

Transverse shrinkage in G-fibers as a function of cell wall layering and growth strain

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Abstract Transverse drying shrinkage was measured at microscopic and mesoscopic levels in poplar wood characterised by an increasing growth strain (GS), from normal to tension wood. Results show that: (a) the drying shrinkage, measured as a relative thickness decrease, was significantly higher for G-layer (GL) than for the other layers (OL), GL shrinkage was not significantly correlated with GS, and OL shrinkage was negatively correlated with GS. (b) In gelatinous fibre (G-fibre), lumen size increased during drying and this increase was positively related with GS, but in normal wood fibre, lumen size decreased during drying. These findings suggest that GL shrank outwards (i.e., its internal perimeter increases), so that its shrinkage weakly affected the total cell shrinkage and the mesoscopic shrinkage was controlled by the OL shrinkage which shrank inwards (i.e., its external perimeter decreases). (c) Measurements done on $7 \times 7 \text{ mm}^2$ thin sections evidenced a negative correlation between transverse shrinkage and GS, significant in T direction but weak in R direction. These observations at both levels allow to discuss the contribution of GL to the mesoscopic shrinkage of tension wood.

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Introduction

Tension wood is a peculiar wood tissue that is often formed in the upper side of leaning trunks and branches in hardwood species (Isebrands and Benseid 1972) and which generates high tensile stress (Wardrop 1964; Fisher and Stevenson 1981; Okuyama et al. 1994) assisting stems or branches to maintain or recover a preferred orientation (Kuo and Timell 1969). It exhibits important changes of the cell wall structure compared with normal wood (Onaka 1949). Normal wood fibres are composed of a middle lamella, a fine primary layer and a large secondary layer (S) divided into three sub-layers, called S_1 , S_2 and S_3 . In many species, such as beech, poplar, oak or chestnut, tension wood contains fibres with a special morphology and chemical composition due to the development of the so-called gelatinous layer (G-layer, noted here GL) replacing S_3 and a part or the whole of S_2 (Saiki and Ono 1971). The GL is known to have a high cellulose content with a high degree of crystallinity (Norberg and Meier 1966; Côté et al. 1969) and to contain microfibrils oriented along the axis of the cell (Fujita et al. 1974). In this study, the cell wall is considered to be composed of two parts: the GL and the other layers (noted OL). OL includes the compound middle lamella (CML) and the sub-layers of S, excluding GL.

This study will focus on the drying shrinkage of tension wood compared with normal wood. Because of its technological consequences, macroscopic longitudinal shrinkage of tension wood has been much more studied than its transverse shrinkage. Tension wood is known to exhibit a higher longitudinal shrinkage than normal wood (Clarke 1937; Chow 1946; Sassus 1998; Jourez et al. 2001; Clair et al. 2003). This result is paradoxical considering the low microfibrillar angle (MFA) in tension wood and the usual positive correlation between MFA and longitudinal shrinkage (Meylan 1972; Timell 1986). Experimental evidence of longitudinal shrinkage of GL itself has been given by Clair and Thibaut (2001) but without explanation of the mechanism. Thus, Yamamoto et al. (2005) stated that the high longitudinal shrinkage in tension wood xylem is induced by the shrinkage of GL in its axial direction. However, few studies have been done on the transverse shrinkage of tension wood and the results are contradictory. Washusen and Ilic (2001) and Clair et al. (2003) reported a higher transverse shrinkage in tension wood, while Arganbright et al. (1970) and Barefoot (1963) observed a lower shrinkage in maple tension wood. In this study, we hope to discern these contradictory results by focusing on the transverse shrinkage at the cell wall layers level. Contrary to Norberg and Meier (1966) who measured the shrinkage of isolated GL, this work considers GL shrinkage in its cellular context. This should allow to understand the consequences of the shrinkage of the cell wall layers on the shrinkage at tissue level. The method used will also allow to avoid the swelling artefact of GL during sample preparation (Clair et al. 2005b) and therefore to obtain quantitative measurements of GL shrinkage. Samples of this study have been chosen according to the residual growth strain (GS) measured on the living tree. It is expected that variations of GL shrinkage will yield qualitative information on the change (or not) in GL structure depending on the stress level. Does GL structure differ between mild and strong tension wood? What are the respective roles of GL and OL in the global shrinkage

of tension wood? In order to answer these questions, the shrinkage will be measured both at cell wall layer and tissue levels, in normal wood and for different levels of tension wood.

