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Original Article

# Applicability of the thermal dissipation method (TDM) for sap flow measurement in teak trees

Takanori SATO*1, Nobuaki TANAKA*1, Katsunori TANAKA*2, Yasunori IGARASHI*3, Natsuko YOSHIFUJI*4, Masakazu SUZUKI*5, Chatchai TANTASIRIN*6

## Introduction

In order to access forest water uptake on a stand scale, it is necessary to quantify water uptake by individual trees and to scale them up to a stand scale. Measurements of tree-to-tree variations in sap flow and within-tree spatial variations (both circumferential and radial) are essential for this procedure (PHILLIPS *et al*., 1996; JAMES *et al*., 2002; DELZON *et al*., 2004; KUMAGAI *et al*., 2005; TATEISHI *et al*., 2008; TSURUTA *et al*., 2010; KUME *et al*., 2011; SATO *et al*., 2012). Estimations of two levels of variability in an actual forest stand require several sap flow sensors. The thermal dissipation method (TDM; GRANIER, 1987), which uses Granier-type sap flow sensors, is both inexpensive and relatively simple to operate. In fact, in recent years, circumferential, radial and tree-to-tree distributions of sap flow were investigated using several Granier-type sap flow sensors (KUMAGAI *et al*., 2005; KUME *et al*., 2010b, 2011). Ease of calculation is an additional advantage provided by the TDM: sap flow averaged over a sensor cross-section is readily obtainable from an empirical equation with only two coefficients that are applicable to various tree species (GRANIER, 1987). Whole-tree water uptake is calculated as the product of sap flow measured by the TDM and sapwood area (e.g., DELZON *et al*., 2004; KUMAGAI *et al*., 2005).

TDM estimates of sap flow are based on an empirical relationship between sap flow and the temperature difference between heated and unheated sensors inserted radially into the xylem. GRANIER (1987) conducted laboratory experiments with two coniferous and one ring-porous species to compare actual sap flow with the temperature difference between sensors. The results suggested that the relationship between sap flow and the temperature difference was uniform regardless of tree species or wood anatomy. Subsequent experiments demonstrated that the TDM can be used to accurately estimate tree transpiration across a range of species (ČERMÁK *et al*., 1992; GRANIER *et al*., 1994; VERTESSY *et al*., 1997; LU and CHACKO, 1998; BRAUN and SCHMID, 1999; CLEARWATER *et al*., 1999; CATOVSKY *et al*., 2002; LU *et al*., 2002; MCCULLOH *et al*.,

＊1 Ecohydrology Research Institute, The University of Tokyo Forest, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Aichi 489-0031, Japan
＊2 Department of Environmental Geochemical Cycle Research, Japan Agency for Marine-Earth Science and Technology, Yokohama, Kanagawa 236-0001, Japan
＊3 Hydrospheric Atmospheric Research Center, Nagoya University, Nagoya 464-8601, Japan
＊4 Forestry and Forest Products Research Institute, Ibaraki 305-8687, Japan
＊5 Graduate School of Agricultural and Life Science, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan
＊6 Faculty of Forestry, Kasetsart University, Bangkok 10903, Thailand

2007; TANEDA and SPERRY, 2008; BUSH *et al*., 2010). Nevertheless, other studies have reported substantial errors when the method was applied to broader range of tree species (GOULDEN and FIELD, 1994; CLEARWATER *et al*., 1999). For example, sap flow is greatly underestimated by the TDM when it is used with ring-porous species (TANEDA and SPERRY, 2008; BUSH *et al*., 2010). The reasons for the discrepancies among these studies are not fully understood, but the problem of underestimation is widely acknowledged in the existing literature.

Radial variation in sap flow in the trunk of ring-porous tree species may be much greater than variation in the trunks of coniferous and diffuse-porous species. Using dye perfusion experiments, UMEBAYASHI *et al*. (2008) demonstrated that the water transport function was greatly restricted in the outermost annual rings of eight ring-porous species growing in a north temperate climate. ANFODILLO *et al*. (1993) inserted the heater into the trunks of ring-porous species to monitor heat dissipation according to sap flow, but they were unable to detect heat dissipation in the outermost annual rings. Variation in sap flow rates across the length of a sensor may account for the underestimations of the TDM (CLEARWATER *et al*., 1999). Thus, the existence of radial variation in sap flow indicates that wide-scale application of the TDM to ring-porous species will require a full exploration of the sap flow distribution in tree trunks. With appropriate sap flow distribution data, it would be possible to determine whether or not the TDM is suited to the species. Most of the previous studies testing the applicability of the TDM to ring-porous tree species have been performed in the laboratory on field-collected branch and stem segments (TANEDA and SPERRY, 2008; BUSH *et al*., 2010). Although it is considered that water transport pattern in the sample segments was quite different from natural condition (RENNINGER and SCHÄFER, 2012), few studies have examined the applicability of the TDM to ring-porous trees growing in natural settings (GRANIER *et al*., 1994). Furthermore, no study has tested the applicability of this method to ring-porous forest canopy trees that are mature and have large diameters.

Teak (*Tectona grandis* Linn. f.) is a well-known ring-porous tree species (CODER, 2011) that is widely planted in tropical regions, including Southeast Asia, the Indian subcontinent, Central America and Africa, because of its considerable commercial value (KRISHNAPILLAY, 2000; KOLLERT and CHERUBINI, 2012). Local water resource management requires information on water uptake by these expanding plantations. The TDM has considerable potential in the measurement of stand-scale water uptake (i.e., transpiration) by teak plantations. However most studies of sap flow distribution in ring-porous species and the applicability of the TDM have been conducted in the north-temperate climate. There is interest to identify the radial distribution of sap flow in ring-porous species standing in tropical climate and testing the applicability of TDM to these species.

The goal of this study, therefore, is to investigate radial distribution of sap flow for teaks and to test the applicability of TDM for this species. Toward this goal, the following field procedure on mature plantation teaks: dye perfusion experiments to investigate the radial distribution of sap flow in tree trunks, and simultaneous measurements of tree water uptake and sap flow using the TDM to compare with the actual water uptake and estimated water uptake by the TDM.

