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ORIGINAL ARTICLE

**Takahisa Nakai · Hisashi Abe · Takeshi Muramoto
Tetsuya Nakao**

# The relationship between sap flow rate and diurnal change of tangential strain on inner bark in *Cryptomeria japonica* saplings

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**Abstract** The relationship between sap flow rates and diurnal fluctuation of stems was investigated in cloned 3-year-old saplings of *Cryptomeria japonica* D. Don grown in a phytotron with irrigation every 2 days. The improved stem heat balance method and a strain gauge were used to measure sap flow rate and diurnal fluctuation of the stem. The sap flow rate reacted to lighting conditions, increasing and decreasing immediately after lights-on and lights-off, respectively. The tangential strain on the surface of the inner bark exhibited a reaction that followed but opposed the reaction of the sap flow rate to lighting conditions. Based on the changes in sap flow rate, there seemed to be four phases in diurnal sap flow: phase $A_1$ began with lights-on, when the sap flow rate increased, and lasted about 2 hours. In the following phase, $A_2$, the sap flow rate remained almost constant at 1.3 g/min for about 10 h, and then declined for about 2 h as lights-off approached. In phase B, the early period of darkness, the sap flow declined quickly and then more slowly, for about 4 h, until the start of the second dark period, phase C, when the sap flow rate became almost constant at 0.05 g/min for about 6 h. The first derivative of each sap flow rate and the corresponding tangential strain were calculated, and the results indicated a negative correlation between the two variables in all periods. In particular, the relationship between the first derivative values exhibited a highly negative correlation in phases $A_1$ and B, expressed as a primary formula. Sap flow rate was found to continue for some time after lights-off, and this compensated for reduced evaporative effects, albeit at a slow rate, over 4 h. The total amount of sap flow in the dark was only about 9% of that in the light, disregarding transpiration in the dark for simplicity. Thus, the total amount of sap flow responsible for swelling of the stem was about 9% of that consumed in transpiration during the light period.

**Key words** 3-year-old cloned sapling · Phytotron · Sap flow rate · Improved stem heat balance method · Strain gauge method

## Introduction

To measure sap flow, there are two nondestructive methods using heat: one focuses on the balance of the heat supplied by a heater in the stem [the stem heat balance (SHB) method], and the other focuses on the heat transfer (the heat pulse method or Granier method[1]). Each method can be divided into two further categories based on whether the amount of heat supplied by the heater is constant.

The SHB methods can be classified into three major types: one with a heater supplying constant temperature difference,[2] one with a heater supplying a constant heating value,[3] and an improved method with the heater supplying a constant heating value.[4] Although SHB methods have an advantage in obtaining sap flow rate for a single tree, they entail the difficulty of using a probe that may be complicated. The heat pulse method[5] and Granier method[1] use relatively simple probes; however, they depend on the value of the cross-sectional area of flow in the stem to convert the flow velocity into the flow rate.

This study primarily aimed to measure the sap flow rate of woody plant (tree) accurately, in which large changes are observed in the sap flow rate, without deeply injuring the test stem. However, we measured the sap flow rate using a new method, which modified an improved type of the SHB method with the heater supplying constant heat[4] to the sapling.

To measure the swelling or shrinkage of the stem, band dendrometer[6–9] and strain gauge methods[10–18] have been generally used until now. The former method allows simple long-term measurement to be made. However, the data obtained by this method is empirically known to underestimate the perimeter of the stem in winter. On the other hand, the latter method has been reported to provide very accurate data for short-term measurements, particularly on

T. Nakai (✉) · T. Muramoto · T. Nakao
Shimane University, Matsue 690-8504, Japan
Tel. +81-852-32-6071; Fax +81-852-32-6071
e-mail: jaja@riko.shimane-u.ac.jp

H. Abe
Japan International Research Center for Agricultural Sciences, Tsukuba 305-8686, Japan

the variation behavior of the xylem differentiation zone. However, for long-term measurements, the measurement data are known to provide somewhat less value than the actual amount of variation (growth rate) because of the effect of injured tissues formed at the site of the affixed strain gauge.