Materials and methods

Experiments were performed on normal and tension wood of poplar (*Populus* cv. I4551). This species is known to produce tension wood containing a characteristic GL and associated with a high longitudinal tensile stress. One 15-year-old tree was chosen according to its tilted shape.

Growth strain measurements

The strain gage method (Yoshida and Okuyama 2002) was used to estimate the longitudinal residual GS at 25 positions around the surface of an inclined poplar trunk at different heights. The GS values are good indicators of the growth stress level within trees of the same species (Fournier et al. 1994). GS is expressed in microstrain dimensionless unit ($\mu\epsilon = \mu\text{m}/\text{m}$). All the values being negative, absolute GS values will be used to simplify representations and analysis. GS values ranging from 100 to 2,275 $\mu\epsilon$ were obtained.

Shrinkage measurement at microscopic level

Samples (one for each GS value, $5 \times 5 \times 5 \text{ mm}^3$) were taken from GS measurement positions. They were maintained in water as soon as they were taken from the tree. None or very few gelatinous fibres (G-fibre) were found under microscope after sectioning the samples with GS equal or less than 610 $\mu\epsilon$. Thus, six samples were chosen for experiments with GS values equidistributed from 610 to 2,275 $\mu\epsilon$ (610, 816, 1,158, 1,450, 1,935 and 2,275 $\mu\epsilon$).

As a normal sectioning method with a sliding microtome results in an uncontrolled swelling and detachment of GL (Clair et al. 2005a, b), embedded wood samples were used and serial-sectioning was performed with a glass knife.

Wood sticks (2 mm in longitudinal direction, $1 \times 1 \text{ mm}^2$ in cross section) were longitudinally cut by splitting to guarantee a good axial orientation. To avoid shrinkage, the samples were always kept in a drop of water during the preparation. They were then cut in the middle of axial direction, perpendicular to the fibres, with a brand new razor blade in order to obtain two matched samples. One sample was dehydrated with ethanol series, then embedded in LR White resin (two exchanges of resin/ethanol mixture for 1 h, followed by two exchanges in pure resin for 1 h, kept 1 day at room temperature, then kept overnight in a capsule at 65°C), the other one was oven dried and then embedded in LR White resin (two exchanges in pure resin for 1 h, kept 1 day at room temperature, then kept overnight in a capsule at 65°C) (Fig. 1). After polymerisation of the resin, all deformations of the tissue are blocked, so that sectioning does not alter the shape and the size of the cell wall layers. This method allows observations of the cells

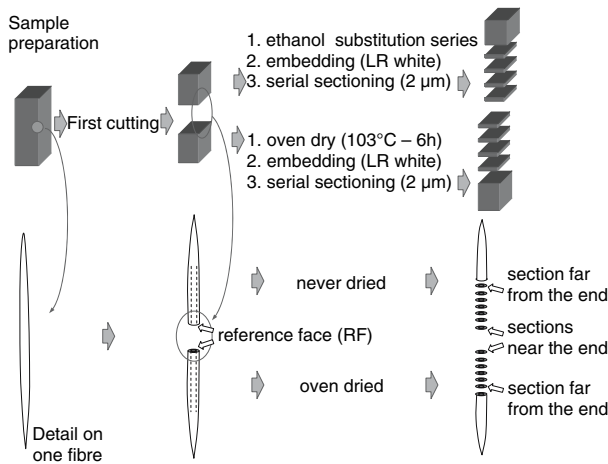


Fig. 1 Experimental protocol and terminology used in the article (Clair et al. 2005a)

from the border to the core of the sample, keeping the morphology as it was before embedding. In the following, the data obtained with the first specimen will be referred to as “wet” values, considering that the replacement of water by ethanol did not alter significantly the cellular morphology of the never-dried wood. In fact, dehydration by ethanol produces some shrinkage, but negligible compared to oven dry shrinkage (unpublished observations made on chestnuts normal wood showing that macroscopic tangential shrinkage is around 0.3% after ethanol exchange and reaches 6% after oven drying). The data obtained with the oven-dried specimen will be referred to as “dry” values.