## Materials and methods

### Plant materials

Experiments on teak were conducted in the Mae Mo teak plantation, which is located in Lampang Province, Thailand (18˚25'N, 99˚43'E; 380 m above sea level). This plantation was established in 1968 by Forest Industrial Organization (FIO). Teak individuals from a 36-year-old teak stand, where an average height and a diameter at breast height (DBH) respectively was 20 m and 22 cm, were selected for our experiments.

In this study site, there were the wet (April to October) and dry (November to December and January to March) seasons in a year under the influence of Asian monsoon. An above-canopy meteorological measurement was conducted on a 40-m high scaffolding tower located 400 m west of the examined stand. The annual amount of precipitation in this area was 1,284 mm, and the average temperature (2000-2004) was 25.8 °C (YOSHIFUJI *et al.*, 2006; IGARASHI *et al.*, 2012).

Teak is a deciduous broadleaved tree classified as ring-porous by its vessel distribution in the xylem. It has large earlywood vessels that are 200-300 μm in diameter arrayed along annual rings, and small latewood vessels with diameters of <100μm (SAEKI, 1982).

## Dye perfusion experiment

To determine the radial distribution of sap flow in the trunks, dye perfusion experiments were conducted for individuals listed in Table 1. Three sample trees differing in DBH were selected and named D1, D2 and D3. The dye perfusion experiments were conducted on the following dates: 2009/11/17, 2012/10/25, and 2012/10/26.

A 1 % acid fuchsin solution was used as the perfusion liquid. The movement of this solution matches that of sap flow, because the dye molecules do not adhere to the vessel walls and move together with the sap through the vessels (IIDA *et al.*, 1992; SANO *et al.*, 2005). Thus, it is supposed that the flow of the acid fuchsin solution matched sap flow movement in the vessels.

The bottles used for injecting the dye solution were attached to tree trunks 90 cm above ground level (Figure 1a). On each tree, a hole, the diameter and depth were 10 and 50 mm, was made through the bark and into the trunk xylem 80 cm above ground level using an electric drill. To avoid xylem vessel cavitation, a simple water reservoir was attached to the tree trunk and the hole was made under water. After made the hole, the dye solution was injected into each hole for a set period of time (Table 1). To avoid leakage of the dye solution, the hole and the bottle outlet were connected with a silicone cap, after which the water reservoir was detached (Figure 1a). Before injecting the dye solution, a hole was bored on the bottle using a gimlet. Following dye injection, the experimental trees were felled and all branches were immediately cut free to prevent further ascent of the dye solution. Sample disks were cut out of the trunks at intervals of 10-100 cm, until the dyed section on the disks surface became ambiguous.

To distinguish the dyed and non-dyed section on the surface of each sample disk, the dyed section was shaved using a chisel and immediately marked out the borders using a ball-point pen. According to examine the surface of disks, radial thicknesses of the bark, sapwood, heartwood and dyed section were measured, and the annual rings of the sapwood, heartwood and dyed area were counted.

The dye ascent velocity ($D_s$; cm $h^{-1}$) was calculated as:

$D_s = h / T \times 60$ Equation (1)

where $h$ (cm) is the height above the injection hole and $T$ (min) is the duration of dye solution injection.

Table 1. Information on experimental teak specimens and details of the dye perfusion experiments.

| | Date of experiment | Tree height (m) | Diameter at brest height (cm) | Sapwood thickness (cm) | Sapwood annual rings (total) | | Aspect of hole | Duration of experiment (total dye injection time min) |
|---|---|---|---|---|---|---|---|---|
| D1 | 2009/11/17 | 20.0 | 16.0 | 1.4 | 11 | (33) | N | 09:30 - 10:30 (60) |
| | | | | 1.5 | 11 | | SE | 09:50 - 10:30 (40) |
| | | | | 1.2 | 10 | | SW | 10:10 - 10:30 (20) |
| D2 | 2012/10/25 | 18.0 | 17.6 | 1.6 | 15 | (32) | N | 11:00 - 11:30 (30) |
| | | | | 1.9 | 13 | | SE | |
| | | | | 1.1 | 8 | | SW | |
| D3 | 2012/10/26 | 23.3 | 28.2 | 2.1 | 10 | (35) | N | 10:30 - 11:00 (30) |
| | | | | 2.0 | 11 | | SE | |
| | | | | 1.5 | 13 | | SW | |

### Absorption experiment

Details of the trees used in the absorption experiment are provided in Table 2. Three sample trees differing in DBH were selected and named A1, A2 and A3. The absorption experiments were conducted on the following dates: 2010/10/23-25, 2011/10/14-17 and 2012/10/27-29.

A water holding collar was attached to each experimental tree 80 cm above ground and sealed with silicone caulk to prevent water leakage (Figure 1b). On the day of the experiment, we used an electric drill and a chisel to cut a groove about 40 mm depth and 20 mm width through the bark and xylem around the circumference of the trunk 90 cm above ground level (See Figure 1b). The groove was deep enough to reach the heartwood. To reduce the effects of xylem cavitation, this operation was performed predawn under the premise that sap does not flow. After visible sawdust on the water holding collar was removed as possible as clearly, the water holding collar was filled with water. Bubbles were removed manually from the surface of the groove cut in the trunk. After water absorption experiment, the sample teaks were felled and measured the sapwood thickness and counted the number of sapwood annual rings at the height of sap flow sensor insertion which was 1.3 m above ground level (Table 2).

The water absorbed by the sapwood was supplied from a measuring cylinder and the amount of supplied water was recorded. The actual absorbed water ($Q_{\_act}$, kg $h^{-1}$) was calculated as follow;

$Q_{\_act} = Q / IT \times 60$ Equation (2)

where $Q$ (kg) was the amount of supplied water during interval and $IT$ (minute) was interval times of water supply. To compare with sap flow measurements, $Q_{\_act}$ was made at 30 min interval by interpolation.

