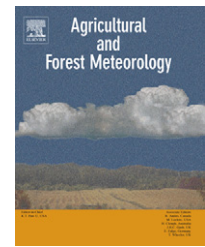


available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/agrformet](http://www.elsevier.com/locate/agrformet)

# Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed

Tomo'omi Kumagai<sup>a,\*</sup>, Makiko Tateishi<sup>a</sup>, Takanori Shimizu<sup>b</sup>, Kyoichi Otsuki<sup>a</sup>

<sup>a</sup> Kasuya Research Forest, Kyushu University, Sasaguri, Fukuoka 811-2415, Japan

<sup>b</sup> Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto 860-0862, Japan

## ARTICLE INFO

### Article history:

Received 4 October 2007

Received in revised form

4 April 2008

Accepted 21 April 2008

### Keywords:

*Cryptomeria japonica*

Granier-type sensor

Sap flux

Scaling

Soil moisture

Stomatal control

## ABSTRACT

Plant–soil system patterns and processes along a slope are among the greatest causes of uncertainty in estimating watershed-scale transpiration ( $E$ ). Tree-to-tree and radial variations in xylem sap flux density ( $F_d$ ), in addition to tree biometrics, were measured over a 2-year period (2005–2006) in two slope stand positions. The areas of interest consisted of an upper slope plot (UP) and a lower slope plot (LP) in a Japanese cedar (*Cryptomeria japonica* D. Don) forest watershed and the environmental controls of stand  $E$  for each plot were compared. Canopy stand  $E$  ( $E_c$ ) and canopy stomatal conductance ( $G_c$ ) in the UP were less than those in the LP during the growing season, while those in the UP were greater than those in the LP over winter. In addition, mean stand  $F_d$  ( $J_s$ ) in the UP was greater than that in the LP over winter, but  $J_s$  values were similar in the UP and LP except in the winter, which allows us to extrapolate watershed-scale  $E$  based on  $J_s$  estimated from  $F_d$  measurements of a partial stand in the watershed. However, this relationship contains a bias and differed between 2005 and 2006. Although there were significant differences in soil moisture conditions between the UP and LP in both years, a systematic relationship between the similarity in  $J_s$  and soil moisture conditions was not found. The bias was due to a tendency for  $J_s$  in the LP to be greater than that in the UP in 2006. This tendency was amplified because  $J_s$  in the LP was greater than that in the UP around an atmospheric humidity deficit ( $D$ ) of 1–1.5 kPa and frequencies of this  $D$  range were higher in 2006 than in 2005. The greater  $J_s$  in the LP at  $D \sim 1$ –1.5 kPa could be explained by the difference in the response of  $G_c$  to  $D$  between the UP and LP. Our results suggest this to be the cause of the similarity in  $J_s$  values for the UP and LP and for the occasional abortion of its similarity. However, even when the bias or the occasional deviation is disregarded, the error in estimating stand  $E$  from a partial stand is so small that it is comparable to an  $F_d$  measurement error. For example, the error when using only the LP was 6.6% for stand  $E$ .

© 2008 Elsevier B.V. All rights reserved.

## 1. Introduction

In Japan, forests cover 64% of the total land area (World Resources Institute, 2004) with the majority situated in mountain regions (Sawano et al., 2005). Since mountains receive higher precipitation and play a role in supplying water

to lowlands, quantifying hydrologic components in montane-forested catchments is critical for water resource management in Japan. Surprisingly, 22% of the total forest area is composed of a single tree species, *Cryptomeria japonica* D. Don (Japanese cedar) (Japan Forestry Agency, 2002). Therefore, understanding water use in *C. japonica* trees is the first and

\* Corresponding author. Tel.: +81 92 948 3113; fax: +81 92 948 3119.

E-mail address: [kuma@forest.kyushu-u.ac.jp](mailto:kuma@forest.kyushu-u.ac.jp) (T. Kumagai).

0168-1923/\$ – see front matter © 2008 Elsevier B.V. All rights reserved.

doi:10.1016/j.agrformet.2008.04.010

crucial step for water resource research in Japan. Recently, a few studies (Kumagai et al., 2005a, 2007; Komatsu et al., 2006a,b) discussed their potential as a water-consumer whereas the emphasis previously in the literature has been on their functions as woody material and as a silvicultural species.

