

# Reaction wood: A wood with altered properties and its formation in woody trees

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Bilal Ahmad Wani, Amina Khan

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## Abstract

Reaction wood possesses altered properties than normal wood and develops in response to gravistimulus in trees. In gymnosperms it is referred as compression wood and develops on the lower side of leaning stems or branches, while in angiosperms it is called tension wood and is formed on the upper side of the leaning stem or branches. Reaction wood performs the function of regulating a tree's form but at the same time is a serious defect in wood utility. This paper describes the factors which lead to the formation of reaction wood and its different properties.

## Introduction

### Properties of Reaction Wood

Reaction wood is modified in its anatomical and chemical properties and is generally formed in response to a non-optimal orientation of the stem or branch caused by prevailing winds, snow, slope, loads, or asymmetric crown shape. When a herbaceous plant is brought out of its equilibrium position in space, inclined or horizontally positioned for example, a longitudinal growth promotion is initiated on its lower side, thus making the stem bend upward. In the case of woody plants, however, an increased longitudinal growth on the lower side is not sufficient for the upward bending. The righting is achieved by the formation of reaction wood, which develops while the tree "reacts" to its changed environment. The properties and induction of reaction wood have been investigated and reviewed by many wood anatomists and physiologists<sup>557273796756</sup>. The type of reaction wood formed in gymnosperms is referred to as compression wood. It develops on the lower side of an inclined shoot or stem, where the tissues seem to be under a "compressive" stress. The most characteristic feature of compression wood is the rounded shape of the tracheids, resulting in intercellular spaces. The cell walls of compression wood are thicker than those in normal wood, and contain more lignin but less cellulose. The primary wall is the same as in normal wood, but the secondary wall lacks the innermost S3 layer, containing only S1 and S2 layers. The tracheid length is reduced and the microfibril angle is much higher than in normal wood. Helical cavities are another very characteristic feature of compression wood, and are responsible for some of the physical properties of this tissue. As a result of these changes, compression wood cells can expand longitudinally during the cell maturation process to perform the function of "pushing" up the shoot or stem<sup>77786739</sup>.

Reaction wood in the arboreal, dicotyledonous angiosperms is called tension wood and is formed on the upper side of a leaning stem, where the tissues are held in "tension". The most outstanding characteristic of tension wood fibers is the presence of a thick, inner cell-wall layer that consists of highly crystalline cellulose, in which the microfibril orientation is nearly longitudinal and parallel to the fiber axis. This so-called gelatinous layer (G-layer) is almost invariably unlignified and is loosely attached to the other cell-wall layers. As G-layer is blue-stained with a fast-green solution, tension wood fibers are easily recognized using this feature subjected to light microscopy. During maturation, tension wood fibers shrink strongly in the longitudinal direction, thereby creating a very strong "tensile" stress to "pull" the leaning stem upright. Besides, the formation of both compression and tension wood is usually paralleled by increased radial growth on the side, causing the stem to be eccentric<sup>50511066636</sup>. The characteristic anatomical and chemical features of tension wood have been the focus of extensive study because they are closely related to the quality of wood and its products<sup>54722250512351820216162</sup>.

There are also some special cases where the patterns of reaction wood formation do not correspond with the group of gymnosperms or angiosperms that the species belongs to. In the Cycadales, which produce very little xylem, no reaction wood has been detected. The Gnetales do not form compression wood. Instead, they can form tension wood tissues. The primitive angiosperm *Buxus*, however, was found to produce compression wood. These genetic characteristics are correlated with the origin and evolution of the species<sup>55678368</sup>.

