I. INTRODUCTION
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Wood is the most important gift that nature has given to the mankind. Its structure and chemistry make it the topmost material for a variety of constructions, wood work industries like plywood, veneers, sports, toys, agricultural implements, matches, scientific and musical instruments. Wood flour is used to manufacture linoleum, plastics and nitroglycerine explosives. Organic compounds such as methanol, acetic acid, acetone, wood turpentine, wood tar and wood gas can be obtained from wood. Saw dust, shavings and excelsior of wood and charcoal are well known energy sources. The wood comprises of various kinds
of cell types, and its quality depends on their structure, orientation and chemistry. In addition to its normal structure and chemistry, wood shows certain variations. Reaction wood is one of such variations, and may be defined as the wood of abnormal structure (Wardrop, 1959), or a variation of normal wood structure (Fisher and Stevenson, 1981). Its occurrence has been recognised long back on upper and lower sides of inclined branches in angiosperms and gymnosperms respectively (Côté, 1968). Because of the high tension and compression forces bringing about such changes in wood it is known as tension or compression wood respectively. Collectively they are known as reaction wood (Cutter, 1978). In the branches of angiosperm trees distribution of tension wood is variable; although usually present on the upper side, it may also be found in the lower side of the branches in many instances (Wardrop, 1964). The reaction anatomy involves changes in tissues of both the upper and the lower halves of inclined branches or stems (Kučera and Philipson, 1977). The vertical upright trunks or branches of many angiosperm species such as *Eucalyptus goniocalyx* (Wardrop, 1964), *Populus* and *Fagus* (Kaeiser, 1955; Trénard and Guéneau, 1975), *Acer rubrum* and some gymnosperm species (Brown, 1974) produce reaction wood without any apparent displacement from
their vertical position (also see Wardrop, 1956, 1964; Hughes, 1965; Scurfield, 1973; Côté, 1977; Wilson and Archer, 1977; Fahn, 1982). Such species offer an excellent source of material for investigation on causes of reaction wood formation (Brown, 1974).

The very first question that we should ask is: "What is the role of reaction wood formation?" Other important questions which have not been fully understood are: "Does it play an active role in the recovery of tilted shoots to vertical? Has it any impact on the quality of the wood? What are the factors bringing about its structural differences?" Our informations on this aspect of wood biology are mainly based on the work on the temperate species. Tension wood is classed as a natural defect of wood due to some of its undesirable properties for construction and processing applications (Côté, 1968). Warping, bowing, buckling, tearing, twisting and collapse of tension wood are serious wood industry problems (Wardrop and Dadswell, 1955b; Cote and Day, 1965). "Dulling" of the saw is another serious problem of the tension wood (Wardrop and Dadswell, 1955b, Lassen, 1959). As the wood of branches forms a major part of the total bulk of wood in a tree, the structure and quality
of the reaction wood produced by them must be known. This may lead us to proper utilization of reaction wood. The tension wood yields greater amount of chemical pulp than that from the normal wood, and it can be defibrated mechanically more easily than the normal wood. It produces a high quality pulp, having 89 to 99 percent alpha cellulose content (Panshin and de Zeeuw, 1980). If we can turn a great majority of low quality wood into tension wood, the pulp industry can be benifited. For either promotion or demotion of the tension wood production, the mechanism of its formation must be known. Our information on this aspect has a number of lacunae, and surprisingly, contribution on these aspects for our own species is none. This serious paucity of information on a very important problem of forest wealth of India prompted me to take up the problem to investigate the structure, histochemistry, and mechanism of tension wood formation in some angiosperm species.