The sap flow technique is a useful methodology for investigating forest water use at temporal and spatial scales because complex terrain and spatial heterogeneity do not limit its applicability (e.g., Wilson et al., 2001; Kumagai et al., 2007; Ford et al., 2007), which is important in a mountainous country like Japan. Furthermore, this technique can examine the effects of species composition on stand, watershed or landscape scale transpiration ( $E$ ) (e.g., Ewers et al., 2002, 2005; Mackay et al., 2002; Pataki and Oren, 2003; Bladon et al., 2006). Despite the robustness of the sap flow technique, three level scaling procedures are required to extrapolate the watershed scale  $E$ , i.e., from within-tree to the tree, from the tree to the stand, and from the stand to the watershed (see Ford et al., 2007). These procedures can be difficult owing to tree-to-tree variations in xylem sap flux density ( $F_d$ ) (Granier et al., 1996a; Wullschlegel et al., 2001; Pataki and Oren, 2003), tree sapwood area ( $A_{S\_tree}$ ) (Kumagai et al., 2005b), and spatial variations in  $F_d$  in the trunk of individual trees (Zang et al., 1996; Lu et al., 2000; Wullschlegel and King, 2000; Delzon et al., 2004b; Kumagai et al., 2005a).

Topographic gradients influence the soil texture and availability of water and nutrients, resulting in plant–soil systems and plant growth patterns along a slope (Sabate et al., 1995; Tokuchi et al., 1999; Hanba et al., 2000; Luizao et al., 2004; Tateno et al., 2004). In particular, Tromp-van Meerveld and McDonnell (2006) reported the relationships between soil moisture, soil depth, and individual tree water use ( $E_T$ ) and their influence on the hillslope water balance, and implied their resultant spatial differences in growth and species distribution along a slope. Two considerations must be kept in mind when we apply sap flow measurements to estimate the watershed scale  $E$ . The first is the difference in tree-to-tree and within-tree variations in  $F_d$  and the second is the allometric relationship between the stem diameter at breast height (DBH) and  $A_{S\_tree}$  between slope positions. In a previous study (Kumagai et al., 2007), we examined slope-position variations in total sapwood area of the stand ( $A_{S\_stand}$ ), the radial trend in  $F_d$ , and the mean stand sap flux density ( $J_S$ ), taking into account the above factors. The results showed that  $J_S$  measured at different positions along the slope was similar during the period studied despite significant variations in environmental factors, e.g., soil moisture conditions, and tree growth, e.g., DBH and tree height. These similarities implied the potential of a relationship for determining the watershed scale  $E$  based on  $J_S$  estimated from  $F_d$  measurements of a partial stand in a watershed.

Although the  $J_S$  values at different slope positions were similar, there were systematic inconsistencies between them, i.e., “biases”, and the studied period was limited to a single growing season. Thus, three questions arise: (1) are the  $J_S$  values at different slope positions similar over a longer period and (2) what factors generated the bias? Additionally, since the tree densities and individual tree sizes along the slope were considerably different despite the forest being of even age

(Kumagai et al., 2007), it would also be interesting to examine (3) the degree of difference in how  $E_T$  respond to soil conditions among the slope positions. To address these questions, we conducted tree-level measurements of  $F_d$  at several depths of sapwood in upper and lower slope plots of a watershed over a 2-year period and compared environmental controls of stand  $E$  for the different plots. The outcome of this study was also used to provide strategies for watershed-scale sap flow estimates of  $E$  and minimize potential errors in the estimate.

## 2. Materials and methods

### 2.1. Study site and meteorological measurements

The experiments were carried out in the Kahoku Experimental Watershed (KHEW), a 2.63 ha evergreen coniferous plantation on Kyushu Island, Japan (33°08'N, 130°43'E, 150–220 m a.s.l.). The watershed is underlain by crystalline schist and the slopes on both sides of the valley are steep (20–40°). The mean annual precipitation for the period 1999–2004 was around 2150 mm with the rainy season occurring from mid-June to early July. The mean annual temperature was around 15 °C with a minimum mean monthly temperature of about 4 °C in January–February and a maximum mean monthly temperature of about 26 °C in August.

