

ORIGINAL ARTICLE

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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

Received: June 30, 1998 / Accepted: December 14, 1998

Abstract Although it is well known that sap exudation during early spring in temperate deciduous trees occurs in response to daytime warming and nighttime cooling, the mechanisms of the process are not yet fully understood. Previous theories suggested that changes in stress in the wood caused by daytime heating and nighttime cooling might be linked with sap flow. Consequently, a study of itaya-kaede maple (*Acer mono*) and shirakamba birch (*Betula platyphylla* var. *japonica*) looked at tangential strains. One-hour intervals for 3 years of the tangential strains on the inner bark of stem and root were measured in itaya-kaede maple and shirakamba birch during the sap exudation season. The measurements indicated different mechanisms of sap exudation in these two trees. During the sap exudation season in late March, when the temperature fluctuated around 0°C, the tangential strain in the root of itaya-kaede maple showed expansion in the daytime and contraction at night. Conversely, in early April the tangential strain in the root of shirakamba birch exhibited contraction in the daytime and expansion at night. The changes in tangential strains in itaya-kaede maple were attributed to conditioning, a known concept used to explain the uptake mechanism of soil water in maple and its exudation during early spring. However, because the change in tangential strain in the roots of shirakamba birch was similar to that found during the rampant season, sap exudation was not attributed to conditioning but to the plentiful supply of water from the roots. The implications of these mechanisms

are that different sap harvesting techniques may be appropriate for different tree species.

Key words *Acer mono* · *Betula platyphylla* var. *japonica*
Inner bark · Sap exudation · Tangential strain

Introduction

During early spring, shirakamba birch (*Betula platyphylla* var. *japonica*) behaves similarly to maple and exudes a large amount of sap from scratched stems.¹ Terazawa¹ noted that shirakamba birch exudation starts later, and continues for a month longer, than maple. In addition, the amount of sap exuded by shirakamba birch reached 10 times that of maple, producing 100–180 l in one season. Based on these dissimilarities, Terazawa¹ concluded that the mechanism of sap exudation in shirakamba birch was different from that of maple.

It has been reported that maple sap exudation is temperature-dependent, with maximum yields coinciding with wood temperature fluctuating above and below 0°C.^{2–4} During the cooling sequence the uptake of soil water has been termed the “conditioning” phase by Marvin.⁵ Despite much research, existing knowledge about the mechanism of conditioning is limited. Various hypotheses involving both vital^{4,6} and physical⁷ mechanisms have been proposed, but none has been validated through observation.

Sap exudation is perhaps related to water status (i.e., xylem water potential, turgor pressure). Xylem water potential changes with turgor pressure in living cells,⁸ inducing deformation of the living cells in phloem and cambium. However, the cell diameter in the xylem is considerably less than that in phloem.⁹ Since 1950 many studies have attributed the change in tree diameter to xylem water potential,^{10–12} although experiments by Lövdahl and Odín¹³ suggested that these changes are mostly caused by shrinkage and swelling in the outer bark due to changes in moisture content. Okuyama et al.⁸ estimated the change in xylem water potential and turgor pressure in living cells through

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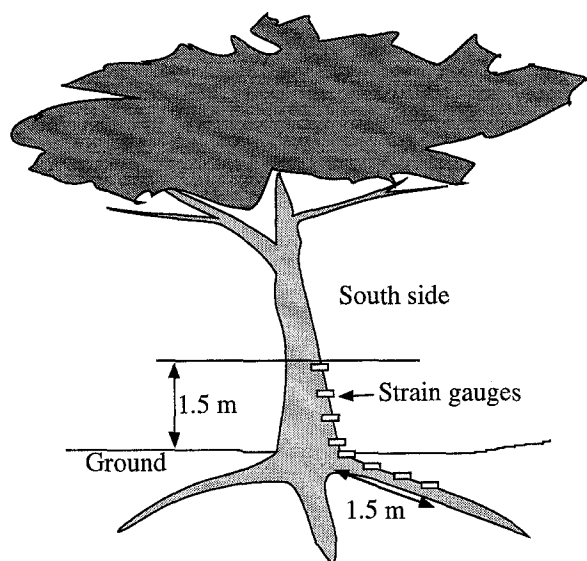


Fig. 1. Layout of the measuring points on the trees

the changes in tangential strain on the inner bark. Their measurement is little affected by the changes in moisture content of air. By measuring the tangential strain on the inner bark, some information about the sap flow may be gained.