Serial cross-sectioning (2.5 μm thickness) was performed with a glass knife and the distance to the initial border of the sample was noted for each section. For each sample more than 100 sections were made to ensure that measured sections were far enough away from the sample border and avoid the border artefact. Sections were mounted on glass slides and were observed under optical microscope.

Images (Fig. 2a) were obtained with a digital camera and measurements were performed with image analysis software Image J (Rasband 1997–2006).

First, measurements were done on 12 fibres per sample to compare the wet and dry wall thickness of the same fibre. However, because of the non-uniformity of the walls thickness along the fibres (Okumura et al. 1977), the thickness values were not comparable. So, statistical trends were searched from new measurements with more repetitions. A total of 25–30 measurements of the double cell wall thickness (i.e., 50–60 single cell wall thickness) excluding (L_1) or including GL (L_2), as well as of lumen perimeter were performed in each sample in both wet and dry states (Fig. 2b). From these measurements, morphometric parameters were obtained as follows:

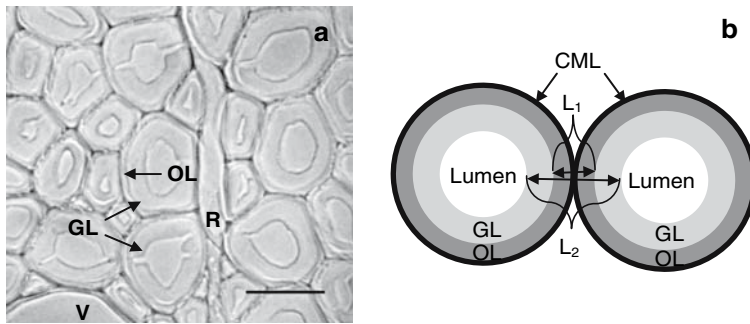


Fig. 2 Shrinkage measurement at cell wall level. *GL* G-layer; *OL* other cell wall layers, including compound middle lamella (*CML*), *S1* and *S2*; *V* vessel; *R* ray; **a** transverse section picture. Scale bar = 20 μm . **b** Morphological model and parameters. L_1 Double other layer (*OL*) thickness; L_2 double all layer (*AL*) thickness

$$\text{All layer (AL) thickness} = L_2/2$$

$$\text{OL thickness} = L_1/2$$

$$\text{GL thickness} = (L_2 - L_1)/2$$

Based on the mean values of these parameters for a given sample, the radial cell wall shrinkage of *AL*, *OL* or *GL* were calculated as the relative thickness decrease between the wet and dry condition. The relative lumen perimeter decrease was used to estimate the tangential cell wall shrinkage at the inner side of the cell wall (i.e., tangential cell wall shrinkages at lumen border).

Shrinkage measurement at mesoscopic level

Samples were taken in the vicinity of the sample used for the microscopic study. Two additional samples were selected to enlarge the spectrum of values including normal wood. Thus, *GS* values of the chosen samples are 168, 405, 610, 816, 1,158, 1,450, 1,935 and 2,275 μe . The five last samples contained G-fibres, and the first three (here called normal wood) did not. Wood sticks ($7 \times 7 \text{ mm}^2$ in cross section) were sectioned (20 μm thick) with a sliding microtome. Two sections for each sample were selected and mounted on glass slides with a drop of water to avoid drying, and covered with cover glass to prevent warping. A very light press was performed with fingers on the cover glass in order to level up the wood sections. Images covering the whole cross sections were taken under microscope before and after the sections were oven dried.

On the images before and after drying, corresponding pairs of points were chosen and their distances were measured using the image analysis software Image J (Rasband 1997–2006). The shrinkage was calculated as the relative distance decrease. For each sample ten measurements were done in tangential (*T*) and ten in radial (*R*) direction.