The forest in the watershed consists mainly of even-aged 50-year-old *C. japonica* stands, and to a lesser degree, *Chamaecyparis obtusa* Endl. (Japanese cypress) stands ranging from 30 to 50 years old. Understory vegetation is dense and consists of various species of evergreen *Quercus* and *Castanopsis* trees. For this study, two *C. japonica* stand plots, an upper slope plot (UP) and a lower slope plot (LP), located less than 100 m from each other on a 20° slope in the watershed were sampled (see Table 1). The UP and LP have similar ground areas and are of identical age; however, while there are more trees in the UP than in the LP, the stand basal area and individual tree sizes in the UP are smaller than in the LP (Table 1). These differences result in a frequency distributions

**Table 1 – Stand characteristics of the two study plots, the upper slope plot (UP) and lower slope plot (LP)**

Characteristic	UP	LP
Plot area (m <sup>2</sup> )	318	321
Age (years)	50	50
Density (trees ha <sup>-1</sup> )	1575	904
PAI <sup>a</sup> (m <sup>2</sup> m <sup>-2</sup> )	3.2–5.4 <sup>b</sup>	4.4–5.7
Mean DBH (cm)	23.8	40.3
Range DBH (cm)	12.5–30.8	23.7–53.3
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	71.7	118.7
Sapwood area <sup>c</sup> (m <sup>2</sup> ha <sup>-1</sup> )	36.3	46.0
Mean height (m)	22	32
Sap flux measurements (trees)	23	15

<sup>a</sup> PAI was measured from 2004 to 2005, and ranges of values denote seasonal variations.

<sup>b</sup> Measured at other slope positions with similar slope height to the UP.

<sup>c</sup> Sapwood area was estimated based on the allometric relationship of each study plot (Kumagai et al., 2007).

of the DBH in the UP and LP that barely overlap. The silhouette area index of leaves plus stems and branches (plant area index; PAI) was measured in the LP from 2005 to 2006 using a plant canopy analyzer (LAI-2000, Li-Cor, Lincoln, NE). The PAI in the LP ranged from 4.4 to 5.7 m<sup>2</sup> m<sup>-2</sup>, implying minor seasonal variation.

A solar radiometer (CM14B, Kipp & Zonen, Delft, Netherlands) and ventilated psychrometer (NH020L, EKO, Tokyo, Japan) were installed at a height of 47 and 42 m, respectively, using a 50-m canopy tower located at the center of the watershed. While the ground level is 20–30 m higher in the UP than in the LP, the canopy height in the UP is around 10 m lower than in the LP (see Table 1). In short, the canopy surface above the slope is somewhat even. Thus, we assumed that radiative energy received by the canopies in the UP and LP and air temperature ( $T_a$ ) and relative humidity (RH) above them were about the same, and these climatic factors measured at the canopy tower were representative of the sampled slope. Whether this assumption is valid will be examined later.

Samples were taken every 30 s for solar radiation ( $R_s$ ) and every 1 min for  $T_a$  and RH, and averaged over 30 min (CR10X, Campbell Scientific, Logan, UT). In an open field located approximately 100 m from the watershed, a tipping bucket rain gauge (RT-5, Ikeda Keiki, Tokyo, Japan) was placed on a waist-height bench.

Volumetric soil moisture content ( $\theta$ ; m<sup>3</sup> m<sup>-3</sup>) and matric potential ( $\psi$ ; m) were measured in each plot at 10, 20, and 40 cm below the forest floor at 30-min intervals (CR10X). A dielectric aquameter sensor (EC-10, Decagon Devices, Inc., Pullman, WA) was used to measure the time series of  $\theta$ . A tensiometer (DIK3151, Daiki, Tokyo, Japan) was used to monitor  $\psi$  at the same depth as  $\theta$  thereby providing the necessary measurements to compute in situ  $\theta$ – $\psi$  curves, i.e., soil water retention curves.  $\psi$  at the inflection point and the air entry on the  $\theta$ – $\psi$  curves revealed the soil pore size distributions (see Kosugi, 1994).

The weighted average of  $\theta$  in the 0–50 cm soil layer was calculated as  $\theta_{0-50} = (15\theta_{10} + 15\theta_{20} + 20\theta_{40})/50$  (where  $\theta_{10}$ ,  $\theta_{20}$  and  $\theta_{40}$  are  $\theta$  at depths 10, 20, and 40 cm, respectively, in m<sup>3</sup> m<sup>-3</sup>). The relative extractable water in the soil ( $\omega$ ; m<sup>3</sup> m<sup>-3</sup>) was calculated using  $\theta_{0-50}$  as  $\omega = (\theta_{0-50} - \theta_r)/(\theta_s - \theta_r)$ , where  $\theta_s$  and  $\theta_r$  are the saturated water content and the residual water content averaged in the 0–50 cm layer, respectively.

