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Tension Wood in Eucalypt Trees

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Abstract

Primary and secondary growths of main and lateral axes of *Eucalyptus gunnii* clone 634 young trees as well as some other aspects related to stem bending were studied in a small group of vertically left and inclined young trees and followed for a period of fourteen weeks. Although all the young trees, i.e. inclined and straight ones, did produce tension wood in the form of G-fibres, tilting was proved to be greatly effective in G-layer formation. Three different types of G-fibres were distinguished, with thin G-layer without an S3; with moderate to thick G-layer with an S3 and "faint" G-layer. The results of this experiment suggest that encountering the interior and exterior stresses the eucalypt employs at least three mechanisms: differentiating secondary xylem gelatinous fibres, eccentricity of growth compatible to G-fibres production and gelatinous fibres in phloem on the upper side of the leaned axes.

Keywords*: Tension wood, gelatinous layer, G-fibre, secondary, growth, stem inclination, Eucalyptus gunnii*

Introduction

In order to investigate the response of wood formation and kinetic lignification under exterior stimulus in *Eucalyptus gunnii* Hook.f., the wood structure was examined for possible tension wood and gelatinous fibres. While a considerable literature has been developed concerning the anatomy of reaction wood in the reorientation of leaning stems, wood characteristics in the stems of straight and non-leaning trees has received little consideration.

Wood formation is a dynamic physiological process and any change in the immediate environment in which the tree is growing can affect the growth and thus its pattern of growth and wood properties.

Most angiosperm trees respond to lean by producing wood with higher tensile stress on the upper side than on the lower side of the lean. The higher stresses usually develop in tension wood fibres identified by their special cell wall layers (Okuyama *et al.* 1994, White *et al.* 1965, Fournier *et al.* 1994).

It is fibre cells that show the most important modifications from an anatomical, mechanical and chemical point of view (Isebrands *et al*. 1972). It is considered to be the response to gravitational stress. There are also reports on its involvement in the efforts of the plant to correct the leaning portions of the main trunk. This stress differential generates an internal bending moment that tends to bend the stem back toward vertical in a righting response (Wilson *et al*. 1996). So mechanisms for righting response are: the development of the higher growth stresses usually associated to production of tension wood on the upper side and the development of eccentric rings (wider in the upper side) that amplify the effect of higher growth stresses by increasing the total force up righting movement in a ring.

Tension wood is usually associated with increased cambial activity and eccentric annual rings in experimentally bent trees in the case of poplar and willow (Jourez *et al.* 2001, Ohta 1979, Robards 1996).

Accentuated growth and anatomical modification do not always occur together. In some plants much more growth is found on the lower side of a branch, whereas the gelatinous fibres appear on the other side, in others reaction anatomy may occur with no asymmetry of growth rings and many woody plants do not produce typical reaction wood at all (Fahn

1990). It is widely assumed that reaction wood adds structural support to unevenly loaded branches and trunk axes and that its formation is the mechanism by which a tree counteracts the effect of changes in axis orientation due to natural or experimental cause. This is accomplished either by axis movement to decrease its bending moment and/or by inducing opposing stresses through newly formed wood (Wilson *et al.* 1979).

Materials and methods

Sampling: The sample trees used in this experiment were grown from cuttings 4-week-old from 4-year-old eucalypt (*Eucalyptus gunnii*) clone 634 trees. Fourteen one year old new saplings were transferred from Toulouse to 'Afocel' green-house (France), where we demon-strated a stem deviation from vertical situation about 30° for half of the young trees. Each stem of determined potted saplings were tied to the supports by plastic bands to make them produce reaction wood continuously (Fig. 1), and after some height increasing, the links to the supports used to be repeated. We measured height and diameter in 3-6 pre-determined points (related to tree morphology) every week and checked the behaviour of inclined trees against leaning and also the others for specific features. Two weeks after leaning the first pair of saplings, i.e. an inclined and a straight one, were cut off and either the others every two week from mid May toward early in August. The upper side of the axis was noted by an ink mark. The stems were divided to three or four 5-cm segments named number 1 to 4 from base (3 cm above ground) to top, respectively, fixed in FAA immediately and sectioned by microtome.

Fixation and embedding for light microscopy: Internodes of eucalypt lateral axis and either stems were sampled at various times, fixed in cold Glutaraldehyde-Paraform-aldehyde-Coffein (GPC), pH=7, for 1-7 days. The samples were then dehydrated in an ascending series of ethanol concentrations and embedded in LKB resin. A few stems were fixed in FAA. Transverse and longitudinal sections for light microscopy were cut with either a rotary or a sledge microtome of 3 or 15 µm in thickness, treated with a variety of stains and histochemical techniques using resin to demonstrate structural features and cell wall composition. These treatments included KMnO4 and Phloro-glucinol-HCl (Maule colour reaction) and also Phloroglucinol ethanol solution and HCl (Wiesner reaction) for lignin (Dadswell *et al*. 1956), Safranin and Alcian blue (FASGA) which stains unlignified tissue in blue and lignified ones in red; Mirand's Reagent which permits a clear distinction between cellulosic and lignified tissue either under UV excitation or light microscopy (Mondolot *et al*. 2001). Toluidine blue 0.5% as general stain; Periodic acid-Schiff (PAS) along with Naphtol blue black for polysaccharides and reserve material and Alune methylene blue and ruthenium red for lignified tissue.