Results and discussion

GS: cell wall radial shrinkage

Figure 3 shows the average values and 95% confidence intervals of GL, OL and AL thickness for different GS levels in wet and dry conditions (as none or very few GL was found in the sample with a GS of $610\text{ }\mu\epsilon$ the GL thickness was regarded as 0 and thereby AL thickness equalled that of OL).

Other layer thickness decreased markedly from normal wood to tension wood (Fig. 3). This confirms that in tension wood, GL replaces a part or the whole of the S_2 layer (Saiki and Ono 1971). AL thickness in normal wood was notably lower than in tension wood (Fig. 3) indicating that the GL is thicker than the replaced layers which exist in normal fibres.

In the five tension wood samples, GL thickness had a significant positive correlation with GS, and OL thickness had a significant negative one (Fig. 3, Table 1). These relations were found both in wet and dry conditions. This clearly demonstrates that GS is a reliable indicator of tension wood severity, associated with more and more pronounced morphological changes. AL thickness did not change significantly with GS in either condition (Fig. 3, Table 1). It implies that G-fibres contain a bigger proportion of GL when the samples have higher GS, as shown recently (Fang et al. 2007).

Figure 4 shows the relationship between GS and cell wall radial shrinkage of GL, OL or AL. Correlation coefficients and significance levels are shown in Table 1. As observed by Norberg and Meier (1966) GL has a very high transverse shrinkage (they measured 15–25% transverse shrinkage in thickness on isolated GL) compared to other layers. In this study, the shrinkage was also much higher in GL (mean value 21.2%) than in OL (mean value 14.2%, Fig. 4). High GL shrinkage could be partly explained by its gel-like structure, and partly by its low lignin content (Furuya et al.

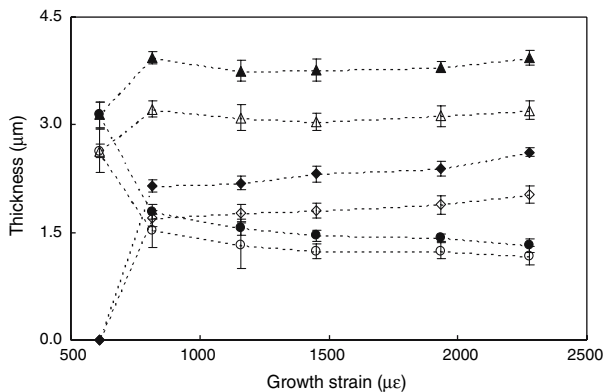


Fig. 3 Thickness variations of GL, OL and AL for different growth strains in wet and dry conditions. Solid triangle AL wet, hollow triangle AL dry, solid diamond GL wet, hollow diamond GL dry, solid circle OL wet, hollow circle OL dry. Error bars show 95% confidence intervals

Table 1 Correlations between parameters for the five samples containing G-fibres, except for the underlined values, which include all six samples

Parameters	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	
Growth strain ($\mu\epsilon$)	(1)	1	**	*	NS	**	*	NS	NS	<u>**</u>	<u>NS</u>
Thickness (μm)											
Wet											
GL	(2)	0.96	1	NS	NS	**	NS	NS	NS	*	NS
OL	(3)	−0.94	−0.88	1	NS	*	**	NS	NS	<u>NS</u>	<u>*</u>
AL	(4)	0.14	0.34	0.15	1	NS	NS	*	NS	<u>NS</u>	<u>*</u>
Dry											
GL	(5)	0.97	0.98	−0.89	0.27	1	NS	NS	NS	*	NS
OL	(6)	−0.89	−0.81	0.99	0.27	−0.84	1	NS	NS	<u>NS</u>	<u>*</u>
AL	(7)	0.03	0.18	0.29	0.94	0.16	0.41	1	NS	<u>NS</u>	<u>NS</u>
Shrinkage (%)											
GL	(8)	0.57	0.71	−0.50	0.49	0.57	−0.43	0.18	1	NS	*
OL	(9)	<u>−0.92</u>	−0.96	<u>0.63</u>	<u>−0.62</u>	−0.94	<u>0.61</u>	<u>−0.60</u>	−0.70	1	<u>NS</u>
AL	(10)	<u>0.63</u>	0.46	<u>−0.87</u>	<u>0.83</u>	0.31	<u>−0.87</u>	<u>0.77</u>	0.89	<u>−0.59</u>	1

