Tension Wood as a Model System to Explore the Carbon Partitioning between Lignin and Cellulose Biosynthesis in Woody Plants

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Tension wood, a specialized tissue developed in the upper side of the leaning stem and drooping branches of angiosperm, is an attractive experimental system attractive for exploring the development and the biochemical pathways of the secondary cell wall formation, as well as the control mechanism of the carbon flux into lignin, cellulose, and hemicellulose. However, the mechanism underlying the induction and the development of the tension wood is largely unknown. Recently, several researchers suggested the possible roles of the plant growth hormones including auxin, gibberellin, and ethylene mainly based on the expression pattern of the genes in this specialized tissue. In addition, expressed sequence tag of Poplar and Eucalyptus provide global view of the genetic control underlying the tension wood formation. However, the roles of the majority of the identified genes have not yet been clearly elucidated. The present review summarized current knowledge on the biosynthesis of tension wood to provide a brief synopsis of the molecular mechanism underlying the development of the tension wood.

Key words: tension wood, lignin, cellulose, secondary xylem

Anatomical Characteristics of Tension Wood

Displacement of stems and branches by wind or mechanical stress in the woody species results in the formation of a reaction wood. In general, tissues differ greatly depending upon whether the woody plant is a gymnosperm or an angiosperm, with the former giving rise to a compression wood and the latter to a tension wood [Timell, 1986]. Tension wood developed upper side of the leaning stems and drooping branch where tensile stress developed [Seafled, 1973; Hellgren et al., 2004]. The formation of the reaction wood in response to the altered gravitational stimuli is believed to be the mechanism developed by the tilted stem and the branches to recover their original upright positions [Hellgren et al., 2004; Timell, 1986]. This mechanism is usually, but not always, associated with the eccentric growth towards the upper side of the leaning stems and branches (Fig. 1a) [Timell, 1986]. Anatomically, the tension wood is characterized by a reduction in size and frequency of the vessels and by an increase in the proportion of the fibers (Fig. 1b) with the latter differing in structure (Fig. 2) and composition from those of the normal wood [Wardrop and Dadswell, 1955]. The fiber in the tension wood is characterized by thick cell walls and a gelatinous (G) layer, which is not found in the normal wood fibers.
Although the G layer has variable thickness, it is often quite massive, normally replacing the innermost secondary cell wall layer, the S3 layer (Fig. 2). However, it can also replace both the S2 (middle layer of secondary cell wall) and the S3 layers or be added to the inside of the S3 layer (Fig. 2). The occurrence of the gelatinous (G) fibers is the most typical feature of the tension wood, even though they do not form in certain species and are quite rarely observed in others [Côté et al., 1969]. The G-layer was believed to be composed entirely or almost entirely of cellulose [Norberg and Meier, 1966; Cronshaw and Morey, 1965; Scurfield and Wardrop, 1963], whose microfibrils are oriented parallel or nearly parallel to the longitudinal axis and have a high degree of crystallinity [Scurfield, 1973; Côté et al. 1969; Mia, 1968]. However, the nature of stimulus and mechanism controlling the altered cellulose microfibril orientation in the tension wood has not yet been fully studied.

**Role of Plant Hormones in Tension Wood Formation**

Tension wood formation was induced not only by the gravitational stimuli but also by mechanical stresses such as those experienced during the clinostat and the centrifuge treatments, or by bending [Wordrop, 1964; Westing, 1965; Westing, 1968]. In addition, many plant growth hormones were suggested to be involved in the formation of the tension wood. For example, auxin redistribution has been regarded to play an essential role in the tension wood formation, because more auxins were detected on the underside of the leaning stems in the dicots [Wordrop 1964; Westing 1965; Westing, 1968]. Moreover, the treatment of auxin transport inhibitor apparently induced the tension wood in the vertical dicot stems by reducing the auxin concentration [Cronshaw and Morey, 1965; Morey and Cronshaw, 1968; Kennedy and Farrar, 1965]. However, a recent study by Hellgren et al. (2004) showed that the formation of the tension wood resulted in no obvious alteration of the IAA balance around the stem upon gravitational induction [Hellgren et al., 2004], suggesting that the redistribution of auxin may not be an essential regulator for the development of the tension wood. However, several Aux/IAA gene families were differentially expressed between the tension and the opposite wood [Moyle et al., 2002; Hellgren et al., 2004], implying that the auxin affects the signaling pathway of the tension wood formation [Hellgren et al., 2004].