Fig. 1- Arrangement of young eucalypt trees in green-house (May 14).

With emphasizing on the presence and distribution of G-fibres in stained transverse sections we examined the distribution of tension wood by an Optimas (Optimas version 6.5.172, 1987-1999 Media Cybernetics, LP.) macro with modification. Tension wood arcs were drawn on a sheet of paper by observing with a drawing stereoscope to a magnification of 25X. Examining these transverse sections as illustrated in Fig. 2A-B the drawings were scanned later and the quantum of differentiation of reaction wood as well as the linear dimensions of its constituent gelatinous fibres were estimated in different regions of all the stems from base to tip (information about tension wood and eccentricity of young trees not

shown). Wiesner and Maüle reactions were employed everywhere the distribution of tension wood was not clear enough. The other related anatomical characteristics were noticed either.

Epifluorescency: Lignification and the loss of lignification were detected by epifluoresceny method which has recently been arranged successfully by Mondolot (Mondolot *et al.* 2001).

Prepared slides were examined using a light microscope Leica DM RXA under visible or ultraviolet light (filter block: A; excitation range: UV; excitation filter: BP 340-380; suppression filter: LP 430 nm). The anatomy of stems was explored by observing thin sections employed a variety of microscopes (Olympus BX 60, Leica DM RXA, Nikon Optiphot). Photomicrographs were prepared by color video and an ordinary camera (Mondolot *et al.* 2001).

Electron microscopy (SEM, TEM): For Scanning Electron Microscopy (SEM) the samples were collected from the first and last trees harvested (i.e. 7 and 1 inclined) fixed in GPC, dehydrated by a series of ethanol, dried to critical point, coated with platinum; mounted by silver paste to the stubs (Chaffey *et al*. 2002) and observed by a Jeol Scanning electron microscope (JSM-6300 II, Electron Microscope, Jeol Ltd. Tokyo, Japan) operated at 15 KV. For Transmission Electron Microscopy (TEM) the samples from the last pair of the trees (14-week-treated) from tension wood and normal wood separately were immediately fixed in glutaraldehyde cacodylate buffer in 4°C for 2 hours; secondary fixation in 1% osmium tetroxide, dehydration by a series of ethanol (10°, 30°, 50°, 70° and 100°) and embeding in Spurr epoxy resin. A Reichert Ultracuts ultramicrotom was used to cut samples by glass and diamond knives to 35-95 nm to obtain sections displaying silver to gold interference colours. Gold, nickel and copper grids were used to keep them which were stained later with uranyl acetate and lead citrate (Chaffey *et al.* 2002) and examined in a Transmission Electron Microscope (TEM, Jeol JEM-1200 EX II, Electron microscope, Jeol Ltd. Tokyo, Japan).

Results

1- Architecture: *Eucalyptus gunnii* is a fast grown species which in green house produced an internode every 4.5 days. The maximum length of each internode hardly exceeds 2 cm. Each internode consists of two leaves against each other which will be wholly changed in shape in later years. The crown was almost symmetrical within the saplings which were left vertically but in tilted ones the branches and so the leaves were further on the upper side. This reaction seems to maintain regulation of the weight by reducing the distance between its standing point and centre of gravity (Wilson 1988).

2- Primary and secondary construction: There is a large rectangular medulla surrounded by primary vascular bundles and parenchymatous tissue in the youngest internode (Fig. 2). The first appearance of secondary growth was observed in the second internode (if one counts from the tip of the branch). The development of secondary xylem occurs in two phases. During the first phase only vessel elements differentiate and the rest of cells remain parenchyma (Fig. 2A-B). Fibres were only differentiated after some growth had occurred. Some workers had found the same pattern of secondary growth in *Arabidopsis* which is used by geneticists as a model for wood formation (Chaffey *et al.* 2002). At first the vessels appear along the two lateral sides of the medulla rectangular and later they spread over the other sides. One can find vessels with lignified cell walls in this stage (internode 2). Vessel elements mature quite early after being produced in cambial zone as evidenced by the thick lignified cell wall in the vessels close to cambium (Fig. 2A). Since at early stages of establishment the tree employs its vessels to bring about the growth substances, early maturation of vessels and even paratracheal parenchyma is highly expected. The time taken for paratracheal parenchyma cells is almost the same as vessels. However, comparing to vessels and parenchyma cells, fibre maturation takes longer time either in first or second growth ring. These differences between duration of vessel and fibre maturation rates were confirmed in some other eucalypts (Ridout *et al.* 1994),

poplars (Mourakami *et al.* 1999) and ashes (Doley *et al.* 1968).

