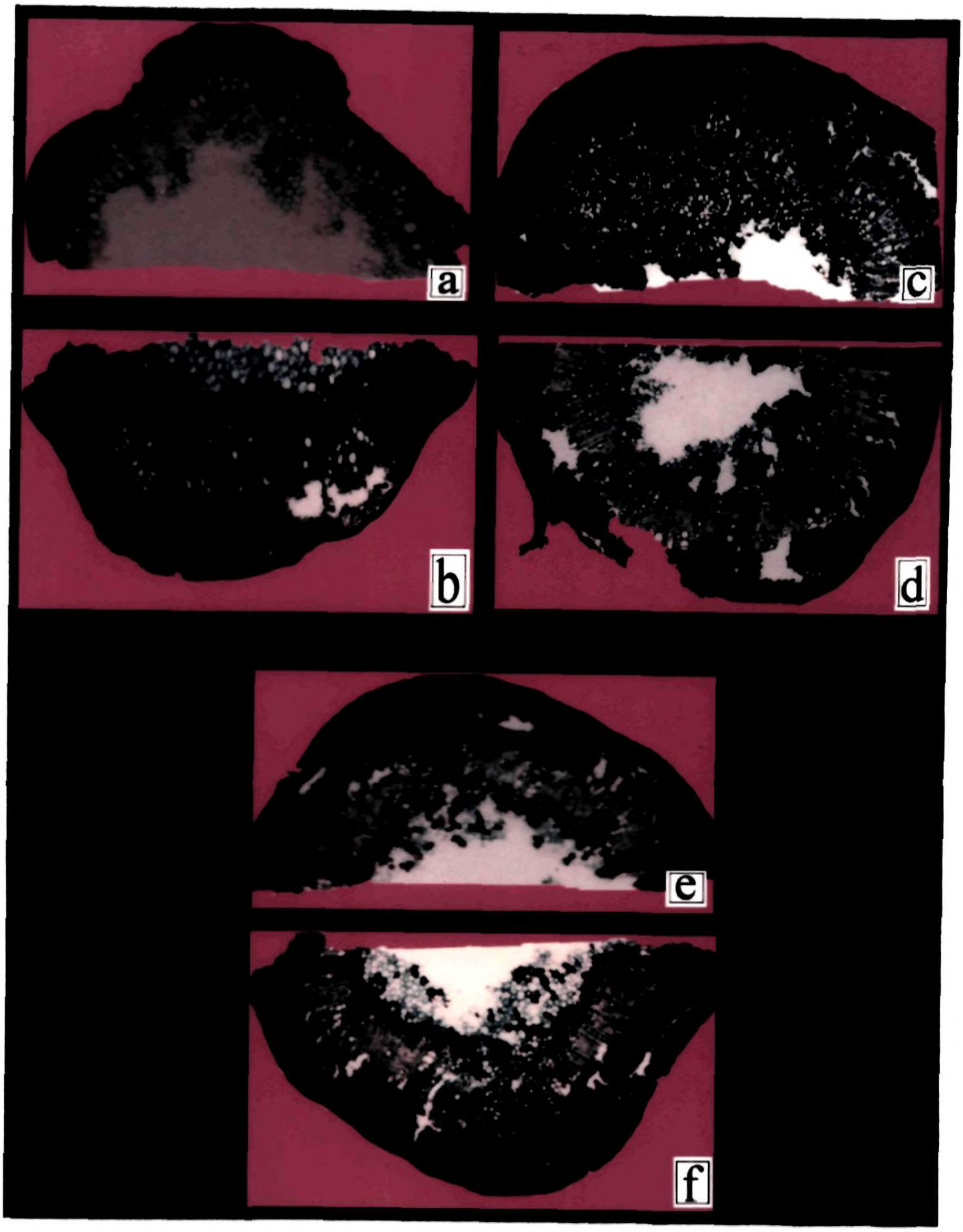


Fig. 35. C.S. of wood from upper and lower halves of the bent axis treated with TIBA and lanolin (control)

a - d : TIBA a. upper half treated with TIBA. X30; b. lower half treated with lanolin. X31; c. upper half treated with lanolin. X22; d. lower half treated with TIBA. X22;

e - f : Lanolin e. upper half treated with lanolin. X22; f. lower half treated with lanolin. X22.

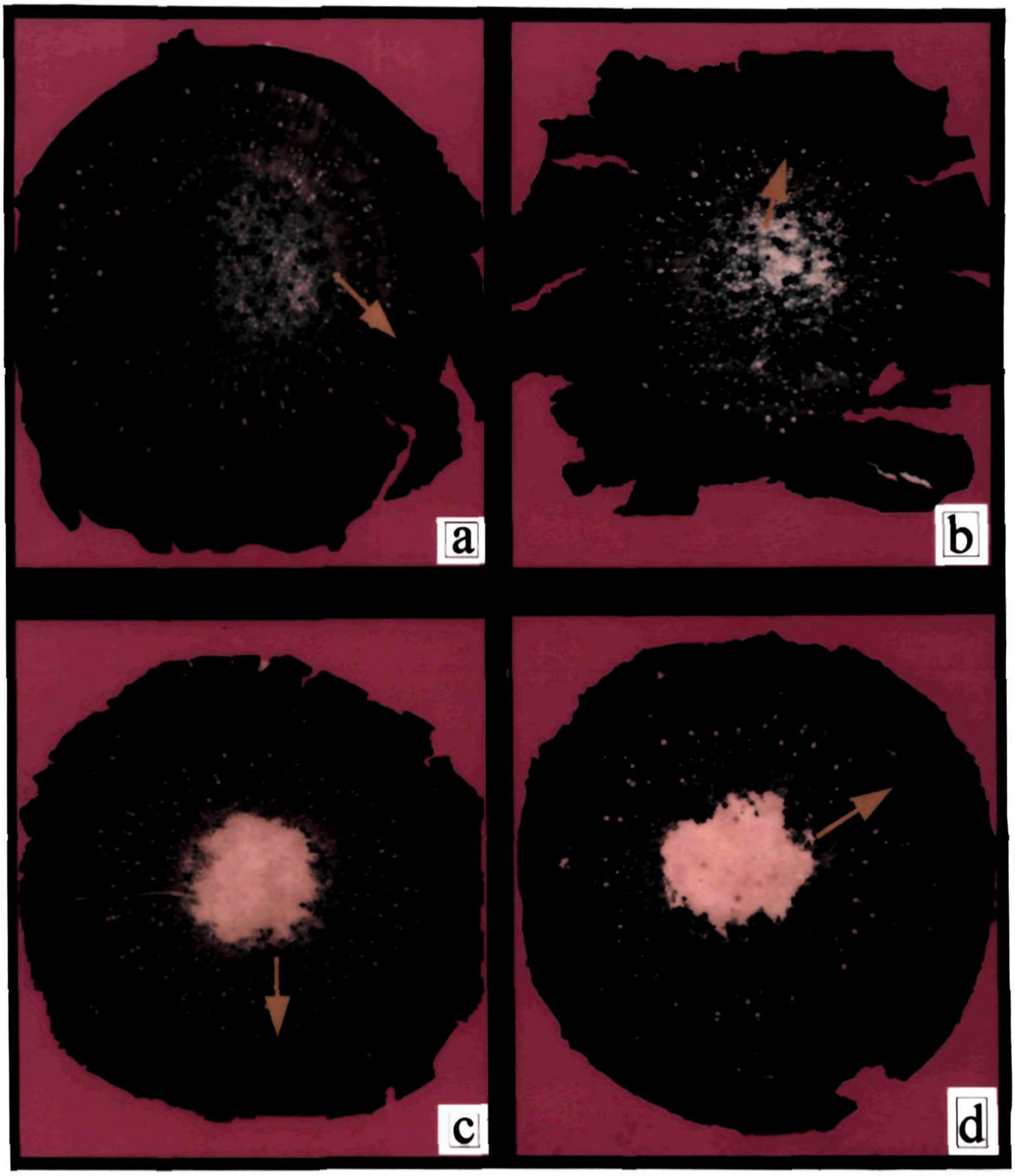


Fig. 36. C.S. of wood showing distribution of tension wood (arrows) in vertical plants treated with lateral application of IAA, GA_3 and TIBA

a. lateral application of IAA on vertical plants. X16;
b. lateral application of IAA on vertical plants (showing high bark tissue formation). X15;
c. lateral application of GA_3 on vertical plants. X10;
d. lateral application of TIBA on vertical plants. X18.