This study used a strain gauge method because the prime objective of this study was to accurately measure variation in the xylem differentiation zone.

## Experimental

### Sample tree and growing condition

Ten cloned saplings of 3-year-old Japanese cedar (*Cryptomeria japonica* D. Don.) planted in Wagner pots with vermiculite were used as the sample trees. The average height of the saplings was 80.3 cm at the beginning of the experiment, and the average diameter of the stems at a road clearance of 12.5 cm was 1.19 cm. The saplings were cultivated by providing 1 liter of nutrient solution every second day (N 50.0 ppm, $P_2O_2$ 25.0 ppm, $K_2O$ 30.0 ppm, $CaO_2$ 20.0 ppm, $MgO_2$ 10.0 ppm, $Fe_2O_3$ 2.0 ppm, Cu 0.1 ppm, Mn 0.1 ppm, Zn 0.1 ppm, B 0.2 ppm, Mo 0.1 ppm, and initial pH 5.2).

Experiments were conducted in a climate-controlled phytotron. The temperature was set at 20° ± 1.0°C, relative humidity (RH) at 75% ± 5.0%, and the day cycle was 14 h of light and 10 h of darkness. The artificial light source in the room was a mixed light of 8 mercury lamps and 12 positive glow lamps. The light intensity was approximately 490.0 ± 5.0 $\mu mol \cdot s^{-1} \cdot m^{-2} / \mu A$ (cloudy weather level) with the light meter (Model L1–189, LI-COR) at a height of 0.8 m from the light source.

The fluctuations of temperature, relative humidity, and illumination in the phytotron are shown in Fig. 1. In this case, illumination was measured with the illumination sensor (IKS-17, Koito).

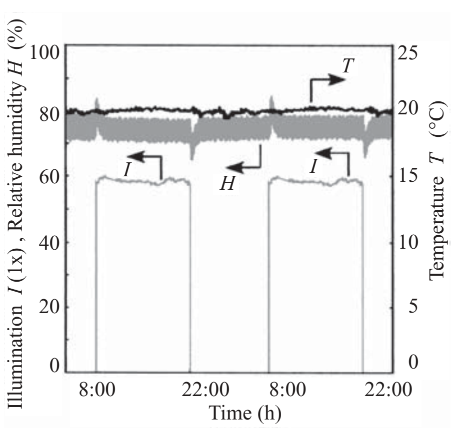



**Fig. 1.** Fluctuation of temperature ($T$), relative humidity ($H$), and illumination ($I$) in the phytotron. *Bent arrows* indicate relevant axes

### Sap flow rate

*Measurement theory*

To measure sap flow rate, the improved SHB method[4] was used. The following is a brief description of the measuring principle: to set up the condition for measurement, the stem segment is wrapped with a strip heater, the heater is covered with heat-insulating materials, and heat energy QH is supplied to the stem segment by the heater connected to a constant-voltage power source. The possible flows of the heat energy are the following five as shown in Fig. 2:

1. QF: heat energy used for heating the sap and carried by upward sap flow
2. QU: heat energy transferred upward through the stem by thermal conduction
3. QD: heat energy transferred downward through the stem by thermal conduction
4. QS: heat energy dissipated into the surroundings after passing through the thermal insulating materials
5. HC: heat energy transferred from/to the internal body of the stem and used for increasing or decreasing the amount of heat storage in the stem

The heat balance equation is given by

$$\mathrm{QH} = \mathrm{QF} + \mathrm{QU} + \mathrm{QD} + \mathrm{QS} + \mathrm{HC} \tag{1}$$

Equation 1 can be rearranged as

$$\mathrm{QF} = \mathrm{QH} - \left(\mathrm{QU} + \mathrm{QD} + \mathrm{QS} + \mathrm{HC}\right) \tag{2}$$

The value of each term of Eq. 2 can be obtained from the following procedures:

1. QH: calculated from the voltage and current of the constant-voltage power supply of the heater

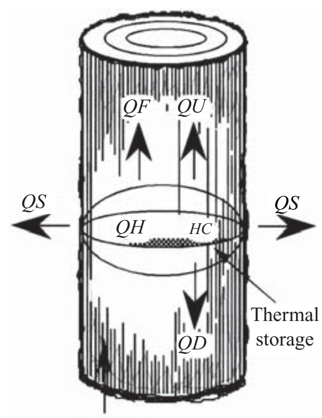



**Fig. 2.** Heat balance of the stem with an installed heater. *QH*, heat energy supplied by the heater; *QF*, heat energy used for heating the sap and carried by upward-moving sap; *QU*, heat energy transferred upward through the stem by thermal conduction; *QD*, heat energy transferred downward through the stem by thermal conduction; *QS*, heat energy dissipated into the surroundings after passing through thermal insulating materials; *HC*, heat energy transferred from/to the internal body of the stem and used for increasing or decreasing the amount of heat storage in the stem

2. QU: calculated as a value proportional to the temperature gradient on the surface of the upper side of stem segment, generated by the heater
3. QD: calculated as a value proportional to the temperature gradient on the surface of the lower side of the stem segment, generated by the heater
4. QS: calculated as a value proportional to the temperature gradient in radial directions in the isolating materials
5. HC: neglected (regarded as zero)

Then the heat energy QF is obtained by substituting these values into Eq. 2. The sap flow rate $F$ is calculated from the following equation with the above-obtained QF,

$$F = \frac{\mathrm{QF}}{\delta\theta \cdot \mathrm{cp}} \tag{3}$$

where cp is specific heat of water ($4.186\,\mathrm{J \cdot g^{-1} \cdot K^{-1}}$), and $\delta\theta$ is the temperature difference between the time just before the sap flow enters the heated section and that just after the sap flow exits the heated section. Because the sap flow velocity cannot be known, the temperatures above and below the heated section are continuously recorded. The temperature change due to heating was calculated from the following two equations based on the time ($\sigma t$) required for the sap flow to pass through the heated section:

$$T_{\mathrm{Before}}(t) = T_{\mathrm{Below}}\left(t - \frac{\sigma t}{2}\right) \tag{4}$$

$$T_{\mathrm{After}}(t) = T_{\mathrm{Above}}\left(t - \frac{\sigma t}{2}\right) \tag{5}$$

Here $T_{\mathrm{Before}}(t)$ and $T_{\mathrm{After}}(t)$ are the temperatures at the time ($t$) before and after the sap flow passes through the center of the heated section, respectively. In addition, $T_{\mathrm{Below}}(t)$ and $T_{\mathrm{Above}}(t)$ are the temperatures at the time ($t$) when the sap passes through the lower edge of the heater and the upper edge, respectively. The reason why $\sigma t$ is considered is that nonsteady properties in the flow rate of the sap flow when passing through woody plants are stronger than those through herb plants. The sap flow rate $F$ can be obtained by using Eqs. 4 and 5, and is expressed by

$$F = \frac{60 \cdot \mathrm{QF}}{\left(T_{\mathrm{After}} + T_{\mathrm{Before}}\right) \cdot a \cdot \mathrm{cp}} \tag{6}$$

where $a$ is a coefficient for calibrating the increment of sap temperature. The coefficient is necessary in case the increment of sap temperature is overestimated or underestimated by reasons of the following examples: (1) the distribution of sap flow velocities in the direction of the circumference varies significantly,[8] or (2) the thermocouples only detect the surface temperature of the stem, so that the temperature increment of sap is measured indirectly. The following equation is used to check the value obtained from Eq. 6,

$$\frac{L}{F/S} = \sigma t \tag{7}$$

If Eq. 7 is not satisfied, $\sigma t$ is to be calculated again and the sap flow rate $F$ is also calculated. Here $L$ is the distance, equal to 7 cm, between the thermocouples located right above and below the heated section, and $S$ is the cross-sectional area of the sap flow in the stem.