## 2.2. Sap flux measurements and sapwood analysis

$F_d$  measurements were conducted using the thermal dissipation method with Granier-type sensors (e.g., Granier, 1987). Each sensor consists of a pair of probes 20 mm long and 2 mm in diameter. The probes were inserted into the sapwood approximately 0.15 m apart. The upper probe, which includes a heater, was supplied with 0.2 W constant power. The heat was dissipated into the sapwood and vertical sap flux surrounding the probe. The temperature difference between the upper heated probe and lower unheated reference probe was then measured and converted to  $F_d$  according to Granier (1987). Sap flow signals were recorded on a data logger (CR10X) with a multiplexer (AM16/32, Campbell Scientific) every 30 s and averaged over 30 min.

For  $F_d$  measurements, 23 and 15 trees were selected in the UP and LP, respectively (see Table 1), so that the number of trees measured in each DBH class corresponded to the frequency distributions of the DBH in the UP and LP (see Kumagai et al., 2007). One to three sensors were inserted into each selected tree at depths of 0–20, 20–40, and 40–60 mm to cover the sapwood, and 20 and 10 trees were used for measurement of the radial  $F_d$  profiles in the UP and LP, respectively. It is noted that sample sizes were confirmed to be sufficient for estimating stand  $E$  in each plot (see Kumagai et al., 2007).

The sensors were positioned about 0.15 m circumferentially apart from each other at a height of about 1.3 m. 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. *C. japonica* trees in the plantation are commonly characterized by a perfectly 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).

In addition, most sensors were placed on the north-facing side of the trees to avoid the sun-exposed side of the trunk and the part of the trunk into which the sensors were inserted was fully insulated to prevent any direct radiation. Although some sensors were not placed on the north-facing side because of topographical obstacles, there was only a slight natural thermal gradient along the trunks of all measured trees, probably because of the closed canopy and shade of the steep slope. Therefore, the data were not corrected for this. It is known that  $F_d$  from sensors positioned on the shaded side of tree crowns is often underestimated (e.g., Oren et al., 1999a). This effect could occur when conduits are straightforward, because spiral conduits generate a uniform sap flow distribution whereas straight vertical conduits offer direct easy paths (see Kubler, 1991). In our study, it was demonstrated in an experiment using dye solution injected into a radial hole bored into the tree trunk that the conduits in *C. japonica* are spiral (data not shown). Thus, we assumed that systematic underestimation of  $F_d$  was not caused by placing sensors on the north-facing side of the tree trunks and that the azimuthal variation in  $F_d$  was included in the tree-to-tree variation in  $F_d$ . Therefore,  $F_d$  was not measured at different orientations within a tree trunk.

Sapwood thickness (in mm) of each sample tree was measured on a core extracted with a 5-mm increment borer about 1.3 m above-ground, and assessed as the mean of two orthogonal measurements. Distinct color differences were used to identify the boundary between sapwood and heartwood.  $A_{S\_tree}$  was obtained from the difference between the stem cross-sectional area beneath the bark and heartwood area assuming that the stem cross-sections were circular. In the sapwood of *C. japonica*, a “white zone”, the moisture content of which is much lower than the heartwood, exists adjacent to the heartwood (e.g., Nobuchi and Harada, 1983; Nakada et al., 1999). Its radial position can be predicted because sapwood thickness can be predicted from the DBH. There is no water movement in the “white zone” (Kumagai et al., 2005a) and its width was assumed to be constant at about 10 mm (data not shown). Note that the dye solution experiment confirmed our ability to identify the boundary

between sapwood and heartwood and the “white zone” in the stem cross-section of *C. japonica*. Therefore, precautions were taken when inserting sensors in the sapwood to ensure coverage of the hydroactive area.

### 2.3. Calculations of $J_s$ , canopy stand $E$ and canopy stomatal conductance

$J_s$  was computed as the area-weighted mean  $F_d$  for the 0–20, 20–40, and 40–60 mm xylem bands of all measured trees within each plot according to Kumagai et al. (2005a, 2007). In addition,  $E_T$  for each tree measured over the entire sapwood was obtained as the sum of the product of  $F_d$  and the sapwood area at each xylem band.  $E_T$  for each individual tree was scaled up to the stand level as (Wilson et al., 2001; Wullschleger et al., 2001; Schäfer et al., 2002; Pataki and Oren, 2003; Kumagai et al., 2005a, 2007)

$$E_C = J_s \frac{A_{S\_stand}}{A_G} \quad (1)$$

where  $E_C$  is the canopy stand  $E$  and  $A_G$  is the ground area.