### Stimuli Inducing Reaction Wood Formation

More than one factor may contribute as an initial stimulus to the induction of reaction wood formation. Compressive and tensile stresses are the originally proposed candidate stimuli thus giving the names for compression and tension wood, respectively<sup>67</sup>. The loop experiments of shoots or branches probably contributed most to the confirmation of gravity vector as the stimulus for

reaction wood formation. These kind of experiments were conducted by several investigators<sup>3233315264715840</sup> and have been repeatedly cited and discussed by later researchers<sup>5573777840131467817</sup>. In the case of vertical loops of conifers, they found that compression wood was formed on the lower side in both the upper and the lower halves of the loops, but not in the vertical portions. Similarly, in the tested broadleaf trees, tension wood was formed on the upper side of both upper and lower portions of the loop, but not in the vertical portions

### Internal control mechanism

Reaction wood formation can also be generated to maintain a proper status of the entire tree even in the absence of any gravitational, compressive, or tensile stimulus<sup>307980</sup>. A well known example is that which is formed in branches of the uppermost whorl when the apical shoot is removed. Reaction wood formation in this case causes a side shoot to bend upward and replace the lost leader. In an experiment of removing one of the branches from the highest whorl of pine trees, compression wood formation was observed along the out flank of the two adjacent branches, and the two branches bent toward each other to reduce the gap between them<sup>76</sup>. The process of reaction wood formation in these cases is controlled by an internal mechanism, but can also be regarded as a response to changed environments.

### Hormonal Control of Reaction Wood Formation

#### Auxin

Plant hormones, auxin in particular, have been intensively studied in revealing the biology of gravitropic responses. The upward bending of tilted herbaceous plants is interpreted by the Cholodny-Went theory as a result of lateral redistribution of auxin, its accumulation on the lower side of tilted stems resulting in the acceleration of longitudinal growth on the same side<sup>1975</sup>.

Many investigations indirectly demonstrated a correlation of elevated auxin level to compression wood formation by local applications of exogenous auxins or auxin regulators. These include examples of artificially induced compression wood formation by the application of IAA or naphthaleneacetic acid (NAA) to vertical shoots or to the upper side of horizontal or inclined shoots<sup>535548737440</sup>. The old model for tension wood formation postulates that gravistimulation (e.g. tilting of stems) causes a difference in auxin level around the stem and an auxin deficiency on the upper side induces tension wood formation. Applied radiolabeled IAA was detected to move towards the lower side of bent or horizontally placed willow and beech stems opposite to the side of tension wood formation<sup>3835</sup>. Direct evidence that auxin concentration is lower on the upper side of inclined hardwood shoots where tension wood forms has been detected using bioassay by several investigators<sup>4836</sup>. A number of application experiments support this postulation<sup>55341617242544451260</sup>

#### Ethylene

Ethylene is a volatile hormone which contributes to many plant functions such as cell division, cell wall synthesis, elongation growth, swelling, curvatures, xylem formation, and response to gravity<sup>127</sup>. Ethylene evolution in tree stems or branches can be enhanced by various kinds of physical stresses such as shaking, bending, and tilting<sup>371559491165825741</sup>. These stresses often locally stimulate cambial activity and wood formation, including reaction wood. A possibility that ethylene plays a role in reaction wood formation has accordingly been considered and investigated. A role for ethylene produced by stem inclination in compression wood formation of conifers has been suggested by several investigators<sup>1594129</sup>. The evidence supporting this hypothesis includes findings that ethylene evolution was greater from the lower sides where compression wood formed than from the upper sides in branches or tilted stems of cypress, spruce, and metasequoia<sup>14128</sup>.

#### Gibberellin

Gibberellins (GAs) are another group of plant hormones that are essential to cambial growth in both woody angiosperms and gymnosperms. Several GAs have been identified in the cambial region, and both endogenous and applied GAs have been found to be possibly related to stem radial increment<sup>23443697042</sup>. Much evidence implies that GAs are involved in tension wood formation. It was reported that GA3 induced tension-wood-like fibers in vertical cherry shoots<sup>26</sup>. Drooping mutants of cherry trees restarted vertical shoot growth following GA3 application, and the formation of tension wood on the upper side was promoted in this occasion<sup>46478</sup>. Throughout this review it seems that information about the mechanism of reaction wood formation has been accumulating less rapidly in recent years than was the case several decades ago. This work highlights the properties and role of plant hormones in the regulation of reaction wood formation.

