

Seasonal change in tangential strain on the inner bark in white birch (*Betula platyphylla* var. *japonica*)

Masato YOSHIDA¹, Yutaka TAMAI²

Yuzou SANO², Minoru TERAZAWA² and Takashi OKUYAMA¹

The aim of this paper is to acquire a growth information from the tangential strain due to changes in turgor pressure in the cells of the cambium and phloem. The strains were measured nondestructively and continuously using strain gauges pasted on the surface of the inner bark of the stem and root of white birch (*Betula platyphylla* var. *japonica*). They showed seasonal changes. As a repeating seasonal pattern, the tangential strain increased year by year. In the season when secondary growth was most vigorous, the tangential strain increased rapidly and then decreased in July and August. Significant amplitude was not seen before the sprout, then both the strain and its amplitude began to increase rapidly accompanying the sprout. In early July, the diurnal strain amplitude showed a peak coinciding with the peak of the strain. The diurnal amplitude of strain disappeared after defoliation. A phase difference in the periodical strain change could not be seen in terms of the height from the ground. In winter season, marked shrinkage was found in the stem. During this season, the rate of dimensional change in the tangential direction per degree Kelvin was 0.0296 (%/K). This value is quite close to the freeze-drying shrinkage of wood, 0.03 (%/K). The most probable cause of shrinkage during winter was the frost-shrinkage caused by the freezing-out of cell wall moisture into the cell lumen.

Keywords: cell-wall extensibility, change in tangential strain, turgor pressure, frost shrinkage, water movement

Introduction

The activity of the interfascicular cambium governs the secondary growth of trees. In order to examine the growth of trees from mechanical point of view, the present research was undertaken focusing on the changes in strain on the stem surface, induced by secondary growth and water stress. The purpose of this investigation was to acquire a growth information from the strain.

Turgor pressure, generated in living cells as the difference between xylem water pressure and osmotic pressure, enlarges the newly produced cells in order to expand the stem diameter. The

changes in stem diameter and turgor pressure have been measured by various methods. Klepper *et al.* (1971) measured the change in stem diameter by a Linear Variable Differential Transformer technique and have discussed the water potential of leaves. Husken *et al.* (1978) and Nonami *et al.* (1987) measured the turgor pressure directly with a pressure probe. Moreover, Lövdahl and Odin (1992) measured the change in stem diameter at the surface of the outer bark using a laser device and their findings showed that changes in diameter occur in response to changes in air humidity at the surface of the stem. Okuyama *et al.* (1995) measured the diurnal change in tangential strain

¹Laboratory of Bio-material Physics, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan.

E-mail: yoshida@agr.nagoya-u.ac.jp

名古屋大学大学院生命農学研究科 生物材料物理学研究室

²Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan.

北海道大学大学院農学研究科

(Accepted: Nov. 14, 2000)

in the inner bark of 3-year-old cedar (*Cryptomeria japonica* D. Don) using the strain gauge technique and they have discussed the diurnal change in turgor pressure around cambium cells. This strain gauge method enables the qualitative monitoring of the relative changes in turgor pressure and cell-wall extensibility in living cells, nondestructively and continuously, as well.

White birch (*Betula platyphylla* var. *japonica*), a kind of deciduous tree, shows distinctive activity in the leaves according to the season, while it exudes much sap in the spring before sprouting (Terazawa 1995). This proves that the driving force of water movement is not only because of leaf transpiration as understood on the basis of cohesion theory. The strain gauge method has been applied to investigate the growth activity of white birch *in situ* which showed significant characteristics of vigorous water movement and much sap flow in the spring (Yoshida *et al.* 1999). The strains measured on an inner bark gave us some information about sap exudation mechanism.

In order to understand the growth behaviour of trees from the mechanical point of view, the tangential strain in a mature white birch tree growing in the field was measured throughout the year. The aim of this paper is to find some information concerning to tree growth from the strain measurements.

Materials and Methods

White birch trees (*Betula platyphylla* var. *japonica* Hara) growing in the Hokkaido University campus was used in this research. This tree was 27 years old, 13 m in height and 38 cm diameter at breast height. We put strain gauges on the following 5 points in the tangential direction: three points were on the south-west side of the stem (40 cm, 150 cm, 400 cm from the ground), one point was on the north side of the stem (150 cm from the ground), and another point was on the south-west side of the root (130 cm arc from the ground).