Thick-walled sclereids are scattered in bundles in the medulla. With age these cells are augmented by late lignification. The bundles are specially concentrated at two poles of medulla in second year of growth. These sclereids are suggested to keep the stele skeleton. Similar lignified sclereids are scattered in bundles in cortex (Fig. 2E).

3- Tension wood: Since it is important to determine, if tension wood is a normal component of the wood before studying its induction under experimental conditions, half of the sample trees were left vertically during the experiment as controls (Dadswell *et al.* 1956). Found gelatinous fibres in the inner portion of the non-leaning *Eucalyptus* and various other tropical hardwoods. In this experiment tilting highly accelerated tension wood production, though, all the young trees either inclined or vertically remained, did produce tension wood in appearance of G-fibres and none of the trees were free of it. Visual observations as well as microscopic examination of vertically left trees (straight) showed that in the cases of high straight and symmetrically grown stems (i.e. trees nos. 17^{st} and 13^{st}) the proportion of gelatinous fibres was either extremely restricted or the values dropped to almost zero (data not shown). This has led us to believe that the presence of gelatinous fibres within a growth increment were associated with the formation of tension wood. Tension wood in turn often is related to tree lean and usually is located on the upper side of leaning trees or stems (Isebrands *et al.* 1972). Rapidly grown wood also has been shown to contain a high proportion of gelatinous fibres (Berlyn *et al.* 1961, Ritter *et al.* 1993, White *et al.* 1965).

Furthermore differences in response to stimulus of stem inclination among differentiating fibres were clear at different heights along the stems. In general the lower the height the higher the response (data not shown). Although some workers believed that because of the high flexibility of the tip of the branches, tension wood is seldom found in this area (Onaka *et al.* 1949).

We found G-fibres on the upper side 1.5 cm away from the tip of the branch after producing only four internodes (Fig. 2D). Further-more, in a lateral branch consisting of 13 internodes, G-fibres were found in 5, 6, 9, 12 & 13^{th} internodes and the others were free of it. It shows the movements of branch to overcome its exceeding weight and to provide the best position for itself (Onaka *et al.* 1949), suggesting differentiating fibres responsible for G-fibres rather than cambium. Generally speaking the number of rows of tension wood fibres increases with increasing time of inclination. Tension percentage achieved its maximum (Tab. 1) after 2 weeks inclination, but decreased gradually during the next weeks and from the 10^{th} week the value raised up again gradually.

It can be concluded that once differentiating fibres have been stimulated by inclination, G-fibre production is extended during next 15 days, but after that if stimulus is continued, there is little response by tree unless after 8 weeks remaining stimulus which is raised up gradually. In Tab. 1 this proceeding can be observed clearly. On the other hand taking into consideration the inclination period, eccentricity percentage plays exactly the same role suggesting cambial cell division rate being related to duration of inclination stimulus. It is hypothesized that the differentiating cells respond to stimulus severely accompanied by cambium accelerated wood cell formation, but not as much as G-fibre production.

Tab. 1- TimeTab. of tension wood production and eccentricity of growth in current growth ring in inclined and straight young trees. The value relates to tree no. 2 inclined which was a slow growing suppressed one. St: straight; in: inclined; TW%: percentage of G-fibres; d_{ecc} %: distance between the real centre and the centre of current growth ring relative to its radius.

TW%							
time(Week)	14	12	10	8	6	4	2
Mean st	10,95	4,17	5,71	6,86	9,52	1,22	4
Mean in	23,19	24,58	14	13,6	25,24	4,9*	33,86

d_{ecc}%							
time(Week)	14	12	10	8	6	4	2
Mean st	11,36	6,96	10,7	3,64	8,72	5,39	2,36
Mean in	16,67	17,4	16,26	7,86	8,54	8,69	21,03

