

# Impact of stem water storage on diurnal estimates of whole-tree transpiration and canopy conductance from sap flow measurements in Japanese cedar and Japanese cypress trees

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## Abstract:

The amount of water stored in the stem introduces uncertainty when estimating diurnal whole-tree transpiration ( $E_T$ ) and canopy stomatal conductance ( $G_C$ ) using sap flow measured at the base of the stem ( $Q$ ). Thus, to examine how  $E_T$  can be calculated from  $Q$ , we obtained  $E_T$  using sap flow and stem water content measurements and a whole-tree water balance equation, and compared it with  $Q$ . In this study, we measured sap flows in 33-year-old individual trees of *Cryptomeria japonica* D. Don and *Chamaecyparis obtusa* Endl. using constant-heat sap flow probes. Sap flows were measured at several depths at the base of the stem, and at the upper trunk as a surrogate of  $E_T$ . Stem water contents were measured at three vertical positions on the trunk using amplitude-domain reflectometry (ADR) sensors. We also measured sapwood volumes of the study trees. Using simultaneous sap flow and stem water content measurements along the tree stem, we confirmed that stem water storage has impacts on the transpiration stream. These include sap flow lags along the tree heights and an enhanced peak of transpiration from stem sap flow. These results enabled us to calculate the correct  $E_T$  by multiplying  $Q$  by 1.18 and shifting its time series forward by 30 min. The  $E_T$  value was then used to calculate  $G_C$  for both tree species. The factor of 1.18 is based on the fact that at noon, the value of  $E_T$  was higher than that of  $Q$ , due to the prolonged  $Q$  during the evening. Establishing the time lag was relatively simple and was determined by comparing  $Q$  and vapor pressure deficit. The multiplier is more challenging to ascertain due to the difficulty in obtaining  $E_T$  correctly. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS *Chamaecyparis obtusa*; *Cryptomeria japonica*; Granier-type sensor; ADR; sapwood

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## INTRODUCTION

Environmental control of canopy transpiration can be characterized in terms of the response of canopy conductance to environmental factors (e.g. Martin *et al.*, 1997; Cienciala *et al.*, 2000; Wullschlegel *et al.*, 2000; Kumagai *et al.*, 2004, 2008). In general, canopy conductance ( $G_C$ ;  $\text{m s}^{-1}$ ) is calculated from the inverted Penman–Monteith equation under the assumptions of negligible heat storage and soil heat flux:

$$G_C = \frac{\gamma \lambda E_C G_a}{\Delta R_n + \rho_a c_p G_a D - \lambda E_C (\Delta + \gamma)} \quad (1)$$

where  $\gamma$  is the psychrometric constant ( $66.5 \text{ Pa K}^{-1}$ ),  $\lambda$  is the latent heat of vaporization of water ( $\text{J kg}^{-1}$ ),  $E_C$  is the canopy transpiration ( $\text{kg m}^{-2} \text{ s}^{-1}$ ),  $G_a$  is the aerodynamic conductance ( $\text{m s}^{-1}$ ),  $\Delta$  is the rate of change of saturation water vapor pressure with temperature ( $\text{Pa K}^{-1}$ ),  $R_n$  is the net radiation above the canopy ( $\text{W m}^{-2}$ ),  $\rho_a$  is the density of dry air ( $\text{kg m}^{-3}$ ),  $c_p$  is the specific heat

of air at constant pressure ( $\text{J kg}^{-1} \text{ K}^{-1}$ ), and  $D$  is the above-canopy atmospheric humidity deficit (Pa).

Recently,  $E_C$  in Equation (1) has been approximated from xylem sap flux density ( $F_d$ ) measurements (Maganani *et al.*, 1998; Oren *et al.*, 1998; Cienciala *et al.*, 2000; Granier *et al.*, 2000; Schäfer *et al.*, 2000; Wullschlegel *et al.*, 2000; Oren *et al.*, 2001; Pataki and Oren, 2003; Delzon *et al.*, 2004; Kim *et al.*, 2008; Kumagai *et al.*, 2008). However,  $E_C$  estimated from  $F_d$  measurements represents water uptake, rather than transpiration. If there is a large capacitive exchange between the transpiration stream and stem water storage, there is a significant time lag between sap flow measured at the base of the stem and transpiration (Martin *et al.*, 1997; Phillips *et al.*, 1997; Goldstein *et al.*, 1998; Kumagai, 2001; Meinzer *et al.*, 2003; Ford *et al.*, 2005). Furthermore, when the stem capacitance is large, an abundance of night time water recharges into the stem because whole-tree transpiration ( $E_T$ ) is higher than the stem sap flow ( $Q$ ) around mid-day (Kumagai, 2001; Phillips *et al.*, 2003; Bohrer *et al.*, 2005; Čermák *et al.*, 2007; Phillips *et al.*, 2009). In practice, many studies have regarded  $Q$  as  $E_T$  after confirmation that the  $Q$  did not lag  $E_T$  (Phillips and Oren, 1998; Ewers and Oren, 2000; Granier *et al.*, 2000), lagged the

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meteorological data to use Equation (1) by the time difference that resulted in the highest correlation of the  $Q$  with the weather data (Martin *et al.*, 1997; Schäfer *et al.*, 2000), or evaluated the time lag using time series models (Ford *et al.*, 2004, 2005; Ewers *et al.*, 2005). However, despite  $Q$  being less than  $E_T$  during daylight hours, few studies have discussed its effect on the prediction of  $E_C$  from  $Q$  (e.g. Phillips *et al.*, 1997).

Intrinsically, the water balance between  $E_T$  ( $\text{g s}^{-1}$ ) and  $Q$  ( $\text{g s}^{-1}$ ) can be expressed as follows:

$$E_T = Q - \frac{dW}{dt} \quad (2)$$

where  $W$  is the stem water storage (g). Thus,  $dW/dt$  denotes an increase or a decrease in stem water amount with time ( $\text{g s}^{-1}$ ).  $E_C$  is expressed per unit area of ground, whereas  $E_T$  is expressed per individual tree. Note that a temporal change in water stored in the foliage was neglected here. We later discuss contributions of water storage in tissues other than sapwood to  $E_T$ . Given that  $Q$  and  $W$  are measured, correct values of  $E_C$  and therefore  $G_C$  can be approximated through Equation (2).