Environmental control of  $E_C$  has been characterized in terms of the response of canopy stomatal conductance ( $G_C$ ) to environmental factors (e.g., Meinzer and Grantz, 1990; Granier et al., 1996b; Martin et al., 1997; Cienciala et al., 2000; Wullschleger et al., 2000; Kumagai et al., 2004). In this study,  $G_C$  was calculated using the simplified form of the Penman-Monteith equation (Monteith and Unsworth, 1990):

$$G_C = \frac{\gamma \lambda E_C}{c_p \rho D} \quad (2)$$

where  $\gamma$  is the psychrometric constant,  $\lambda$  is the latent heat of vaporization of water,  $c_p$  is the specific heat of air at constant pressure,  $\rho$  is the density of dry air, and  $D$  is the above-canopy atmospheric humidity deficit. Furthermore,  $G_C$  was calculated as a daily average conductance using mean daytime  $D$ , thermodynamic variables based on mean daytime  $T_a$ , and  $E_C$  summed over 24 h but divided by daylight hours only (Phillips and Oren, 1998), and as an average of half-hour  $G_C$  values around noon (1100–1300 LT). Since for a daily average and a midday  $G_C$ ,  $E_C$  was obtained as daily values by integrating the sap flow over one day and averaged values only around noon, we assumed the effect of stem capacitance to be small (see Kumagai et al., submitted for publication, hereinafter referred to as submitted manuscript, 2007). The decoupling coefficient,  $\Omega$ , of *C. japonica* canopies was calculated according to Jarvis and McNaughton (1986) as 0.1–0.15 (Kumagai et al., submitted for publication). In general, the boundary conductance of conifers is sufficiently large, and we confirmed *C. japonica* canopies are aerodynamically well coupled to the atmosphere. Under these conditions, we removed the  $G_C$  values obtained on rainy days (as the  $F_d$  data were subject to noise) and when  $D < 0.1$  kPa in calculating the daily average  $G_C$  (see Phillips and Oren, 1998) and when  $D < 0.6$  kPa in calculating the midday  $G_C$  (see Ewers and Oren, 2000).

To facilitate the interpretation of the influence of environmental variables on  $G_C$ , we used a multiplicative-type function

(e.g., Jarvis, 1976), which is described by Granier and Bréda (1996) and Pataki and Oren (2003) as

$$G_C = \frac{R_s}{R_s + a} (b + m \ln D)(c + d \log_{10} \Theta) \quad (3)$$

where  $a$ ,  $b$ ,  $c$ ,  $d$ , and  $m$  are empirical parameters to be estimated through non-linear regression analysis.  $R_s$ ,  $D$  and  $\Theta$  in Eq. (3) have the same time resolution as a daily average or midday  $G_C$ . Note that when a value of  $R_s$  reflects non-limiting light,  $b$  and  $m$  are the reference value of  $G_C$  (i.e., the value of  $G_C$  at  $D = 1$  kPa) and the sensitivity of  $G_C$  to  $D$  (i.e.,  $-\partial G_C / \partial \ln D$ ), respectively (see Oren et al., 1999b, 2001).

## 3. Results

### 3.1. Environmental and sap flow data

Daily environmental data for the study period are shown in Fig. 1. Maximum  $T_a$  reached 35 °C between late July and early August in both 2005 and 2006. Minimum  $T_a$  was –5.3 °C in February.  $T_a$ , and therefore  $D$  showed a seasonal variation.  $D$  and daily total  $R_s$  were low from mid-June to mid-July in both 2005 and 2006 due to the regular rainy season in Japan. It should be noted there was an appreciable difference in soil moisture conditions between the UP and LP.  $\theta_{0-50}$  in the LP was always higher than that found in the UP throughout the studied period because of the lower porosity of soils in the UP. Soil water retention curves suggest the frequency distributions of soil pore size in the LP is significantly high in the large pore size region, while that in the UP is evenly distributed with a low (negative high)  $\psi$  at the air entry (data not shown). This resulted in much lower water extraction  $\psi$ , and thus much lower  $\psi$  in the UP during dry spells despite the similar range of  $\theta_{0-50}$  variations in the plots. In addition, there was a remarkable contrast in the soil moisture conditions between the 2005 and 2006 growing seasons, i.e., from April to October. Occasional severe dry spells ( $\psi$  at 20 cm depth ( $\psi_{20}$ ; m)  $\leq 2.0$  m) occurred in 2005 that rarely appeared in 2006 (although a severe dry spell occurred from September to November).