It is most widely assumed that the reaction wood formation is an active and endogenous mechanism within a tree for the normal reorientation of axes in some species, and that it adds the structural support to unevenly loaded branches and trunk axis (Wardrop, 1959;
Fisher and Stevenson, 1981). The extensive production of reaction wood on the upper side of lateral branch makes it grow upright in Hura (Tomlinson, 1978). In stems, which previously were displaced from their natural vertical direction, reaction wood is generally presumed to be responsible for bending them back to vertical; and reaction wood formed in branches is thought to overcome the effect of gravitational force tending to bend them below their natural positions relative to the stem (Boyd, 1977). Instead of viewing the differentiation of reaction wood as merely an anatomical response to exogenous changes, Fisher and Stevenson (1981) see it as a genetically programmed and active part of normal tree development. To understand such active role of reaction wood in trees, they introduced the concept of tree architecture which involves the orientation, and sometimes reorientation, of lateral branches and the leader axis.

Though the occurrence of tension wood is often more difficult to recognize than compression wood (Côté, 1977), there are several features in the surface appearance of wood that indicate the presence of tension wood (Panshin, de Zeeuw and Brown, 1964). In sawing (Marra, 1942; Dadswell and Wardrop, 1949; Wardrop and Dadswell, 1955b;
Côté, 1968, 1977), planning, turning (Desch and Dinwoodie, 1981) and rotary peeling of fresh lumbers, the surface of tension wood areas show wooly nature (Dadswell and Wardrop, 1954). The dried and dressed discs of the wood show silvery sheen (Côté, 1968, 1977), and sometimes they show darker colour than normal wood in some Australian species (Dadswell and Wardrop, 1949). Horizontal or leaning branches of angiosperms show eccentric growth on upper side with tension wood in their upper half (Priestly and Tong, 1927; Hartmann, 1932; Panšhin et al., 1964; Côté, 1968, 1977; Brown, 1974). However, surface features of wood are not always dependable for identification of tension wood in angiosperms. Only the microscopic study would be reliable for its indication (Fisher and Stevenson, 1981). In some species, the tension wood appears in the form of either arcs or dense areas (Robards, 1966; Fisher and Stevenson, 1981) or complete circles (Westing, 1968; Kučera and Philipson, 1977; Fisher and Stevenson, 1981).

The principal anatomical feature of the tension wood is the occurrence of gelatinous fibers (tension wood fibers) which completely or partially replace normal wood fibers (Côté, 1977). Metzger (1908) recognized them as characteristic of reaction wood for the first time.
Hardwoods of *Fraxinus* and *Tilia* are devoid of gelatinous fibers in their tension wood. However, such tension woods show drastic reduction in lignin content, and in the thickness of secondary wall (Panshin et al., 1964). Two types of tension wood are recognised: compact and diffused. The compact type is one in which the fibers with partially or wholly un lignified cell walls are found in either a particular region of the stem or dense areas or arcs, and the diffused type is one in which the modified fibers are scattered singly or in small groups among normal fibers (Wardrop and Scaife, 1956; Fahn, 1982).