*Cryptomeria japonica* D. Don. (Japanese cedar) and *Chamaecyparis obtusa* Endl. (Japanese cypress) plantation forests cover about 20% of Japan's total land area (Japan Forestry Agency, 2002). Hence, understanding water use of these tree species and environmental control of their transpiration is critical for water resource management. However, their potential as water-consumers receives much less attention than their functions as woody materials and a silvicultural species (Kumagai *et al.*, 2005, 2007; Komatsu *et al.*, 2006a,b). Therefore, the goal of this study was to investigate how to obtain the  $G_C$  from  $F_d$  measurements in *Cr. japonica* and *Ch. obtusa* trees. To do this, we calculated 'non-corrected  $G_C$ ' ( $G_{C\_Nco}$ ) using  $Q$  as  $E_T$ , and 'corrected  $G_C$ ' ( $G_{C\_co}$ ) using the measured  $E_T$ , and then compared the non-corrected and corrected values. Before using the  $G_{C\_co}$ , the stem water budget described by Equation (2) was first validated with detailed measurements of the stem moisture components in *Cr. japonica* and *Ch. obtusa* trees as described below.

## MATERIALS AND METHODS

### Study Site and Meteorological Measurements

These experiments were carried out in a uniformly aged 33-year-old *Cr. japonica* and *Ch. obtusa* stand in the Shiiba Research Forest, Kyushu University (32° 22'N, 131° 09'E). Both *Cr. japonica* and *Ch. obtusa* are major plantation species in Japan. The study site, situated in the central Kyushu mountain range at approximately 860 m above sea level, has a mean annual temperature of 13.6 °C and a mean annual precipitation of 3500 mm.

An 18-m research tower was constructed on a 4-m mound within the stand. Two *Cr. japonica* and one *Ch. obtusa* adjacent to the tower were used for the study (Table I). The live crowns of the studied trees had a typical formation, that is the distribution of their leaf

Table I. Characteristics of study trees, and number and positions of sensors<sup>a</sup>

	<i>Cr. japonica</i>		<i>Ch. obtusa</i>
	E750	E751	J816
Height (m)	21.2	21.2	18.1
Diameter at 1.3 m (cm)	36.5	34.8	28.3
Crown area (m <sup>2</sup> )	9.8	9.8	17.6
Sapwood thickness (mm)	53 (1.3), 58 (9.9), 59 (13.8)	57 (1.3), 60 (10.1), 57 (13.9)	27 (1.3), 29 (7.8), 27 (12.3)
[measurement height (m)]			
Height at base of live crown (m)	5.5	5.0	7.7
Heights of sensors (m)			
Sap flux density	1.3 (a, b, c), 10.6 (a), 19.5 (a)	1.3 (a, b, c), 9.7 (a), 19.4 (a)	1.3 (a), 7.4 (a), 16.4 (a)
Volumetric water content of stem	1.1, 10.2, 18.4	1.3, 10.2, 18.3	1.3, 7.7, 12.5

<sup>a</sup> Sap flux density was measured at three depths: a, 0–20 mm; b, 20–40 mm; c, 40–60 mm.

area is likely to be represented by a bell-shaped curve. This distribution pattern is characterized by maximum leaf area values at the midpoints of the tree top and the base of the live crown (Tadaki, 1976). The tower enabled access to the trunks of the studied trees at any height. Micrometeorological conditions were measured using a solar radiometer (CM06E, Kipp & Zonen, Delft, Netherlands), a net radiometer (CNR1, Kipp & Zonen, Delft, Netherlands), a temperature and relative humidity sensor (HMP45D, Vaisala, Helsinki, Finland), a cup-anemometer (Model 03 102, R. M. Young Co., Traverse City, MI), and a tipping bucket rain gauge (RT-1D, K. Hattori & Co., Ltd., Tokyo, Japan) installed at the top of the canopy. Soil matric potential was measured in the stand at 0.1, 0.2, 0.4 and 0.8 m below the forest floor (DIK3150, Daiki, Tokyo, Japan).

The study was carried out on 4–18 August, 2005, when environmental conditions were ideal for these analyses. During this time, there was no rainfall and soil conditions were moist. There were appreciable day-to-day variations in radiation, temperature and humidity. Thus, we could effectively examine the response of  $E_T$  to those environmental variables.

### Sap Flux and Stem Water Storage Measurements

We measured  $F_d$  according to the thermal dissipation method using Granier-type sensors (e.g. Granier, 1987). Each sensor consists of a pair of probes 20 mm long and 2 mm in diameter. Probes were inserted in the sapwood approximately 150 mm apart. The upper probe contained a heater that was supplied with 0.2 W of constant power. The heat was dissipated into the sapwood

and the vertical sap flux surrounding the probe. The temperature difference between the upper heated probe and lower unheated reference probe was measured and converted to  $F_d$  according to Granier (1987).

For each tree, we measured  $F_d$  at breast height, mid-height and near the top of the trunk (Table I). The sensors at mid-height were positioned below the live crown for the *Ch. obtusa* tree and above the live crown for the *Cr. japonica* trees (Table I). Considering the tree biomass descriptions of Tadaki (1976), we can assume that approximately 60% of total leaf area was above the middle sensors in *Cr. japonica* trees, and approximately 5% above the top sensors. For the *Ch. obtusa* tree, 100% of total leaf area was above the middle sensors, and approximately 20% above the top sensor. Three sensors were inserted into each *Cr. japonica* tree at depths of 0–20, 20–40 and 40–60 mm at the breast height of the stem, so that sapwood was completely covered (Table I). For sensor access to 20–40 and 40–60 mm depths, bigger holes were created in the trunk to enable installation of the sensors at the deeper positions of the sapwood. Sensors at the 40–60 mm depth were in contact with nonconducting wood, but errors in calibrating the Granier-type sensors were considered to be small because in this study sap flux density at 40–60 mm was at most  $0.01 \text{ mm s}^{-1}$  (Clearwater *et al.*, 1999). Furthermore, the value of  $Q$  in the 40–60 mm xylem band is only approximately 5% of that in the total sapwood; thus, data were not corrected. The studied trees were grown in a well-managed plantation, and were characterized by a circular stem cross-section and circumferentially constant sapwood thickness. Therefore, we assumed the azimuthal variation in  $F_d$  to be small (e.g. Vertessy *et al.*, 1997).

The stems of these tree species taper off near the top of the tree, so the stem diameter near the tree top is very small. Therefore, the stem near the tree top is assumed to have relatively small capacitance (Čermák *et al.*, 2007), and is assumed to be isotropic in terms of the dependence of leaf transpiration on crown illuminance (Burgess and Dawson, 2008). Hence, we measured  $F_d$  with probes installed near the top of each tree ( $F_{d,\text{top}}$ ) as a surrogate for  $E_T$  (Goldstein *et al.*, 1998; Meinzer *et al.*, 2003; Phillips *et al.*, 2003).