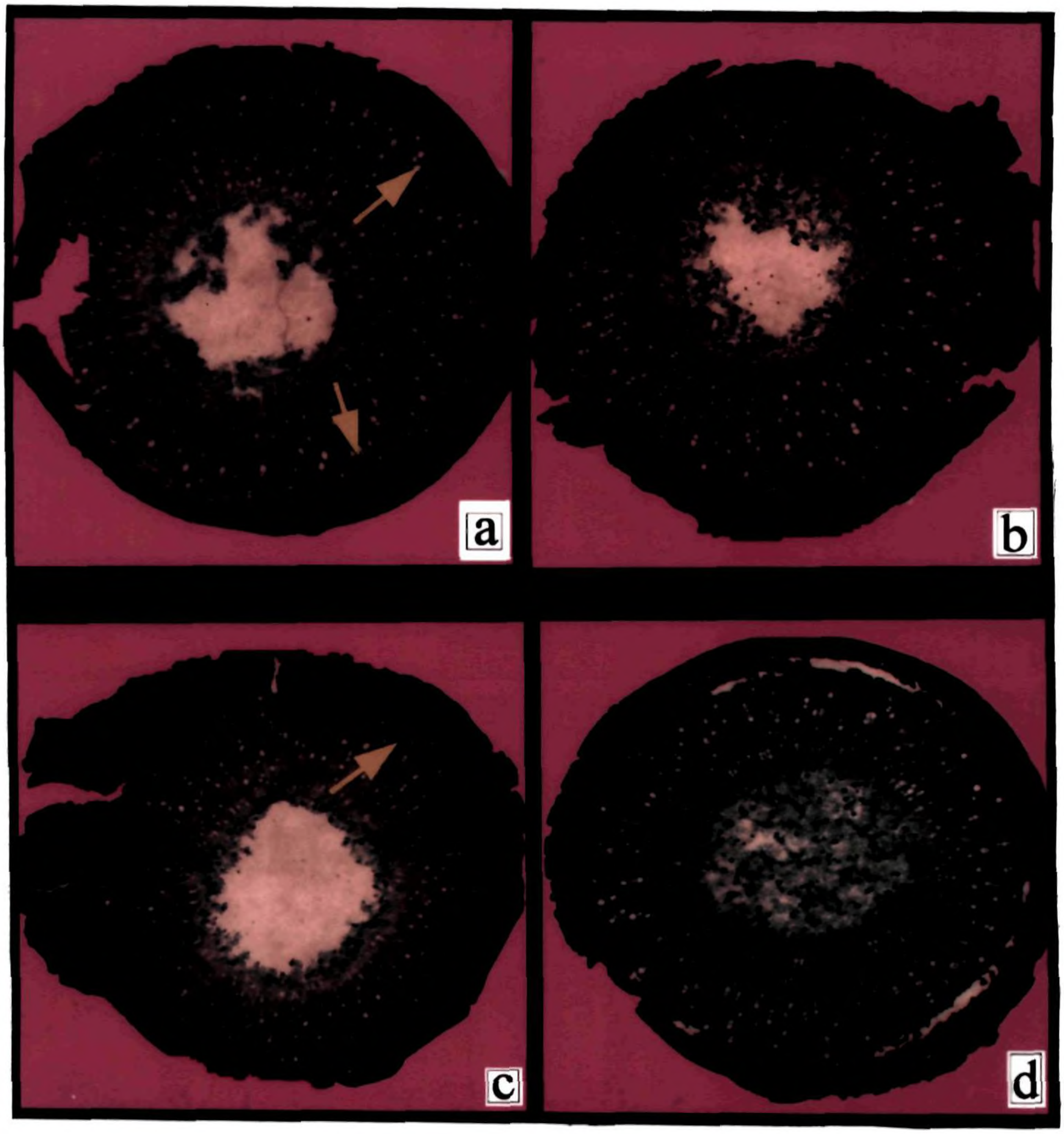


Fig. 37. C.S. of wood showing distribution of tension wood (arrows) in vertical and inclined plants treated with lateral application of IAA and TIBA

a. lateral application of lanolin on vertic⁻ˡly growing plants(control). X15;
b. lateral application of IAA on vertical plants through the excision of bark. X13;
c. lateral application of IAA on plants bent at 45^0. X13; d. lateral application of TIBA on plants bent at 45^0. X13.

CHAPTER 5

DISCUSSION

5.1 Distribution pattern of tension wood in *Hevea brasiliensis*

The investigation on tension wood is of both practical and scientific importance. Tension wood formation is generally considered as a modification of normal wood structure of hardwood species and its occurrence causes problems in various sectors of timber utilization. This is mainly due to the heterogeneous nature of wood and its elements, which have different orientation, architecture, chemical composition, physical and mechanical properties. Hence a better understanding of the structure, distribution and proportion of tension wood in *Hevea brasiliensis* would assist to develop technological solutions in overcoming various problems associated to the industrial utilization of rubber wood.

Formation of compact and diffuse types of tension wood in *Hevea brasiliensis* is a common phenomenon as in other hardwood species (Clark, 1937; Ghosh and Rao, 1958; Hughes, 1965; Ollinmaa, 1956; Bamber, 1976). In rubber wood, the distribution of tension wood is not restricted to a specific zone (Sharma and Kukreti, 1981; Vijendra Rao *et al.*, 1983; Reghu *et al.*, 1989a) as in other hardwoods such as *Populus deltoids* (Kaeiser, 1955), *Terminalia cattappa* (Fisher and Stevenson, 1981), *Sassafras officinale*

(Kucera and Philipson, 1977) *Polyalthia longifolia, Azadirachta indica* and *Mangifera indica* (Reghu, 1983). It is distributed in the upper and lower parts of inclined trunks and branches as well as in vertical trunks. In the present study the compact bands of tension wood were more concentrated in the peripheral and inner zones of the wood in all the clones except in RRII 105, indicating that its formation is more pronounced in the juvenile wood than the mature wood. Jaccard (1938) and Munch (1938) reported that in angiosperm trees, the outer peripheral xylem is in a state of more tensile stress compared to the xylem near the central zone. It has also been established that the formation of tension wood is associated with the tensile stress (Metzger, 1908; Munch, 1938; Sinnot, 1952; Scurfield and Wardrop, 1962) and the present study also confirms this view.

The distribution pattern of tension wood at different height levels within trees showed considerable variation in *Hevea* as reported by Fisher and Stevenson (1981) in various other broad-leaved trees. Sharma and Kukreti (1981) and Reghu *et al.* (1989a) also reported similar type of variation in certain *Hevea* clones.

It is a well known fact that rubber plantations are mostly established in hilly and undulating terrain areas with prominent environmental stresses such as wind, phototropic movements, crown imbalance etc. These uncontrollable stresses normally influence the movement of tree canopy exerting some intrinsic growth stress in the tree trunk, triggering the development of tension wood fibres. The undulating terrain and wind blow also tends the trees to bend and exert tensile stress on the upper portion of the bent axis leading to the formation of tension wood. According to Tomlinson (1978), the formation of tension wood in the lower side of the inclined axis helps the oblique or horizontal branch to restore its ortho-tropical orientation, whereas its formation in the upper half of the tilt axis prevents the branches from further bending below the horizontal plane under its weight.

The formation of tension wood in the vertical stems is not brought out either by the differential growth of the cambium or the lateral displacement of auxins (Brown, 1974). Taylor (1968) believed that the formation of tension wood in non-leaning trees is due to the crown movement in its attempt to obtain sufficient light in dense forest. Nonetheless, Kaeiser (1955), Wardrop (1964), Hughes (1965), Scurfield (1973) and Wilson and Archer (1977) attribute the formation of tension wood in the vertical axes due to the growth stress or loading stress associated to crown imbalance or a little lean. Timell (1973) reported that tension wood formation needs at least 2^0 deflection of the axes from vertical. Therefore, in nature, rubber trees are growing under various stresses (like wind, imbalanced canopy, load of canopy etc) and likely to form certain amount of tension wood even in vertical axes. Hence, the view that tension wood can be present randomly in the tree trunk and branches (Dadswell and Wardrop, 1949) and that tension wood should be considered as a normal component of wood (Wilson and Archer, 1977) holds good.