Fibers in the tension wood part of the stem are longer than the normal fibers in the opposite side of the stem (Chow, 1946; Onaka, 1949; Nečesný, 1958). Contrary to this, Dadswell and Wardrop (1954) showed that the tension wood fibers may either be longer or shorter than, or equal in length to the normal fibers. In experimentally induced reaction wood of *Fagus*, the fiber length was identical to that in normal wood (Sachsse, 1961). In *Populus alba*, the reaction wood fibers are narrower than those in the wood opposite to it. In cross section, reaction wood fibers appear rectangular, whereas, those in the wood opposite to reaction wood the fibers are
polygonal (Onaka, 1949; Wardrop, 1964). Tips of tension wood fibers show fewer bifurcations and other distortions than do the tips of normal fibers (Burns, 1942). The most characteristic modification of tension wood fibers is the occurrence of gelatinous-or G-layer as a part of secondary wall (Panshin et al., 1964; Côté, 1968, 1977). This special wall layer, which is usually equal to or greater in thickness than S_2 layer of cell wall, makes the secondary wall of tension wood fibers thicker than that of the normal fibers (Panshin et al., 1964). G-layer appears thick or swollen in cross section and nearly fills the fiber lumen (Côté, 1968). In some fibers the G-layer is convoluted (Wardrop, 1959, 1964; Scurfield and Wardrop, 1962; Côté, 1968), giving the impression that it is attached only loosely to other layers of the secondary wall (Côté and Day, 1962; Côté, 1968, 1977). The G-layer of tension wood fibers stains green and the remaining secondary wall stains red with safranin and fast green or light green (Jutte, 1956). On hydration the G-layer swells and nearly fills the fiber lumen (Fisher and Stevenson, 1981). During microtomy the G-layer in most of the cells gets displaced in the direction of cutting. This artifact indicates loose attachment of G-layer with S-layers.
(Côté, 1968, 1977). The convolutions of G-layer represent various developmental stages of cell wall thickening. In some species, however, convoluted G-layers occur even in mature cells. Wardrop (1964) and Côté (1968) gave detailed picture of wall thickening and patterns of convolutions associated with it. The unconvoluted G-layers of mature cells become convoluted when swollen in reagents such as nitric acid (Onaka, 1949). G-layer is multilamellate (Casperson, 1960, 1961a,b, 1963, 1967, 1968; Côté and Day, 1962; Scurfield and Wardrop, 1962; Casperson and Hoyme, 1964; Wardrop, 1964; Norberg and Meier, 1966; Scurfield, 1967; Casperson, Jacopian and Philipp, 1968) and refracts light (Panshin et al., 1964), and gives gel-like appearance when viewed under light microscope (Panshin et al., 1964; Wardrop, 1964). It is usually un lignified (Wardrop and Dadswell, 1948; Wardrop, 1964; Côté, 1977) or lignified to a very limited degree (Wardrop, 1964; Côté, 1968). Lignin may be absent in one or more layers of secondary wall ($S_1-S_2$). This general lack of lignin in the secondary wall is the primary characteristic of tension wood development. G-layer consists predominantly of cellulose (Wardrop and Dadswell, 1948; Jayme, 1951; Norberg and Meier, 1966; Côté, 1968; Timell, 1969; Furuya,
Takahashi and Miyazaki, 1970; Côté, 1977) that is highly crystalline (Wardrop and Dadswell, 1955a; Wardrop, 1964). Either $S_2$ or $S_3$ layer of the secondary wall is replaced by G-layer, or such a layer may be formed in addition to the normal three layers of the secondary wall in tension wood fiber (Wardrop and Dadswell, 1955a). A fourth kind of tension wood fiber wall consisting of $P + S_1 + G +$ another layer or layers may also occur. These extra layers differ from G-layer in their optical and chemical properties (Scurfield, 1973). The texture of the cell wall layers, other than G-layer, appears to be basically similar to that of normal fiber wall (Wardrop, 1964).

Initial studies on the fine structure of tension wood fibers are made by Jaccard and Frey (1928) and Münch (1938) who showed that the molecular (micellar) orientation in the un lignified layer of the cell wall was approximately axial. These studies were followed by those of Wardrop and Dadswell (1948, 1955a), Preston and Ranganathan (1947), Jutte (1956), and Wahlgren (1957). The G-layer is a sheath of cellulose microfibrils oriented about $5^\circ$ from the long axis of the cells (Marra, 1942; Onaka, 1949; Wardrop and Dadswell, 1955a; Ollinmaa, 1961; Côté and Day, 1962). In tension wood fibers the pit chamber
is reduced with a slit-like canal oriented almost parallel to the fiber axis. Walls of tension wood fibers show slip planes and compression failures (Wardrop and Dadswell, 1948; Patel, 1964; Sachsse, 1965; Robards, 1967; Côté, 1968; Côté, Day and Timell, 1969).