*Measurement of sap flow*

To measure the sap flow rate, a specialized sap-flow-rate measuring device (TUH-22, HydroTeck, Shiga, Japan) was used. The device is composed of a heater, thermocouples, and insulation. The surface asperities of the outer bark of the stem segment were removed with a knife to make the surface smooth. Sheets with polyvinylidene chloride were wrapped around the surface of the stem to prevent the stem becoming dry. The heater, as shown in Fig. 3, with a width of 5 cm was mounted over the polyvinylidene chloride sheet around the stem at a height of 15 cm from the ground. Eight thermocouples were attached to the stem segment at locations above and below the heater as indicated in Fig. 3. A layer of insulating material was wrapped threefold around the stem segment fitted with the heater and thermocouples. A thermocouple used to measure heat energy dissipated outside was attached inside the first and second layers of the insulating materials, respectively. To confirm whether the sap flow drifts inside the stem of the test tree, the position of each thermocouple was shifted by a constant angle in the circumferential direction. The sap flow rate was measured each time the position was changed. No significant difference in the sap flow rate was detected and flow rates were almost the same even if thermocouples were shifted.

*Measurement fluctuation of the stem*

To determine the fluctuation of the stem surface, the outer bark of the stem was carefully removed and the tangential strain on the surface of the inner bark was measured with a strain gauge (Tokyo Sokki, gauge length 5 mm) by the single-active-gauge and three-wire-connection method. In this measurement, cyanoacrylate adhesives (CN-E, Tokyo

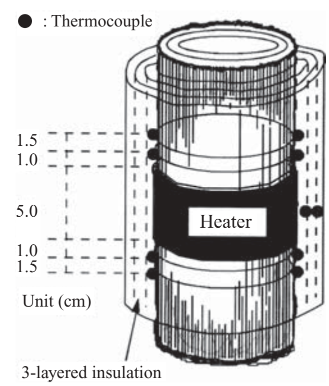



**Fig. 3.** Structure of the heater system used in this study. Four thermocouples were located above the heater and four below. To measure the energy flow that escaped horizontally to the outside, two thermocouples were located inside the insulation: one in the inner interlayer and another in the outer interlayer

Sokki) was used for bonding the strain gauge to the inner bark surface. The measuring points with strain gauges were covered with Vaseline and aluminum sheet to protect them from shrinkage and direct light irradiation. The installed sap-flow-rate measuring device and strain gauge are shown in Fig. 4.

## Results and discussion

### Effect of the nonsteady properties of sap flow rate on the measured sap flow rate

As mentioned above, it is well known that the nonsteady properties of the sap flow rate in woody plants are stronger than those in herb plants. The sap flow rate considering the nonsteady properties was plotted against time, along with the sap flow rate obtained when neglecting them (Fig. 5). The black line in Fig. 5 shows the former, and the gray line shows the latter. As a result, although it was not more remarkable than the high standing tree,[19] there was a clear difference between the values. Namely, it was clear that the nonsteady properties in the sap flow rate must be considered in the young tree.