As Phillips *et al.* (2009) pointed out, detection of a time lag between  $F_d$  and  $F_{d,\text{top}}$  might be affected by the aspect of the trunk at the position where the sap sensor was placed. In this study, the aspects differed at each measurement height. In addition, a tracking experiment using dye solution injected into tree trunks showed that there are spiral conduits in these studied tree species. Thus, we assumed that our methods appropriately evaluated the time lag.

Stem volumetric water content ( $\Theta$ ;  $\text{m}^3 \text{ m}^{-3}$ ) was monitored using amplitude-domain reflectometry (ADR). Each probe consisted of four 3-mm-diameter stainless steel rods inserted into the stem. The lengths of the rods (60 mm) covered the entire sapwood depth. Although the tips of the rods are most sensitive, this characteristic was considered to be included in the ADR readings derived

from empirical relationships using “target sapwood samples”. The ADR measurement is based on the relationship between the apparent dielectric constant ( $\epsilon_b$ ) of the stem and  $\Theta$  as is the case for time-domain reflectometry (TDR) measurement (Constantz and Murphy, 1990; Holbrook and Sinclair, 1992; Wullschleger *et al.*, 1996). The TDR dielectric constant is obtained from the speed at which an electromagnetic wave is propagated through a water-bearing material. ADR is calculated from the impedance of the rod array varying with the impedance of a water-bearing material, resulting in more stable readings.

ADR measurements were made using an amplitude-domain reflectometer (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK) at three heights on each studied tree (Table I). The positions of the ADR sensors in relation to the base of the live crown were the same as those described for the Granier-type sensors (Table I). Temperature effects on the ADR measurements were small because of the closed canopy; furthermore, the sensors were fully insulated from direct radiation. An empirical relationship is typically derived to convert  $\epsilon_b$  measurements to  $\Theta$ . Wullschleger *et al.* (1996) derived a general relationship for different species and for segments of each sample tree. We checked Wullschleger’s equation in the laboratory using segments from lower and upper positions along the stem of *Cr. japonica* and *Ch. obtusa* trees. For both species, the results corresponded with Wullschleger’s relationship for the segments from the upper stem positions. However in lower stem positions, there were more significant variations. As a result, we used the relationships corresponding to the measured tree species and their measurement positions (data not shown).

Micro-meteorological data, sap flow data, and stem water content data were recorded on a data logger (CR10X, Campbell Scientific, Logan, UT) with a multiplexer (AM16/32, Campbell Scientific). Sampling occurred every 30 s and data were averaged every 30 min.

#### Sapwood Area and Volume Analysis

We estimated sapwood area and volume biometrically, as described by Čermák *et al.* (2007). We measured stem diameter and sapwood thickness at three vertical positions along the stem of each studied tree, and each value was the mean of two orthogonal measurements at each position. Sapwood thickness (in mm) was measured with a ruler on a core extracted with a 5-mm increment borer. Distinct color differences were used to identify the boundary between sapwood and heartwood. As a result, we obtained the relationship between the stem ( $y$ ) and heartwood ( $y'$ ) radii and the stem length from tree tip ( $x$ ) of each studied tree. The third-order polynomial, which has previously been proved to be useful for approximating stem curves of *Cr. japonica* and *Ch. obtusa*, was fitted to both  $x-y$  and  $x-y'$  relationships. Integration of the polynomial gave the stem and heartwood volumes of each tree. In this study, the stem of each tree was divided

into three parts: lower, middle and upper parts. Table II shows the stem volume and the sapwood volume, which was calculated by subtracting heartwood from stem volume, for each of the three parts. One ADR probe was inserted to each part, and its value was assumed to represent  $\Theta$  of each part of the stem.

#### Calculation of Whole-Tree Transpiration, Canopy Conductance and Decoupling Coefficient

We calculated  $E_T$  using measured  $Q$  and  $dW/dt$  values through Equation (2). A similar concept has been used elsewhere, e.g. Čermák *et al.* (2007). We obtained  $Q$  as the sum of the product of the sap flux density ( $F_{d\ i}$ ) and the cross-sectional sapwood area ( $A_{S\ i}$ ) at each sensor position,  $i$ , as follows:

$$Q = \sum_{i=1}^n F_{d\ i} A_{S\ i} \quad (3)$$

where  $n$  is the number of positions measured along the xylem. Our experiment using a dye solution injected into a radial hole bored into a tree trunk confirmed that there was no water movement in the heartwood. Hence, we assumed that the major variation in stem water storage occurs in the sapwood volume, and thus  $dW/dt$  can be calculated as follows:

$$\frac{dW}{dt} = \frac{d(V_{S\_A}\Theta_A + V_{S\_B}\Theta_B + V_{S\_C}\Theta_C)}{dt} \quad (4)$$

where  $V_{S\_A}$  and  $\Theta_A$ ,  $V_{S\_B}$  and  $\Theta_B$ , and  $V_{S\_C}$  and  $\Theta_C$  are the sapwood volumes and  $\Theta$  of the stem sections A, B, and C (Table II), respectively.

We calculated  $G_{C\_Nco}$  and  $G_{C\_co}$  by Equation (1) using  $E_C$  as  $1.0 \times 10^{-3} T_D Q$  and  $1.0 \times 10^{-3} T_D E_T$ , respectively [where  $T_D$  is tree density ( $0.116 \text{ trees m}^{-2}$ ) for both *Cr. japonica* and *Ch. obtusa* stands]. The decoupling coefficient,  $\Omega$ , was calculated according to Jarvis and McNaughton (1986),

$$\Omega = \frac{\Delta/\gamma + 1}{\Delta/\gamma + 1 + G_a/G_C} \quad (5)$$

Note that  $G_{C\_Nco}$  or  $G_{C\_co}$  were input into Equation (5) as  $G_C$ . Using wind speed above the canopy and logarithmic law,  $G_a$  was calculated by setting the roughness length and zero-plane displacement as 1/10 and 2/3

of the stand height, respectively. The relative importance of radiative ( $E_{eq}$ ;  $\text{kg m}^{-2} \text{ s}^{-1}$ ) and advective ( $E_{imp}$ ;  $\text{kg m}^{-2} \text{ s}^{-1}$ ) energy for  $E_C$  were estimated using the following equations:

$$E_C = \Omega E_{eq} + (1 - \Omega)E_{imp} \quad (6)$$

where

$$E_{eq} = \frac{\Delta R_n}{\lambda(\Delta + \gamma)} \quad (7)$$

$$E_{imp} = \frac{\rho_a c_p}{\lambda \gamma} G_C D \quad (8)$$

(McNaughton and Jarvis, 1983). The equilibrium evaporation rate,  $E_{eq}$ , depends only on the energy supply (radiation) and would be obtained over an extensive surface of uniform wetness. The imposed evaporation rate,  $E_{imp}$ , is 'imposed' by the atmosphere on the natural canopy surface through the effect of  $D$ , so that evaporation is proportional to the physiological conductance.