If differences in above-canopy climatic factors between the UP and LP caused by topographical differences influence estimates of environmental control of  $E$  in the UP and LP, the effects would be minimized using data around midday, when solar elevation is highest. In this study, we compared ratios of daily  $J_s$  between UP and LP with those of midday  $J_s$  between UP and LP, and observed the calculation results were the same (*t*-test,  $P = 0.14$ ). Therefore, our assumption is thought to be valid.

Responses of daily  $J_s$  and  $E_C$  to  $D$  and  $R_s$  patterns, and thus their seasonal variations are evident in Fig. 2a and b. On the other hand,  $G_C$  during the growing seasons was low from July to August despite the relatively high  $R_s$  (Fig. 2c).  $J_s$  in the UP was greater than that in the LP during the winter (Fig. 2a). It should also be noted that UP values in the winter remained comparable to the values in the other seasons. The relative difference between  $J_s$  values in the UP and LP plotted by the daily minimum  $T_a$  clearly indicated that  $J_s$  in the UP was greater than that in the LP when the minimum  $T_a$  was below 0 °C, i.e., DOY 341, 2005 to DOY 79, 2006. Thus, this period was defined as “winter” in this study. Except in winter,  $J_s$  values

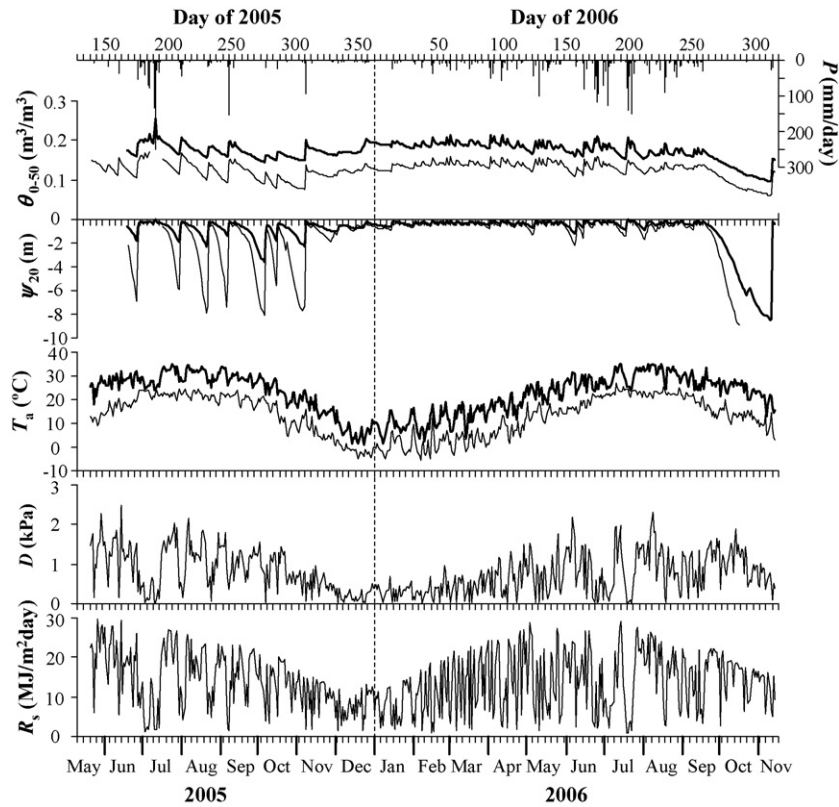


Fig. 1 – Yearlong climatic data (DOY 139, 2005 to DOY 317, 2006, May 19, 2005 to November 13, 2006). Reading from the top: daily precipitation ( $P$ ; bars, right scale), volumetric soil moisture content in the 0–50 cm soil layer ( $\theta_{0-50}$ ) in the UP (thin line) and LP (thick line), soil matric potential at 20 cm depth ( $\psi_{20}$ ) in the UP (thin line) and LP (thick line), daily maximum (thick line) and minimum (thin line) air temperature ( $T_a$ ), mean daytime atmospheric humidity deficit ( $D$ ; thin line), and daily total solar radiation ( $R_s$ ; thin line).