This paper investigates the changes in tangential strains and the corresponding mechanism of sap exudation during early spring on the inner bark of the stem and root in itaya-kaede maple (*Acer mono* Maximowicz) and shirakamba birch (*Betula platyphylla* var. *japonica* Hara) according to Okuyama's method to estimate the mechanism of sap exudation.

Materials and methods

The experimental trees were two 12-year-old maples (itaya-kaede, *Acer mono* Maximowicz) and two 27-year-old birch (Shirakamba, *Betula platyphylla* var. *japonica* Hara) located at the Hokkaido University campus at latitude 43°03' N and longitude 141°20' E, which is in the subarctic zone climatically. The itaya-kaede maples were 10 and 11 m in height and 12 cm in diameter at breast height (DBH). The shirakamba birch were 12 and 13 m in height with 28 and 38 cm DBH, respectively.

Measurements consisted of tangential and longitudinal strains on the inner barks of the stem and root, taken with strain gauges using Okuyama's method.⁸ The measuring points on the stems were 50 cm apart vertically and up to 1.5 m above ground, facing south. Each measuring point had a pair of gauges. With the same orientation and distance the strain gauges were placed on the upper side of the roots in a 1.5 m arc from the trunk to the root tip (Fig. 1). The outer bark was removed with a knife, and strain gauges of 10 or 30 mm length (Kyowa KFG-10-120-C1-11, Kyowa KFG-30-

120-C1-11) were glued with cyanoacrylate adhesives (Kyowa CC-33A) onto the surface of the inner bark in both tangential and longitudinal directions. The measuring points were protected from moisture loss and direct light with Vaseline, vinyl, and aluminum sheets. To eliminate errors incurred from changes in temperature, the conventional three-wire method was used to connect the gauges to a strainmeter (NEC San-ei Logger mate DL-1200). The precision of the measurement was $\pm 0.001\%$.

The temperature on the surface of the tree stems and roots was measured by thermocouples. After placing strain gauges, the roots were covered with soil. Beginning in March 1995, measurements on shirakamba birch were taken at 1-h intervals for 3 years. The measurements on itaya-kaede maple began in 1997. To eliminate potential errors due to instrument wear, the strain gauges were replaced with new ones every 3 months. The position of the replaced strain gauges was chosen as close as possible to the old ones to minimize the measuring error. The water in the phloem was observed when the strain gauges were replaced. The beginning of sap exudation was identified by tapping.

Results and discussion

Tangential strain of itaya-kaede maple

The tangential strains on the inner bark of the stems during the severe cold season showed sharp variations in mid-March (Fig. 2). These observations were similar at all measuring points on the stems. The tangential strain decreased at temperatures below 0°C, measured on the stem, and rose to the original values at temperatures above 0°C. Because frozen phloem was found during the severe cold season, "frost shrinkage" could have played a role. Specifically, it has been suggested that large contractive strains break the cell wall, and moisture migrates into the lumens of xylem cells, causing frost shrinkage.¹⁴ Subsequent to the sap exudation period, the strains were almost constant, with small diurnal fluctuations. With the appearance of new leaves on the stem shoots, the tangential strains and the diurnal changes started to increase (Fig. 2).

Sap exudation began on March 10, 1997, and continued for 2 weeks (Fig. 3). During this time the temperature on the surface of the stem fluctuated above and below 0°C. Despite the variations in temperature, the longitudinal strain remained constant, whereas the tangential strain did not. As the temperature dropped below 0°C, a small increase in the tangential strain was recorded and was attributed to expansion during ice formation in the xylem and phloem cells. With further decreases in temperature the tangential strain was also reduced, perhaps related to frost shrinkage. As the temperature rose above 0°C the tangential strain increased, reaching the original value before ice formation.