All statistical analyses were performed using MATLAB software with a Signal Processing Toolbox and Statistics Toolbox (The MathWorks Inc., Natick, MA).

## RESULTS AND DISCUSSION

We investigated  $F_d$  at 0–20 mm depth and changes in stem water content at breast height, mid-height and near the tree top of the trunk (Table I) of *Cr. japonica* and *Ch. obtusa* trees for 5 days (Figure 1). There were apparent lags between  $F_d$  at the three heights;  $F_d$  at the highest position started to flow, and  $F_d$  proceeded to flow at lower positions after that (Figure 1a,b). At breast height,  $F_d$  was much lower than that at other heights, but there were not clear differences in  $F_d$  between mid-height and near the tree top. It should also be noted that  $F_d$  at higher positions showed more distinct variations over time compared with those at breast height; probably because  $F_d$  is very sensitive to environmental factors (Čermák *et al.*, 2007; Burgess and Dawson, 2008).

For *Cr. japonica*, the most significant diurnal changes in stem water content were measured at breast height (Figure 1c). Diurnal changes were less apparent at higher positions. Furthermore, there were appreciable lags between the stem water changes at the three heights;

Table II. Studied trees' stem and sapwood volumes used for calculating stem water storage<sup>a</sup>

Species	Heights			Stem volume (sapwood volume)			
	A (m)	B (m)	C (m)	A (m <sup>3</sup> )	B (m <sup>3</sup> )	C (m <sup>3</sup> )	Total (m <sup>3</sup> )
<i>Cr. japonica</i>							
E750	0–5.7	5.7–14.3	14.3–21.2	0.485 (0.286)	0.380 (0.286)	0.083 (0.077)	0.948 (0.649)
E751	0–5.8	5.8–14.3	14.3–21.2	0.513 (0.300)	0.414 (0.299)	0.064 (0.062)	0.991 (0.661)
<i>Ch. obtusa</i>							
J816	0–4.5	4.5–10.1	10.1–18.1	0.262 (0.180)	0.236 (0.181)	0.094 (0.088)	0.592 (0.449)

<sup>a</sup> A, B and C denote lower, middle and upper parts of tree stem, respectively.

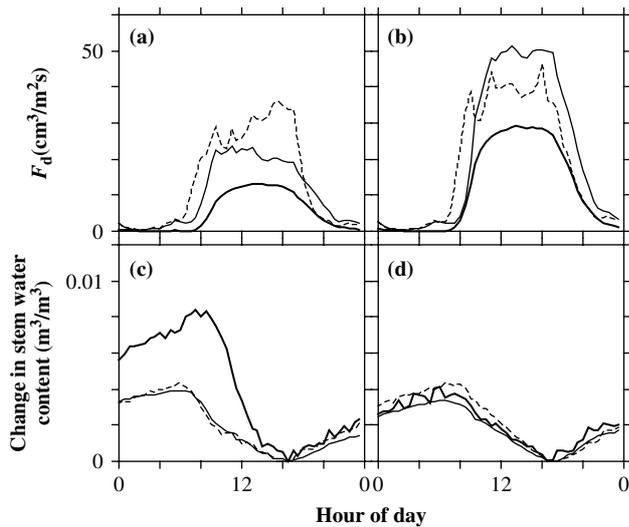


Figure 1. Average diurnal variation in sap flux density at 0–20 mm depth ( $F_d$ ) (a, b) and stem water content (c, d) at lower (thick solid line), mid (thin solid line) and higher heights (broken line). See Table I for details. Values are from trees E750 (a, c) and J816 (b, d). Measurements were taken on 10–14 August, 2005

the reduction in the stem water content started at higher positions, and moved progressively down the tree trunk over time. Interestingly, the start of the increase in  $F_d$  was synchronized with the decrease in stem water content at each height. In *Ch. obtusa*, there were few differences in the changes of stem water content and their time lags among the three heights (Figure 1d).

Figure 2 shows diurnal patterns of  $E_T$ ,  $Q$  and  $dW/dt$  on days with high and low solar radiation ( $R_S$ ) and  $D$ . Decreases in stem water storage ( $-dW/dt$ ) started 0.5–1.0 h earlier than  $Q$ , which can be attributed to the water uptake from sapwood tissue. The maximum  $-dW/dt$  occurred in the morning, while  $Q$  peaked at approximately noon. During the evening,  $Q$  was prolonged, while  $W$  increased in the afternoon and evening. In summary,  $W$  was used for transpiration

until noon. Approximately 0.5–1.0 h after  $W$  started to decrease,  $Q$  started to increase (Kumagai, 2001). While  $E_T$  in the morning and afternoon was largely attributed to  $Q$ , the  $W$  deficit compensated for the transpiration stream. In the evening,  $Q$  was used for recharging  $W$ . As a result,  $E_T$  occurred only during daylight hours, and  $Q$  continued during the evening. The highest value in  $E_T$  occurred around noon, and was higher than that of  $Q$ . The patterns of  $E_T$  appeared to be similar to those of either  $R_S$  or  $D$ . Note that the highest value of  $E_T$  was observed on the day when both  $R_S$  and  $D$  were high (4 August 2005; Figure 2a,e).