Though the general structure of vessels of tension wood is unchanged from their counterparts in the normal wood, they are smaller and less numerous (Onaka, 1949; Wardrop, 1959, 1964; Beiguelman, 1962; Panshin et al., 1964; Côté, 1963; Kučera and Philipson, 1977; Fisher and Stevenson, 1981). Ray and vertical parenchyma of tension wood are unmodified, and they do not show great modifications of their cell wall structure (Wardrop, 1964; Côté and Day, 1965; Côté, 1968). Onaka (1949) noted the reduction in xylem parenchyma of tension wood. Very often the parenchyma gets compressed by surrounding reaction fibers, and sometimes they may obliterate (Scurfield and Wardrop, 1962). In reaction wood the proportion of vasicentric parenchyma gets reduced (in the species in which such distribution of axial parenchyma is common in the normal wood) due to the reduced number of vessels (Wardrop, 1964). Scurfield and Wardrop (1962) reported the reduced number of rays in reaction wood than that in normal one. In *Populus monilifera*
the number of rays is greater in tension wood than that in normal one (Kučera and Nečesaný, 1970). On the contrary Kučera and Philipson (1978) showed less number of rays in reaction side of the leaning branch than that in the normal one in *Pseudowintera colorata*, and pointed out that the rays of the former are narrower and longer than those of the latter. Rays are uniseriate and rarely biseriate in upper side of the leaning branch, whereas, those in the lower side are 2–4 seriate and occasionally seven cells wide in *Aristotelia serrata* (Kučera and Philipson, 1977).

The chief abnormal physical properties of tension wood are: unusually high longitudinal shrinkage (Akins and Pillow, 1950; Pillow, 1950; Terrel, 1952; Wahlgren, 1957; Ollinmaa, 1961; Côté, 1968), high tensile strength, low compressive strength (Wardrop and Dadswell, 1948), and high shrinkage (Côté, 1977). Tension wood has abnormally high longitudinal and tangential shrinkage as compared to those of compression wood (Desch and Dinwoodie, 1981). Fresh cut tension wood is low in tensile strength, but when air-dried its tensile strength is higher than that of normal wood (Klauditz and Stolley, 1955; Côté, 1968). The toughness and specific gravity are higher in tension wood
than those in the comparable normal wood (Klauditz and Stolley, 1955; Lassen, 1959).

The tension wood has high cellulose (Klauditz and Stolley, 1955), glucose (Gustafsson, Ollinmaa and Saarnio, 1952), galactose (Timell, 1969) and ash contents (Ollinmaa, 1961); low starch (Hillis, Humphreys, Bamber and Carl, 1962), lignin (Marra, 1942; Chow, 1946; Jayme, 1951; Bland, 1961), xylose (Meier, 1962), mannose (Meier, 1962), pentosan (Ollinmaa, 1961), glucomannan (Timell, 1969), total water (Wardrop, 1964) and mobile water contents (Wardrop, 1959) as compared to those in normal wood. Arabinose content has been reported to be either low (Gustafsson et al., 1952) or high (Meier, 1962) in tension wood.

The G-layer contains a small amount of some carbohydrates other than cellulose, such as xylose, mannose, galactose, arabinose and pectic materials, and high ash content (Furuya, Takahashi and Miyazaki, 1970). G-layer often shows intense activity of enzyme peroxidase (Wardrop, 1964; Scurfield, 1972, 1973). The cells of reaction wood have low lignin content in their walls (Jayme, 1951; Wardrop, 1964). On the other hand Côté (1977) showed high degree of lignification in the non-
gelatinous layers of the cell wall of tension wood fibers. Here, \( S_1 \) layer shows, probably, a little more lignification than that in normal wood fibers. The \( S_2 \) layer may either be more or less lignified than \( S_1 \) (in a reaction fiber), but almost invariably it is more lignified than \( S_2 \) of normal wood fibers.

Tension wood differentiation can be induced in small angiosperm trees by leaving them undisturbed in a horizontal position for 24 hr or more (Casperson, 1960). Studies on the experimental induction of tension wood have been carried out by several wood biologists, and a number of theories explaining the mechanism of reaction wood formation are floated by them. These theories relate the formation of tension wood to three mechanisms: response to stress, response to gravity, and response to various intrinsic factors operating within the plant (Wardrop, 1959).