After removing the outer bark carefully, the strain gauges were pasted on the inner bark surface along the tangential direction by means of a cyanoacrylate adhesive (Kyowa CC-33A). Strain gauges 10 mm or 30 mm long (Kyowa KFG-10-120-C1-11, Kyowa KFG-30-120-C1-11) were used. A strain gauge was also glued on a point on the south-west side of the stem along the longitudinal direction (150 cm from the ground) to check the stability of the device throughout the measurement period. To avoid moisture evaporation and direct irradiation by sunlight, the strain gauges and the inner bark surfaces were covered with Vaseline, a vinyl sheet and aluminum foil. To cancel the signal drift due to temperature changes, the strain gauges were connected to a strain meter (NEC San-ei Logger mate DL-1200) by the three-wire method. The stem surface temperature and the soil temperature near the point of measurement on the root were measured by means of thermocouples. Strains and temperatures were measured at 1-hour intervals (1 minute intervals for an exceptional period) for three years starting in 1994.

The longitudinal strain at the point near the tangential strain was extremely constant throughout the entire period of measurement, and the output due to temperature changes was negligible as compared to the tangential strain values as shown in Fig. 1. The strain gauges were replaced with new ones only when the output became unstable.

A strain gauge on the inner bark was torn in the middle when the strain exceeded the upper limit of the gauge (nominal value 2%). The affixed strain gauge was found to follow the strain of the inner bark well without aberration. Therefore, the errors in tangential strain attributable to the system of measurement can be considered to be small because it was measured using the same system as that for longitudinal strain.

Results and Discussion

Diurnal change in tangential strain

During growing season, repeated diurnal changes in tangential strain were observed as it gradually increased (Fig. 1). The tangential strain started to contract at sunrise, showing maximum contraction at noon and then gradually expanding thereafter. This finding indicates that within the stem repeated diurnal expansion and contraction of the living cells occurs while the stem undergoes secondary growth. The same result was reported for Japanese cedar (*Cryptomeria japonica* D. Don) and Japanese black pine (*Pinus thunbergii* Parl.) by Okuyama *et al.* (1995).

In studies of cotton plants (*Gossypium hirsutum* L.), Klepper *et al.* (1971) showed that the stem diameter decreases when the water potential of the leaves decreases due to high transpiration. Similarly, Herzog *et al.* (1995) working with Norway spruce observed that the stem diameter

decreased when the rate of water movement in the stem was higher. These results indicate that the stem diameter (tangential strain on the stem surface) decreases in the daytime during transpiration when the rates of water loss from the leaves as well as the rate of water movement in the stem are high.

Yearly change in tangential strain and its amplitude

Throughout the three-year observation period, a similar pattern of variation in the tangential strain was observed every year (Fig. 2). The strain began to increase from May to July and decreases once or twice between July and September, while sharp fluctuations were observed in the frost season. The trend of the tangential strain increased year by year according to the thickening of the stem.

Figure 3A is an enlarged part of the time course of changes in tangential strain between April 1994 and July 1995 shown in Fig. 2. The

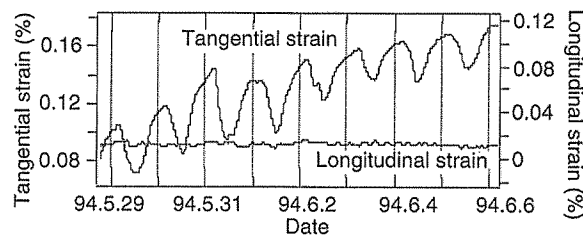


Fig. 1. The typical time course of changes in tangential strain and longitudinal strain for a 1-week period during the growing season. The vertical broken lines indicate twelve o'clock in every night.