### References

1. Abeles FB, Morgan PW and Saltveit ME Jr. 1992. Ethylene in Plant Biology, 2nd edn. Academic Press, San Diego.
2. Aloni R. 1988. Vascular differentiation within the plant. In: Roberts LW, Gahan PB.
3. Aloni R. 1979. eds. Vascular Differentiation and Plant Growth Regulators. Springer-Verlag, New York. 39-62.
4. Aloni R. 1991. Wood formation in deciduous hardwood trees. In: Raghavendra AS, ed Physiology of Trees. John Wiley &

5. Araki N, Fujita M, Saiki H and Harada H. 1982. Transition of the Wber wall structure from normal wood to tension wood in *Robinia pseudoacacia* L. and *Populus euramericana* Guinier. *Mokuzai Gakkaishi*. 28:267-273.
6. Archer RR. 1987. *Growth Stresses and Strains in Trees* (Springer series in wood science). Springer-Verlag, New York.
7. Baba K. 2003. Structure and formation of reaction wood. In: Fukushima K, Funada R, Sugiyama J, Takabe K, Umezawa T, Yamamoto H, eds. *Secondary Xylem Formation – Introduction to Biomass Science*. Kaiseisha Press, Otsu. 76–80 (in Japanese).
8. Baba K, Adachi K, Take T, Yokoyama T, Ito T and Nakamura T. 1995. Induction of tension wood in GA3-treated branches of the weeping type of Japanese cherry, *Prunus spachiana*. *Plant Cell Physiol*. 36:98-988.
9. Barker JE. 1979. Growth and wood properties of *Pinus radiata* in relation to applied ethylene. *N. Z. J. For. Sci*. 9:15-19.
10. Bentum ALK, Côté WA Jr, Day AC and Timell TE. 1969. Distribution of lignin in normal and tension wood. *Wood Sci Technol*. 3:218-231.
11. Blake TJ, Pharis RP and Reid DM. 1980. Ethylene, gibberellins, auxin and the apical control of branch angle in a conifer, *Cupressus arizonica*. *Planta* 148:64-68.
12. Blum W. 1971. Über die experimentelle Beeinflussung der Reaktionsholzbildung bei Fichten und Pappeln. *Ber. Schweiz. Bot. Ges.* 80: 225-251.
13. Boyd JD. 1976. Basic cause of differentiation of tension wood and compression wood. Part I, II. *Drev. Vysk*. 21:57–66; 133-144.
14. Boyd JD. 1977. Basic cause of differentiation of tension wood and compression wood. *Aust. For. Res.* 7:121-143.
15. Brown KM and Leopold AC. 1973. Ethylene and the regulation of growth in pine. *Can. J. For. Res.* 3:143-145.
16. Casperson G. 1965. Über endogene faktoren derreaktionsholzbildungl. Wuchsstoffapplikation an kastanienepikotylen. *Planta* 64:225-240.