Table 2. Information on experimental teak specimens and details of the procedures for the absorption experiments and sap flow measurements.

| | Date of experiment | Tree height (m) | Diameter at breast height (cm) | Sapwood thickness (cm) | Sapwood annual rings | (total) | Positions of sensors aspect | Depth (cm) |
|---|---|---|---|---|---|---|---|---|
| A1 | 2010/10/23-25 | 21.9 | 27.0 | 2.5 | 8 | (31) | N | 0-1, 1-2, 2-3 |
| | | | | 1.2 | 9 | | E | 0-1 |
| | | | | 1.9 | 9 | | S | 0-1 |
| | | | | 2.8 | 9 | | W | 0-1 |
| A2 | 2011/10/14-17 | 21.2 | 16.0 | 1.8 | 15 | (26) | N | 0-1, 1-2 |
| | | | | 1.6 | 15 | | S | 0-1 |
| A3 | 2012/10/27-29 | 22.8 | 22.9 | 1.6 | 12 | (36) | N | 0-1, 1-2 |
| | | | | 2.1 | 11 | | E | 0-1 |
| | | | | 2.1 | 10 | | S | 0-1 |
| | | | | 1.8 | 12 | | W | 0-1 |

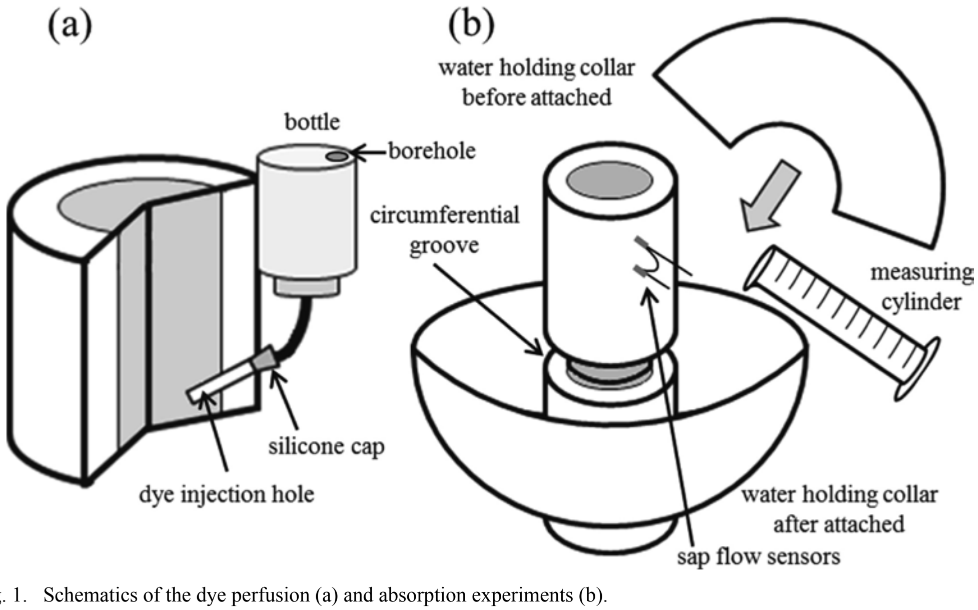


Fig. 1. Schematics of the dye perfusion (a) and absorption experiments (b).
The diameter and depth of the drilled dye injection hole were about 10 mm and 50 mm, respectively. The hole was bored on the bottle using a gimlet. The depth and width of the circumferential groove were about 40 mm and 20 mm, respectively. In the dye perfusion experiment, the bottle and dye injection hole were connected through a silicone cap. In the absorption experiment, water absorbed from the sapwood was supplied with a measuring cylinder. Sap flow sensors were installed 1.3 m above ground level and two or four directions.

### Sap flow measurement

Sap flow measurements on the teaks using the TDM were conducted during the course of the absorption experiments. Details of the sap flow measurement on each experimental tree are provided in Table 2. To determine the spatial (circumferential and radial) variation in tree trunk, sap flow sensors were installed to measure sap flow at a depth of 0-1 cm on 2-4 trunk directions (north, east, south, and west), and at a depth of 1-2 cm depth on a north direction. Sap flow sensors were installed 1.3 m above ground level (Figure 2(b)).

The sap flux density averaged over the sensor cross-section ($F_d$; cm $h^{-1}$) was measured by the TDM using Granier-type sensors (GRANIER, 1987). A Granier-type sensor consists of two aluminum tubes, each containing a copper-constantan thermocouple thermometer connected by a constantan wire. Two tubes were inserted into the sapwood at a vertical separation distance exceeding 15 cm. The upper tube contained a constantan heating element supplied with a constant electric power. The sensor length was 10 mm and the power supply was set to 0.15 W (following the protocol of JAMES *et al.*, 2002). The heat generated by the upper sensor was dissipated by sap flow, and the temperature difference between the two thermocouples ($\Delta T$) varied with the sap flow rate. Voltage occurs according to $\Delta T$ (Seebeck effect) and was recorded at 10- or 30-s intervals using a data logger (CR10X, CR23X; Campbell Scientific, Logan, UT, USA), then averaged over 10- or 30-min intervals.

The non-linear relationship between $\Delta T$ and $F_d$ is expressed as follows (GRANIER, 1987):

$$F_d = a \times \left(\frac{\Delta T_{max} - \Delta T}{\Delta T}\right)^b \times 3600 \times 100 \quad \text{Equation (3)}$$

where $\Delta T_{max}$ is the maximum $\Delta T$ when the sap flow was assumed to be zero. In our study, the maximum value of $\Delta T$ on each day was defined as $\Delta T_{max}$ (IIDA *et al.*, 2003). The values of coefficients *a* and *b* was determined to be $1.19 \times 10^{-4}$ and 1.23 by GRANIER (1987) who conducted calibration experiments using two coniferous (*Peseudotsuga menziesii* and *Pinus nigra*) and one ring-porous (*Quercus pedunculata*) species. The values of *a* and *b* have been corroborated by additional calibration experiments using other tree species (CABIBEL and DO, 1991; KÖSTNER *et al.*, 1998).