Unlike the stems, the tangential strain of the roots was not affected by ground temperatures just above 0°C during

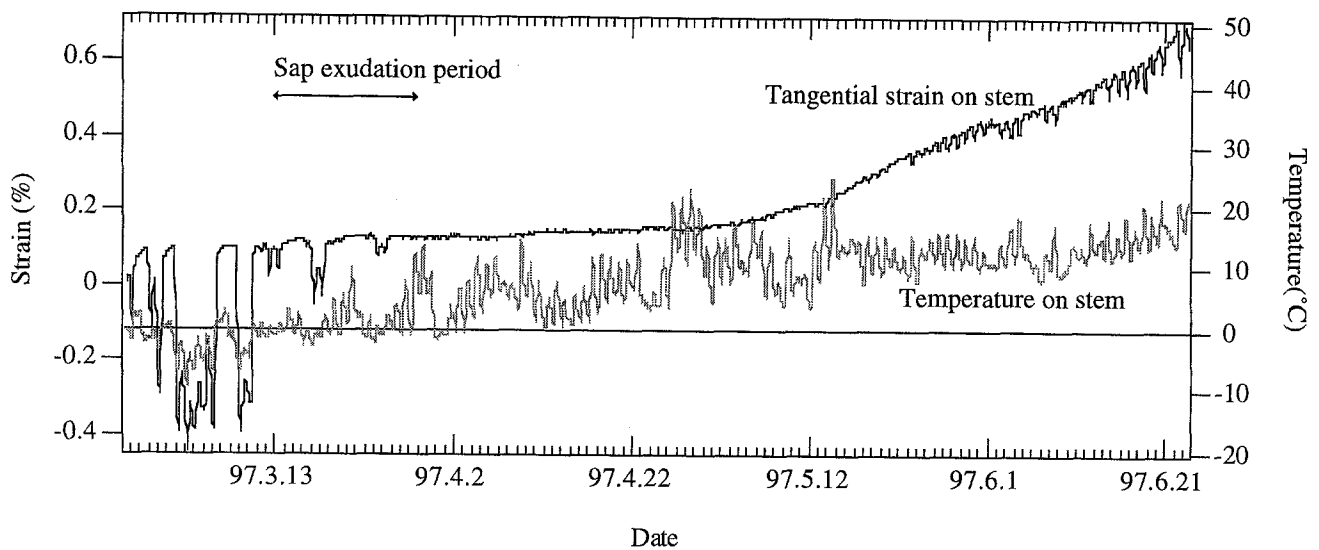


Fig. 2. Seasonal changes of tangential strain and temperature of the stem in itaya-kaede maple, measured at the surface of the inner bark in a mid position (*Acer mono*). (Other positions show similar results)

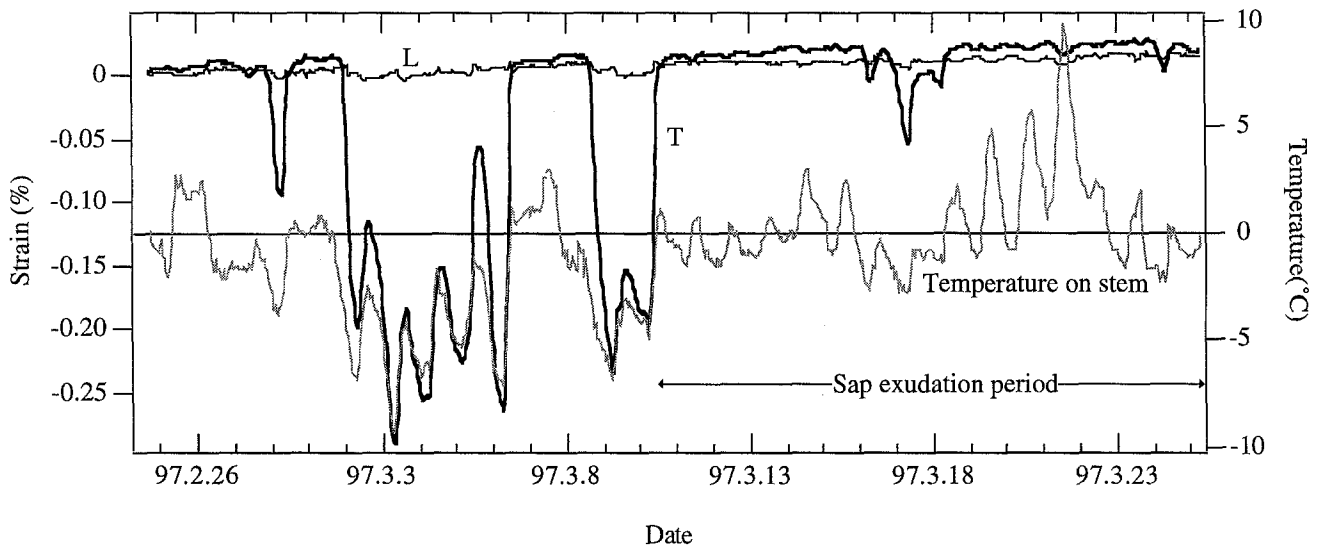


Fig. 3. Diurnal changes of tangential strain and temperature on the surface of the inner bark of the stem in itaya-kaede maple (*Acer mono*) during the sap exudation season. L, longitudinal strain; T, tangential strain