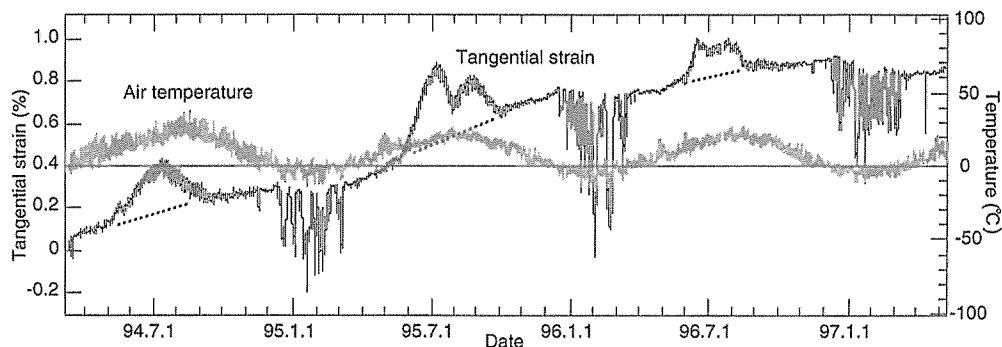


Fig. 2. Variations in tangential strain and air temperature over a three-year period, between May 1994 and March 1997.

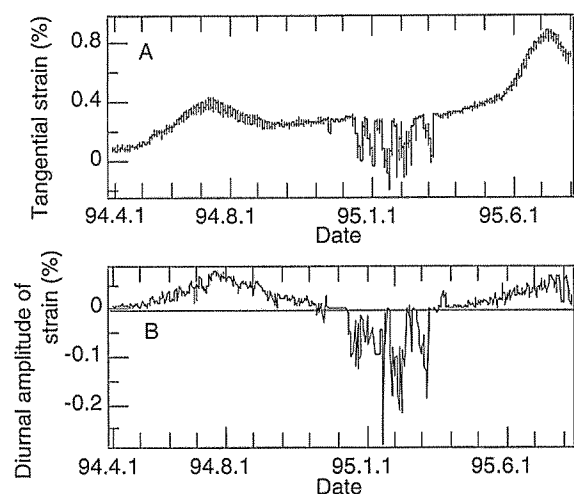


Fig. 3. Variations in tangential strain (A) and its diurnal changes in the amplitudes of tangential strain (B) over a one-year period, from April 1994 to July 1995. Diurnal amplitudes were read from Fig. 3A.

strain started to increase in early spring and there was a large increase beginning in the sprouting season. It decreased in July and August and was almost constant toward the winter.

The diurnal changes in the amplitude of the strain throughout the year was from Fig. 3A as the difference between the maximum strain just before day-break and the minimum strain around noon each day (Fig. 3B). Significant amplitude was not seen before the sprout, then both the strain and its amplitude began to increase rapidly accompanying the sprout. In early July, the diurnal strain amplitude showed a peak coinciding with the peak of the strain in Fig. 3A. The diurnal amplitude of strain disappeared after defoliation.

Peak of tangential strain in summer

One or two peaks of the strain occurred in summer. This phenomenon was not found in the measurement of stem diameter at the surface of outer bark. The increase and decrease in the strain during summer would not be due to the thickening or shrinkage of the xylem, but due to the changes in turgor pressure resulting from excess water absorption in the cambium and the phloem (Figs. 2 and 3A). The diurnal and yearly changes

in turgor pressure appear as tangential strain synchronously (Okuyama *et al.* 1995). The absolute turgor pressure as well as the diurnal change in turgor pressure increase with the sprout and they reach their maximum values in early summer. In this season, imbibition by the roots becomes intensive, while water transpiration in the leaves becomes lively. However in the hot season, the xylem water pressure decreases because water transpiration exceeds water imbibition. Then the absolute turgor pressure and the diurnal changes in the strain decrease towards autumn. After all, the substantial thickening growth, represented by the dotted line, connects the two strains just before sprouting and just after the leaves fall (Fig. 2).

Strain caused by freezing

Marked shrinkage was closely related to freezing of the stems (Figs. 2 and 4). Many species in the frigid zones are frozen due to temperatures below zero and accordingly frost cracks occur in the stem. Some researchers have discussed the frost shrinkage of moist wood which contains as much water as green wood at temperatures below 0°C (Kubler 1983; Neely and Himelick 1987). According to these reports, wood that contains sufficient water shrinks considerably at temperatures below 0°C. Neely and Himelick (1987) explained that at temperatures below 0°C, shrinkage occurs because of internal freeze-drying as moisture migrates from the cell walls into ice loci in the lumen of empty cells. For example, in the case of European oak, the rate of tangential shrinkage is around 0.03 (%/K) over the range of temperature from -10 to 0°C (Kubler 1983).