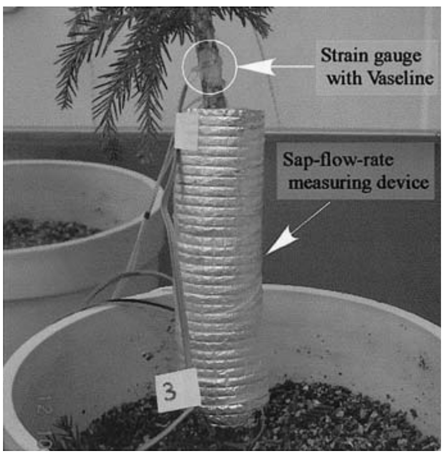



**Fig. 4.** Apparatus used to measure sap flow rate and tangential strain

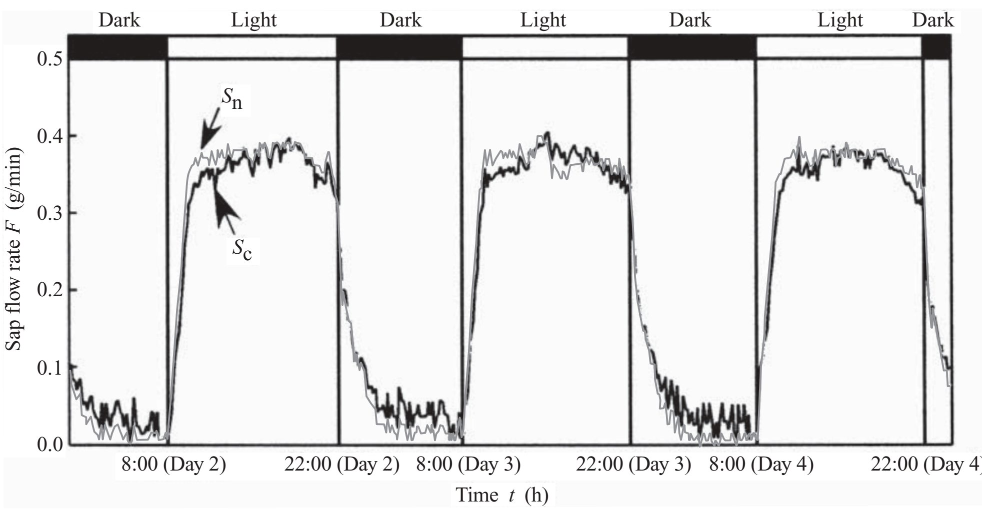
### Diurnal fluctuations of sap flow rate and tangential strain of inner bark surface in stem

Changes in sap flow rate and tangential strain during a 14-h light period and a subsequent 10-h dark period are shown in Fig. 6. The sap flow rate and tangential strain on the surface of inner bark each showed almost the same repeating patterns of diurnal fluctuation every day throughout the duration of measurement.

In accordance with the diurnal fluctuation, the daily pattern can be divided into four phases: two phases during the light period and two phases during the dark period. The diurnal fluctuation of sap flow rate is shown in Fig. 7. The former two phases are phase $A_1$ in which the sap flow rate increased rapidly with elapsed time after lighting and phase $A_2$ in which the sap flow rate stayed at a nearly constant value (approximately 1.3 g/min) and tended to decrease slightly (on day 3 it remained at a nearly constant value without decreasing because of irrigation). The latter two phases are phase B in which the sap flow decreased rapidly with elapsed time after lights-off, and phase C in which the sap flow rate stayed at a nearly constant value (approximately 0.05 g/min). With saplings used in this study, the durations were about 2 h for phase $A_1$, about 10 h for the nearly constant section of phase $A_2$, about 2 h for the decreasing section of phase $A_2$, about 4 h for phase B, and about 6 h for phase C.

On the other hand, the amount of tangential strain on the surface of the inner bark began to decrease (the stem shrank) slightly after the increase in the sap flow rate due to the onset of light. After the sap flow rate reached a constant value, the rapid shrinkage of the stem stopped. After that, there was little swelling or shrinkage fluctuation up to the time at which the dark period started. As the sap flow rate rapidly decreased after lights-off as described above, the

**Fig. 5.** Relationship between sap flow rate considering the nonsteady properties of the sap flow rate ($S_c$) and sap flow rate neglecting the nonsteady properties of the sap flow rate ($S_n$)