the sap exudation period (Fig. 4). Although the diurnal changes in tangential strain of the roots also occurred as new leaves appeared in May 1997, the amplitude of the root strains were larger than those of the stems during sap exudation. During the sap exudation period of the root, which began in mid-March and continued for 2 weeks, the temperature on the surface of the root was constant at 0°C, regardless of the change in the stem temperature from -2.5° to +5°C (Fig. 5). This figure also shows that the variations of the tangential strain in the root followed that of the temperature above ground.

Variations in tangential strain could be associated with the water-uptake characteristics of maple during the conditioning stage. Also, it could be related to the absorption of water in response to freezing due to apoplastic ice forma-

tion in gas-filled spaces (i.e., xylem fiber cells), as discussed by Milburn and O'Malley.⁷ Their study suggested that during the cooling sequence water is taken up by the tree. During nighttime, when the temperature is below 0°C, ice forms in the fiber lumina, compressing the air in the xylem fiber lumina. Subsequently, the warmer daytime temperatures release the compression force as the ice thaws and cause sap exudation from the stems.

Based on these ideas, the results of the current investigation suggest that during the cooling sequence water in the root moved to the stem and decreased the tangential strains in the root. Subsequently, as the temperature rose, water from thawing ice filled up the root cells and increased the tangential strain of the root (Fig. 5). If the stem had a tap at this time, sap would have exuded.

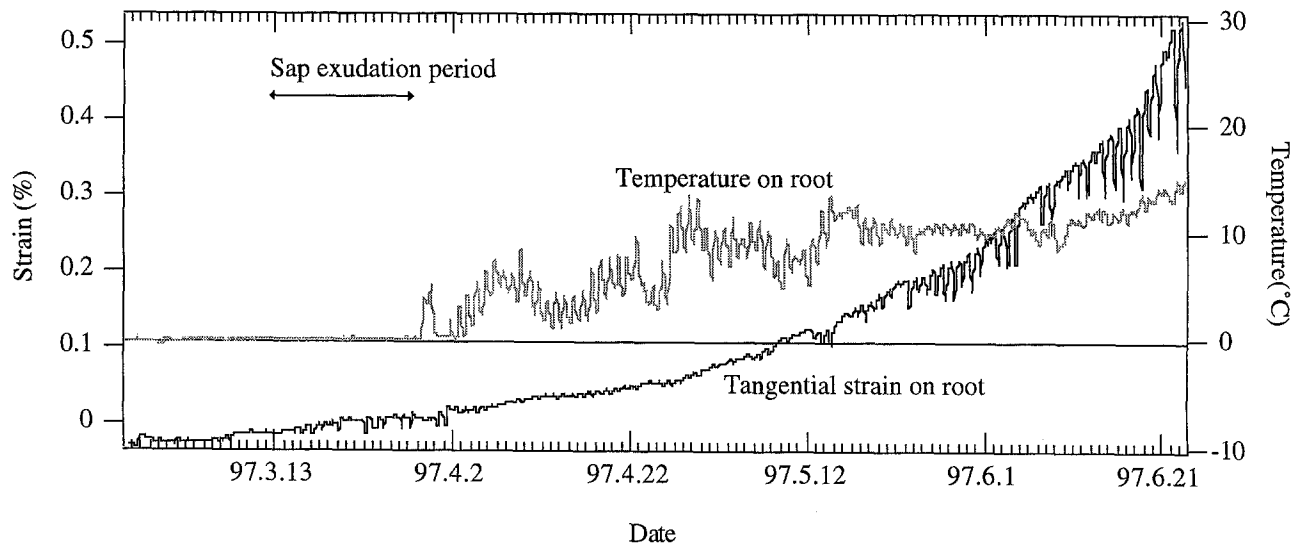


Fig. 4. Seasonal change of tangential strain and temperature on the surface of the inner bark of the root in itaya-kaede maple (*Acer mono*)