Other plant growth hormones such as gibberellin, ethylene, and cytokinins were not regarded to play any roles in the tension wood formation for the long time, because their exogenous applications did not affect the formation of the reaction wood [Pharis et al., 1972; Wareing et al., 1964; Hejnowicz and Tomaszewski, 1969; Wilson and Archer, 1977]. However, a recent work by Funada et al. (2008) clearly demonstrated that the exogenous application of gibberellin to the vertical stems of four angiosperm species induced the tension wood formation where gibberellin was applied (Fig. 4). Ethylene was also proposed to be involved in the formation of the tension wood, because the gene coding the ACC oxidase of poplar displayed an asymmetric expression between the tension and the opposite woods [Andersson-Gunnerås et al., 2003]. In addition, its expression was mediated by the gravitational stimuli, which is known to be an important signal for initiation of the tension wood development [Andersson-Gunnerås et al., 2003]. Transcript analysis provided the evidence that ethylene is an important regulator of the tension wood formation due to the finding that the gene encoding amino-cyclo-propane (ACC) oxidase was highly overexpressed in the tension wood [Pilate et al., 2004]. Taken together, the plant hormones are now regarded as essential regulators of the tension wood formation. However, the molecular mechanisms underlying the hormonal control of the tension wood formation are yet largely unknown.

**Biosynthesis of Cellulose in Tension Wood**

The content of cellulose in the tension wood is much higher than in the opposite wood [Timell, 1986]. In addition, the tension wood develops a cellulose-enriched gelatinous layer (G-layer) next to the lumen of the fiber (Fig. 2) [Norberg and Meier, 1966; Cronshaw and Morey, 1965; Scurfield and Wardrop, 1963], which is generally not found in the normal fiber. The G-layers have been...
often described as a pure cellulose layer with highly crystalline microfibrils orientated nearly parallel to the longitudinal axis [Wardrop, 1965]. In aspen, PtrKOR (Korrigan endoglucanase, CesA) mRNA was extensively localized to where the tension wood formed, whereas the PtrlKOR expression was significantly suppressed in the opposite wood [Bhandari et al., 2006]. In addition, four cellulose synthase genes, PtrlCesA1, PtrlCesA2, PtrlCesA3, and PtrlKOR were coexpressed with the highly crystalline cellulose in the tension wood fiber as demonstrated by in situ hybridization technique [Bhandari et al., 2006], implying the roles of the cellulose synthase [CesA] gene in the tension wood formation. In addition, the CesA gene expression was highly upregulated in response to the tensile stress [Bhandari et al., 2006]. Analysis of the differentially expressed genes in the tension wood implied that the tension wood formation involves reprogramming of the carbohydrate metabolism, that is, the increased activities for the cellulose biosynthesis and the pectin degradation [Anderson-Gunnerås et al., 2006]. In addition, the transcriptome analysis suggested that the overall carbon flux to the biosynthetic pathway of the cell wall matrix carbohydrates significantly decreased in the tension wood of the poplar [Anderson-Gunnerås et al., 2006].

Recent analysis of the poplar EST library indicated that the fasciclin-like arabinogalactan protein gene family was significantly up-regulated in the tension wood [Anderson-Gunnerås et al., 2006]. For example, the expression level of fasciclin-like arabinogalactan protein of the poplar (PtFLA12 K, PtFLA12E, and PtFLA12V) was approximately 18 times higher in the tension wood than that in the opposite wood at transcription level [Anderson-Gunnerås et al., 2006]. Because the animal fasciclin-like arabinogalactan protein was shown to play a role in the cell adhesion and communication, the significant increase of the fasciclin-like arabinogalactan protein transcript could be correlated with the signaling pathway of the tension wood formation. However, the roles of the fasciclin-like arabinogalactan protein in the tension wood have not been uncovered.

**Lignin Biosynthesis During Tension Wood Formation**

The lignin content of the tension wood significantly decreases by about 20% of the cell wall dry weight compared with those of the normal and the opposite woods [Timell, 1969; Donaslon, 2001]. In general, the angiosperm lignins mainly contain coniferyl and sinapyl units (Fig. 3) roughly in equal proportions, together with a small amount of interunits derived from the p-coumaryl alcohol. In the tension wood fiber, however, the syringyl unit is predominantly detected in the secondary cell wall of the fiber cell type [Terashima et al., 1998; Joseleau et al., 2004]. Although decreases in the lignin content and guaiacyl unit (G in Fig. 3) of the tension wood lignin have previously been reported, little is known about the lignin modification associated with the tension wood development.