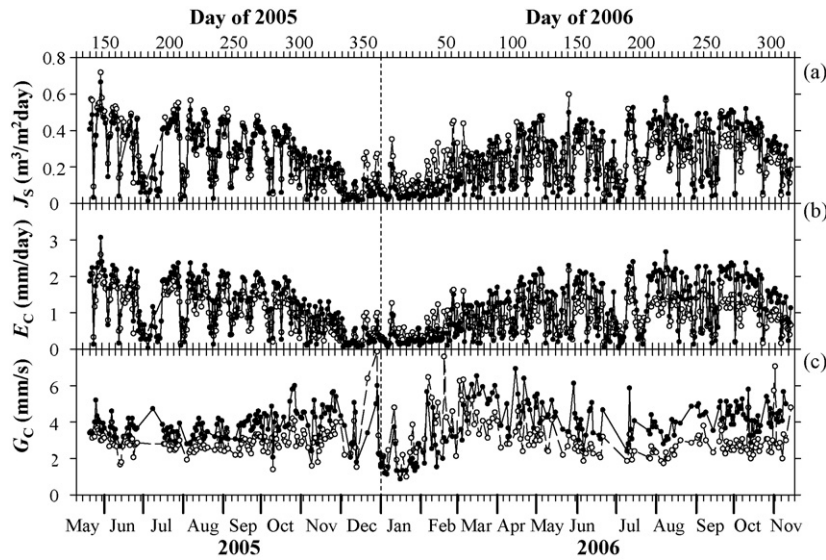
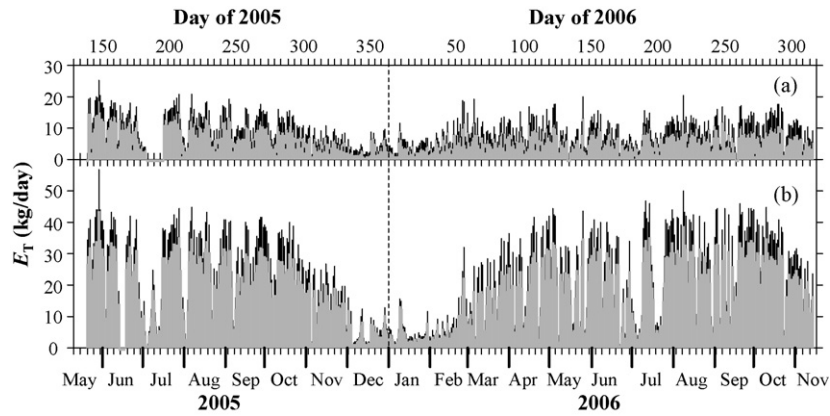


Fig. 2 – Seasonal patterns of (a) daily mean stand sap flux density ( $J_s$ ), (b) daily canopy stand transpiration ( $E_c$ ), and (c) daily canopy conductance ( $G_c$ ) in the UP (broken lines with open circles) and LP (solid lines with closed circles). Note that symbols are linked with lines even though there are days of missing data within the intervals.



**Fig. 3 – Daily mean water use of individual trees ( $E_T$ ; gray bars) in the UP (a) and LP (b). Vertical black bars represent one standard deviation.**

were similar in the plots for 2005, but greater for the LP than for the UP in 2006 (Fig. 2a). In addition, the difference apparently increased in 2006 (Fig. 2b and c) although  $E_C$  and  $G_C$  were greater in the LP than in the UP throughout the study period.

Fig. 3 further compares  $E_T$  in the UP and LP. Maximum  $E_T$  in the UP reached  $20 \text{ kg day}^{-1}$ , whereas that in the LP surpassed  $40 \text{ kg day}^{-1}$ . Considering that the  $J_S$  values for the UP and LP were similar and that tree size was much larger in the LP than in the UP, a correlation can be seen between tree size and  $E_T$  along the slope.