The estimated absorbed water using the TDM ($Q_{\_cal}$; $kg^3$ $h^{-1}$) was calculated as follows:

$$Q_{\_cal} = (F_{d\_0\text{-}1} \times A_{s\_0\text{-}1} + F_{d\_1\text{-}2} \times A_{s\_1\text{-}2} + F_{d\_2\text{-}3} \times A_{s\_2\text{-}3})\ /1000 \quad \text{Equation (4)}$$

where $F_{d\_0\text{-}1}$, $F_{d\_1\text{-}2}$ and $F_{d\_2\text{-}3}$ are $F_d$ values measured at a depth of 0-1, 1-2 and 2-3 cm, respectively, and $A_{s\_0\text{-}1}$, $A_{s\_1\text{-}2}$ and $A_{s\_2\text{-}3}$ are the sapwood areas ($cm^2$) occupied at each depth by the sap flow sensor. To consider the circumferential variation in $F_{d\_0\text{-}1}$, $Q_{\_cal}$ was calculated using averaged $F_{d\_0\text{-}1}$ values for two or four directions, and $F_d$ values for just one direction. Each of the calculated $Q_{\_cal}$, $F_{d\_1\text{-}2}$ and $F_{d\_2\text{-}3}$ value was used for northerly direction.

To compare the diurnal pattern of $F_d$ in experimental and non-experimental trees, sap flow measurements were conducted to other teak trees standing in the plantation simultaneously. The relative $F_d$ values measured on the non-experimental trees were indicated in Figure 3 (gray dashed lines).

## Results

### Dye perfusion experiment

The maximum dye ascent heights, maximum $D_s$ values, and numbers of dyed annual rings on sample disks at breast height and maximum dye accent height are summarized in Table 3. The circumferential variation in the maximum dye ascent heights for D1 (Table 3) may be attributed to differences in the total dye injection time on each of the trunk sides (Table 1): the highest and lowest dye ascent heights were observed for directions with the longest (northerly direction) and shortest (southwesterly direction) dye injection times (Table 1), respectively. For D2 and D3, the maximum dye ascent heights differed considerably by directions (Table 3) even though the total dye injection time was consistent (30 min) in the two individuals (Table 1), indicating large circumferential variation in sap flow in the trees. Consequently, the maximum $D_s$ varied from 440 to 2,840 cm $h^{-1}$ (Table 3).

The number of dyed annual rings on sample disks cut at breast height (0.4 m above the dye injection height) varied from five to seven (Table 3), indicating that some vessel conduits are functional for at least five years. At the maximum height of dye ascent, the outermost annual ring was dyed in all directions, and the number of dyed annual rings varied from three to five, except in a sample taken from the SW direction in D3, which had only one dyed annual ring (Table 3). As an example of dyed disk samples, Figure 2 presents photos of the northern part of D3 disk surfaces. At the maximum dye ascent height, the dyed area was distributed around annual ring boundaries (Figure 2b). On the other hand, at the breast height, such a preferential distribution of dyed area could hardly be found and in-between areas of annual rings were also stained (Figure 2a). However during our visual observations, we were unable to find any relationship between functionality and the anatomical features of the vessels (i.e., between the vessels in earlywood and latewood).

## Sap flow based on the TDM

Figure 3 shows the diurnal patterns in $F_d$ (for the three individuals listed in Table 2), in relation to the above-canopy solar radiation ($S_d$) and atmospheric vapor pressure deficit (VPD). The bold horizontal solid lines indicate the periods of water supply to the water holding collar. Before removing xylem, the diurnal pattern of $F_d$ corresponded well with $S_d$ in all individuals examined (Figure 3). On the other hand, the diurnal pattern of $F_d$ after removing xylem was depressed in comparison with the relative $F_d$, particularly in A3 (gray dashed line in each panel of Figure 3). The changes in the diurnal pattern of $F_d$ were most obvious at a depth of 0-1 cm

Table 3. Results of dye perfusion experiments for each sample teak and the direction of the dye injection hole.

| | Direction | Maximum dye ascent height from the dye injection point (m) | Maximum *Ds* (cm h$^{-1}$) | Number of dyed annual rings (total rings in sapwood) | |
|---|---|---|---|---|---|
| | | | | *0.4 m above dye injection point | Maximum dye height |
| D1 | N | 8.7 | 870 | 5 (11) | 4 (13) |
| | SE | 4.2 | 630 | 6 (10) | 3 (12) |
| | SW | 2.7 | 810 | 5 (11) | 4 (14) |
| D2 | N | 2.2 | 440 | 6 (15) | 3 (16) |
| | SE | 3.2 | 640 | 6 (13) | 3 (14) |
| | SW | 7.2 | 1440 | 6 (8) | 4 (12) |
| D3 | N | 14.2 | 2840 | 7 (10) | 5 (8) |
| | SE | 9.2 | 1840 | 7 (11) | 5 (10) |
| | SW | 7.2 | 1440 | 7 (13) | 1 (8) |

*breast height (1.3 m above ground)

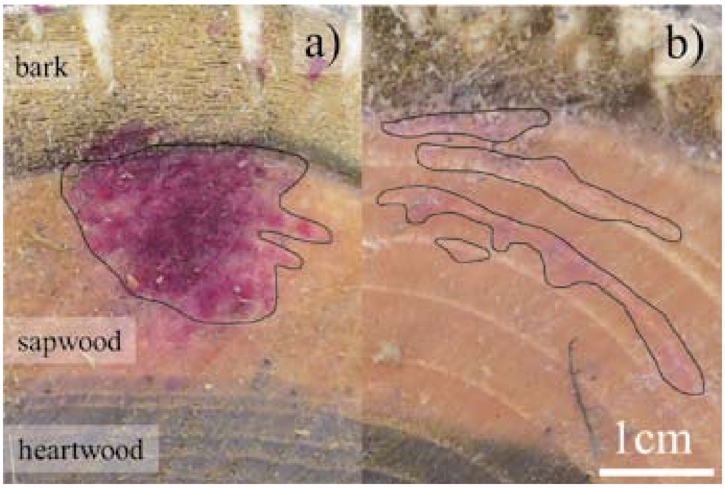


Fig. 2. Surfaces of dyed disks cut 0.4 m (a) and 14.2 m (b) above the dye injection point on the north side of D3. The peripheries of the marked areas in each figure enclose dyed sections are visible to the naked eye.

across all direction of A1. For A3, these shifts in pattern were most obvious at a depth of 0-1 cm for all direction and at 1-2 cm depth on the northerly facing trunk side (Figure 3). $F_d$ declines might be attributed to vessel clogging by minute dust particles in the water holding collar, although most visible dust had been removed, and the effect of cavitation while removing the xylem. Anyhow the illustrated diurnal patterns of $F_d$ after the xylem removals in Figure 3 should be taken as those different from relative $F_d$. However, for the purpose of comparing with $Q_{\_act}$ and $Q_{\_cal}$, the obtained $F_d$ data could be used.