We calculated daily water use of the trees using the  $E_T$  value and compared it with daily water use calculated using the  $Q$  value. No significant differences in water use were observed among the studied trees throughout the study period [analysis of variance (ANOVA),  $P = 0.19$ ]. Figure 3 shows that there was a strong correlation between the values obtained using two calculations (i.e. using  $E_T$  and  $Q$ ); the slope and the intercept of the regression line were close to unity and zero, respectively ( $y = 1.06x$ ,  $R^2 = 0.97$ ). These data indicate that the daily water balances of the stem reservoirs were estimated to be zero. Furthermore, the low variability among the estimates of daily  $E_T$  and  $Q$  values indicates that the measurements of  $W$  and  $Q$  were valid. It should also be noted that maximum daily water use by *Cr. japonica* individuals was approximately  $30 \text{ kg day}^{-1}$ , and by *Ch. obtusa* individuals,  $20 \text{ kg day}^{-1}$  (Figure 3). Our data indicate that the obtained daily  $Q$  values that were used to calculate water use were reasonable and representative of the studied site (Kumagai *et al.*, 2005).

Many studies have investigated the contribution of  $W$  to  $E_T$  (Waring *et al.*, 1979; Schulze *et al.*, 1985; Loustau *et al.*, 1996; Andrade *et al.*, 1998; Goldstein *et al.*, 1998; Kobayashi and Tanaka, 2001; James *et al.*, 2003; Meinzer *et al.*, 2003; Phillips *et al.*, 2003; Meinzer *et al.*, 2006; Čermák *et al.*, 2007). The estimates for  $W$ 's contribution

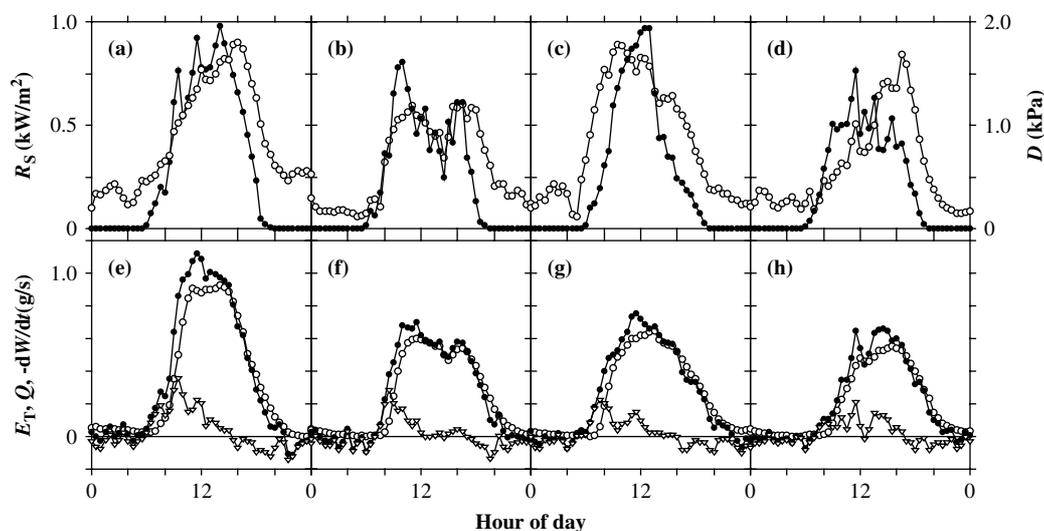


Figure 2. Diurnal pattern of solar radiation (a–d) ( $R_S$ ; closed circle) and atmospheric humidity deficit ( $D$ ; open circle). Whole-tree transpiration (e–h) ( $E_T$ ; closed circle), stem sap flow ( $Q$ ; open circle), and increase/decrease in stem water amount with time ( $-dW/dt$ ; triangle) for tree E750 on (a, e) 4, (b, f) 6, (c, g) 11, and (d, h) 14 August, 2005

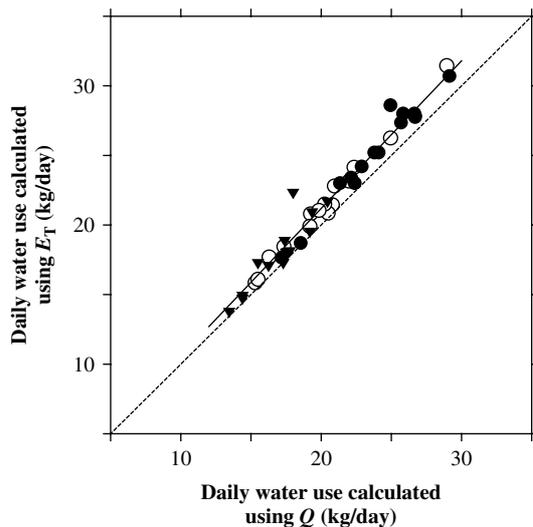


Figure 3. Comparison between daily water use calculated using whole-tree transpiration ( $E_T$ ) and stem sap flow ( $Q$ ) for trees E750 (open circle), E751 (closed circle) and J816 (triangle) throughout the study period (4–18 August 2005). Solid line:  $y = 1.06x$ ,  $R^2 = 0.97$ ; 1 : 1 line (dotted line) is also presented

to  $E_T$  have varied widely (from 2 to 50%). In our study, 15–33% of the transpired water was extracted from the water stored in the stem sapwood in both *Cr. japonica* and *Ch. obtusa* trees. It is also interesting to compare the total stem volume and the ratio of sapwood to the total stem volume between our study trees and the old-growth Douglas fir tree studied by Čermák *et al.* (2007). In our studied trees, the total stem volume and the ratio of sapwood volume were 0.592–0.991 m<sup>3</sup> and 66.7–75.8%, respectively (Table II), compared with 16.993 m<sup>3</sup> and 30.1% for the large Douglas fir tree. According to Kumagai (2001), the temporal change in stored water in foliage is only about 10% of that in the stem in *Cr. japonica*. This implied that the contribution of water stored in foliage to  $E_T$  could be neglected in this study. It should be also noted that Čermák *et al.* (2007) reported that total water stored in needles and branches was less than 10% of that in the stem in their studied Douglas fir.

The contribution of  $W$  to  $E_T$  cannot be ignored, and must be accounted for by determining the differences between  $E_T$  and  $Q$ . Generally, these differences have been corrected using the time lag between  $Q$  and an appropriate driving variable such as  $D$ , which is an easily accessible surrogate for  $E_T$  (e.g. Schäfer *et al.*, 2000). However, as Schäfer *et al.* (2000) pointed out, using a time lag may correct for shifts in the time series of  $Q$  relative to  $E_T$ , but does not correct for the diffusion of the  $E_T$  signal measured as  $Q$  at the base of the stem (Phillips *et al.*, 1997; Ewers and Oren, 2000). We emphasize that in this study we attempted the correct estimation of whole-tree transpiration  $E_T$  using ADR measurements and detailed whole-tree sapwood volume analysis. In addition, it should be noted that it is significant to quantify water storage capacity or capacitance of the stem using a technique that is independent of sap flow measurements (Phillips *et al.*, 2009).