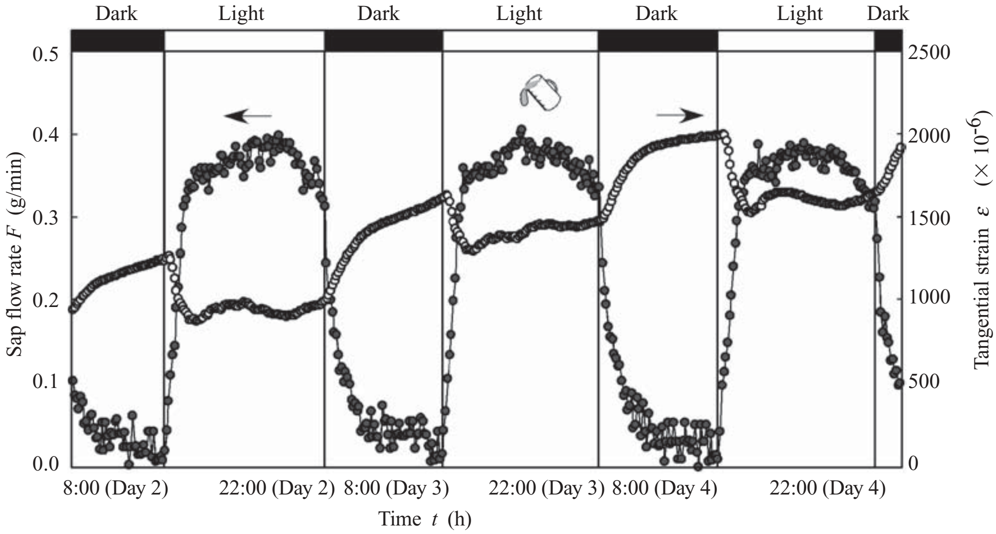



**Fig. 6.** Changes in sap flow rate (*filled circles*) and tangential strain measured on the surface of the inner bark (*open circle*). Lighting period (*white bars*), 14h; dark period (*black bars*), 10h

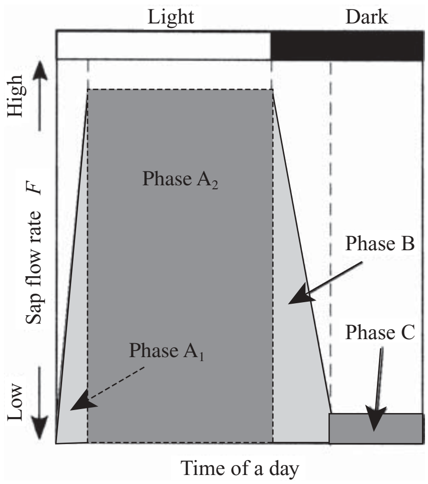



**Fig. 7.** Diurnal fluctuation of sap flow rate. See text for explanation of *phase $A_1$*, *phase $A_2$*, *phase B*, and *phase C*

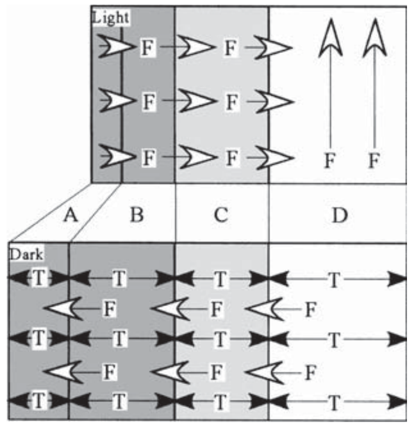



**Fig. 8.** Diagram for water transport and cell expansion in the stem with transpiration. *A*, cambial and inner bark zone; *B*, expanding zone; *C*, developing zone; *F*, water flow (*white arrows*); *T*, pressure potential (*black arrows*)

tangential strain significantly increased (the stem swelled). The stem swelled significantly before the sap flow rate reached the minimum value. The increase in the tangential strain became gentle concurrently with the sap flow rate reaching the minimum value. In other words, we can speculate the change as follows. For about 4h after the dark period started, the sap kept flowing to compensate the water content lost in the stem during the light period. However, 4h later, the shortage of water in the stem was rectified to some extent and the pressure gradient of water potential in the stem became small and the amount of water drawn from the soil became small.