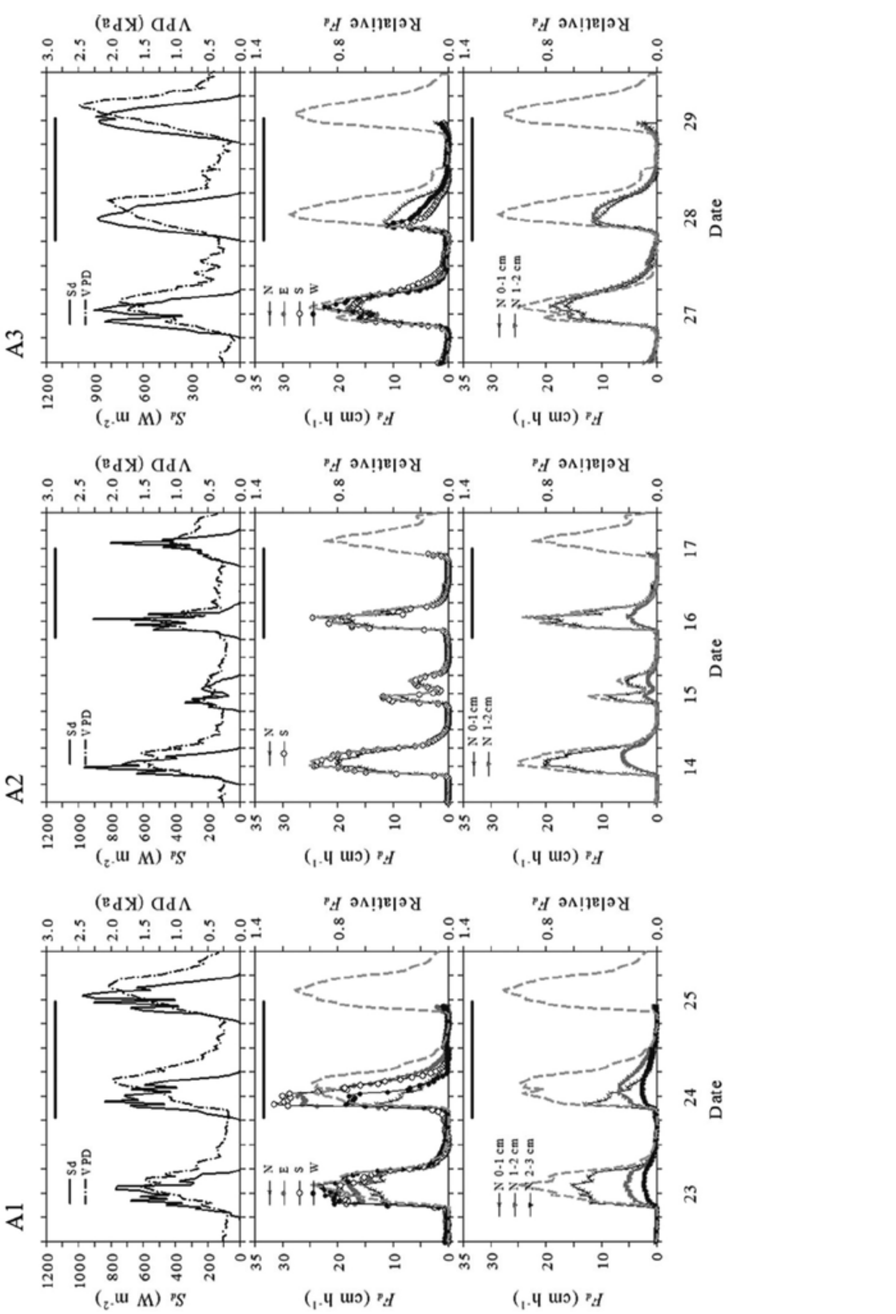


Fig. 3. Diurnal patterns in solar radiation ($S_d$), atmospheric vapor pressure deficit (VPD) and sap flux density ($F_d$).
A1 was measured at 2010/10/23-25. A2 was measured at 2011/10/14-17. A3 was measured at 2012/10/27-29. The upper box shows the $S_d$ and VPD, the middle box shows the circumferential variation of $F_d$ and the lower box shows the radial variation in $F_d$. The gray dashed line was the relative $F_d$ measured from other teak trees standing in Mae Mo plantation at the same time. The horizontal solid line indicates the period of supplying water to the water holding collar.

## Comparison of $Q_{\_act}$ and $Q_{\_cal}$

Figure 4 compares the diurnal patterns in $Q_{\_act}$ and $Q_{\_cal}$ for the three teak tree listed in Table 2. In general, $Q_{\_cal}$ underestimated $Q_{\_act}$ in all individuals, even when circumferential variation in $F_{d\_0\text{-}1}$ was taken into consideration (see the dashed lines in Figure 4); the underestimations were more pronounced for A1 than for A2 and A3. Table 4 lists details for the amount of $Q_{\_act}$ and $Q_{\_cal}$ calculated from 07:00 on the first experimental day through 07:00 on the next. The amount of $Q_{\_cal}$ for A1 was 14.64 kg (i.e., 14.5 % of the amount of $Q_{\_act}$). The amount of $Q_{\_cal}$ for A2 and A3 were 44.1 % and 62.4 % of the corresponding $Q_{\_act}$, respectively (Table 4).