Table III. Regression statistics for comparisons among canopy conductances ( $G_C$ ) calculated from measured whole-tree transpiration ( $E_T$ ), stem sap flow ( $Q$ ) and  $E_T$  calculated from  $Q$  taking into consideration the lag and difference in the peak between measured  $E_T$  and  $Q$  ( $E_{T,cal}$ )

Variable	Slope	Intercept (cm s <sup>-1</sup> )	R <sup>2</sup>	RMSE (cm s <sup>-1</sup> )
<i>Cr. japonica</i>				
E750				
$G_{C,Nco}$	0.93	-0.07	0.79	0.12
$G_C E_{T,cal}$	1.06	-0.01	0.89	0.06
E751				
$G_{C,Nco}$	0.92	-0.04	0.88	0.11
$G_C E_{T,cal}$	1.00	0.05	0.79	0.11
<i>Ch. obtusa</i>				
J816				
$G_{C,Nco}$	1.00	-0.06	0.93	0.07
$G_C E_{T,cal}$	0.97	0.05	0.86	0.07

Regression model is  $y = \text{slope } x + \text{intercept}$ , where  $y$  is  $G_C$  calculated from  $E_T$  ( $G_{C,co}$ ), and  $x$  are  $Q$  ( $G_{C,Nco}$ ) or  $E_{T,cal}$  ( $G_C|E_{T,cal}$ ). Coefficient of determination ( $R^2$ ) and root-mean-squared error (RMSE: cm s<sup>-1</sup>) are shown. Each regression analysis contains 102 points.

Higher  $E_T$  around noon extracts water from the stem water storage, and as a result, the value of  $E_T$  is higher than that of  $Q$  at approximately noon. We expected that there would be a relationship between the amount of water depleted in the stem from the early morning to mid-afternoon and the  $E_T$  or atmospheric evaporative demand, and we expected that this relationship could be used to estimate the difference between  $E_T$  and  $Q$  around noon. However, we did not find any clear relationship (data not shown). Then, we examined the relationship between the peak values of  $E_T$  and  $Q$  for all study trees throughout the study period. We determined average values for  $E_T$  and  $Q$  around noon (1100–1300 LT) and compared their ratios. This ratio did not differ between the studied trees (ANOVA,  $P = 0.40$ ). Figure 4 compares the averaged peaks of  $E_T$  and  $Q$ . A repeated measures ANOVA revealed that they were significantly different ( $P < 0.0001$ ). Forcing the regression line through the origin showed that despite differences among study trees and the measurement dates, the averaged peak of  $E_T$  was explained by that of  $Q$ , thereby suggesting that they were strongly correlated (slope = 1.180,  $R^2 = 0.89$ ). This factor of 1.18 explains that  $E_T$  peaked higher than  $Q$  around noon because of the prolonged  $Q$  during the evening (Figure 2).

In *Cr. japonica*, the time lag between  $F_d$  at 0–20 mm at higher and at middle heights was approximately 60 min, and was the same (60 min) between middle and lower heights (Figure 1). In *Ch. obtusa*, there was a time lag of approximately 90 min between higher and middle heights, while the time lag between middle and lower heights was unclear. In *Cr. japonica*, the time lag between stem water content at higher and at middle heights was unclear, but was approximately 120 min between middle and lower heights. In *Ch. obtusa*, those time lags were 30–60 min and unclear, respectively. The

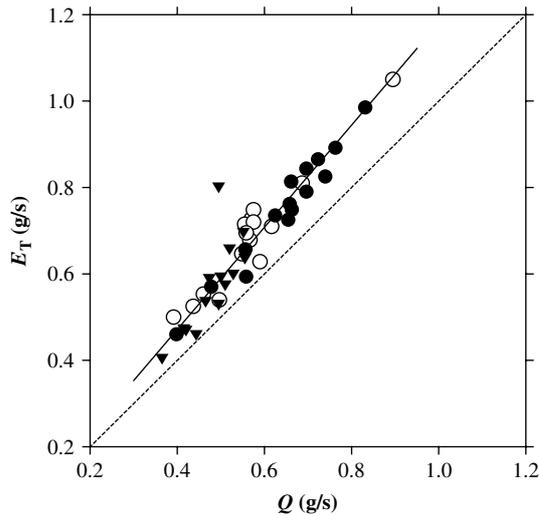


Figure 4. Comparison between average whole-tree transpiration ( $E_T$ ) and stem sap flow ( $Q$ ) around noon (1100–1300 LT) for trees E750 (open circle), E751 (closed circle) and J816 (triangle) throughout the study period (4–18 August 2005). Linear regression was forced through origin: solid line;  $y = 1.18x$ ,  $R^2 = 0.89$ ; 1:1 line (dotted line) is also presented

inconsistencies in the lags between  $F_d$  and the stem water content might result from the lack of connectedness among the conduits at 0–20 mm depth at the various heights. Nevertheless, and notably, we confirmed the existence of lags between sap flow at higher and lower positions of the tree by simultaneously using sap flow measurement and another independent technique, i.e. ADR measurement (Burgess and Dawson, 2008; Phillips *et al.*, 2009).

The lag between  $F_{d\_top}$ , which is a surrogate for  $E_T$ , and  $R_S$  or  $D$  was determined using cross-correlation analyses of their time series as shown in Figure 5. In all studied trees,  $F_{d\_top}$  lagged 30 min behind  $R_S$  (Figure 5a), whereas  $F_{d\_top}$  was correlated with  $D$  without a lag (Figure 5b). Cross-correlation analyses of  $F_{d\_top}$ ,  $Q$ , and  $E_T$  time series showed that time lags between  $F_{d\_top}$  and  $Q$  were 30 min (E751) and 60 min (E750 and J816) (Figure 6a), but between  $F_{d\_top}$  and  $E_T$  were 0 (E750 and E751) and 30 min (J816) (Figure 6b). Thus, in these studied trees,  $E_T$  instantaneously responds to changes in  $D$ , and the time lag between  $E_T$  and  $Q$  is 30–60 min.

From the information obtained, we assumed that for all study trees,  $E_T$  is 1.18 times  $Q$  (i.e.  $E_T = 1.18 \times Q$ ) for daylight hours and precedes  $Q$  by 30 min. Thus, we can also calculate the whole-tree transpiration from  $Q$ , taking this assumption into consideration ( $E_{T\_cal}$ ), and evaluate the predictive skills of  $E_{T\_cal}$ .