Correlation coefficients (Pearson) are given in the lower left half of the matrix and significance levels (2-tailed) in the upper right half

NS not significant

* Significant at 0.05 level; ** significant at 0.01 level

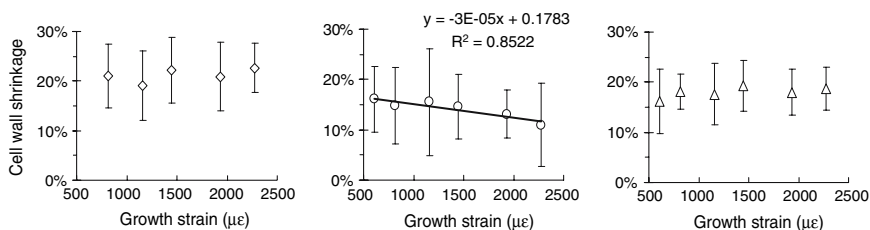


Fig. 4 Relations between GS (in $\mu\epsilon$) and cell wall radial shrinkage. Diamond GL, circle OL, triangle AL. Error bars show 95% confidence intervals

1970; Wada et al. 1995; Pilate et al. 2004) as Bosshard (1956) and Panshin and de Zeeuw (1980) proposed that the increase in shrinkage is associated with a decrease in lignin content.

For tension wood samples, GL thickness linearly increased with the increase of GS (Fig. 3), but its shrinkage changed very little (Fig. 4) and no significant correlation was found (Table 1). It suggests that structure and composition of GL do not vary when GS increases but only their thickness. AL shrinkage was not significantly correlated with GS, but related significantly with GL shrinkage for the five tension wood samples (Fig. 4, Table 1). High GL proportion in the cell wall can explain this phenomenon.

Other layer shrinkage had a very significant negative correlation with GS (Fig. 4, Table 1). This fact can be given two explanations.

First, it could be explained by a change in the proportion of CML and S_2 in the cell wall. In the cell wall of normal wood, the proportion of CML is very low compared to S_2 , which plays a dominant role in transverse shrinkage. In tension wood, the higher the GS, the thicker the GL and the thinner the OL (Fig. 3). However, CML seems to remain constant, so that the decrease in OL thickness originates from a decrease in S_2 thickness (S_2 visible in wood with low GS becomes invisible in high GS samples). Matsumoto (cited by Kelsey 1963) reported that he could not detect any shrinkage in the CML of Japanese red pine, and therefore concluded that the shrinking does not take place in the CML, which is highly lignified, but in S_2 . Then the increase of OL thickness would be linked to the increase of its shrinkage up to a maximum when the CML is negligible compared to S_2 . This expectation is confirmed by the comparison of OL shrinkage versus its thickness (Fig. 5).

Second, some authors reported that the concentration of lignin is considerably higher in OL of G-fibres than in the corresponding layers of normal fibres (Timell 1969; cited by Pilate et al. 2004). So this could be another possible reason for the decrease of OL shrinkage from normal wood to tension wood, as the increase in lignin content is associated with a decrease in shrinkage (Bosshard 1956; Panshin and de Zeeuw 1980). But there is no evidence that the concentration of lignin in OL increases with the increase of GS in tension wood.

GS: lumen size change after oven drying

Some authors observed that in normal wood cell, the lumen size varies only slightly during drying compared to macroscopic shrinkage, reducing in very light wood and augmenting in dense wood (Keylwerth 1951; Kelsey 1963). It indicates that during drying cell wall shrinks inwards: the thickness reduction is driven by the decreases of the external diameter, proportional to the external perimeter. In our study, for the normal wood sample without GL the lumen perimeter reduced nearly by 10% after oven drying, yielding a positive tangential shrinkage of the inner side of the cell