The formation of tension wood in the upper and lower parts of bent axis restricts further bending of rubber trees in natural environment. The causative factors responsible for the occurrence of tension wood in the lateral zones of the tree trunk in rubber trees may be attributed to the transmission of the internal growth stress from the upper and lower parts of the bent axis towards the lateral sides. Hence it is reasonable to substantiate the view of Fisher and Stevenson (1981) that tension wood formation has an active role in the normal architectural development of trees. In this context, the distribution pattern of compact and diffuse tension wood in *Hevea* may have some role to influence the modification of the normal cellular structure of rubber wood thereby altering its properties and qualities to a great extent.

5.2 Proportion of tension wood in mature trees

In the present study all the clones except RRIM 600 showed an increasing trend in the proportion of tension wood from base to top of the tree trunk. Similar results were also reported earlier in clone PB 86 (Reghu *et al.*, 1989a), PB 260 and RRIM 600 (Sulaiman and Lim, 1992) and in certain unspecified *Hevea* clones (Sharma and Kukreti, 1981; Vijendra Rao *et al.*, 1983). In RRIM 600 the proportion of tension wood was maximum in the middle zone of the trunk and this observation was in accordance with the reports of Dayer (1955), Wardrop (1956) and Reghu (1983) in certain hardwood species. Sulaiman and Lim (1992) also reported significant clonal variability in the proportion of tension wood in PB 260 and RRIM 600. But in the present investigation no significant clonal variability was observed indicating that the proportion of tension wood in mature trees of *Hevea* clones may vary according to the intensity of environmental factors where it grows.

5.3 Proportion of tension wood in the immature phase

Majority of clones in the present study showed a high proportion of tension wood in the immature growth phase. For example, in clones like Tjir 1 and GT 1, the proportion of tension wood was almost double in the immature phase than the mature phase. The clone RRIM 600 had a more or less equal proportion of tension wood in both mature and immature stages. The proportion of tension wood in the mature stage of

RRII 105 was almost 10% less than that of its immature phase. Among the 10 clones, clone Gl 1 was observed with the least incidence of tension wood (14.32%).

In this context, it is reasonable to believe that the triggering factors responsible for the formation of tension wood may be more active in the immature stage than in the mature stage. Therefore, the early growth phase of fast growing trees like rubber, may be more flexible to tissue modification and hormonal imbalance resulting in tension wood formation.

5.4 Proportion of tension wood in bud-grafted and tissue culture plants

The present study revealed that the proportion of tension wood was more in tissue culture plants than that of bud-grafted plants in the immature stage. This is the first report on the comparison between tissue culture plants and bud-grafted plants with respect to tension wood formation.

Bud-grafting is a vegetative propagation technique commonly used for the massive multiplication of planting materials for rubber cultivation. During bud-grafting the root stocks are raised from polyclonal seeds and scions (bud wood) from different clones. Since the stocks and scions are of different genetic entities, the possibility of 'stock-scion interaction' exists in bud-grafted plants. On the contrary, the tissue culture plants used for the present study are raised through micro propagation technique, called somatic embryogenesis, and hence the genetic configuration is always uniform. Therefore, it is assumed that the increase in the proportion of tension wood in tissue culture plants may be a genetic character and such plants are probably more prone to tension wood formation than bud-grafted plants. Moreover, the differentiating media used for somatic embryogenesis contained high concentration of the growth regulator

Gibberellic acid. It is widely believed that Gibberellic acid induces tension wood formation (Reghu, 1983; Yoshida *et al.*, 1999) and enhance cambial activity (Digby *et. al.*, 1964; Shiniger, 1971) and respiratory rate in plants (Koto, 1956; Weller *et al.*, 1957; Nielsen and Berquist, 1958; Halevy, 1964; Adams, 1969). Hence the increase in the proportion of tension wood in tissue culture plants may also be attributed to the activity of Gibberellic acid in the early growth phase.

5.5 Directional effect of tree leaning on tension wood formation

Growth eccentricity in leaning stems and branches is a common phenomenon in angiosperms and gymnosperms (Cote and Day, 1962) The asymmetrical growth of the stem together with the formation of tension wood and compression wood in angiosperms and gymnosperms, respectively has been considered as a mechanism by which the normal predetermined growth position of the stem is retained or re-attained (Sinnot, 1952) Moreover, these features of secondary growth play an active role in the normal architectural development of the tree (Tomlinson, 1978; Fisher and Stevenson, 1981). Patel *et al.*, (1984) studied the direct relationship between growth eccentricity and specimen angle in *Kigellia pinnata* and reported that the growth eccentricity decreased with increase in specimen angle. Fisher and Stevenson (1981) extensively studied the influence of tension wood formation in tree architecture in various hardwood species including *Hevea brasiliensis* and classified *Hevea* under Raugh's model of tree architecture, where the orientation of the tree axis increased with a corresponding increase in the development of tension wood fibres in the upper and lower parts of the bent axis. The authors further proved that the increase in the leaning angle of branches in *Hevea brasiliensis* initiated tension wood formation in the lower side of the bent axis.

The correlation between the angle of leaning, growth eccentricity and proportion of tension wood in mature growth phase of rubber trees, in the present investigation, revealed that the angle of inclination increased from base to top of the tree trunk where as the percentage of growth eccentricity showed a reverse trend.

The highly significant correlation between angle of leaning and tree height was in accordance with the similar findings made by Akachuku and Abolarin (1989). This is presumably due to the fast growing nature of rubber trees in association with effect of internal growth stress resulting from the movement of canopy and axis displacement as suggested by Wardrop (1964), Hughes (1965), Scurfield (1973) and Wilson and Archer (1977).

In three clones viz. RRII 105, GT 1 and Tjir 1 the growth eccentricity gradually increased with a corresponding increase in tree height. Similar type of growth eccentricity has also been reported earlier by Patel *et al.* (1984) in *Kigellia pinnata.*

Patel *et al.* (1984) reported a decrease in growth eccentricity with an increase in leaning angle as observed in RRIM 600 in the present study. Kaeiser and Boyce (1965) did not find any correlation between leaning angle and eccentricity as observed in the case of RRII 105, Tjir 1 and GT 1. Hence the growth eccentricity may be increased or decreased with tree leaning in relation to variation in the rate of cambial activity in upper and lower parts of the inclined axis.

None of the clones in the present investigation showed significant correlation between leaning angle and proportion of tension wood indicating that changes in axis orientation may not be a major factor to enhance tension wood formation in *Hevea.* The influence of factors such as internal growth stress and increased longitudinal tensile stress caused by uncontrollable movement of canopy due to wind blow etc. leads to various structural changes in the wood fibres during secondary growth, thus switching over to tension wood formation in *Hevea brasiliensis*.

It has already been reported that tension wood formation is associated with pith eccentricity in many broad leaved species (Wardrop, 1964; Harris, 1977; Timell 1986) and also in *Hevea* (Reghu *et al.*, 1989a). Akachuku and Abolarin (1989) studied pith eccentricity and its association on tension wood formation in *Tectona grandis* and proved the non-relationship between the degree of pith eccentricity and the proportion of tension wood formation. The results of the present study is in accordance with this view as revealed by the non-correlation between pith eccentricity and proportion of tension wood. Hence the magnitude of pith eccentricity need not be considered as a criteria to ascertain the extent of tension wood formation in *Hevea.* The remarkable increase in the cambial activity towards one side of the axis and the suppression of meristematic activity on the opposite side may be responsible for growth eccentricity.

5.6 Proportion of tension wood in tapped and untapped regions within trees

A comparative analysis on the quantity of tension wood between tapped and untapped trees could not be possible due to the non-availability of tapped and untapped trees of identical age in mature plantations. Hence an attempt has been made to ascertain the extent of tension wood formation in tapped and untapped zones within trees.

In three clones viz. Tjir 1, RRII 105 and RRIM 600, tension wood formation was more in the untapped region of the trunk (at 300 cm height) than the tapped region (at 60 cm height). While in GT 1 the proportion of tension wood was identical in both tapped and untapped regions.

The reduction in the proportion of tension wood in the tapped region of trees may be attributed to the reduction in the rate of cambial activity inhibited by wound hormones as suggested by Brown (1937). In fact tapping is a continuous wounding process to extract latex from rubber tree. During this process, major portions of the photosynthates are diverted to latex production which in turn limits the differentiation of wood elements as well as the synthesis of cell wall materials. Hence it is reasonable to assume that tapping practices may reduce the development of tension wood fibres in *Hevea.* Since the present study gives only an indication to the variation in the proportion of tension wood in tapped and untapped zones within trees, a systematic comparison between tapped and untapped trees of identical age only helps to explain the role of tapping, if any, on tension wood formation in rubber.