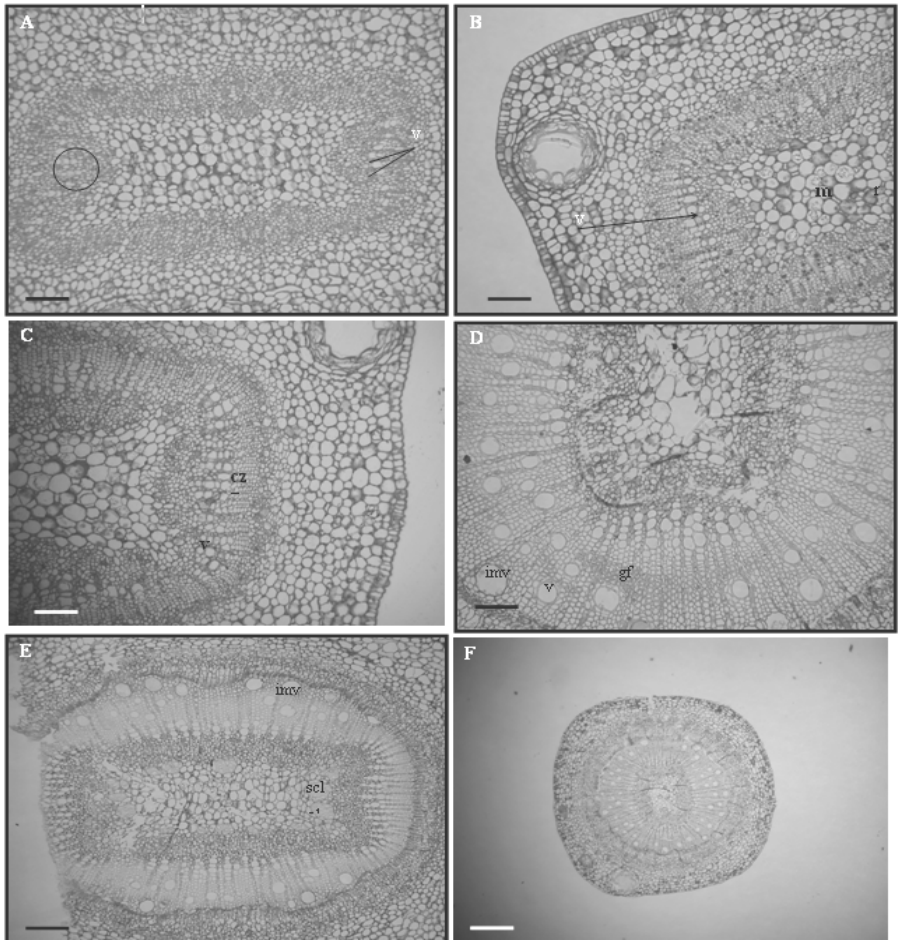

Fig. 2- Internodes of a lateral branch of *Eucalyptus gunnii* from tip to base respectively. (A) Cross section of second internode, the initiation of first phase of secondary growth. A row of lignified vessels is shown along the two lateral sides of pith rectangular (circle and arrows), bar=50 µm. (B) Third internode, the number of lignified vessels are increasing and along two other lateral sides of pith rectangular the vessels are present. Note that no fibre is differentiated yet, bar=50 µm. (C) 4th internode of the same material. The number of vessels are growing large, bar=50 µm. (D) Fifth internode, note that fibre differentiation and G-fibre production is commenced simultaneously, bar= 50 µm. (E) 7th internode, the sclerenchyma inside medullae are fully lignified and arranged along the four lateral sides of medullae, bar=100 µm. (F) The cross section of 8th internode, note the absence of G-fibres in this and previous section, bar = 200 µm.

Although the rate of eccentricity decreasing according to inclination duration is not as high as G-fibre differentiation, it is clear that during the remaining stimulus their trends are the same. Comparing to great loss of vessel differentiation in high stimulated period, the slow responding period to stimulus is marked by changing vessel number to its normal value which is characteristic of the tree (Fig. 3F).

4- Reaction anatomy:

Fibres in secondary xylem: in dicotyledons reaction wood characteristically has G-fibres which completely or partially replace normal wood fibres. The G-layer is swollen and nearly fills the fibre lumen when hydrated and stained with aqueous toluidine blue and often undulating or detached when dehydrated (Fisher *et al.* 1981). There are at least three different types of gelatinous fibres present in the specimens. They can be assumed as with: Thin G-layer without S3; moderate to thick G-layer with S3 (Fig. 4) and often convoluted; and very faint G-layer within the intermediate zone between the growth ring and latewood. The faint ones are not always easy to trace.