17. Casperson G. 1968. Wirkung von wuchs-und hemmstoffen auf die kambiumtätigkeit und reaktionsholzbildung. *Physiol. Plant* 21:1312-1321.
18. Chaffey N, Barlow P and Sundberg B. 2002. Understanding the role of the cytoskeleton in wood formation in angiosperm trees: hybrid aspen (*Populus tremula* £ *P. tremuloides*) as the model species. *Tree Physiol* 22:239-249.
19. Cholodny N. 1926. Beiträge zur analyse der geotropischen reaction. *Jahrb. Wiss. Bot.* 65:447-459.
20. Clair B, Thibaut B and Sugiyama J. (2005). On the detachment of the gelatinous layer in tension wood fiber. *J Wood Sci* 51:218-221.
21. Clair B, Ruelle J, Beauchêne J, Prévost MF and Fournier M. 2006. Tension wood and opposite wood in 21 tropical rain forest species 1. Occurrence and eYciency of the G-layer. *IAWA J* 27:329-338.
22. Cote WA and Day AC. 1965. Anatomy and ultrastructure of reaction wood. In: Côté WA Jr (ed) *Cellular ultrastructure of woody plants*. Syracuse University Press, Syracuse. 391-418.
23. Cote WA, Day AC and Timell TE. 1969. A contribution to the ultrastructure of tension wood fibers. *Wood Sci Technol* 3:257-27.
24. Cronshaw J, and Morey PR. 1965. Induction of tension wood by 2,3,5- tri-iodobenzoic acid. *Nature* 205, 816–818
25. Cronshaw J, and Morey PR. 1968. The effect of plant growth substances on the development of tension wood in horizontally inclined stems of *Acer rubrum* seedlings. *Protoplasma* 65:379-391.
26. Denhard B, and Feucht B. 1971. Zur reaktionsholzbildung bei *Prunus avium*. *Holzforschung* 25:169-174.
27. Dolan L. 1997. The role of ethylene in the development of plant form. *J. Exp. Bot.* 48:201-210.
28. Du S, and Yamamoto F. 2003b. Ethylene evolution changes in the stems of *Metasequoia glyptostroboides* and *Aesculus turbinata* seedlings in relation to gravity-induced reaction wood formation. *Trees* 17:522-528.
29. Eklund L, and Klintborg A. 2000. Ethylene, oxygen and carbon dioxide in woody stems during growth and dormancy. In: Savidge RA, Barnett JR, Napier R, eds. *Cell and Molecular Biology of Wood Formation*. Bios Scientific, London.43-56.
30. Fisher JB and Stevenson JW. 1981. Occurrence of reaction wood in branches of dicotyledons and its role in tree