Figure 7 shows comparisons among  $E_T$ ,  $E_{T\_cal}$  and  $Q$  bin-averaged by time of day. Despite the simplified modification,  $E_{T\_cal}$  captured the canonical form of the measured  $E_T$  for both *Cr. japonica* and *Ch. obtusa* trees (Figure 7a, b). When  $Q$  was multiplied by 1.18,  $E_T$  and  $E_{T\_cal}$  were similar during the daylight hours (see also that there were significant discrepancies between  $E_T$  and  $Q$ ), while  $E_{T\_cal}$  was overestimated in the evening and before dawn.

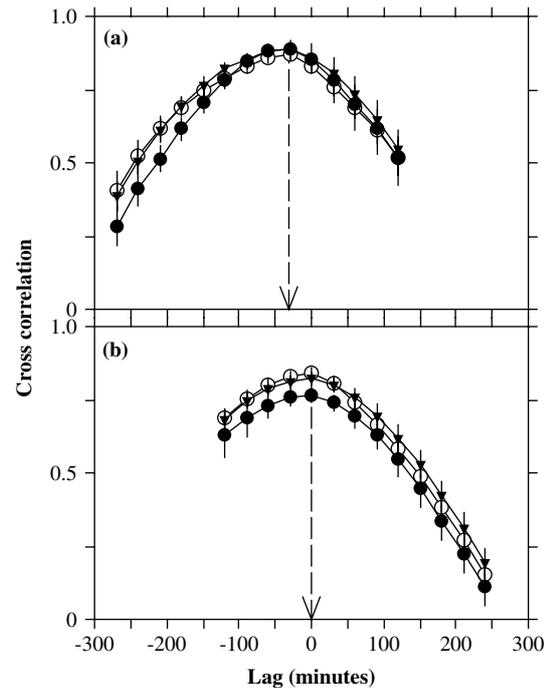


Figure 5. Cross-correlation coefficient (a) between solar radiation and xylem sap flux density measured near the tree top ( $F_{d\_top}$ ) and (b) between atmospheric humidity deficit and  $F_{d\_top}$ . Open circle, E750; closed circle, E751; triangle, J816. Vertical bars represent one standard error. Arrow denotes maximum cross-correlation coefficient for each tree

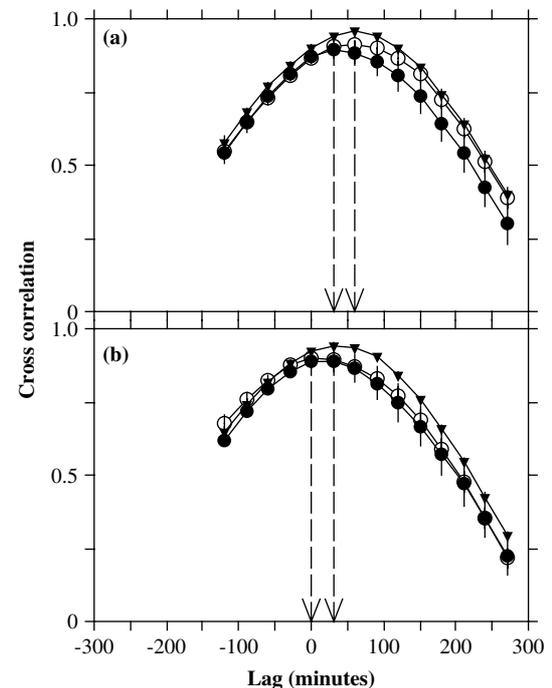


Figure 6. Cross-correlation coefficient (a) between stem sap flow and xylem sap flux density measured near the tree top ( $F_{d\_top}$ ) and (b) between whole-tree transpiration and  $F_{d\_top}$ . Open circle, E750; closed circle, E751; triangle, J816. Vertical bars represent one standard error. Arrow denotes maximum cross correlation coefficient for each tree

Figure 8 shows comparisons of  $G_C$  calculated from measured  $E_T$  ( $G_{C\_co}$ ), from  $Q$  ( $G_{C\_Nco}$ ), and from  $E_{T\_cal}$  bin-averaged by time of day. The difference between  $G_{C\_co}$  and  $G_{C\_Nco}$  was approximately 30% around noon.

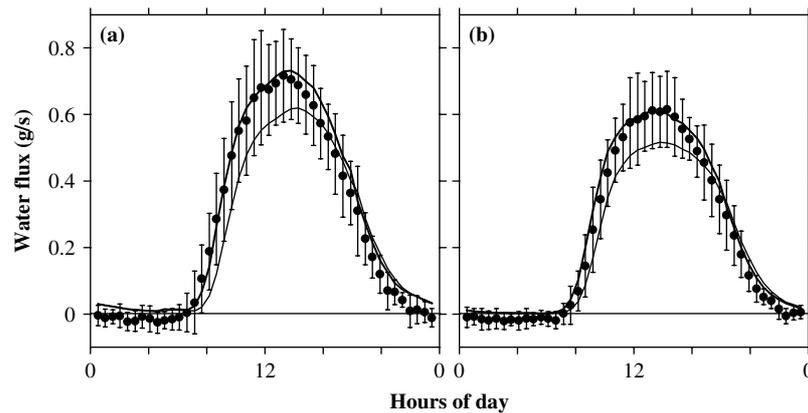


Figure 7. Average temporal variation in measured whole-tree transpiration ( $E_T$ ; solid circle), stem sap flow ( $Q$ ; thin line) and  $E_T$  calculated from  $Q$  taking into consideration the lag and difference in the peak between measured  $E_T$  and  $Q$  ( $E_{T\_cal}$ ; thick line) for trees E750 (a) and J816 (b). For reference, one standard deviation of the measured binned  $E_T$  is also shown