Figure 5 shows the relationship between $Q_{\_act}$ and $Q_{\_cal}$ for all individuals. The broken lines represent 1:1 ratios, and the gray solid lines are fitted regression lines. The regressions show that the hourly $Q_{\_cal}$ was lower than the hourly $Q_{\_act}$. The points in the regressions plots were scattered in an approximately elliptical pattern, especially in the graph for A3. For periods when the sap flow was increasing, $Q_{\_cal}$ relatively underestimated $Q_{\_act}$, but when the sap flow was decreasing, $Q_{\_cal}$ relatively overestimate $Q_{\_act}$. The hourly $Q_{\_act}$ and $Q_{\_cal}$ were positively correlated except in the case of A3 (A1; $r$=0.99, A2; $r$=0.89, A3; $r$=0.54).

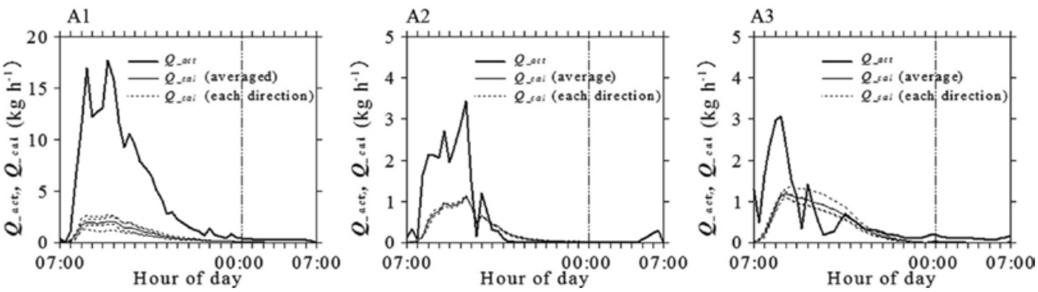


Fig. 4. Diurnal patterns of hourly $Q_{\_act}$ and $Q_{\_act}$.
$Q_{\_act}$ is represented by thick solid lines; $Q_{\_act}$ is represented by thin lines. Thin dashed lines represent estimated water uptake calculated as sap flux density ($F_d$) in each direction.

Table 4. Comparisons between the amount of $Q_{\_act}$ and $Q_{\_act}$.
The amount of $Q_{\_act}$ and $Q_{\_act}$ calculated from 07:00 on the first experimental day through 07:00 on the next.

| Experimental trees | A1 | A2 | A3 |
|---|---|---|---|
| $Q_{\_act}$ (kg) | 101.15 | 13.42 | 13.72 |
| $Q_{\_cal}$ (kg) | 14.64<br>max: 18.46 (E)<br>min: 10.17 (N) | 5.92<br>max: 6.00 (S)<br>min: 5.85 (N) | 8.56<br>max: 10.18 (N)<br>min: 7.52 (S) |
| ratio | 6.91 | 2.27 | 1.60 |

## Discussion

The dye perfusion experiment revealed the sap flow velocity in teak trunk vessels. The maximum $D_s$ ranged from 440 to 2,840 cm $h^{-1}$. Previous dye perfusion experiments revealed that the dye ascent speed in the trunks of coniferous and diffuse-porous species was about 50 to 80 cm $h^{-1}$ (SUZUKI, 1990; TAKIZAWA *et al*., 1996). Thus, the sap flow velocity in teak trunks is much larger than in coniferous and diffuse-porous species trunks.

In the dye perfusion experiment, we visualized the sap flow distribution in teak trunks. At the maximum height of dye ascent, the number of dyed annual rings varied from one to five, and the dye was concentrated around annual ring boundaries (Table 3, Figure 2). However, we could not distinguish dyed earlywood or latewood sections in our visual observation. In teak trees, the diameter of vessels in earlywood ranges from 200 to 300 μm, but in latewood it is <100 μm (SAEKI, 1982). The velocity of water in a channel is proportional to the fourth power of its internal radius (Hagen-Poiseuille Law). Since the vessel diameter is large, the sap flow velocity must also be large (TYREE and ZIMMERMANN, 2002). The water transport function of large diameter earlywood vessels is restricted to the outermost annual ring in cool temperate climates (TANEDA and SPERRY, 2008; UMEBAYASHI *et al*., 2008; BUSH *et al*., 2010; SATO *et al*., 2010). Our experiment was conducted during the wet season, when the outermost annual ring retained a water transport function. Moreover, our experiment revealed that the dyed section around the annual ring boundary was across more than one annual ring. Thus, the sap flow gradient between earlywood and latewood in a single annual ring was large, and it was consistent across consecutive annual rings, producing a wave-like pattern in the sap flow profile.

The cause of restricted the water transport function of large diameter earlywood vessels in the outermost annual ring in ring-porous species standing in cool temperate climate is that the freezing cavitation of large diameter earlywood vessels during winter is likely responsible for destruction of the transport function in older vessels (TYREE and ZIMMERMANN, 2002). In contrast, we showed that tropical teaks, which are never exposed to freezing, are able to maintain their water transport function across multiple annual rings. Thus, the sap flow distribution of tropical teaks differs that of other ring-porous species in cool temperate climates.

We measured $Q_{\_act}$ in mature teaks in a plantation and compared them with $Q_{\_cal}$. $Q_{\_cal}$ underestimated $Q_{\_act}$ in our experimental trees. The ratio of underestimation varied between approximately one half and one sixth (Table 4). An elliptical form in the scatter relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$ indicates a hysteresis, especially in A3 (Figure 5). This result indicates that the ratio of underestimation differed between periods of increasing and decreasing sap flow. However, the relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$ was linear in cases other than A3 (Figure 5); hysteresis between $Q_{\_act}$ and $Q_{\_cal}$ was less obvious in A1 and A2. Thus, a linear fit regression was inappropriate for A3.