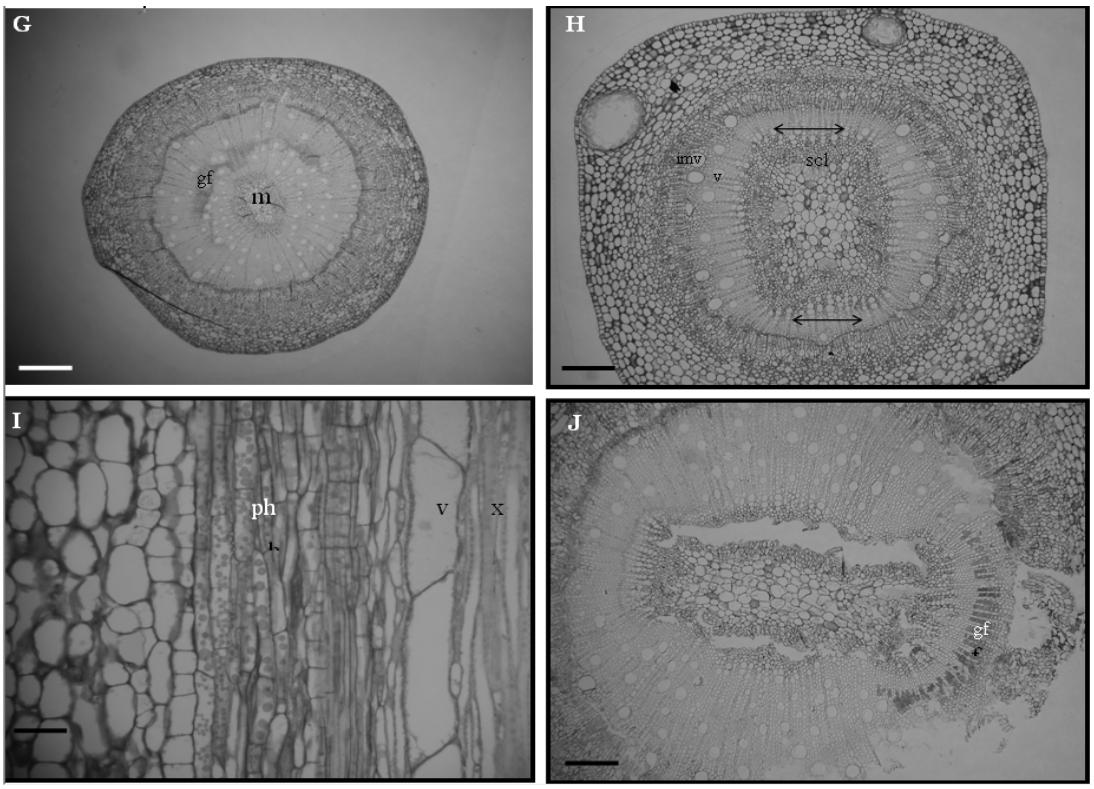

Fig. 2- Continued. (G) Cross section of 9th internode, note the presence and extension of G-fibres, bar=200 µm. (H)10th internode, showing the absence of G-fibres, note the reduced rate of vessel differentiation in the two lateral sides which at first the vessels were differentiated (arrows), bar=100 µm. (I) Longitudinal section of 11th internode through cambial zone, showing vessel elements, bar=50 µm. (J) Cross section of the last internode (base of the branch) with G-fibres not as much as the 9th internode, bar=100 µm. v=vessel, cz= cambial zone, scl= sclerenchyma, gf=G-fibre, imv=immatured vessel, ph=phloem, x=xylem, wo=wound, r=ray, gri=growth increment

In balsam poplar, portions of the wood samples were machined poorly when lacking high concentration of gelatinous fibres and samples with high concentrations of gelatinous fibres didn't exhibit visible evidence of the so-called "white ring" which is a marked zone in cross section identifiable to the naked eyes knowing to make some problems when wood is machined. It was suggested that the presence of "incipient" tension wood may contribute to poor machining properties (Ritter *et al.* 1993). If these two types of identified tension fibres, i.e. faint and incipient ones were the same, this can lead us to believe that they are mainly produced at the end of active period of growth.

When the production of tension wood is highly active (i.e. 2 weeks after leaning) there is no distinguishable border between differentiating and gelatinous fibres and it can be seen that immediately after division, the cells are differentiated to G-fibres. In such cases the only slightly graduation of G-layer formation can be noticed (Fig. 3H). In less active periods of tension wood production and either in the opposite wood the process of differentiation and lignification can be identified more clearly. Although the material in cells in the proximity of the cambium was not to be identified, since a β-glucosidase ought to be encountered somewhere along the route leading to lignin (Freudenberg 1964), it is probably traceable in 1-10 cells in radial files from cambium. Interestingly, they are all present in cells with identical G-layers, if were located close to cambial zone. The results suggest the process of lignification to be continued after G-layer formation (Fig. 3C).