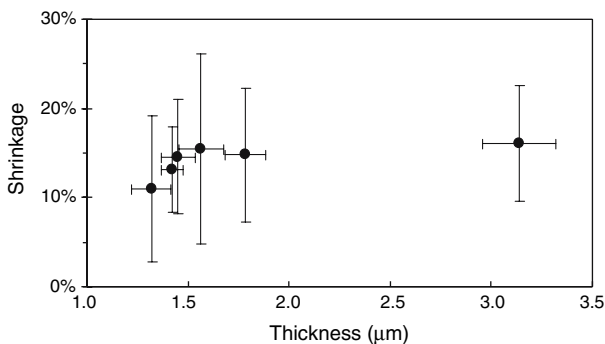


Fig. 5 Relation between the thickness and the shrinkage of the OL. Error bars show 95% confidence intervals

wall (Fig. 6). On the contrary for the G-fibres in tension woods, lumen augmented notably (negative shrinkage) and this effect was stronger with the increase of GS, i.e., with the increase of GL thickness (Figs. 3, 6). This behaviour of G-fibres can be explained by the absence of S_3 layer and indicates the weaker transverse rigidity of G-layer compared to S_2 .

With these results it cannot be concluded whether or not GL also shrinks inwards (its external perimeter decreases), but it can be deduced for certain that it does shrink outwards (its internal perimeter increases). This conclusion will be used in the following discussion of tension wood shrinkage at the mesoscopic level.

GS: mesoscopic shrinkage

Figure 7 shows the relationships between GS and mesoscopic shrinkage in both T and R directions. The average values of T shrinkage varied from 6.3 to 8.3%, while those of R shrinkage varied from 3.5 to 4.7%. A paired-samples t test was performed. The values of T and R shrinkage were paired according to the piece of wood from which they originate. The result showed that T shrinkage was significantly higher than R shrinkage ($P < 0.001$). In normal wood T shrinkage is about 1.4–2 times higher than R one (Kelsey 1963; Panshin and de Zeeuw 1980; Skaar 1988); according to our finding hygroexpansion is also highly anisotropic in tension wood.

A very significant negative correlation (Pearson $r = -0.939$, $P < 0.001$ with 2-tailed test) was found between T shrinkage and GS (Fig. 7), irrespective of the presence of G-fibres. It indicates that from normal wood to tension wood, T shrinkage decreases with the increase of GS. This result is contrary to the results from Washusen and Ilic (2001) and Clair et al. (2003), obtained on massive wood.

No significant relationship (Pearson $r = -0.461$) was found between R shrinkage and GS (Fig. 7). R shrinkage fluctuated a lot and the mean values varied in a very narrow range in spite of a high change of GS (Fig. 7).

For transverse shrinkage in both T and R directions, similar results were reported by Arganbright et al. (1970) and Barefoot (1963) on massive wood of maple and yellow-poplar, respectively, and Barefoot stated that the decrease in T shrinkage is

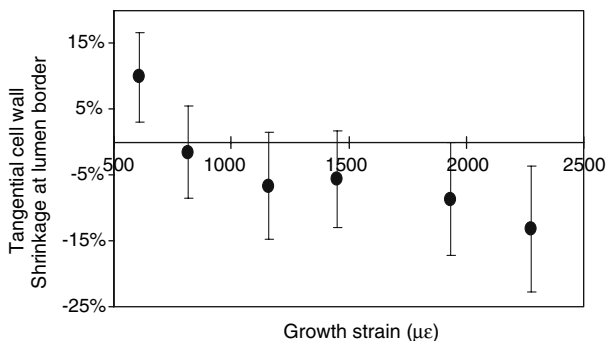


Fig. 6 Tangential cell wall shrinkages at lumen border for samples with different GS ($\mu\epsilon$). Positive value means decrease, negative means increase. Error bars show 95% confidence intervals