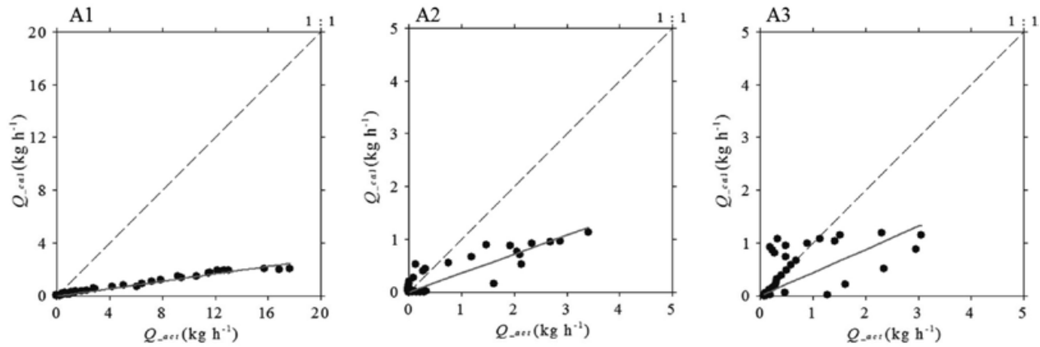


Fig. 5. Relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$.
Broken lines represent ratios of 1:1; gray solid lines are fitted regression line. The correlation coefficients ($r$) for A1,A2 and A3 are 0.99, 0.89 and 0.54, respectively.

Several earlier studies calibrated the TDM in diverse woody species. Some reported satisfactory TDM performance for a variety of trees, including gymnosperms with tracheid (GRANIER, 1987; ČERMÁK *et al*., 1992; CATOVSKY *et al*., 2002), tropical tree species (LU and CHACKO, 1998; LU *et al*., 2002; CLEARWATER *et al*., 1999; MCCULLOH *et al*., 2007), diffuse-porous species (BRAUN and SCHMID, 1999; CLEARWATER *et al*., 1999; CATOVSKY *et al*., 2002; TANEDA and SPERRY, 2008; BUSH *et al*., 2010) and ring-porous species (CATOVSKY *et al*., 2002; GRANIER *et al*., 1994). However, other reports indicated that TDM calculated sap flow substantially underestimated actual sap flow in diffuse-porous species (TANEDA and SPERRY, 2008; HULTINE *et al*., 2010; STEPPE *et al*., 2010), ring-porous species (TANEDA and SPERRY, 2008; BUSH *et al*., 2010) and bamboo (KUME *et al*., 2010a). BUSH *et al*. (2010) calibrated the TDM in four ring-porous (*Elaeagnus angustifolia*, *Gleditsia triacanthos*, *Quercus gambelii* and *Sophora japonica*) and two diffuse-porous (*Populus fremontii* and *Tilia cordata*) species, demonstrating that the TDM severely underestimates actual sap flow in only ring-porous species. TANEDA and SPERRY (2008) also conducted a TDM calibration using the ring-porous species *Q. gambelii* and the diffuse-porous species *Acer grandidentatum*; they found that the underestimation was more serious for *Q. gambelii*. Likewise, MONTAGUE and KJELGREN (2006) compared the actual water uptake of containerized diffuse-porous (*Pyrus calleryana*, *Populus detoides* and *Liquidambar styraciflua*) and ring-porous (*Q. rubur* × *Q. bicolor*) species with TDM-based estimates and found the most serious underestimations by the TDM in the ring-porous tree. These comparative studies indicate that TDM measurement of sap flow produces a greater error for ring-porous than for diffuse-porous tree species. The current study shows that, also in ring-porous teak, TDM underestimates actual sap flow indeed.

After completion of the absorption experiments, we felled the sample teaks to measure the width of sapwood at the height of sap flow sensors inserted (Table 2). The differences in xylem colors allowed us to distinguish sapwood from heartwood. On the north-facing sides of A1, A2, and A3, sapwood widths were 2.5, 1.8, and 1.6 cm, respectively. Thus, the sap flow sensors installed on tree sides with northerly direction covered the entire sapwood area. The sections of the sap flow sensors at 2-3 cm and 1-2 cm depths were located in heartwood. CLEARWATER *et al*.

(1999) indicated that the value of $F_d$ was underestimated because the sections of sap flow sensor is inserted in the non-conducting area (i.e., heartwood). Thus, $F_{d\_2\text{-}3}$ in A1 and $F_{d\_1\text{-}2}$ in A2 and A3 will be underestimated and the $Q_{\_cal}$ calculated using equation (4) will be also underestimated compared with $Q_{\_act}$.

We determined $\Delta T_{max}$, the maximum value of $\Delta T$ at which the sap flow rate is assumed to be zero, for each day following the protocol of IIDA *et al*. (2003). $\Delta T_{max}$ occurred in the predawn hours or early in the morning on all experimental days. However, water absorption by A1 and A3 continued through the night (Figure 4). For A3 in particular, water absorption occurred in the early morning hours of day 28 when $\Delta T$ was maximal. The value of $F_d$ may have been underestimated because we determined $\Delta T_{max}$ when sap was flowing (LU *et al*., 2004), resulting in an underestimated $Q_{\_cal}$ value (for A3) compared to $Q_{\_act}$.

The high velocity sap flows in ring-porous species may provide partial explanations for these underestimations. In the TDM, heat generated by the sensor is transferred to the sap and transported by the flow. However the large sap flow velocities in large diameter earlywood vessels prevent temperature equilibration between the sensor and sap. ANFODILLO *et al*. (1993) inserted a heater into tree trunks to observe heat transfer by thermographic procedures and found no thermal loading in the outermost annual rings of the ring-porous species (*Fraxinus excelsior*) under high transpiration conditions at 11 o'clock. They thus proposed that the temperature of the rapidly flowing sap could not be raised sufficiently (ANFODILLO *et al*., 1993). We believe that this was also the case for our teak trees.