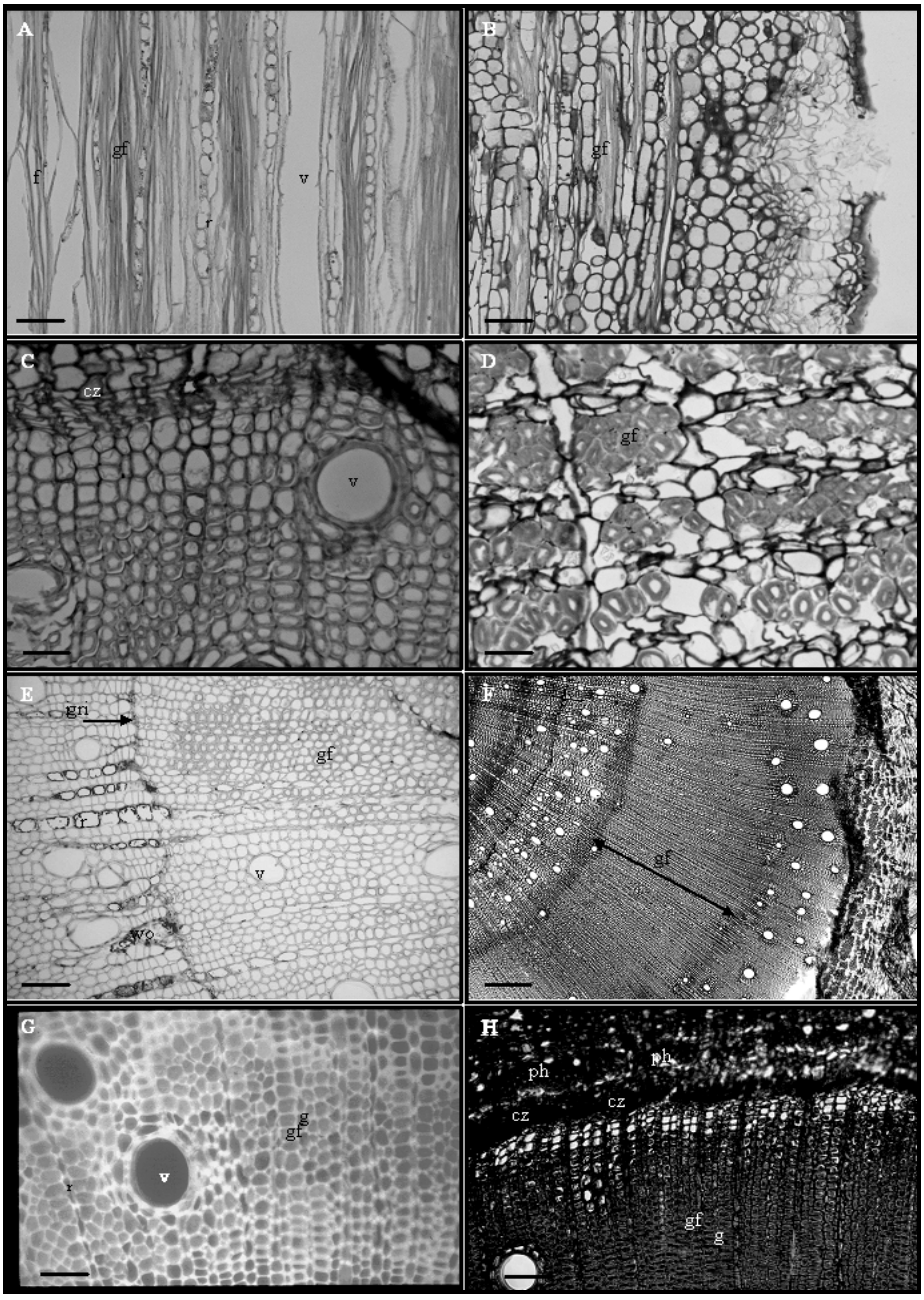

Fig. 3- G-fibres in secondary xylem and phloem. (A) Longitudinal section (sectioned at 3 µm and stained with FASGA), showing gelatinous fibres in secondary xylem, bar=50µm. (B) Same material but stained with PAS+Naphtol blue black, showing G-fibres in cortex, bar= 50µm. (C) Transverse section showing cambial zone at the top, immature fibres in the middle and gelatinous fibres still in maturation process, stained with FASGA, bar=20 µm. (D) G- fibres in cortex; bar=20µm. (E) Wound in secondary xylem in the growth ring zone. Note G-fibres close to the wound at the same side, bar=25 µm. (F) Cross section of a 8-week-trial inclined tree sectioned at 15 µm, stained with Safranin-Alcian blue, showing the extended vessel-less area of tension wood, followed by an area with default number of vessels. Note that both areas are located in latewood, bar=200 µm. (G) UV micrograph of a transverse section of G-fibre zone, auto fluorescence of lignin in the walls of vessels is highlighted, bar=200 µm. (H) Transverse section of (sectioned at 15 µm and stained with Azure II) of a 2-week-trial inclined tree, showing the process of G-fibres production and highly stimulation of cambium and differentiating cells, bar=50 µm. For abbreviations see Fig. 2.