The differential growth of stems and branches which usually accompanies reaction wood formation led several early workers to conclude that reaction wood develops as a response to mechanical stress (Metzer, 1908). Boyd (1977) opined that the reaction wood was formed in response to imposed stress. Berlyn (1961), Wardrop (1964), Robards...
(1966) and Fisher and Stevenson (1981) showed a linear relationship between the degree of lean in shoot axis and the amount of tension wood formed. If the shoot axis is bent artificially, the tension wood develops on its upper side, i.e., the side undergoing tension. This led to the view that tension wood is a morphological response to the presence of tensile stress in a branch or a stem (Wardrop, 1959).

The experiments of vertical loops of stem by Jaccard (1938) demonstrated the association of contraction with tension wood formation. The contraction originates in the growth stress on the stem (Münch, 1938). The origin of such stresses is, to some extent, obscure. Nonetheless, Jacobs (1945) pointed out that they may arise by some change in cell wall texture associated with differentiation of fibers from cambium. Yet another view explains that an asymmetrical development of the stem alone would bring about an asymmetrical distribution of growth stress which can effect movements of orientation of branches and stems (Jacobs, 1945).

Jaccard (1919, 1938), Onaka (1949), and Hartmann (1949) carried out some experiments to find out the role of gravity in the formation of reaction wood in angiosperms.
In reality, the weight of displaced stems or horizontal branches is an indirect manifestation of gravitational forces, and several workers have expressed the idea that the formation of reaction wood is a reaction to the influence of gravity rather than tissue stress (Ewart and Mason-Jones, 1906; Jaccard, 1919). Jaccard (1938) from his vertical loop experiments showed that the reaction wood is always formed on the upper side of the loops irrespective of tension or compression stress. When gravitational forces were replaced by continuous centrifugal forces, reaction wood could be formed in the upright stems (Brown, 1974). When conifers and angiosperms were slowly rotated on horizontal klinostats neither compression nor tension wood could be induced (Wershing and Bailey, 1942; Wardrop, 1964).

If a branch is displaced obliquely downward tension wood is formed on the upper side, and if the branch is displaced upward tension wood is formed on the lower side (Jaccard, 1919; Hartmann, 1949; Dyer, 1955; Wardrop, 1956). In both of these experiments the orientation of the branch was altered in relation to the gravitational field. All the conflicting results lead us to think that some intrinsic factors must be involved in governing the orientation of branch (Wardrop, 1964).
Boyd (1977) maintained that an initial internal strain might be the active inductive force for reaction wood formation. Defoliation can bring about reduction in the quantity of reaction wood, but unless the terminal bud is removed its formation can not be stopped (Wardrop, 1959).