The G-layer has often been described as being mostly composed of pure cellulose, based on the results of the
histochemical staining and sugar analysis obtained by 
means of the ultrasonic treatment [Pilate et al., 2004]. 
Ruel et al. [1999] studied the distribution of the lignin 
subunits in Eucalyptus gunnii and revealed that the S2 
layer of the secondary cell wall of the tension wood has a 
lower amount of the guaiacyl-syringyl subunits than 
those of the opposite and the normal woods. In situ 
hybridization of Populus deltoids tension wood further 
demonstrated that the syringyl units of the lignin were 
detected in the G-layer of the tension wood fiber (Fig. 4) 
[Joseleau et al., 2004], which opened the possibility of a 
partial lignification of the G-layer with the syringyl unit, 
rather than being in a pure cellulose state.

Differential regulation of the genes in the shikimate acid 
and the phenylpropanoid pathways were observed, especially 
at the early stages [Pilate et al., 2004; Anderson-
Gunnerås et al., 2006]. Anderson-Gunnerås et al. [2006] 
showed that the transcripts of shikimate kinase, chorismate 
synthase, prephenate dehydratase, and phenylalanine 
ammonia lase (accession number PU02719) significantly 
decreased in the tension wood. They also noticed that 
transcripts of the genes in the down-stream enzymes of 
caffeoyl-CoA, i.e., caffeoyl-CoA O-methyltransferase 
(CCoAOMT2, accession number PU02461), cinnamoyl-
CoA oxidoreductase (CCR1, accession number PU0003), 
ferulate-5-hydroxylase (F5H, PU01148), and caffeic acid 
O-methyl transferase (COMT1, PU02638) greatly decreased 
in the tension wood [Anderson-Gunnerås et al., 2006]. 
The transcriptional down-regulation of these genes 
clearly explains the reduced amount of coniferyl alcohol-
derived guaiacyl units (G in Fig. 3) in the G-layer of the 
tension wood fiber. Interestingly, the expression of genes 
involved in the glycosylation of monolignol also greatly 
decreased in the tension wood [Anderson-Gunnerås et al., 
2006], implying that the glycosylation of the monolignols 
during the process of monolignol transport to the 
liningfying cell wall was inhibited, which, in turn, explains 
the reduced extent of the lignification in the tension 
wood. Genes involved in the monolignol polymerization, 
laccase and peroxidase, were also greatly down-regulated 
in the tension wood [Pilate et al., 2004]. Therefore, the 
lignin biosynthesis in the tension wood appears to be 
regulated at multiple points including the monolignol 
biosynthesis, monolignol glycosylation, transportation to 
the cell wall, monolignol coupling for lignin polymerization, 
and specific deposition within the secondary cell wall.

Interestingly, Akiyama et al. [2003] investigated the 
ratio of erythro and threo forms of β-O-4 structures of 
the tension wood lignin in the yellow poplar. They demonstrated 
that the content of the erythro form of β-O-4-linked lignin 
was higher than that of the threo form of lignin in the 
tension wood, implying a stereoselective regulation of the 
lignin polymerization during the tension wood formation. 
Taken together, the lignin biosynthesis during the tension 
wood formation appeared to be very tightly regulated, 
spatially and temporally, as well as stereochemically.

Discussion

The inducible formation of the tension wood together 
with the altered cellulose and the lignin biosynthesis 
provide an excellent system to dissect the mechanism 
of cellulose biosynthesis and down-regulation of the lignin 
biosynthesis during the secondary xylem formation in the 
woody tissues. However, the genes involved in this 
process have only recently started to be reported 
[Anderson-Gunnerås et al., 2006; Paux et al., 2005], with 
most of them not yet functionally characterized. However, 
the transcriptome analyses of Populus and Eucalyptus 
tension woods provided a more global view of the carbon 
flux redirected from cellulose-, hemicellulose-, and 
lignin-rich sub-layers of the normal secondary cell wall 
into the cellulose-rich G-layers with the lignin modification 
during the tension wood formation. Transcript profiling 
of the tension wood also highlighted the candidate genes 
that could be important regulators responsible for the 
characteristic features of the tension wood [Paux et al., 
2005]. The functional characterization of these genes will 
greatly help to expand the understanding of the carbon 
partitioning between the cell wall carbohydrates and the 
lignin biosynthesis, thereby providing tools for the 
metabolic engineering of the lignocellulosic material as 
a desirable biofuel.

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