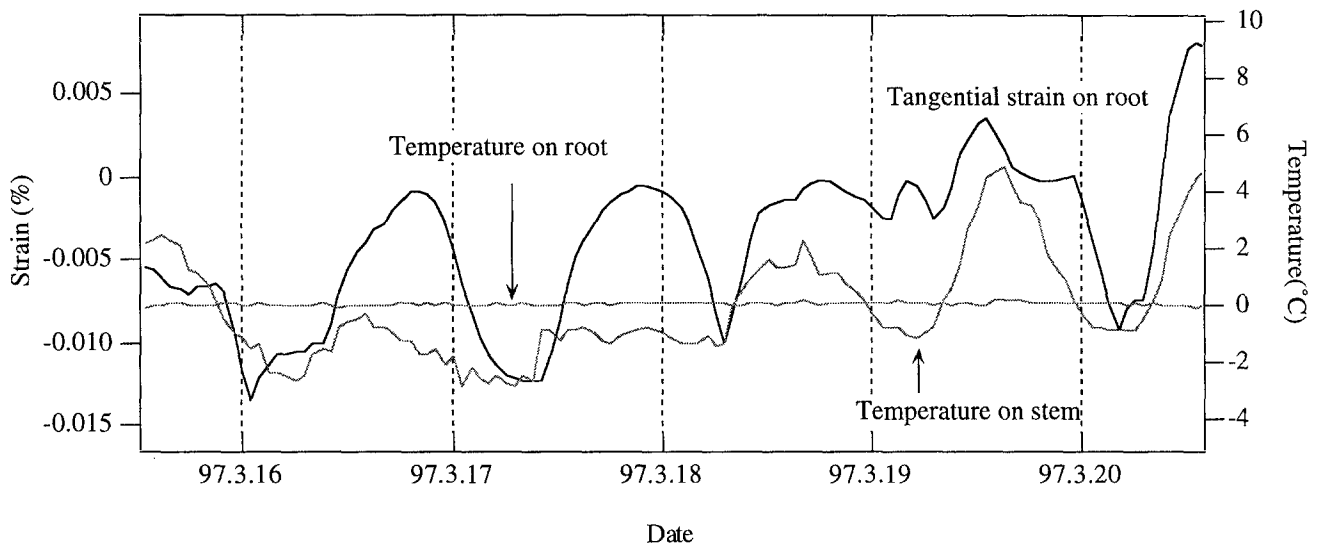


Fig. 5. Diurnal changes of tangential strain of the root in itaya-kaede maple (*Acer mono*) during the sap exudation season. Vertical broken lines indicate midnight

Milburn and O'Malley reported that during sap exudation the diametral changes were not found on the stem.⁷ The measurements in our study generally conform with their results, as the tangential strain of the stem was almost constant, with the exception of subzero days during sap exudation (Fig. 3).

Tangential strain of shirakamba birch

From February to March of every year throughout this research, large contractive strains were measured on the surface of the inner bark of the stem in shirakamba birch (Fig. 6). During the severe cold season, when frozen phloem cells were found, the occurrence of large contractive strains

was attributed to frost shrinkage, as was the case with itaya-kaede maple. During the sap exudation period in April, the tangential strain in the stems was almost constant. After this period the diurnal change in the tangential strains gradually increased. Within the same year, the observations from both trees and all measuring points indicated similar results. Because of the similarity in results of the two years of experimentation, this report includes only those of 1997.

The sap exudation in these trees correlated with a rapid increase in underground temperature (Fig. 7). This was simultaneous with the diurnal change of the tangential strain of the root. The tangential strain of the roots decreased slowly during sap exudation and began to increase. Shirakamba birch showed a characteristic change in the tangential root strains during the sap exudation period.