architecture. Bot. Gaz. 142:82-95.

31. Hartmann F. 1932. Untersuchungen über Ursachen und Gesetzmäßigkeit exzentrischen Dickenwachstums bei Nadel- und Laubbäumen. Forstwiss. Cbl. 54: 497-517, 547-566, 581-590, 622-634.
32. Jaccard P. 1919. Nouvelles Recherches sur L'accroissement en Épaisseur des Arbres. Foundation Schnyder von Wartensee, Zürich.
33. Jaccard P. 1938. Exzentrisches Dickenwachstum und anatomisch-histologische Differenzierung des Holzes. Ber. Schweiz. Bot. Ges. 48:491-537.
34. Kennedy RW and Farrar JL. (1965). Induction of tension wood with the anti-auxin 2,3,5-triiodobenzoic acid. Nature 208:406-407.
35. Lachaud S. 1987. Xylogénèse chez les dicotylédones arborescentes. V. Formation du bois de tension et transport de l'acide indole acétique tritié chez le Hêtre. Can. J. Bot. 65:1253-1258.
36. Leach RWA and Wareing PF. 1967. Distribution of auxin in horizontal woody stems in relation to gravimorphism. Nature 214:1025-1027.
37. Leopold AC, Brown KM and Emerson FH. 1972. Ethylene in the wood of stressed trees. HortScience 7:715.
38. Lepp NW and Peel AJ. 1971. Distribution of growth regulators and sugars by the tangential and radial transport systems of stem segments of willow. Planta 99:275-282.
39. Lin JX and Li ZL. 1993. Comparative anatomy of normal wood and compression wood of masson pine (*Pinus massoniana*). Acta Bot. Sin. (in Chinese with an English abstract). 35:201-215.
40. Little CHA. 1967. Some Aspects of Apical Dominance in *Pinus strobus* L. Ph D Thesis, Yale Univ. New Haven.
41. Little CHA and Eklund L. 1999. Ethylene in relation to compression wood formation in *Abies balsamea* shoots. Trees 13:173-177.
42. Little CHA and Pharis RP. 1995. Hormonal control of radial and longitudinal growth in the tree stem. In: Gartner BL, ed. Plant Stems: Physiology and Functional Morphology. Academic Press, New York. 281-319.
43. Little CHA and Savidge RA. 1987. The role of plant growth regulators in forest tree cambial growth. Plant Growth Regul. 6:137-169.
44. Morey PR and Cronshaw J. 1968a. Developmental changes in the secondary xylem of *Acer rubrum* induced by various auxins and 2,3,5-triiodobenzoic acid. Protoplasma 65:287-313.
45. Morey PR and Cronshaw J. (1968b). Induction of tension wood by 2,4-dinitrophenol and auxins. Protoplasma 65:393-405.
46. Nakamura T, Saotome M, Ishiguro Y, Itoh R, Higurashi S, Hosono M. 1994. The effects of GA<sub>3</sub> on weeping of growing shoots of the Japanese cherry, *Prunus spachiana*. Plant Cell Physiol. 35: 523-527.
47. Nakamura T, Saotome M and Tanaka H. 1995. Weeping habit and gibberellin in *Prunus*. Acta Horticult. 394:273-280.
48. Necessary V. 1958. Effect of ?-indoleacetic acid on the formation of reaction wood. Phyton 11:117-127.
49. Nelson ND and Hillis WE. 1978. Ethylene and tension wood formation in *Eucalyptus gomphocephala*. Wood Sci. Technol. 12:309-315.
50. Norberg PH and Meier H. 1966. Physical and chemical properties of the gelatinous layer in tension wood fibers of aspen (*Populus tremula* L.). Holzforschung 20:174-178.
51. Norberg PH and Meier H. 1966. Physical and chemical properties of the gelatinous layer in tension wood of aspen (*Populus tremula* L.). Holzforschung 20:174-178.
52. Onaka F. 1935. Über die Rotholzordnung bei Nadelbäumen. J. JPN. For. Soc. (in Japanese). 17:680-693.
53. Onaka F. 1940. Über den einfluß von heteroauxin auf das Dickenwachstum, besonders die Rotholzbildung der Bäume. J. JPN. For. Soc. (in Japanese). 22:573-580.
54. Onaka F. 1943. Studies on compression- and tension-wood. Bull Wood Res Inst Kyoto Univ 1:1-88.
55. Onaka F. 1949. Studies on compression- and tension-wood. Mokuzai Kenkyu, Wood Res. Inst. Kyoto. Univ. 1:1-88 (in Japanese with an English resume).
56. Plomion C, Leprovost G and Stokes A. 2001. Wood formation in trees. Plant Physiol. 127:1513-1523.