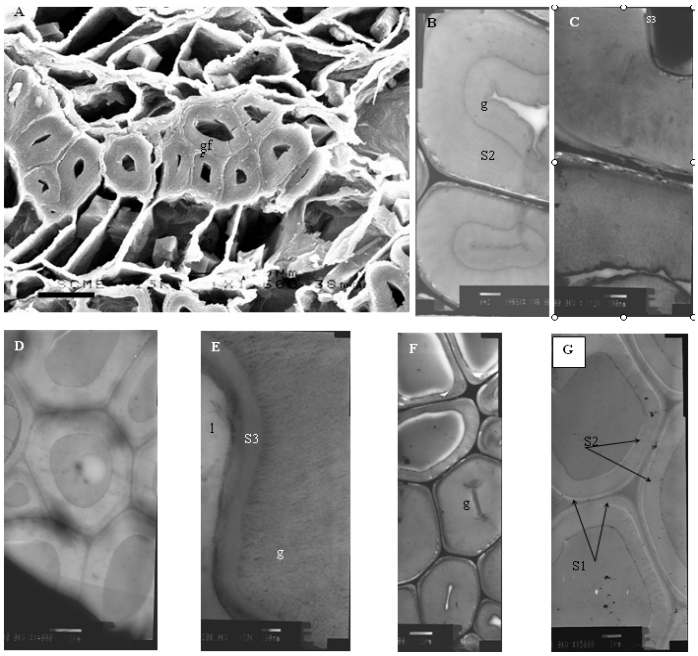

Fig. 4- G-fibres in phloem and xylem. (A) Scanning electron micrograph of a transverse section of secondary phloem zone in a 14-week-trial inclined tree showing G-fibres, bar =10 µm (B, C, D, E, F and G) transmission electron micrographs of secondary xylem. (B) Intermediate G-layer, bar=1 µm. (C) Thick G-layer, bar=0.5 µm. (D) Normal fibres, bar=2 µm. (E) Thick G-layer with S3, bar=0.1 µm. (F) Normal and G-fibres. Note the highly lignified middle lamellae, bar=2 µm. (G) Normal fibres showing layers of secondary wall, bar =1 µm.

In this investigation the transition from normal to tension wood formation migrated abruptly as seen in cross sections and a few longitudinal tangentially ones. Fig. 5 shows the three types of G-fibres and either presence of thin and thick G-layer in the same radial file demonstrating that there is no systematically and gradually formation of G-fibres.

Fibres in secondary phloem: It has been reported in a gymnosperm (*Gnetum gnemon*) that gelatinous fibres are developed in secondary phloem and cortex which may function as tension fibres. Since secondary xylem of tilted stems showed little eccentricity of development and no reaction anatomy, the importance of reaction tissues in maintaining the distinctive architecture of the tree was confirmed (Tomlinson 2001).

In present experiment the gelatinous fibres were present in the secondary phloem as well as in cortex at the upper side of most of the leaning stem (Fig. 3B, D). Interestingly none of the vertically left young trees produced gelatinous fibres in their phloem or cortex even if they had produced gelatinous fibres in their secondary xylem due to the natural stresses. Hence the results indicate the general distribution of gelatinous fibres in seed plants. Furthermore, gelatinous fibres are common in the bark of many *Ephedra* species (Carlquist 1989) which seems an additional structural aspect related to its growth habit as a climber (Lev-Yadun 1999). It seems that the plant employs its extra-xylary tissue as a complementary solution for re-orientation. In Fig.4A a bundle of secondary phloem gelatinous fibres is shown.

Wounds: Wounds may be caused by injuries, water deficits or mechanical bending stresses (Tremnerud 1999). Wounding may cause cellular abnormalities. In general trees react the wounding by forming a mass of traumatic cells which is composed of thin-walled parenchyma cells irregular in size and shape. In *Eucalyptus*, gum canals are referred to as gum veins or kino veins. In present experiment wounds were found especially in inclined trees (Fig. 3E).

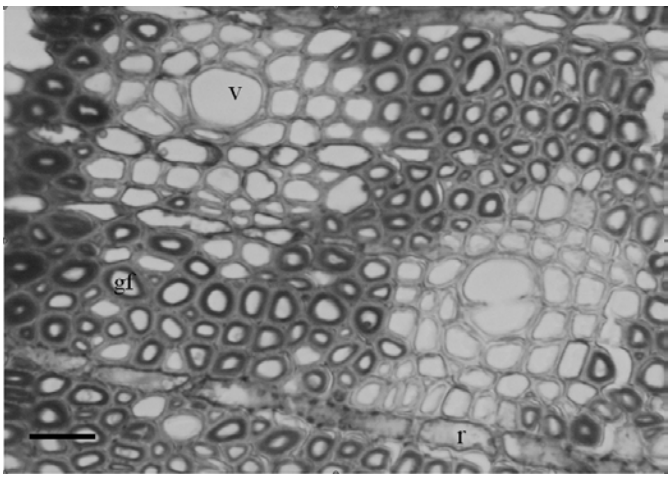

Fig. 5- Cross section of a 12-week-trial inclined tree showing presence of thin and thick G-layer in the same radial file. Cambial zone is located on the left side, bar = 20 µm

Frequently they were located on growth increment zone and sometimes within the second growth increment. In all cases typical wounds were only formed after some growth had occurred. Only two of the vertically left trees produced wounds i.e. trees numbers 11 and 15 which were known as naturally leaned samples. Only one of the inclined samples (7 in 2 week's trial) didn't produce wounds at all which can be assumed as not to have enough time to respond the stimulus. In the last harvested tree (1 in 14 week's trial) beside the preformed wound the initiation of new wound was markedly found.

Conclusion

Due to experimental bending, young trees of *Eucalyptus gunnii*, made immediate response by differentiating G-fibres of different types, reducing vessel differentiation and eccentricity of growth. Although tension wood is a normal component of *Eucalyptus gunnii* tilting accelerated highly its production. Examining the internodes of lateral branches confirmed the immediate responding to self-weight stimulus in early stages of growth. The presence of G-fibres within a few internodes and not all of them successively, lead us to think about the responsibility of differentiating fibres to produce G-fibres rather than cambium. It seems that division process in cambium is highly accelerated simultaneously which causes eccentricity of growth. Furthermore, gelatinous fibres are usually formed in phloem and even cortex suggesting a complementary solution for re-orientation of stems.