As shown in Fig. 4, the tangential strain increased slightly just before the air temperature decreased to 0°C and it decreased rapidly as the air temperature dropped, while the longitudinal strain remained almost constant. Reading the changes in both strain and temperature on subzero days, we plotted them in Fig. 5. The rate of dimensional change in the tangential direction per degree Kelvin was 0.0296 (%/K). This value was

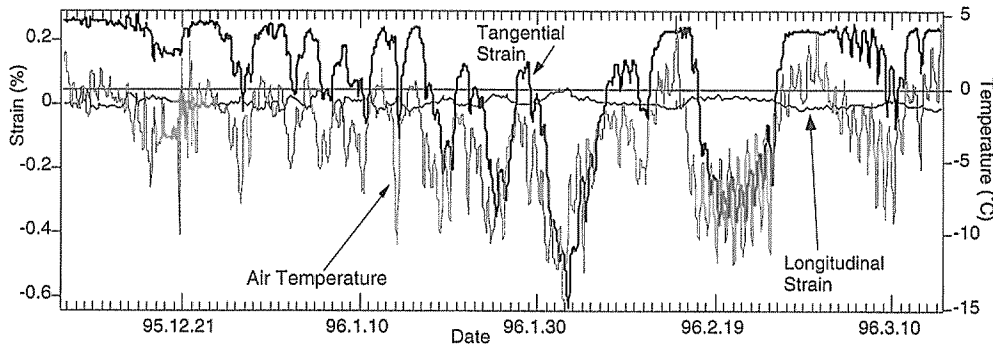


Fig. 4. Strain caused by freezing. Variations in tangential strain, longitudinal strain and air temperature during winter season from 1995 to 1996.

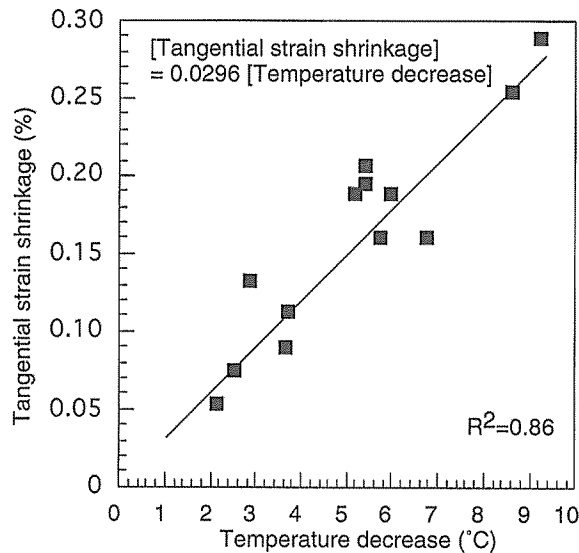


Fig. 5. The rate of dimensional change in the tangential direction against below-zero temperature. Tangential strain shrinkage and temperature decrease were read from Fig. 4 as the differences between two points of the strain and the temperature (max. - min.).

too large to simply be considered as the shrinkage coming from the thermal shrinkage of the ice in the lumen because the coefficient of thermal expansion of ice was known to be only 0.005 (%/K). On the other hand, this value was quite close to the freeze-drying shrinkage 0.03 (%/K) reported by Kubler (1983). Therefore, the most probable cause of shrinkage during winter was the frost-shrinkage caused by the freezing-out of cell wall moisture into the cell lumen. A part of the

thermal shrinkage of the ice in the lumen or between the gaps in the cell wall appeared as the wood shrinks, too. Though considerable shrinkage may be caused by several unknown factors, the fundamental cause of this phenomenon is freezing of the stems.

Phase difference in tangential strain

A phase difference in the periodical tangential strain change could not be seen in terms of the

height from the ground during the 1-minute interval of measurement (Fig. 6). These tangential strains varied in a manner clearly opposite to the changes in air temperature. It was thought that a tree could be considered to be like a series of tubes arranged in a longitudinal row and the change in water potential caused by transpiration in the leaves spreaded longitudinally in a moment.

Phase differences in the tangential strain were observed at measuring point on different sides (not shown in the figure). This was thought to be due to differences in the transpiration peak depending on the side, as the time when the leaf received the greatest sunlight and the maximum air temperature was dependent on the side. To be concrete, at the measuring point on the east side of the stem, both shrinkage and swelling seemed to occur earlier than on the west side because the east side received light earlier in the morning and became shaded earlier in the afternoon.