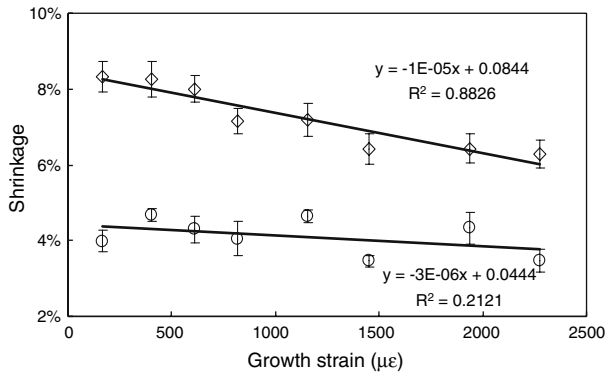


Fig. 7 Tangential (diamond) and radial (circle) shrinkages versus growth strain. Error bars show 95% confidence intervals

due to a decrease in specific gravity, while *R* shrinkage is controlled by fibril angle and specific gravity. The fact that the shrinkage was measured here on sections may have particular mechanical consequences when compared to massive wood. The glass and cover glass may have kept the section sufficiently plane, nevertheless the section was free from straining in its normal direction, the longitudinal with respect to wood. It was a situation of plane stress, whereas the core of a massive wood would express plane strains; both cases are expected to differ by some Poisson's effects which ought to be checked by further analysis.

We concluded from the above results obtained at microscopic level that during drying the cell wall shrinks inwards in a normal wood cell, but in tension wood the GL shrinks outwards (Fig. 8). This means that GL shrinkage, however big it is,

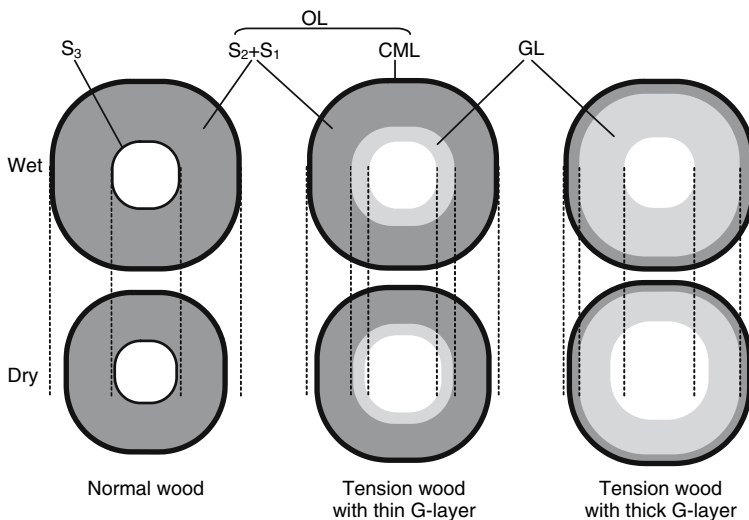


Fig. 8 Three shrinkage scenarios starting from the same cell and lumen size, depending on the proportion of the cell wall layers. *OL* other layers, *CML* compound middle lamella, *GL* gelatinous layer

weakly affects the total cell shrinkage and that the mesoscopic shrinkage is controlled by OL shrinkage, which is essentially influenced by the secondary wall shrinkage. The higher the GS, the thinner the secondary wall and the lower the transverse shrinkage (Figs. 3, 4). The difference between *T* and *R* shrinkage is supposed to be due to the parenchyma rays which prevent part of the radial strain.

Conclusions

From this study the following conclusions are drawn:

- The thickness of normal wood cell wall was notably lower than that of the tension wood cell wall including GL, but markedly larger than that of the other layers excluding GL. In tension wood the thickness of GL and OL increased and decreased, respectively, with the increase of GS.
- The drying shrinkage, measured as a relative thickness decrease, was significantly higher for GL than OL. There were not significant correlations between GS and GL or AL shrinkage, but a negative one was observed with OL shrinkage.
- In G-fibre, lumen size increased during drying and this increase was positively related with GS, but in normal wood fibre lumen size decreased during drying in our observations. These findings suggest that GL shrank outwards (i.e., its internal perimeter increases), so that its shrinkage weakly affected the total cell shrinkage and the mesoscopic shrinkage was controlled by the OL shrinkage which shrank inwards (i.e., its external perimeter decreases).
- At tissue level, based on the observations on sections *T* shrinkage was notably higher than *R* both in normal and tension wood. Both *T* and *R* shrinkages were negatively correlated with GS; however, the correlation was clear for *T* but weak for *R*.

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