TDM underestimation in ring-porous species may also be explained by a non-uniform sap flow distribution over the sap flow sensors. CLEARWATER *et al*. (1999) showed that when there was a large sap flow gradient over the sensor, the sap flow estimated by the average $\Delta T$ at the sensor underestimated the actual sap flow because of the nonlinear relationship between sap flow and $\Delta T$ (Equation 3). A large sap flow gradient over the sensor is more likely to occur when part of the sensor is inserted into heartwood with no water transport function, and when the water transport function is limited in the outermost annual ring, which is the case in ring-porous species. CLEARWATER *et al*. (1999) showed that the degree of underestimation increased in proportion to the area of non-conducting tissue in the trunk, and they proposed a correction procedure for modifying the original Granier calibration (Equation 3) by taking into account the proportions of conducting and non-conducting tissues sampled by the sap flow sensor. In our comparison of $Q_{\_act}$ and $Q_{\_cal}$, the ratio of underestimation for A1 was larger than for A2 and A3 (Table 4). Interestingly, A1 had wider annual rings (i.e., a lower ring density) in its sapwood than the other two trees (Table 2). Thus the sap flow sensor in A1 was exposed to fewer annual rings than the sensors in A2 and A3. The width of earlywood does not vary across the widths of the annual rings. In contrast, the width of latewood, which comprises small-diameter vessels and non-conducting tissue, varies across the widths of the annual rings (SHIMAJI *et al*., 1985). Even teak which is ring-porous species standing in the tropical climate has this tendency (PRIYA and BHAT, 1999). Therefore, because the sap flow sensor inserted into A1 will be exposed to a large latewood area, the ratio of underestimation in A1 will be larger than those in A2 and A3.

## Conclusions

To test the applicability of the TDM to mature plantation teak trees, dye perfusion experiments and simultaneous measurement of water uptake and sap flow using the TDM were conducted. Teak had the large sap flow velocity compared with coniferous and ring-porous species. The teak trees exhibited water transport across more than one annual ring. Based on the vessel distribution in the annual rings of ring-porous species, and the relationship between vessel diameter and sap flow velocity, we propose that large diameter earlywood vessels have water transport functions across more than one annual ring. We compared the actual water uptake with the uptake estimated by the TDM. The relationship between the actual and estimated water uptake was the linear or hysteretic. We found that the two rates were not congruent; in all cases, the TDM produced underestimates, and the degree of underestimation varied among teaks. Thus, estimates of sap flow velocity by the TDM are strongly affected by the unique sap flow distribution in teak tree trunks; the number of functional annual rings is an important determinant of sap flow underestimation measured by the TDM. To explore seasonal change in sap flow using TDM in teak, it might take into consideration of the seasonality of xylem formation especially during the wet season which formation of xylem is active (PRIYA and BHAT, 1999).

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## Summary

To determine the radial distribution of sap flow and to test the applicability of the thermal dissipation method (TDM) for measurements of sap flow velocity in mature, ring-porous teak trees, dye perfusion experiments and simultaneous measurement of water uptake and sap flow using the TDM were conducted. The dye perfusion experiments revealed the sap flow velocity in teak trunks is much larger than in coniferous and diffuse-porous species. According to visual observation of the surface of stained disks, the number of dyed annual rings varied from one to five, and the dye was concentrated around annual ring boundaries. In our absorption experiments, the TDM underestimated the actual water uptake, and the degree of underestimation varied among the sample teak. The extent of underestimation was greatest in a sample with an annual ring density lower than those in two other samples. Thus, the conducting area on the sap flow sensor will change according to the number of annual rings, and the degree of underestimation therefore will vary between individuals. Our dye perfusion and absorption experiments indicated that the large sap flow velocity and non-uniform radial sap flow distribution in teak trunks make it difficult to estimate water uptake by the TDM in teak trees. However we found a linear or hysteretic relationship between the hourly actual and TDM-estimated water uptake. This study indicated that the output of a Granier-type sensor is affected by the anatomical features of the xylem. Exploration of seasonal changes in teak sap flow by the TDM should take into consideration the seasonality of xylem formation.

**Keywords**: teak, thermal dissipation method, absorption experiment, dye perfusion experiment, ring-porous

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# 環孔材であるチークを対象とした熱消散法による樹液流計測の適応可能性の検討

佐藤貴紀*[1]・田中延亮*[1]・田中克典*[2]・五十嵐康記*[3]・吉藤奈津子*[4]・

鈴木雅一*[5]・タンタシリン　チャチャイ*[6]

＊1 東京大学大学院農学生命科学研究科附属演習林
＊2 独立行政法人海洋研究開発機構
＊3 名古屋大学地球水循環研究センター
＊4 国立研究開発法人森林総合研究所
＊5 東京大学大学院農学生命科学研究科
＊6 カセサート大学林学部

**要　　旨**

熱帯に生育する環孔材樹種であるチークを対象として，樹幹内の樹液流動の分布を明らかにするために染色実験を行い，熱消散法による樹液流計測が適応可能であるかどうかを検証するために実吸水量と樹液流計測によって算出された推定吸水量との比較を行った。染色実験により，チーク樹幹内には仮道管材や散孔材樹種と比較して非常に速い樹液の流動が存在していることが明らかとなった。染色された円板表面の観察から，複数の年輪に渡って樹液流動が起こっていること，速い染色液の上昇が年輪付近に存在していることが明らかとなった。吸水実験の結果，推定吸水量は実吸水量に比べて過小評価となることが明らかとなった。そして，過小評価の割合は個体ごとに異なっていた。辺材を構成する年輪数が少なかった個体において，過小評価の割合が他の個体と比較して大きかった。以上の結果は，樹液流センサー上における年輪の数によって樹液流センサー上の通水部分の割合が変化するために，過小評価の割合が個体ごとに変化することを示唆している。染色実験及び吸水実験の結果から，チーク樹幹内における非常に速い樹液流動と半径方向における不均一な樹液流動が，熱消散法によるチーク樹液流量の推定を難しくしていることが示唆された。チークを対象とした熱消散法による樹液流計測は樹液流センサー上における材の特徴に大きな影響を受けることが考えられる。そのため，熱消散法によってチーク樹液流動季節変化を調べる場合，材形成の季節変化を考慮する必要が考えられた。

**キーワード**：チーク・熱消散法・吸水実験・染色実験・環孔材樹種