According to Klepper *et al.* (1971), stem diameter, leaf water potential and leaf relative water content are all closely related to the net radiation at the top of the canopy. They further discussed the observation that leaves on the east and west side of a plant show slight but consistent differences in diurnal water potential patterns. Our

results were consistent with their findings. Moreover, according to Molz and Peterson (1974), the rate of water transport between the xylem and phloem is temperature dependent.

Tangential strain in root and soil temperature

The root tangential strain increased year by year in the same manner as in the case of the stem (Fig. 7). During the summer seasons (July 1996, August 1997), peaks of tangential strain were observed. Therefore, also in the case of the root, the substantial growth could be represented by the dotted line in Fig. 7.

The soil temperature varied between 0 and +20°C over a one-year period. The amplitude of the changes in soil temperature was smaller than that of the air temperature. Robitaille *et al.* (1995) reported that the soil temperature at a deeper point in the ground is lower in the summer and higher in the winter, similar to our results. Compared with the air temperature, the soil temperature hardly reached below the freezing point. Freezing did not occur in the root during the first winter (1996-1997), as the high negative strain observed in the stem did not occur in the root. However, the soil temperature decreased to slightly below the freezing point and consequently great

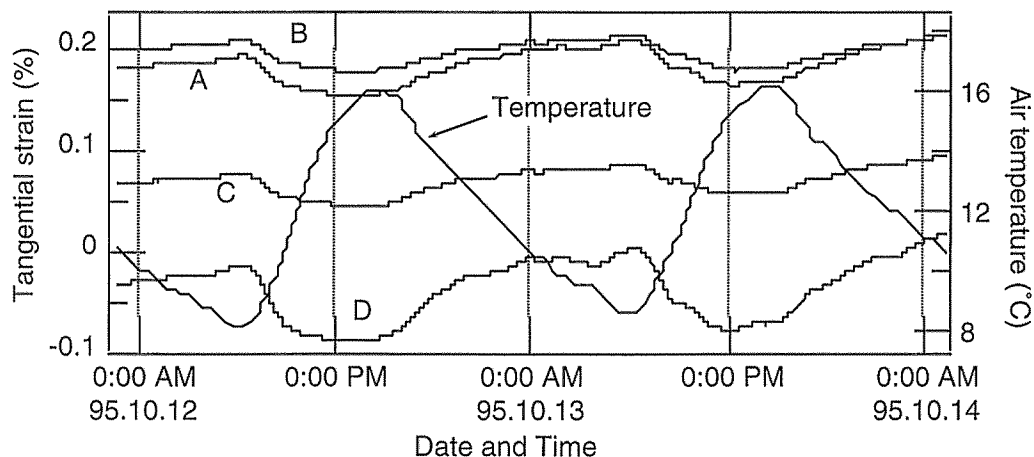


Fig. 6. Tangential strain at several heights from the ground. Each measuring point was set at a different height and all faced to the south-west. The points A, B and C on the stem were 40 cm, 150 cm, and 400 cm from the ground, respectively. Point D was on the root, 130 cm from ground level. To detect the precise time lag between each value, measurements were carried out at 1-minute intervals.

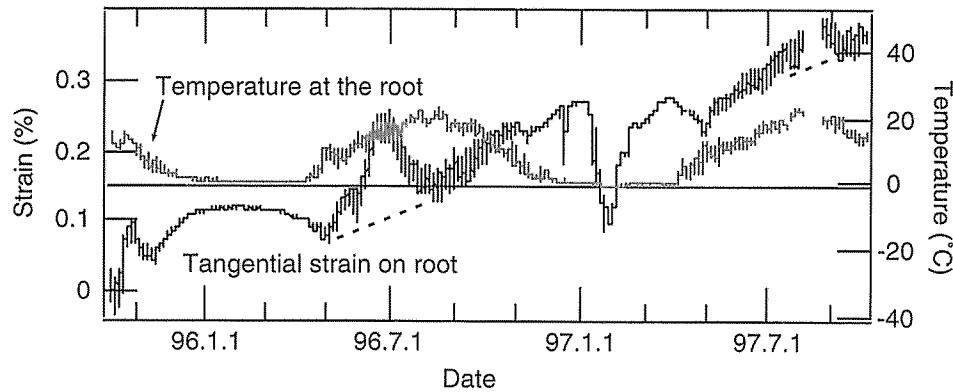


Fig. 7. Variations in root tangential strain and soil temperature over a two-year from 1995 to 1997.

negative strain was observed from January to February in 1997. During this period, the root was thought to be frozen.