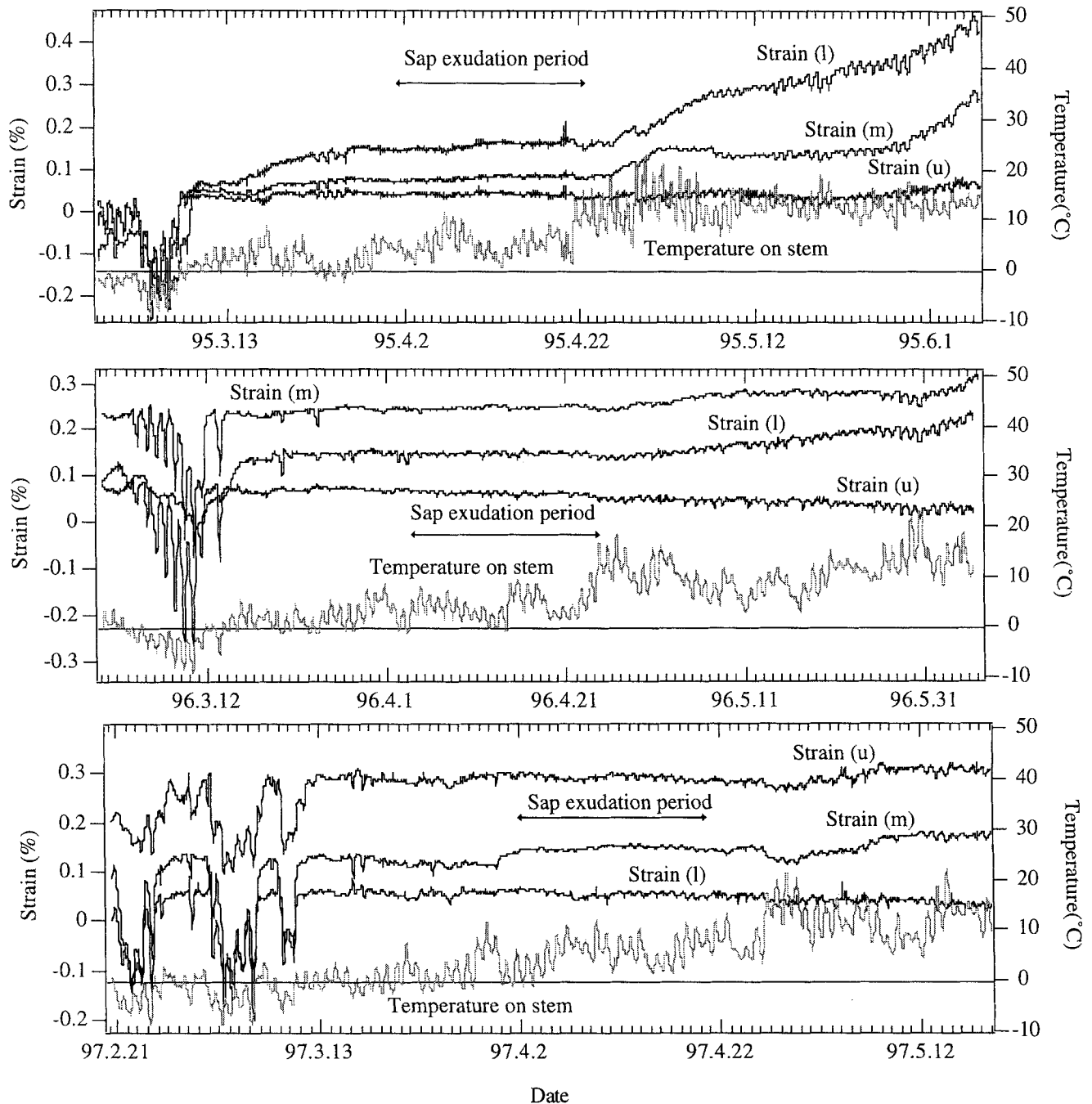


Fig. 6. Seasonal change of tangential strain and temperature on the surface of the inner bark of the stem in shirakamba birch (*Betula platyphylla* var. *japonica*) from 1995 to 1997. Strain (u), tangential

strain on stem in upper position; strain (m), tangential strain on stem in middle position; strain (l), tangential strain on stem in lower position

From April 4, 1997, sap exudation was simultaneous with a rise in root temperature (Fig. 8), regardless of the stem temperature, suggesting that the strain of the root is related to the root temperature, rather than the stem temperature.

Comparison of the sap exudation mechanism in itaya-kaede maple and shirakamba birch

During sap exudation itaya-kaede maple and shirakamba birch showed different tangential strain behaviors on the

inner bark of the roots (Fig. 9). The strain of itaya-kaede maple increased with an increase in stem temperature, whereas that of shirakamba birch decreased. Klepper et al.¹⁵ and Okuyama et al.⁸ noted a decrease in the stem diameter when the water potential of the leaves decreased due to high transpiration rates. Herzog et al. showed that the flow rate of sap in the stem inversely affected the diameter.¹⁶ These studies indicate that during the growing season the tangential strain on the surface of the inner bark decreases with an increase in temperature, as evidenced by