It is evident from Fig. 6, that the increase or decrease in the tangential strain was closely related to the increase or decrease of the sap flow rate. These results supported a model showing water transport and cell expansion, which we proposed from information of the bioelectrical potential and the radial transport of water containing inorganic materials (Fig. 8).[11,12] Namely, the model as shown in Fig. 8 suggests that xylem is divided into four parts: the cambial and phloem zone (zone A), expanding zone (zone B), developing zone (zone C), and mature xylem zone (zone D). The water was transported through the apoplastic passageways and diffused into the tissue from zone D to zone A when transpiration was restricted in the dark period. As a result, cations such as $K^+$ and $Ca^{2+}$ in the water were distributed in high concentration in zone A and gradually decreased toward the inner part of the xylem through zones B and C. In contrast, when transpiration was accelerated during the light period, water mainly flowed through vessels in zone D and was transported to the upper part of the sapling. Then, water containing inorganic constituents in zones A, B, and C was drawn toward zone D.

From the midpart to the last half of the light period on day 3, the diurnal fluctuation was somewhat different from that on the other measuring days. This difference is attributed to the effect of irrigation as described above. As shown in Fig. 6, the sap flow rate decreased and the tangential

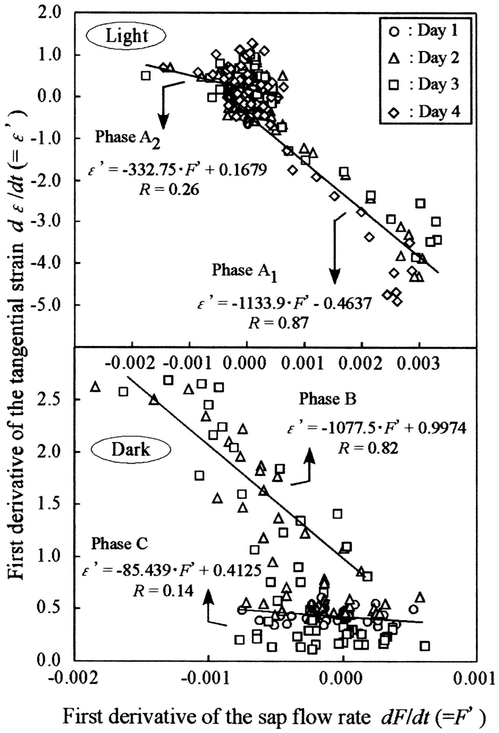



**Fig. 9.** Relationship between the first derivative of the tangential strain [$d\varepsilon/dt$ ($= \varepsilon'$)] and that of the sap flow rate [$dF/dt$ ($= F'$)]. *Solid lines* show regression lines

strain increased just after irrigation. This tendency was very similar to the correlation between sap flow rate and tangential strain just after lights-off.

## Relationship between sap flow rate and tangential strain of inner bark surface in stem

To further study the relationship between the sap flow rate and tangential strain, the first derivative of the sap flow rate [$dF/dt$ ($= F'$)] and that of the tangential strain [$d\varepsilon/dt$ ($= \varepsilon'$)] were compared (Fig. 9). The derivatives indicate the degree of variation with time for the sap flow rate and tangential strain, respectively.

The analytical results of the data during the light and dark periods including the previously classified four phases are presented in Fig. 9. In any of the four phases, there is a negative correlation between $F'$ and $\varepsilon'$. The detailed description of the correlation in each phase is as follows: for phase $A_1$, there is a strong negative correlation between $F'$ and $\varepsilon'$. It reveals that the tangential strain tends to decrease concurrently with the increase of the sap flow rate. For phase $A_2$, there is a weak negative correlation between $F'$ and $\varepsilon'$. As is evident from Fig. 6, the sap flow rate is nearly constant. In more detail, the tangential strain tends to decrease or increase with increase or decrease of the sap flow rate. For phase B, there is a strong negative correlation as seen in phase $A_1$. In other words, the tangential strain tends to increase with the decrease of the sap flow rate. For phase C, there is a very weak negative correlation between $F'$ and $\varepsilon'$. As is evident from Fig. 6, the sap flow rate maintains a nearly constant value at almost zero. In more detail, the tangential strain tends to increase with the decrease in the sap flow rate.