5.7 Tension wood formation and wind damage

The mechanism of tree failures such as trunk snap, branch snap and root snap .in relation to wind loading and tensile / compressive stresses in forest trees has been studied extensively by Matthck and Bethge, (1990). It has been proved that the wind generally affects the weakest point of the tree where tensile / compressive stress is very prominent. The wind load acting on a tree initially transmitted to the root-stem transition zone and the resultant forces later acting away from the root stem transition zone towards the upper trunk zone. Wind breakage starts by de-lamination of the root stem transition zone at the wind exposed side of the tree. The de-lamination weakens the resistance of the tree on the tensile side (upper side) of the inclined axes leading to fibre buckling at the compression side (lower side). This results in the fibre rupture at the tensile stressed region of the tree. If the wind blow is sufficiently strong, especially on trees growing in an inclined direction, this de-lamination may occur and initiate a crack running up the tree. Large amplitude of tree canopy may cause additional bending supported by wind loading. This leads to maximum tree failure through fibre rupture on the upper side and fibre breaking on the opposite side leading to trunk snap. Matthek and Bethge, (1990) further proved that formation of buttress roots reduce the delaminating forces and protect the tree from wind breakage.

In view of the above mechanism, it is inferred that the intensity of tensile stress in leaning trunk in hard wood species like *Hevea* increase the proportion of tension wood by producing unlignified and weak gelatinous fibres and hence fibre rupture is possible in such tension wood zones leading to trunk snap.

The present study revealed that in *Hevea brasiliensis* the trunk snap phenomenon may have some relation to tension wood formation as per the mechanism of wind breakage in trees as described by Matthek and Bethge (1990). However the exact mechanism of wind breakage in rubber plantations and the direct role of tension wood in this phenomenon is yet to be elucidated in detail.

5.8 Visual identification of tension wood

Researchers so far concentrated on the identification of tension wood fibres at microscopic level through various staining procedures. The identification and demarcation of tension wood zone at macroscopic level would help to avoid such weakest zones during sawing operations. In Poplar, Grzeskowiak *et al.* (1996) tried to demarcate tension wood and normal wood zone by using a combination of Zinc Chloride and Iodine. In the present study aqueous zinc chloride solution is mixed with aqueous potassium iodide and iodine solution to form zinc-chloro iodide. When the reagent is applied on fresh wood disc, the zinc-chloro iodide reacted with the unlignified cellulosic G- layer of tension wood fibres giving the brownish pink colour. The application of this reagent on the cut ends or the surface of the sawn planks in green condition was found to be suitable for demarcating tension wood zones as brownish pink clouration in contrast to the yellow colour in normal wood zones. Studies on the economic feasibility of this macroscopic staining procedure and its extensive utilization in the primary rubber wood processing sectors like selective / differential sawing patterns would help to avoid tension wood zones to a considerable extent, as this reagent is very cheap, non-toxic and eco-friendly.

5.9 Structural studies on tension wood

5.9.1 Fiber length

The size of the cambial initials is an important parameter which determine the size of wood elements (Philipson *et al.*, 1971). The variation in the size of cambial initials bringing about variations in the dimensions of wood elements, and are associated with the frequency of transverse divisions, size difference between parent and daughter cells and the preferential loss of initials (Philipson and Butterfield, 1967). Hence the study of wood elements explains the history of cambial cells.

Generally tension wood is considered as the abnormal tissue produced by the cambium in tune with gravitational stimulus induced by the displacement of the axis from its equilibrium position (Wardrop, 1964; Cote *et al.*, 1969; Fisher and Stevenson, 1981). From mechanical point of view, tension wood fibres are highly susceptible to longitudinal shrinkage (Fournier *et al.*, 1990). It is the wood fibre that show the most important anatomical, mechanical and chemical modifications during tension wood formation. Therefore all the modifications occurred in wood fibre must be observed simultaneously to explain the particular behavior of tension wood tissues and its derivatives (Kaeiser and Boyce, 1965). Very often the formation of tension wood on the upper side of the inclined stems and branches in association with growth eccentricity, is related to the proliferation process in the cambial zone (Campredon, 1953; Jane, 1956; Koch *et al.*, 1968).

In many hardwood species, tension wood fibres are longer than normal wood fibres (Chow, 1946; Onaka, 1949; Ollinmaa, 1961; Rao, 1983). Nevertheless, they may shorter or longer or equal in length than NF (Dadswell and Wardrop, 1956).

In the present investigation an attempt has been made to understand the extent of dimensional variation (length and width) of normal and tension wood fibres of *Hevea brasiliensis*. In all clones, the length and width of normal and tension wood fibres increased from pith to periphery. This result is in confirmation with the earlier reports in the clones PR 107 and RRIM 600 (Amin, 1986), and in PB 86 (Reghu *et al.*, 1989a).

The fibre length was inversely related to the radial growth of axis and increased duration of cambial division brings about differentiation of longer fibres (Wardrop, 1964). In the present study, it was observed that the tension wood fibres were shorter than normal wood fibres in all clones as reported by Reghu *et al.* (1989a) in the clone PB 86. Investigations of Amin (1986) and Reghu *et al.* (1989a) revealed that an increase in length of fibres from pith to periphery with longer fibres near the bark region. Even though a steady increase in fibre length was not observed, the longest fibre was observed in the peripheral zone. Similar reports were also reported in other hardwood species (Dinwoddie, 1961; Taylor and Wooten, 1973). Amin (1986) opined that at a certain stage of fibre development, the ultimate length is obtained from the fusiform initials of the cambium and it is believed that any external forces such as tapping, climatic changes, responses to leaf fall etc. during fibre development influences variation in fibre length.

Amin (1986) and Bhat *et al.* (1984) did not find any significant difference in the fibre length of *Hevea brasiliensis* between different height levels. Similar trend was also observed in all the clones of the present study. According to Fahn (1982) the length of fibres differ from that of fusiform initials, due to the intrusive growth and division of differentiating fusiform initials. Hence the variations in fibre length between normal wood fibres and tension wood fibres may be attributed to the variation in the rate of division and intrusive growth of fibre primordia. It has also been reported that the fibre length is inversely related to the radial growth of the axis. An increased duration of cambial division brings about the differentiation of longer fibres and eccentricity of radial growth of axis, whereas an increased rate of radial division causes radial growth increment and differentiation of shorter fibres (Wardrop, 1964). Taking these aspects into consideration, it appears that the decrease in the length of tension wood fibres observed in all the clones studied may be due to the increased rate rather than the increased duration of cambial division during the differentiation of tension wood.

5.9.2 Fibre width

In all the clones studied, the width of tension wood fibres was significantly higher than that of normal wood fibres indicating that tension wood fibres were short and broad as reported by Reghu *et al.* (1989a) in clone PB 86. The fibre width and wall thickness of both type of fibres are varied at different height levels and even between clones. The increased fibre width and wall thickness observed in the basal portion of the tree trunk may be attributed to the increase in the thickness of secondary walls due to ageing, as the fibres present in the basal portion of the tree trunk are ontogenically mature compared to those found in the upper portion of the trees.

5.9.3 Fibre wall thickness

Okumura *et at.* (1977) reported that the increase in the wall thickness of tension wood fibres was mainly due to the increase in the thickness of the unlignified cellulosic G-layer of the secondary wall. In the present study the wall thickness of tension wood fibres was significantly higher than that of normal wood fibres in all the clones due to the increase in the thickness of G-layer in the former. Hence the increase in the thickness of G-layer associated with its unlignified nature makes tension wood fibres more weak and thus leads to various wood working problems such as dimensional instability, warping, shrinkage, collapse etc.

5.9.4 Length and width of vessel elements

The variation in the length and width of vessel elements was not significant at different height levels in all the clones studied. Though significant clonal variability was observed in vessel length, the width of vessel elements was not statistically significant. Nevertheless the length of vessel elements did not show any consistent increase or decrease from pith to periphery. However, the vessel length was maximum in the peripheral zone. This result was in accordance with the earlier reports that the length of vessel elements in the wood contiguous to the bark zone could be increased up to 3.1% than those vessels contiguous to the pith. (Lenze, 1954; Carlquist, 1988; and Jourez *et al.*, 2001).