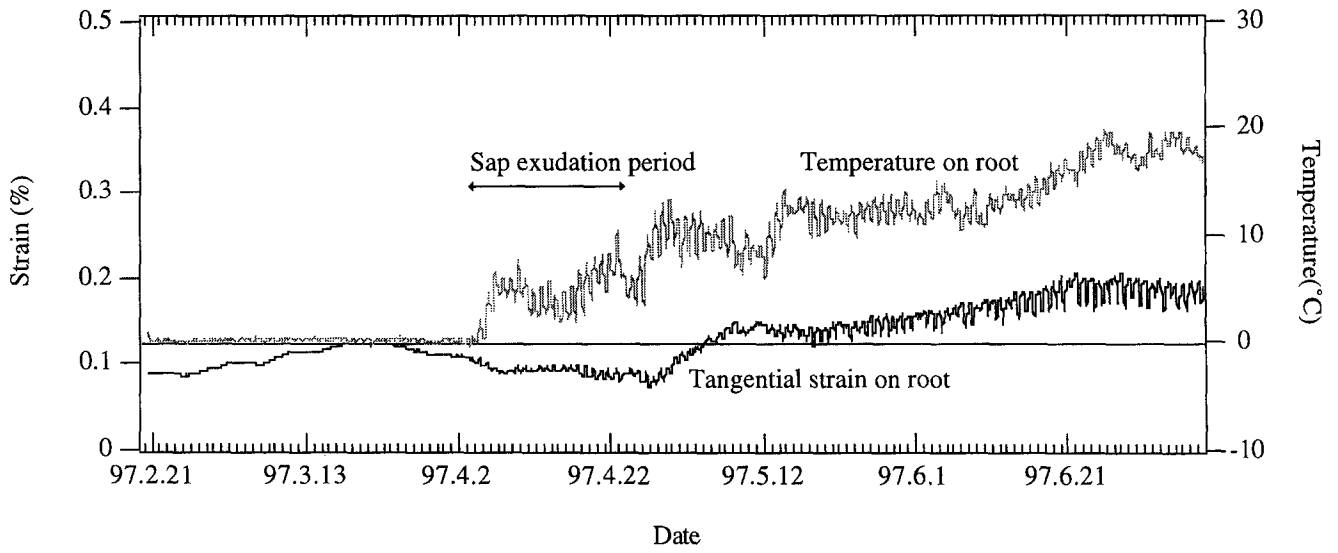


Fig. 7. Seasonal change of tangential strain and temperature on the surface of the inner bark of the root in shirakamba birch (*Betula platyphylla* var. *japonica*)

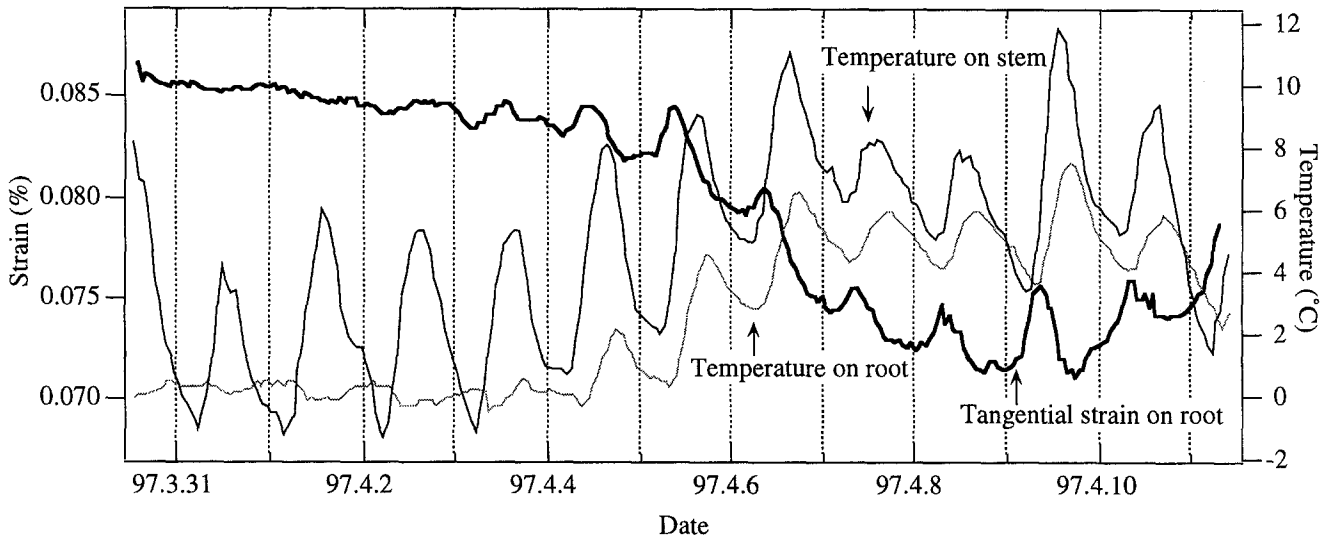


Fig. 8. Diurnal change of the strain of the root in shirakamba birch (*Betula platyphylla* var. *japonica*) during sap exudation. The vertical broken lines indicate midnight