In inclined stems or branches, their lower side has higher concentration of auxin than the upper side (Nečesaný, 1958; Parups, 1970; Fisher, Burg and Kang, 1974). A large school of wood biologist believes that the formation of tension wood is a developmental response to auxin deficiency or reduced auxin level on the upper side of the stem (Sinnott, 1952; Wardrop, 1956; Nečesaný, 1958; Casperson, 1963; Cronshaw and Morey, 1965, 1968; Kennedy and Farrar, 1965; Morey and Cronshaw, 1966, 1968a, b, c; Brown, 1974). Nečesaný (1958) demonstrated that a differential distribution of IAA and other growth regulating substances in the stem can induce reaction wood differentiation. Casperson (1964) showed that a horizontally placed, decapitated epicotyl of *Aesculus hippocastanum* produced tension wood only when supplied with auxin through the cut surface. In the erect stem of *Acer rubrum* seedlings treated with low concentration of auxin, a thick
ring of tension wood below the treatment site was developed (Morey and Cronshaw, 1968c). When the upper side of the leaning stems, in which reaction wood was already differentiated, was treated with IAA further differentiation of reaction xylem was reduced (Nečesaný, 1958). The application of IAA to the lower side of such stems did not have any influence on reaction wood formation. DNP (2,4-dinitrophenol) also induces tension wood formation in internodes when applied locally (Morey and Cronshaw, 1968c). However, the application of auxin alone does not induce tension wood formation (Wardrop, 1959). The presence of endogenous auxin and eccentric distribution of endogenous auxin inhibitor are closely correlated for tension wood formation (Kennedy and Farrar, 1965; Morey and Cronshaw, 1966; Westing, 1968). TIBA, an auxin antagonist, suspends polar auxin transport, and promotes the formation of tension wood when applied to upright twigs of Acer rubrum (Cronshaw and Morey, 1965). Application of IAA or 2,4-D unilaterally to the erect epicotyls of Aesculus hippocastanum L. induces tension wood formation on the side opposite the site of application (Casperson, 1963, 1965b). Auxin inhibits the development of tension wood when applied along the upper side of the axis in horizontally
placed seedling of *Acer rubrum* (Cronshaw and Morey, 1968), *Populus alba* (Nečesaný, 1958), and a number of other species (Casperson, 1965a). However, when gibberellic acid and kinetin are applied along the upper side of the axis in horizontally placed seedlings of *Acer rubrum* the tension wood development occurred in its normal pattern (Cronshaw and Morey, 1968). Casperson (1964) showed that kinetin prevented the tension wood formation. Morey and Cronshaw (1968a,b) demonstrated that GA can induce more tension wood than TIBA. If auxin is applied with TIBA and GA the differentiation of tension wood is markedly inhibited. In gymnosperms high auxin levels promote compression wood formation, and in angiosperms low auxin levels promote tension wood formation (Brown, 1974). High auxin accumulation occurs on the upper side of a branch when pulled upward, in response to epinastic effect, and induces tension wood on its lower side where the auxin concentration is low. This explanation appears logical, but such a physiological balance of auxin under natural conditions is yet to be clearly demonstrated (Brown, 1974). IT 3456 morphactin is also known to suppress the tension wood formation in *Aesculus hippocastanum* (Smolinski, Saniewski and Pieniazek, 1974).
From the above summary of the present state of information on reaction wood formation and its relation to various factors, it is clear that the picture does not develop to its fullest satisfaction. As mentioned earlier, no information is available on our own species regarding the reaction wood anatomy. Moreover, the knowledge particularly in relation to comparative dimensional aspects of rays is very meagre. A useful tool for the assessment of the biological activity of the living cells is the histochemistry. Histochemical techniques enable us to identify and localize specific substances within the tissues (Stevens, 1975). A little information is available regarding starch content, and no information is available on the comparative histochemistry of lipids and proteins in normal and reaction woods. Storage of food material is a very active biological process in plant cells. The identification and localization of reserve metabolites and enzymes help us in understanding their distribution and possible interrelationships. Starch and lipids being important storage products in wood, the knowledge of their distributional pattern in normal and reaction woods may provide some useful information leading us to better understanding of reaction wood formation. There is a need for further investigation.
on the process of lignification in reaction xylem, especially in relation to the causes of decreased lignification, and the relation of this process to the increased synthesis of polysaccharides involved in the development of the gelatinous layer (Wardrop, 1964). Inspite of extensive research on the subject, the triggering mechanism of reaction wood formation is not completely understood.

To elucidate further some of the problem on the subject, and to add some more dimensions to the approach of investigation which may help better understanding of mechanism involved in the formation of reaction wood, the present work was planned on the following lines:

1. Morphology, distribution and general structure of tension wood.
2. Dimensional aspects of fibers and vessels.
3. Analysis of rays.
4. Histochemistry of (a) starch, (b) insoluble carbohydrates (excluding starch), (c) cellulose, (d) lipids, (e) proteins, (f) lignin, (g) enzyme peroxidase, and (h) enzyme succinate dehydrogenase.
5. Experimental studies on reaction wood formation using the following techniques:
(a) effect of angle of leaning of the stem on reaction wood formation;
(b) effect of leaves and growing buds on reaction wood formation;
(c) vertical loop experiment to understand the effect of gravity on reaction wood formation;
(d) effect of growth substances, on horizontally bent seedlings, on reaction wood formation; and
(e) lateral application of IAA on reaction wood formation.

The present thesis describes my observations along the above lines of investigation followed by discussion in light of the information already available on the subject.