5.9.5 Number of pores

As the distribution pattern, frequency and size of pores generally determine the chemical impregnation capacity of rubber wood during wood preservation, a detailed analysis of pores, especially the number and area occupied by them in tension wood and normal wood assumes significance.

In *Hevea*, the pores are evenly distributed as solitary or radial multiples of 2 to 3 or rarely more (Reghu, 2002). It has been reported that number, size and area occupied by pores are less in tension wood zone in comparison to normal wood zone in many hardwood species (Onaka, 1949; Scurfield and Wardrop, 1962; Cote and Day, 1965; Milvia, 1965; Rao, 1983; Reghu, 1983; Jourez *et al.*, 2001). A reduction in the number of pores in tension wood zone, even up to 33% has been observed in Poplar Jourez *et al.*, (2001). Nevertheless, Kucera and Philipson (1978) did not find any reduction in the number of pores in tension wood zone of *Pseudowintera colorata*. However, in the present investigation the number of pores was significantly less in tension wood zones of two clones *viz.* RRII 105 and RRIM 600, whereas in GT 1 and Tjir 1, it was reverse. As the proportion of tension wood was higher in the former two clones and lower in the latter two clones, it is evident from this study that the variation in the number of pores in *H. brasiliensis* was negatively correlated with the quantity of tension wood formed.

5.9.6 Total area occupied by pores

In all the clones investigated, irrespective of the tree height, the total area occupied by pores per unit cross sectional area of wood was reduced in tension wood zone. This result is concomitant with the earlier studies in various species (Onaka, 1949; Scurfield and Wardrop, 1962; Cote and Day, 1965; Milvia, 1965; Rao, 1983;

Reghu, 1983; Jourez *et al.*, 2001), confirming that tension wood formation in rubber wood is associated with a reduction in wood porosity which limits the impregnation capacity of wood preservatives during rubber wood processing.

5.9.7 Average area of pores

In poplar (*Populus euramericana*) Jourez *et al.* (2001) reported increased average pore area in tension wood zone than normal wood zone. This is in accordance with the present observations in RRII 105 and RRIM 600. However, in GT1 and Tjir 1, the average pore area was less in tension wood zone as reported by Chow (1946), Onaka (1949), Barefoot (1965), Hoster (1972) and Beiguelman (1962) in various hardwood species.

It is important to note that in primary clones like GT 1 and Tjir 1, even though the number of pores per unit area was increased in tension wood zone, the area occupied by them was decreased mainly due to the reduction in the average pore area unlike in hybrid clones like RRII 105 and RRIM 600, where the reduction in total area of pores in tension wood zone was directly related to the reduction in the number of pores per unit area.

In general, the analysis of pores in the present study revealed that the formation of tension wood in *Hevea* tends to intensify the structural modifications in rubber wood to a great extent. As the increase in wood porosity is a desirable parameter for rubber wood processing especially for the easy impregnation of preservatives, those clones having high quantity of tension wood reduce the preservative penetration and impregnation capacity. Hence the impact of these structural modifications of rubber wood especially the reduction in wood porosity needs further investigation in technological point of view.

5.9.8 Frequency of rays

The magnitude of variation in the frequency of rays in wood depends on the number and growth of ray cells, and it varies not only in different species but also within species or individual tree (Panshin and de Zeeuw, 1964). Variation in the morphology, distribution and dimension of wood rays in relation to tension wood formation has already been reported earlier (Chow, 1946; Kucera and Neccessany, 1970; Kucera and Philipson, 1978; Rao *et al.*, 1982; Rao, 1983; Reghu, 1983). The dimension of rays, fibres and vessels are inter-related. The dimension of rays may decrease with an increase in the amount of tension wood (Kucera and Bariska, 1972). It has been reported that the frequency of rays increased in tension wood zone than normal wood zone in poplar (Jourez *et al.*, 2001); *Samania saman* and *Cassia siamea* (Rao *et al.*, 1982) and in *Mangifera indica* (Reghu, 1983). In the present study also the frequency of rays was higher in tension wood zone than normal wood zone in RRII 105, RRIM 600 and Tjir 1. Whereas in GT 1 the trend was just the reverse as reported by Ollinmaa (1961); Scurfield and Wardrop (1962), Reghu (1983), Rao (1983) in various hardwood species.

5.9.9 Height, width and height / width ratio of rays

The present study revealed that the formation of tension wood is associated with an increase in ray height with a corresponding decrease in ray with. This phenomenon has also been noticed earlier in various hardwood species such as in *Mangifera indica, Polyalthia longifolia* (Reghu, 1983), *Pseudowintera colorata* (Kucera and Philipson, 1978) *Tectona grandis* (Rao *et al.*, 1982) and *Acacia auriculiformis* and *Leucaena leucocephala* (Rao, 1983). Similarly the height / width ratio of rays also showed considerable increase in tension wood zones in all the clones

It is pertinent to note that rubber wood is highly susceptible to biological deterioration soon after felling mainly due to the high content of soluble sugars and starch in the parenchyma cells including rays. In this context it is reasonable to believe that increase in the frequency of rays in tension wood makes rubber wood more susceptible to biological deterioration.

In general, the occurrence of tension wood in *Hevea brasiliensis* is the most conspicuous natural defect leading to various structural modifications affecting its practical utility. As the environmental factors such a growth habits, leaning direction of trees, tree architecture, branching habits leading to imbalanced crown etc are important parameters governing the intensity of tension wood formation, a systematic and coordinated approach towards tension wood formation in *Hevea brasiliensis* is unavoidable in a long term perspective with the objective of enhancing rubber wood utilization and further value addition.

5.10 Histochemical studies

Information on the histo-chemical status and distribution of reserve metabolites such as starch, lipids and proteins in the wood tissue in relation to tension wood formation is very scanty in general and *Hevea brasiliensis* in particular. Reghu and Patel (1984) studied the distribution of starch and lipids in tension wood of three angiosperm species *viz. Azadirachta indica*, *Mangifera indica* and *Polyalthia longifolia*. Their study revealed that these metabolites in the wood elements must have some different levels of accumulation and distribution in tension wood and normal wood. Such metabolites are also known to have prime importance in other aspects of wood biology like the formation of heartwood and discoloured wood (Hillis, 1977; Patel and Bhat, 1981).

Starch is formed in the tonoplast of plants, as an end product of carbon fixation, preferably from sucrose (Ziegler, 1964; Strafford, 1965; Preiss and Levi, 1980). A large portion of the photosynthates is utilized for the growth and development of plants, a considerable part of it is being used for respiration and the surplus portion is accumulated in the storage tissue which are eventually being utilized for respiration (Kramer and Kozlowski, 1979).

The occurrence of lipid in the storage cells of wood also have close relationship to starch accumulation with respect to their relative amount, as lipids are probably synthesized from starch (Higuchi *et al.*, 1967). Kramer and Kozlowski (1979) and Bhat (1981) suggested that though the protein content in the woody tissue is very little, its presence is very significant in the physiological activity of the tree. The cells with high protein content are likely to have high metabolic activity since some of the proteins may be enzyme proteins. In the tension wood zone of *Azadirachta indica* and *Mangifera indica*, Reghu (1983) reported the close relationship between starch and protein content, where the cells rich in starch have very little protein and those cells poor in starch have more protein content indicative of the differential metabolic status of tension wood tissues.

5.10.1 Starch

The clone RRII 105 has been used in the present study to understand the histo-chemical status of starch, lipid and total protein contents in tension wood and normal wood. In comparison to normal wood, the number and total area occupied by starch grains was considerably reduced in the tension wood zone and the levels of reduction in these two parameters were about 45% and 26% respectively. Nevertheless the average area of starch grains was increased up to 26.5% in the normal wood zone than in tension wood zone. An increase in the average area of starch grains in tension wood zone corresponding with the decrease in the number and total area occupied by starch grains reflects the decrease in the frequency of starch bearing cells in tension wood zone. Jaccard (1938), Hillis *et al.* (1962), Rao (1983), Reghu (1983) and Reghu and Patel (1984) also reported a reduction of starch reserves in the tension wood in various hardwood species indicating that tension wood formation is usually associated with the depletion of starch reserves.

5.10.2 Lipids

Other than starch, the most conspicuous form of reserve metabolites found in the parenchyma tissues in wood are the lipids (Holl, 1975). The lipid content increases towards heartwood boundary with simultaneous decrease of starch reserves during heartwood formation (Higuchi *et al.*, 1967). In *Azadirachta indica*, *Polyalthia longifolia* and *Mangifera indica*, Reghu and Patel (1984) observed considerable reduction in the accumulation of lipids in tension wood zone than in normal wood zone. However, in the present study, the histochemical localization of lipids was very negligible in both normal and tension wood zones. As heartwood formation is virtually absent in *Hevea*, the non accumulation of lipids may be quite natural.