57. Rinne P. 1990. Effects of various stress treatments on growth and ethylene evolution in seedlings and sprouts of *Betula pendula* Roth and *B. pubescens* Ehrh. *Scand. J. For. Res.* 5:155-167.
58. Robards AW. 1965. Tension wood and eccentric growth in crack willow (*Salix fragilis* L.). *Ann. Bot.* 29:419-431.
59. Robitaille HA and Leopold AC. 1974. Ethylene and the regulation of apple stem growth under stress. *Physiol. Plant* 32:301-304.
60. Robnett WE and Morey PR 1973. Wood formation in *Prosopis*: Effect of 2,4-D, 2,3,5-T, and TIBA. *Am. J. Bot.* 60:745-754.
61. Ruelle J, Clair B, Beauchêne J, Prévost MF and Fournier M. 2006. Tension wood and opposite wood in 21 tropical rain forest species 2. Comparison of some anatomical and ultrastructural criteria. *IAWA J* 27:341-376.
62. Ruelle J, Yoshida M, Clair B and Thibaut B. 2007. Peculiar tension wood structure in *Laetia procera* (Poepp.) Eichl. (Flacourtiaceae). *Trees* 21:345-355.
63. Scurfield G. 1973. Reaction wood: Its structure and function. *Science* 179:647-655.
64. Sinnott EW. 1952. Reaction wood and the regulation of tree form. *Am. J. Bot.* 30:69-78.
65. Telewski FW and Jaffe MJ. 1986. Thigmomorphogenesis: The role of ethylene in the response of *Pinus taeda* and *Abies fraseri* to mechanical perturbation. *Physiol. Plant* 66:227-233.
66. Timell TE. 1969. The chemical composition of tension wood. *Svensk Papperstidning* 72:173-181.
67. Timell TE. 1986. *Compression Wood in Gymnosperms*, Springer-Verlag, New York. Vol. 1-3.
68. Tomlinson PB. 2001. Reaction tissues in *Gnetum gnemon* – A preliminary report. *IAWA J.* 22:401-413.
69. Wang Q, Little CHA and Odén PC. 1995. Effect of laterally applied gibberellin A4/7 on cambial growth and the level of indole-3-acetic acid in *Pinus sylvestris* shoots. *Physiol. Plant* 95:187-194.
70. Wang Q, Little CHA, Sheng C, Odén PC and Pharis RP. 1992. Effect of exogenous gibberellin A4/7 on tracheid production, longitudinal growth and the levels of indole-3-acetic acid and gibberellins A4, A7 and A9 in the terminal shoot of *Pinus sylvestris* seedlings. *Physiol. Plant* 86:202-208.
71. Wardrop AB. 1956. The nature of reaction wood. V. The distribution and formation of tension wood in some species of *Eucalyptus*. *Aust. J. Bot.* 4:152-166.
72. Wardrop AB. 1964. The reaction wood anatomy of arborescent angiosperms. In: Zimmermann MH, ed. *The Formation of Wood in Forest Trees*. Academic Press, New York. 405-456.
73. Wardrop AB. 1965. The formation and function of reaction wood. In: Côté WA Jr, ed. *Cellular Ultrastructure of Woody Plants*. Syracuse Univ Press, Syracuse. pp. 373-390.
74. Wardrop AB and Davies GW. 1964. The nature of reaction wood VIII. The structure and differentiation of compression wood. *Aust. J. Bot.* 12:24-38.
75. Went FW. 1926. On growth accelerating substances in the coleoptile of *Avena sativa*. *Proc. K. Akad. Wet. Amsterdam.* 30:10-19.
76. Westing AH. 1965a. Compression wood in the regulation of branch angle in gymnosperms. *Bull. Torrey. Bot. Club* 92:62-66.
77. Westing AH. 1965b. Formation and function of compression wood in gymnosperms. *Bot. Rev.* 31:381-840.
78. Westing AH. 1968. Formation and function of compression wood in gymnosperms II. *Bot. Rev.* 34:51-78.
79. Wilson BF and Archer RR. 1977. Reaction wood: Induction and mechanical action. *Ann. Rev. Plant Physiol.* 28:23-43.
80. Wilson BF and Archer RR. 1983. Apical control of branch movements and tension wood in black cherry and white ash trees. *Can. J. For. Res.* 13:594-600.
81. Yamamoto F. 2002. Cambial activity and radial growth in trees. In: Nagata H, Sasaki S, eds. *Ecological Tree Physiology*. Buneido Publishing, Tokyo (in Japanese). 123-155.
82. Yamamoto F and Kozłowski TT. 1987c. Effects of flooding, tilting of stems, and ethrel application on growth, stem anatomy, and ethylene production of *Acer platanoides* seedlings. *Scand. J. For. Res.* 2:141-156.

83. Yoshizawa N, Satoh M, Yokota S and Idei T. (1993). Formation and structure of reaction wood in *Buxus microphylla* var. *insularis* Nakai. *Wood Sci. Technol.* 27:1-10.