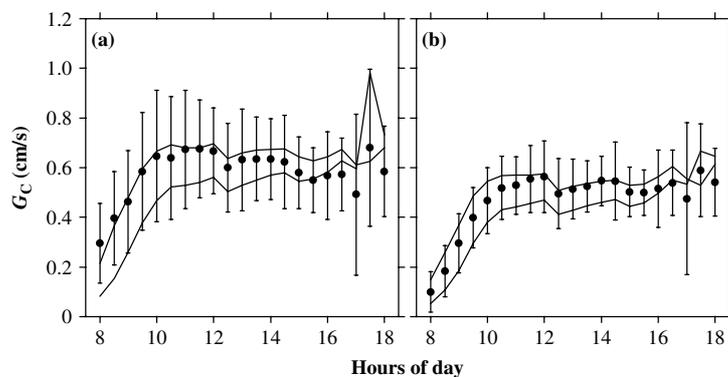


Figure 8. Average temporal variation in measured (solid circle) canopy conductance ( $G_C$ ),  $G_C$  calculated from  $Q$  (thin line) and  $G_C$  calculated from  $E_T$  taking into consideration the lag and difference in the peak between measured  $E_T$  and  $Q$  (thick line) for trees E750 (a) and J816 (b). For reference, one standard deviation of the measured binned  $G_C$  is also shown

It should be noted that  $G_{C\_Nco}$  overestimated  $G_{C\_co}$  early in the evening, due to  $Q$  being prolonged during the evening (Figure 7). However,  $G_C$  calculated from  $E_{T\_cal}$  clearly reproduced the canonical form of  $G_{C\_co}$  for both *Cr. japonica* and *Ch. obtusa* trees (Figure 8a, b). Table III presents the statistical parameters of the comparisons between  $G_{C\_co}$  and  $G_{C\_Nco}$  and the  $G_C$  calculated from  $E_{T\_cal}$  for all study trees. It is clear that the simplified modification, which consists of multiplying  $Q$  by 1.18 and shifting it forward 30 min, improves the predictive accuracy of  $G_C$  calculation for all studied trees.

Phillips and Oren (1998) and Ewers and Oren (2000) suggested that relatively large errors in  $E_T$  estimated from  $Q$  occur only early and late in the day due to measurement errors and the effects of  $W$ . They implied that filtering out data from early and late daytime hours could correct for the diffusion of the  $E_T$  signal measured as  $Q$ . For example, to calculate  $E_T$  from  $Q$ , Schäfer *et al.* (2000) used a time lag with this filtering. However in this study, it is clear that unless  $Q$  was multiplied by 1.18, there would be a large disagreement between  $E_{T\_cal}$  and  $E_T$  (Figure 7). This also suggests that compensating for only the time lag resulted in a large error in estimation of  $G_C$  (Figure 8).

In addition,  $\Omega$  was calculated from  $G_{C\_co}$ , from  $G_{C\_Nco}$ , and using the  $G_C$  from  $E_{T\_cal}$  bin-averaged by time

of day. Data from these three calculation methods are compared in Figure 9. The hourly pattern of  $\Omega$  was similar to  $G_C$ , although the afternoon increase was more prominent. For most of the day, because  $G_{C\_co}$  was higher than  $G_{C\_Nco}$ ,  $\Omega$  calculated from  $G_{C\_co}$  was higher than that determined from  $G_{C\_Nco}$ . The overestimation of  $G_{C\_Nco}$  early in the evening may cause an overestimation of the  $\Omega$  calculated from  $G_{C\_Nco}$ . Note that any estimation of  $\Omega$  at approximately noon was around 0.1–0.15, implying that canopies of *Cr. japonica* and *Ch. obtusa* trees are aerodynamically well coupled to the atmosphere. Coniferous forests have received the most attention in this regard (e.g. McNaughton and Jarvis, 1991). Thus, for estimating the  $G_C$  of *Cr. japonica* and *Ch. obtusa* trees, we can use the simplified form of the Penman-Monteith equation after Whitehead and Jarvis (1981) (same as Equation (8)).

By comparing  $G_{C\_co}$  and  $G_{C\_Nco}$ , we examined how  $G_C$  can be estimated from sap flow measurements at the base of the stem. From the results, we then developed a strategy to estimate  $G_C$ ; that is, by multiplying sap flow rates by 1.18 and shifting its time series forward by 30 min. Our study also suggested that finding the time lag is relatively easy. This is because comparison between sap flow measurements and meteorological variables was sufficient for determination, but finding the multiplier is

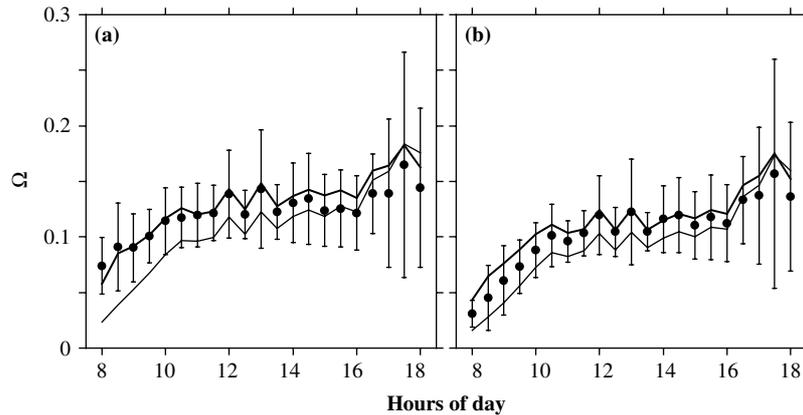


Figure 9. Average temporal variation in measured (solid circle) decoupling coefficient ( $\Omega$ ),  $\Omega$  calculated from  $Q$  (thin line) and  $\Omega$  calculated from  $Q$  taking into consideration the lag and difference in the peak between measured  $E_T$  and  $Q$  (thick line) for trees E750 (a) and J816 (b). For reference, one standard deviation of the measured binned  $\Omega$  is also shown

more demanding because it is difficult to estimate real whole-tree transpiration accurately.

Recently, Burgess and Dawson (2008) raised an issue about the effects of the tree stem capacitance on the transpiration stream, such as sap flow lags along tree heights. Using sap flow measurements and another independent technique, i.e. the ADR measurement (Phillips *et al.*, 2009), we confirmed that tree stem capacitance does have significant impacts on the transpiration stream. This result enabled us to examine the impact of stem water storage on  $G_C$  estimation. It should be noted that our conclusions resulted from studying just three sample trees in a single, well-kept, uniformly aged plantation, during a specific and short time period. However, because only one unit of the lag and multiplier was derived through this experiment regardless of the different individuals, we believe that the findings here are applicable to the sap flow estimates of  $G_C$ , at least in the studied *Cr. japonica* and *Ch. obtusa* stand, and so are a first step in the  $G_C$  estimation of *Cr. japonica* and *Ch. obtusa* trees. Therefore, to estimate  $G_C$  using sap flow measured at the base of the stem, further research is required into the effects of different tree sizes and soil moisture conditions (Phillips *et al.*, 1997).

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