It is a well known fact that the starch and lipids undergo various levels of metabolism during the synthesis of heartwood extractives (Hillis, 1977). Similarly such metabolic activities may also occur at various level during tension wood formation in *Hevea* as indicated by low starch and lipid content in the tension wood zone. These metabolites might have been utilized to a large extent for the development of cellulosic gelatinous layer formation in tension wood fibres.

5.10.3 Total protein

It has been reported that *in Azadirachta indica* and *Mangifera indica*, the protein content is more in tension wood zone than in normal wood zone whereas *in Polyalthia longifolia*, the protein content is more or less same in both wood types (Reghu, 1983). As very few cells showed the localization of protein in the present study, a systematic comparison between tension wood and normal wood zones with respect to the protein status could not be possible.

5.10.4 Cellulose

Cellulose in the cell wall is deposited in the form of micro fibrils which determine the wall properties. The G-layer of tension wood fibres is composed of highly crystalline cellulosic micro fibrils (Cote, 1977) and it is virtually free from lignin deposition (Wardrop and Dadswell, 1948). The cellulose content varies form species to species ranging from 40-98.5% (Norberg and Meier, 1966; Cote *et al.*, 1969; Timell, 1969; Wilson, 1981). The histochemical test of G-layer in the present study showed a high deposition of cellulose in tension wood fibres especially in the G-layer in contrast with the secondary wall of normal wood fibres.

As the layers of the fibre wall are composed of cellulosic microfibrils embedded in the matrix of polysaccharides and lignin (Hepworth and Vincent, 1998), its strength properties are related to the quantity of lignin bio-polymers present in the matrix which binds the cellulosic microfibrils together. Hence the unlignified nature of G-layer of tension wood fibres reduces the strength of cell wall leading to abnormal shrinkage, swelling and detachment from the adjacent walls while cutting. Hence the high content of cellulose and low level of lignin in tension wood fibres may play a major role in the reduction in the strength and durability of rubber wood.

5.10.5 Lignin

Lignins are phenolic polymers in the cell wall and have played a major role in the adaptation of plants to terrestrial life. It provides mechanical support to the plant tissues and allowing for novel defense strategy against pathogen attack (Boudet *et al.*, 1996). The deposition of lignin in plant cell wall accounts for 15 – 36% dry weight of the wood (Boudet, 2000). Lignins are formed by the oxidative polymerization of 3-Hydroxy-cinnamol alcohols commonly referred to as mono-lignols such as p-Cumeryl, Coniferyl and cinapyl alcohol, that give rise to Hydroxiphenylguacyl and Syringyl residues of lignin, respectively (Grima and Goffener, 1999). Kumar and Singh (1976) proved that lignin helps in cementing, anchoring and stiffening of cellulose microfibrils, thereby conferring strength and protection of cell wall against physical, chemical and biological damages.

The G-layer of tension wood fibres may be unlignified (Wardrop and Dadswell, 1948, 1955a; Onaka, 1949; Sachsse, 1965; Norberg and Meier, 1966; Robards, 1967; Bentum *et al.*, 1969) or partially lignified (Scurfield and Wardrop, 1963). The lignin content in the primary and secondary cell wall of tension wood fibres excluding G-layer is comparatively less than that of normal wood fibres (Chow, 1946; Lange, 1954; Wilson, 1981).

In the present study the localization of lignin in the cell wall of normal wood fibres was higher than that on the non-gelatinous wall of tension wood fibres. The gelatinous layer of tension wood fibres is devoid of lignin in *Hevea brasiliensis*. This observation was in accordance with the report of Reghu (1983) in *Azadirachta indica* and *Polyalthia longifolia*. As revealed by the histochemical tests, the inter cellular spaces and corners of the fibres and middle lamella of tension wood fibres had high packing density of lignin indicating that the lignin deposition initiates in the inter cellular regions as reported by Scurfield (1967). Hence the increased G-layer formation in tension wood fibres associated with the decreased lignin deposition in the remaining walls as reported by Dadswell and Wardrop (1956) is applicable to *Hevea brasiliensis* also.

Inspite of a number of explanations put forth by various investigators, the understanding of the mechanism by which the G-layer remains unlignified is still obscure. It is assumed that the metabolism may be directed towards the increased synthesis of cellulose required for the formation of G-layer leading to the development of unlignified tension wood fibres (Dadswell and Wardrop, 1954), or major fraction of photosynthates required for lignin biosynthesis may be diverted to the synthesis of cellulosic G-layer formation. The second view is supported by deficiency of lignin precursors in tension wood fibres produced from carbohydrates (Correns, 1961). It is not clear whether the lignin biosynthetic pathway and mechanism of its regulation in tree species, in general and wood tissue in particular, vary under different conditions of environmental stresses.

It has been reported that low level of IAA reduces lignification (Klee and Romano, 1994) and deficiency of auxin leads to tension wood formation (Neccessany, 1958; Casperson, 1963, Kennedy and Farrar, 1965; Cronshaw and Morey, 1968; Morey and Cronshaw, 1966, 1968a, 1968b, 1968c; Robnett and Morey, 1973). Hence the lack of lignin in gelatinous layer may have some relation with auxin deficiency affecting the formation, activity and regulation of lignin precursor enzymes such as Cinnamol Co-enzyme Reductases (CCR) and Cinomyl Alcohol Dehydrogenase (CAD) in the specific mono-lignol biosynthesis pathway as suggested by Grima and Goffener (1999).

5.11 Factors affecting tension wood formation

Inspite of a series of hypotheses and explanations put forth to explore the causative factors and mechanism of tension wood formation, the most reliable and acceptable explanation is yet to be elucidated. Hence a comprehensive and in-depth review at various angles is highly essential for a better understanding of the factors affecting tension wood formation in *Hevea brasiliensis.*

5.11.1 Angle of leaning on tension wood formation

The leaning angle of the axes has been suggested as one of the important factors, triggering tension wood formation in angiosperms and compression wood formation in gymnosperms (Berlin, 1961; Manwiller, 1967; Arganbright and Bensend, 1968; Tomlinson, 1978; Fisher, 1978; Fisher and Stevenson, 1981). Jaccard (1919, 1938) ; Onaka (1949) and Hartman (1949) observed maximum tension wood formation at a displacement of 90^0 from vertical and beyond 90^0 displacement its formation get reduced and further development of tension wood usually stops when the axis turns upside down. In *Salix fragilis*, Robards (1966) reported that the optimum level of tension wood formation attained at 120^0 angle from vertical. Nevertheless, the studies conducted by Reghu (1983) in one year old seedlings of *Azadirachta indica* proved that the induction of tension wood was maximum at 45^0 inclination and with the increased degree of displacement, its proportion was reduced considerably. In the present study, it was observed that tension wood formation was maximum at 90^0 displacement from the vertical in eight month old seedlings of *Hevea brasiliensis* as reported by Jaccard (1919; 1938), Onaka (1949) and Hartman (1949). It appears, therefore, that the relationship between the degree of displacement of the axes and the proportion of tension wood may be species specific and cannot be generalized for all hardwood species.

Even though the distribution and proportion of tension wood in *Hevea* varies at different displacement angles, the angle of inclination of tree axes can be considered as one of the crucial factors responsible for tension wood formation in *Hevea brasiliensis,* especially in younger stages, because at this immature growth phase the plants are more flexible to various forms of external stimuli.

5.11.2 Defoliation on tension wood formation

Wardrop (1961) and Reghu (1983) showed that defoliation may reduce tension wood formation and its formation cannot be inhibited unless the growing shoot tip is removed. The bent stem axis of *Hevea brasiliensis* after defoliation showed a reduction in tension wood formation in comparison to bent axis with intact leaves. Defoliation experiments in vertically growing plants also showed considerable reduction in tension wood formation compared to those plants grown vertical with intact leaves. The present study also showed that the proportion of tension wood was reduced even up to 50 – 75 % in defoliated plants than that of un-defoliated plants, irrespective of bending and vertical orientation. This may be due to the inadequate supply of photosynthates required for cell wall formation, especially the formation of G-layer in tension wood fibres.