Acknowledgments

This study was supported financially by a Grant-in-Aid for Scientific Research (08456083, 10306010 and 10460072) from the Ministry of Education, Science, and Culture of Japan.

Literature cited

- Herzog K.M., Hasler R. and Thum R. (1995) Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. *Trees* 10: 94-101.
- Husken D., Steudle E. and Zimmermann U. (1978) Pressure probe technique for measuring water relations of cells in higher plants. *Plant Physiol.* 61: 158-163.
- Klepper B., Browning V.D. and Taylor H.M. (1971) Stem diameter in relation to plant water status. *Plant Physiol.* 48: 683-685.
- Kubler H. (1983) Mechanism of frost crack formation in trees - a review and synthesis. *Forest Sci.* 29: 559-568.
- Lövdahl L. and Odén H. (1992) Diurnal changes in the stem diameter of Norway spruce in relation to relative humidity and air temperature. *Trees* 6: 245-251.
- Molz F.J. and Peterson C.M. (1974) Location of low temperature flowbarrier in stems. *Plant Physiol.* 54: 652-653.
- Neely D. and Himelick E.B. (1987) Freeze-crack-related measurements on *Platanus × acerifolia* trees. *Forest Sci.* 33: 239-244.
- Nonami H., Boyer J.S. and Steudle E.S. (1987) Pressure probe and isopiestic psychrometer measure similar turgor. *Plant Physiol.* 83: 592-595.
- Okuyama T., Yoshida M. and Yamamoto H. (1995) An estimation of the turgor pressure change as one of the factors of growth stress generation in cell walls; diurnal change of tangential strain of inner bark. *Mokuzai Gakkaishi* 41: 1070-1078.
- Robitaille G., Boutin R. and Lachance D. (1995) Effects of soil freezing stress on sap flow and sugar content of mature sugar maples (*Acer saccharum*). *Can. J. For. Res.* 25: 577-587.
- Terazawa M. (1995) Shirakamba birch, splendid forest biomass: potential of living tree tissues. In *Tree Sap* (Terazawa M., McLeod C.A. and Tamai Y. eds.), pp. 7-12. Hokkaido Univ. Press, Sapporo.
- Yoshida M., Yamamoto O., Tamai Y., Sano Y., Terazawa M. and Okuyama T. (1999) An investigation of change in tangential strain on the inner bark of the stem and root of *Betula platyphylla* var. *japonica* and *Acer mono* during sap season. *J. Wood Sci.* 45: 361-367.

シラカンバ内樹皮における 接線方向ひずみの季節変動

吉田正人・玉井 裕・佐野雄三・寺沢 実・奥山 剛

形成層帯と師部の膨圧変動によって幹の接線方向にはひずみ変動が現れる。本研究は、このひずみから樹木の成長に関するどんな情報が得られるかを検討した。シラカンバを用い、幹と根の内樹皮表面にひずみゲージを貼り、接線方向ひずみの非破壊・連続測定を行った。接線ひずみは季節ごとに特有の変動を示しながら、年々増加していた。ひずみは、二次成長が始まる時期に急激に増加し、7月から8月にかけて一旦減少した。萌芽の前はひずみに日振幅はなかったが、萌芽に伴い、日振幅もひずみ絶対値も増加した。7月初旬に日振幅が最大となり、その時、ひずみ絶

対値もその年の最大値を示した。落葉後は日振幅は見られなかった。地上高の違いによる、ひずみ位相のズレは確認されなかった。厳冬期には、著しいひずみの減少が生じた。この時期の温度変化に対するひずみ減少率は、 $0.0296\%/K$ であり、これは木材の凍結乾燥収縮率の $0.03\%/K$ にきわめて近い。細胞内腔で形成された氷の発達のため、細胞

壁の水分が内腔へと移動し、細胞壁が凍結乾燥されたことが、厳冬期の著しいひずみ減少のおもな要因と思われる。

キーワード：細胞壁伸展性，内樹皮接線ひずみ，膨圧，低温乾縮，水分移動