Here we discuss the relation between respective phases as follows. As previously described, both phase $A_1$ and phase B are light-sensitive phases in which a responsive reaction occurs for a period following lighting and lights-off. With the regression line, the slope of phase $A_1$ is somewhat smaller than that of phase B. The reason is that, as shown in Fig. 6, the decrease in the sap flow rate after lights-off is different between before and after the tangential strain responds to lights-off. In other words, the decreasing rate of sap flow just after lights-off is almost equivalent to the increasing rate of sap flow just after lighting. After the response of the tangential strain begins, or equivalently, the swelling begins, the decreasing rate of sap flow becomes somewhat smaller. This change brings about the difference between the gradients of phase $A_1$ and phase B. On the other hand, in phase $A_2$ and phase C in which the sap flow rates are nearly constant, the slope of phase $A_2$ is larger than that of phase C during the light period. The reason for this difference is, as shown by Fig. 6, that the change in the sap flow rate and the tangential strain during the light period is greater than that during the dark period.

## Estimation of sap flow utilized for swelling of trunk

The total amount of sap flow is calculated from each phase: phase A (14 h) including phase $A_1$ and phase $A_2$ during the light period, phase B (about 4 h) in the first half of the dark period, and phase C (about 6 h) in the second half of the dark period. The total amount of the sap flow is derived by integrating over each zone interval of the diurnal fluctuation graph of the sap flow rate shown in Fig. 6. The results are as follows: phase A (0800–2200 hours; light period): 1000.6 g, phase B (2200–0200 hours; dark period): 71.5 g, and phase C (0200–0800 hours; dark period): 20.2 g.

The calculated values are the average of data for day 2 and day 3. If we compare them, the total amount of the sap flow during the dark period is about 7% of that during the light period for phase B, and about 2% for phase C, respectively (about 9% in total during the dark period). To be more specific, this study showed that the total amount of the sap flow during the dark period is about 9% of that during the light period. Conversely, the total amount of the sap flow, which flows through the stem and consumed for transpiration, is about 11 times larger than that used for the swelling of the stem during the dark period. This figure is very high. It was reported that the total amount of the sap flow during the dark period is about 8.5% of that during the light period for a standing 17-year-old Japanese cedar.[20] Although these percentages are almost the same regardless of tree age, it wants to make this point to be the continuation problem.

The above calculation assumes, for convenience, that saplings do not transpire at all during the dark period. In actuality, saplings are thought to transpire slightly during the dark period. Therefore, we will conduct further measurements of transpiration in more detail and carry out an accurate calculation in the future.

## Conclusions

Cloned 3-year-old Japanese cedar saplings were grown by controlling light quantities, temperature, humidity, and mineral nutrients in a phytotron in which the day length was set at a light period of 14h (a dark period of 10h). The sap flow rate of saplings and the amount of swelling or shrinkage (tangential strain of inner bark surface in the stem) were measured to study the relation between them in detail by using both the improved SHB method, with a heater supplying constant heat, and the strain gauge method.

The results revealed that, at first, the sap flow rate responded to lighting and lights-off and then the tangential strain changed with a time lag. Furthermore, according to the diurnal fluctuation of sap flow rate, the fluctuation over a day was classified into the following four phases: two phases (phase $A_1$ and phase $A_2$) during the light period, and two phases (phase B and phase C) during the dark period. A strong relationship between the sap flow rate and the tangential strain in those phases was found. More specifically there was a relatively strong negative linear relationship between them in the phases (phase $A_1$ and phase B) from just after switching between the light and dark periods to the time the sap flow rate reached a constant value. Even in the other regions (phase $A_2$ and phase C), there was a weak negative linear relationship.

On the other hand, a comparison of the total amount of the sap flow during the light and dark periods was made in this study. As a result, it became evident that the total amount of the sap flow during the dark period, i.e., that used for swelling of the stem, is about 9% of the total amount consumed in transpiration during the light period, assuming that transpiration during the dark period is negligible.

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