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References

Berlyn G.P. 1961: Factors affecting the incidence of reaction tissue in *Populus deltoids*. *Bartr*. *Iowa State J. Sci.* **5(3):** 7-424.

Carlquist S. 1989: Wood and bark anatomy of the New World species of *Ephedra*. *Aliso* **12:** 1-483.

Chaffey N., Cholewa E., Regan S., Sundberg B. 2002: Secondary xylem development in *Arabidopsis*: a model for wood formation. *Physiol. Pl.* **114:** 4-60.

Dadswell H.E., Wardrop A.B. 1956: The importance of tension wood in timber utilization. Australian Pulp and Paper Industry. *Techn. Assoc. Proc.* **10:** 30-42.

Doley D., Layton L. 1968: Effects of growth regulating substances and water potential on the development of secondary xylem in *Fraxinus*. *New Phytol*. **67:** 579-594.

Fahn A. 1990: Plant anatomy. 4th ed. Pergamon Press, Oxford.

Fisher J.B., Stevenson J.W. 1981: Occurrence of reaction wood in branches of dicotyledons and its role in tree architecture. *Bot. Gaz*. **142(1):** 82-95.

Fournier M., Bailleres H., Chanson B. 1994: Tree biomechanics: growth, cumulative pre-stresses and reorientations. *Biomim.* **2:** 229-251.

Freudenberg K., 1964: The formation of lignin in the tissue and in vitro. In: Zimmermann M.H. (ed.), The formation of wood in forest trees. Academic Press, London.

Isebrands J.G., Bensend D.W. 1972: Incidence and structure of gelatinous fibers within rapid-growing eastern cottonwood. *Wood and Fiber* **4(2):** 61-71.

Jourez B., Riboux A., Leclercq A. 2001: Anatomical characteristics of tension wood and opposite wood in young inclined stems of poplar (*Populus euramericana* CV."GHOY"). *IAWA J.* **22(2):** 133-157.

Lev-Yadun S. 1999: Eccentric deposition of secondary xylem in stems of the climber *Ephedra campylopoda* (Gnetales). *IAWA J.* **20(2):** 165-170.

Mondolot L., Roussel J.L., Andary C. 2001: New application for an old lignified element staining reagent. *The Histochem. J.* **33:** 379-385.

Mourakami Y., Funada R., Sano Y., Ohta J. 1999: The differentiation of contact cells and isolation cells in the xylem ray parenchyma of *Populus maximoviczii*. *Ann. Bot*. **84:** 429-435.

Ohta S. 1979: Tension wood from stems of poplar (*Populus* × *euramericana* C.V.) with various degrees of leaning. *Mokusai Gakkaishi* **9**: 610-614.

Okuyama T., Yamamoto H., Yoshida M., Hattori Y., Archer R.R. 1994: Growth stresses in tension wood: role of microfibrils and lignification. *Ann. Sci. For*. **51:** 291-300.

Onaka F. 1949: Studies on compression and tension wood. *Wood Res. Bull*. No.1, Kyoto University, Kyoto, Japan. Translation No. **93**, Forest Prod. Lab. Dept. the Sec. State, Ottawa, Ontario, Canada. 1956.

Ridout B.G., Sands R. 1994: Quantification of the processes of secondary xylem fibre development in *Eucalyptus globolus* at two height levels. *IAWA J.* **15:** 417-424.

Ritter D.C., Kroll R.E., Gertjejansen R.O. 1993*:* Zones of gelatinous fibres in *Populus balsamifera* L. *Wood Fiber Sci*. **25 (2):** 198-208.

Robards A.W. 1996: The application of the modified sine rule to tension wood production and eccentric growth in the stem of crack willow (*Salix fragilis* L.). *Ann. Bot.* **30:** 513-523.

Tomlinson P.B. 2001: Reaction tissues in *Gnetum gnemon*: a preliminary report. *IAWA J*., **22(4):** 401-413.

Tremnerud E., Valinger E., Sundberg B. 1999: Induction of resin pockets in seedlings of *Pinus sylvestris* L. by mechanical bending stress during growth. *Holzforsch.* **53:** 386-390.

White D.J.B., Robards A.W. 1965: Gelatinous fibers in ash (*Fraxinus excelsior* L.). *Nature* **205:** 816-818.

Wilson B.F. 1988*:* The growing tree. The University of Massachusetts Press.

Wilson B.F., Archer R.R. 1979: Tree design; some biological solutions to mechanical problems. *Biosci.* **29:** 293-298.

Wilson B.F., Gartner B.L. 1996: Lean in red alder (*Alnus rubra*): Growth stress, tension wood and righting response. *Can. J. For. Res*. **26:** 1951-1956.