In this context, it is pertained to note that the removal of leaves brings down the auxin concentration and influence tension wood formation considering the hypothesis that auxin deficiency induces tension wood formation. Moreover, due to defoliation, the photosynhtates required for cell wall formation, especially the formation of gelatinous layer in tension wood fibres, may be highly reduced.

5.11.3 Gravitational response on tension wood formation

Another important causative factor influencing the formation reaction wood (both tension wood in angiosperms and compression wood in gymnosperms), is tensile stress on the upper side and compressive stress on the lower side of the leaning axes, respectively (Metzger, 1908; Munch, 1938; Sinnot, 1952). Ewart and Mason (1906), Jaccard (1919, 1938), Burns (1942), Hartman (1949), Wardrop (1964) suggested that the gravity to be a causative fundamental factor for reaction wood formation. To substantiate the theories of tensile / compressive stresses and gravity, vertical loop experiment has been conducted in *Hevea brasiliensis*. Tension wood formation was observed in the upper side of the upper half of the loop, where tensile stress is exerted and also in the lower half of the loop where compressive stress was exerted. Within these positions, the proportion of tension wood was more or less identical in the upper and the lower parts of the loop irrespective of tensile / compressive stresses. In the lateral part of the loop the formation of tension wood was observed in the outer zone where tensile stress was exerted which is in accordance with the results of the loop experiment conducted by Reghu (1983) in *Azadirachta indica*. It is interesting to note that in vertical loop experiment, the lateral parts of the loop, which are assumed to be vertical and free from leaning and gravitational influence, also showed tension wood formation. Hence the causative factors responsible for tension wood formation in the lateral side may be attributed to the transmission of tensile / compressive stresses from the upper and lower parts of the loop in this regions.

5.11.4 Effect of growth regulator on tension wood formation

5.11.4.1 Indole acetic acid (IAA)

It has been reported that the formation of tension wood is related to low level of auxin in hard wood species (Neccessany, 1958; Casperson, 1963; Kennedy and Farrar, 1965; Cronshaw and Morey, 1968; Morey and Cronshaw, 1966, 1968a, 1968b, 1968c; Robnett and Morey, 1973). The exogenous application of auxin in high concentration on the upper half of artificially bent seedlings of *Populus alba* and *Populus monilifera* inhibited tension wood formation whereas its application in the lower half did not show any effect on tension wood formation (Neccessany, 1958). In *Acer rubrum* (Cronshaw and Morey , 1968) and *Azadirachta indica* (Reghu, 1983), the application of IAA on the upper half inhibited tension wood formation. The present study also showed an inhibitory effect of IAA on tension wood formation in both bent and vertical experiments in comparison to untreated control plants.

The geo curvature of the axes is believed to result in redistributions of auxin migrated from the upper side to the lower side (Wareing *et al.*, 1964) and the deficiency of auxin in the upper side causes induction of tension wood (Kennedy and Farrar, 1965; Leach and Wareing, 1967; Cronshaw and Morey, 1968; Morey and Cronshaw, 1966; 1968a, 1968b, 1968c; Robnett and Morey, 1973). In the present study such a movement of exogenous IAA from upper to lower half, in bending experiment, was not possible as the two halves were partitioned with a cover glass. When the upper half of the bent stem was treated with IAA, formation of wood tissue was reduced and bark formation increased in association with the inhibition of tension wood formation. Hence the applied IAA might have been used up for bark formation rather than the development of wood tissue, thus making the upper half deficient in auxin resulting into the inhibition of tension wood formation.

Similar trend was also noticed in other experiments where IAA was applied in the lower half. The inhibition of tension wood in the lower half where exogenous IAA was applied may be attributed to the excess auxin status in this tissue both from the exogenous and endogenous auxin due to geotropic response.

When IAA was applied laterally on erect stem through bark incision, tension wood was formed on the side opposite to the site of application and also in the lateral side as reported in *Aesculus hippocastanum* and *Acer rubrum* (Morey and Cronshaw, 1968c). In the control experiment (lanolin alone) also tension wood was formed in high proportion. The formation of tension wood in this case may also be due to the deficiency of auxin caused by accelerated rate of cambial division as reported by Kennedy and Farrar (1965), Morey and Cronshaw (1968a, 1968b).

It is a well known fact that auxin is essential for cell division. Hence the cambial cells on the side opposite to the site of treatment might get enriched with high level of IAA for enhancing meristematic activity. A small portion of the bark was removed prior to the lateral application of IAA through incision. This created a partial discontinuity of IAA flow from the tip of young buds. Hence at the wounding site , IAA accumulated in high concentration which might have been moved laterally for increased cambial activity. High concentration of IAA in the site of application might have been affected the cambial activity by inhibiting the formation of wood fibres.

5.11.4.2 Gibberellic Acid (GA_3)

Gibberellins are terpenoid compounds made up of isoprene units. Gibberellic acid (GA_3) induced inter-node elongation in certain types of plants by stimulating stem growth both by cell elongation and cell division (Davies, 1998). The regulation of cell division by GA_3 is believed to regulate the transition between G_2 and M-phase of cell cycle (Davies, 1998). The activity of endo-transglucosylase (XET) has been correlated with GA_3 induced growth and may interact with expansins to promote cell wall loosening (Davies, 1998). On the basis of kinetics of growth of cell cycle, Sauter and Kenede (1992) proposed that the first effect of GA_3 is to induce cell elongation in the intercalary meristems. GA_3 can overcome genetic dwarfism and affect cell expansion in presence of auxin (Davies, 1998). GA_3 is naturally found in high levels in young leaves and this can delay leaf senescence.

The exogenous application of GA_3 induced tension wood formation in the upper and lower halves of the bent axis in *Azadirachta indica* (Reghu, 1983). Studies on the negative geotropic growth stress in GA_3 conducted by Yoshida *et al.* (1999) in *Prunus spachiata* proved high amount of tension wood formation, indicating that GA_3 generates growth stress leading to tension wood formation. In the present study also the application of GA_3 induced tension wood formation in the upper and lower parts of the bent axis. In this context, it is believed that the branches treated with GA_3 likely under tensile stress in the longitudinal direction, especially in the early stages of growth making it positively geotropic to initiate tension wood formation as reported by Yoshida *et al.* (1999). It is also pertinent to note that application of GA_3 increase cambial division (Digby *el al.*, 1964; Shiniger, 1971) leading to the differentiation of unlignified gelatinous fibres in *Hevea brasiliensis*. However, the actual regulatory effect of GA_3 on tension wood formation is yet to be elucidated as the movement of GA_3 in plant system is slower than that of IAA transport (Jacobs, 1998).

5.11.4.3 Tri-iodo Benzoic Acid (TIBA)

2,3,5-Triidobenzoic acid (TIBA) act as a growth hormone with anti-auxin effect in plant system which show direct competition with auxin or by blocking auxin movement in plants (Kennedy and Farrar, 1965). It has been reported that the exogenous application of TIBA promote auxin deficiency and induce tension wood formation in hardwood species (Kennedy and Farrar, 1965; Reghu, 1983). Morey and Cronshaw (1968a, 1968b & 1968c) induced tension wood formation through the combined application of TIBA and GA_3 in *Azer rubrum*. However, the apical application of TIBA in bent axis of *Hevea brasiliensis* in the present investigation did not induce tension wood formation whereas its lateral application on vertical shoots induced tension wood formation. Hence the antagonistic activity of TIBA against auxin is found to work only in vertical shoots in the case of *Hevea brasiliensis*. The reason for non induction of tension wood in the bending experiments is yet to be elucidated.

Based on the above observations and discussions of the present investigation, it is evident that the mechanism of tension wood formation need not be related with a single factor and there must be a combination of various factors. As tension wood formation is tricky and complex, a combination of various factors as described below may be applicable at various levels and intensities in rubber trees leading to the formation of tension wood.

(i) the movement of canopy brought about by various factors like wind, gravity, weight or phototropism makes the axis tilted

(ii) this type of leaning generates tensile stress and under this stress conditions the rate and duration of cambial activity may vary,

(iii) leaning also lead to the variation on the movement of hormones and enzymes on the upper and lower parts of the bent axis,

(iv) due to the changed hormone level the differentiation and development of wood tissues and metabolism of food reserves may alter,

(v) the variation in the metabolism bring about the changes in the cell wall formation (especially unlignified cellulosic G-layer formation)

Due to the lack of coordinated research programme a perfect answer to identify the causative factors responsible for tension wood formation is extremely difficult as the investigation on tension wood formation *in vivo* is not possible. Avoiding tension wood formation in rubber tree is not possible, but to control its deleterious effect is highly essential. To achieve this goal appropriate technology development through multi-disciplinary - coordinated research assumes significance from a long-term perspective.