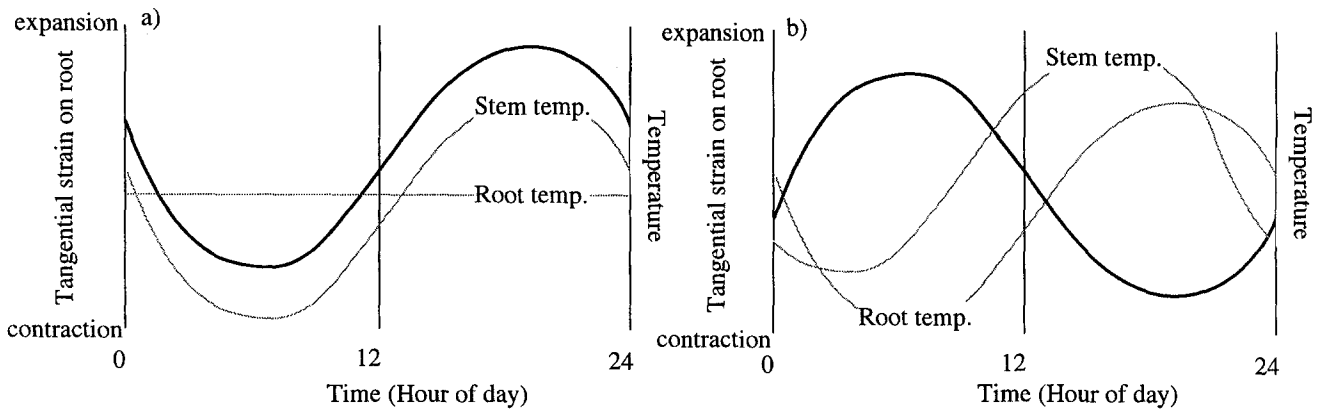


Fig. 9. Typical diurnal change, over 24h, of tangential strain (**bold line**) on the surface of the root inner bark of itaya-kaede maple (*Acer mono*) (a) and shirakamba birch (*Betula platyphylla* var. *japonica*) (b)

a decrease in xylem potential and turgor pressure in the living cells.

During sap exudation, when the temperature of the root was almost 0°C, the change in tangential strain of the root in itaya-kaede maple were completely contrary to that found during the growing season (Fig. 5). This finding suggests that the roots did not imbibe positively during the sap season. The change in tangential strain of the root in itaya-kaede maple could be attributed to “conditioning.” When the temperature of the stem reached below 0°C, water froze and ice developed in the xylem cell lumina. To supply water to the stem, the diameter of the root was thought to be decreased, causing a decrease in the tangential strain of the root.

With regard to shirakamba birch, sap exudation was not related to conditioning, as no ice was found in the xylem and phloem cell lumina. The tangential strain of the root decreased during the daytime and increased at night. Because during the sap exudation period leaves are not developed and their water requirement is absent, the driving force for absorption of water by the roots may be a result of root pressure. Tangential strain decreased as the temperature rose; and, owing to increased water absorption, sap flow intensified in the root. The amount of sap exudation recorded in the shirakamba birch trees was 10 times that of maple.¹ It is assumed that maple sap is derived from the melting of ice frozen in the xylem cell lumina by “conditioning”; thus sap volume may be limited by space in the xylem cell lumina. However, in shirakamba birch the sap comes from water absorbed in the root, and so there is no limitation to its volume.

Conclusions

The results indicate different mechanisms of sap exudation for *Acer mono* and *Betula platyphylla* var. *japonica*. In the case of *A. mono*, changes in tangential strain are explained by the notion of conditioning, which is known to be the main mechanism of soil water uptake in maple during sap exudation. Conditioning was not applicable in the case of *B. platyphylla* var. *japonica*. Sap exudation in *B. platyphylla*

var. *japonica* is ascribed to the supply of plentiful water from the roots.

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

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