CHAPTER 6

SUMMARY

Detailed investigations were carried out on the structure, distribution and formation of tension wood in *Hevea brasiliensis* (wild. ex. Adr. de Juss.) Muell. Arg., with the main objectives : (1) extent of tension wood with special reference to clonal variability; (2) distribution pattern and directional effect on tension wood formation in mature trees; (3) extent of tension wood formation in immature plants; (4) tension wood formation in tissue culture plants and budgrafted plants; (5) role of tension wood in wind damage; (6) distribution and proportion of tension wood in tapped and untapped zones; (7) structural modification of wood elements during tension wood formation and (8) identification and demarcation of tension wood in rubber wood logs through macroscopic staining. The study also aimed at identification of factors affecting tension wood formation in the immature growth phase.

Data were recorded on the distribution pattern, proportion and structure of tension wood in mature trees of four clones *viz*. Tjir 1, GT 1, RRIM 600 and RRII 105, selected from the Central Experiment Station of Rubber Research Institute of India at Chethackal, Ranni. Data were also recorded on the proportion of tension wood in immature growth phase in ten month old bud grafted plants of 10 clones viz. Tjir 1, Gl 1, GT1, PB 5/51, PB 217, PB 235, RRIM 600, RRIM 623, RRIM 703 and RRII 105.

Data recorded on tree leaning, growth eccentricity and proportion of tension wood at different height levels of the tree were correlated to ascertain the directional effect on tension wood formation.

Eight month old tissue culture plants and budgrafted plants of the clone RRII 105 were selected to compare the extent of tension wood formation. Mature trees of RRII 105 were selected to study the role of tension wood on wind damage. An eco-friendly macroscopic staining procedure, using a combination of Zinc Chloride, Iodine and Potassium iodide, was developed for the easy identification and demarcation of tension wood zones in rubber wood logs.

Four month old seedling plants were used to investigate the causative factors responsible for tension wood formation. Budgrafted plants of the clone RRII 105 at the age of eight months were used to study the effect of growth regulators on tension wood formation.

Important structural characters recorded were proportion of tension wood, dimensional variation of wood elements, analysis of pores and rays in both normal and tension wood zones. Histochemical localization of starch, lipids, total proteins, cellulose and lignin were also attempted in normal and tension wood zones..

Experiments on the factors affecting tension wood formation includes (1) angle of leaning; (2) angle of leaning with defoliation; (3) gravitational stimulus; (4) exogenous application of growth regulators such as Indole-3-acetic acid (IAA), 2-3-5-Triiodobenzoic acid (TIBA) and Gibberellic acid (GA_3) on inclined and vertical axes.

The data generated were subjected to detailed statistical analysis viz. Analysis of variance, (ANOVA), paired t-test and correlation coefficients.

In mature trees, compact arcs of tension wood were formed in both the vicinity of the pith and peripheral regions of the tree trunk as white wooly lustrous zones. The proportion of tension wood in all the four clones ranged from 16.75 to 26.49%. The variation in the quantity of tension wood formed at different height levels of the trunk was significant only in RRIM 600. However the variation between clones was not statistically significant. The G-layer of tension wood fibres was well developed in all the clones and showed partial or total detachment from the adjacent walls.

The proportion of tension wood in 10 clones at the juvenile phase ranged from 14.32 to 49.97%, and the variation among the clones was significant. The study revealed that the plants at the juvenile stage is more flexible to tissue modification leading to tension wood formation in *Hevea brasiliensis*.

The correlation studies revealed that the tree height, angle of leaning and pith eccentricity did not play any significant role in tension wood formation in the mature trees of *Hevea brasiliensis*. The proportion of tension wood was significantly reduced in the tapped zones of three clones *viz.* Tjir 1, RRIM 600 and RRII 105 than the untapped zone, whereas in GT 1 the trend was just the reverse. The formation of tension wood was relatively high in tissue culture plants (27.49%) than the budgrafted plants (12.75%) in the immature growth phase.

Quantitative analysis of tension wood in trunk snapped trees due to wind, revealed that the proportion of tension wood was significantly higher in the zone of wind break compared to the zone below and above the point of break. It may be assumed that the stress exerted by wind blow leads to fibre buckling in the lower side of the inclined trunk followed by the rupture of tension wood fibres in the upper side.

Tension wood zones turn brownish pink in Zinc-chloro-iodide by the surface application on freshly sawn wood discs. The colour specificity was not observed when this formulation was applied on dried and fungus infected wood discs. Hence this macroscopic staining procedure could be used effectively for the easy identification and demarcation of massive zones of compact tension wood, during primary wood processing such as selective / differential sawing operations to eliminate tension wood.

The length of tension wood fibres was significantly lower than normal wood fibres in all the clones studied. The variation in fibre length at different height levels within trees and between clones was not significant. Width of tension wood fibres was significantly higher than that of normal wood fibres and the variation at different height levels and between clones was significant. The wall thickness of tension wood fibres was significantly higher than that of normal wood fibres. Variation in length of vessel elements with respect to tree height was not significant whereas between clones, it was significant. The variation in the width of vessel elements at different height as well as between clones was not significant. Frequency of pore was reduced in the tension wood zone than normal wood zone but the variation was significant only in RRII 105. The total area occupied by pores per unit C.S. area of wood was also reduced in the tension wood zone and the difference was significant only in GT 1. Reduction in the average area of pores in tension wood zone was observed in GT 1 and Tjir 1 while in RRII 105 and 600, the trend was just reverse. The frequency and height of rays was increased in tension wood zone than normal wood zone and the variation was not significant. Width of rays was lower in tension wood zone than that of normal wood zone in all the clones and the difference was significant in GT 1, RRIM 600 and RRII 105. The height / width ratio of rays was higher in tension wood zone than normal wood zone and the variation was significant in all the clones except Tjir 1.

The total number and area occupied by starch grains in the parenchymatous tissues per cm^2 C.S area was reduced in tension wood zone up to 45% and 26%, respectively compared to normal wood zone. The average area of grains was increased in tension wood zone up to 26.5% than normal wood zone. Localization of lipids and total proteins was negligible in both normal and tension wood zones. G-layer of tension wood fibres was cellulosic and unlignified. The fibre wall except the G-layer of tension wood fibres showed low level of lignification in contrast to the normal fibres.

Seedlings bent at 90^0 showed maximum tension wood formation (39.6%) and minimum (23.75%) at 45^0 inclination. Tension wood was formed in the upper side of the axis bent at 90^0 and 135^0 whereas its formation was restricted on the lower side of the axis bent at 45^0 from vertical.

The formation of tension wood was reduced up to 50-75% in defoliated seedlings bent at 45^0, 90^0 and 135^0 from vertical probably due to the inadequate supply of photosynthates required for G-layer formation.

Dense mass of tension wood was formed on the upper zone of the upper and lower parts of the loop under tensile and compressive stresses respectively, indicating the role of gravity on tension wood formation. The causative factors responsible for tension wood formation on the outer zone of the lateral part of the loop may be attributed to the transmission of tensile / compressive stresses from the upper and lower part of the loop.

Application of IAA at 500 ppm concentration on the upper and lower halves of the inclined and decapitated plants inhibited tension wood formation. Similar inhibitory effect on tension wood formation was also observed through the lateral application of IAA on vertical plants. However, application of IAA through bark incision on vertical plants induced tension wood formation. Application of TIBA on the upper and lower halves of the decapitated bent plants also suppressed tension wood formation, but its lateral application in vertical plants induced tension wood formation. Application of GA_3 induced tension wood formation in the upper and lower halves of the decapitated bent plants.

The present investigation indicated that the mechanism of TW formation *Hevea brasiliensis* is related to the influence of various factors at various levels and intensities as follows :

The movement of canopy brought about by various factors like wind, gravity, phototropism etc. makes the axis tilted. The tilted axis generates various internal/ external stresses and under this stress condition the rate and duration of cambial activity may vary. Leaning also leads to the variation in the level of hormones / enzymes in the upper and lower parts of the bent axis. Due to the changed hormonal level the differentiation and development of wood tissues and metabolism of food reserves may alter and the variation in the metabolism causes changes in the cell wall formation (the unlignified cellulosic G-layer).

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