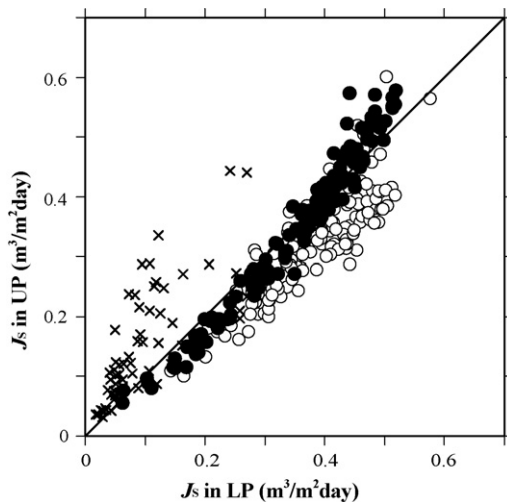
### 3.2. Comparisons of $J_S$ values in the UP and LP

Information on what factors in the UP and LP impact  $J_S$  would be useful for extrapolating larger-scale  $E$  from  $J_S$  estimated in single and partial plots (Kumagai et al., 2007). Thus, considering Fig. 2a, we compared  $J_S$  in the UP and LP in each studied period of 2005 (DOY 139–340 in 2005), winter (DOY 341 in 2005

to DOY 79 in 2006), and 2006 (DOY 80–317 in 2006) in Fig. 4. Note that the extraordinarily high  $J_S$  (DOY 148, 2005), partly due to high  $T_a$  and  $D$  uncommon in May in this region, was excluded from the analysis as an outlier hereinafter. In the winter,  $J_S$  was clearly much higher in the UP than in the LP. In 2005, the  $J_S$  values in the LP were highly correlated with those in the UP ( $R^2 = 0.94$ ; slope equal to 1.00), and the difference between these two quantities was not significantly different from zero (paired t-test,  $P = 0.12$ ). However, in 2006,  $J_S$  was significantly higher in the LP ( $P < 0.0001$ ).

The relationship between  $J_S$  values in the UP and LP over the study period was non-linear and contained a bias. Therefore, taking into consideration the difference in soil moisture conditions between 2005 and 2006 (see Fig. 1), it is logical to expect that this bias might be caused by the soil moisture conditions. However, in this study, we did not find a clear relationship between  $J_S$  and the soil moisture condition ( $\theta_{0-50}$  and  $\psi_{20}$ ) in the UP and LP (Fig. 5a and b). It should also be noted there were no clear relationships between  $J_S$  and soil moisture at specific soil layers (data not shown).

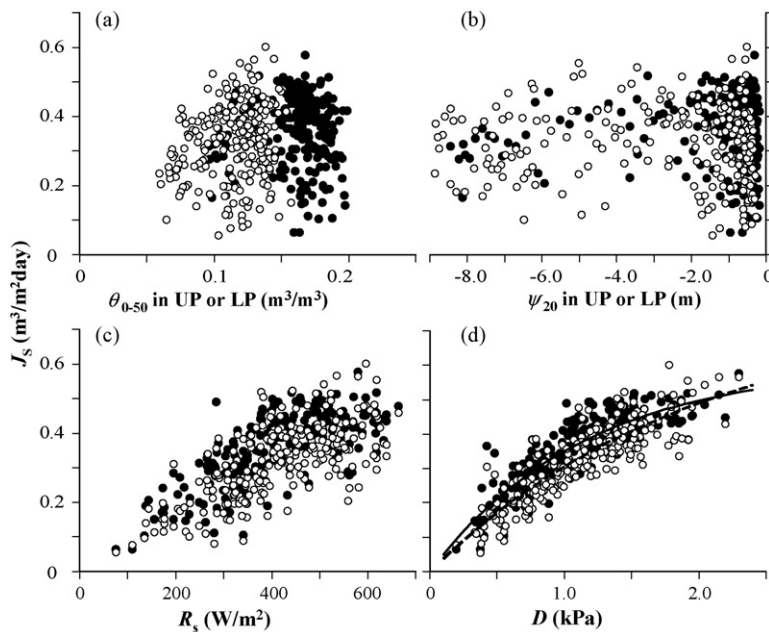
Fig. 5c and d shows the relationships between  $J_S$  in the UP and LP and  $R_s$  and  $D$ . Exponential saturations of  $R_s$  and  $D$  were fitted to  $J_S$  in the UP and LP by nonlinear regression analysis (e.g., Ewers et al., 2007). While the  $J_S$  in the UP and LP was moderately explained by  $R_s$  ( $R^2 = 0.50$  and  $0.57$  in the UP and LP, respectively), high correlations between  $D$  and the  $J_S$  values were observed ( $R^2 = 0.77$  and  $0.78$  in the UP and LP, respectively). Furthermore, we obtained the  $R^2$ -values from correlations of  $R_s$  and  $D$  with  $E_T$  of each tree in the UP and LP, and found they were related to DBH (Fig. 6). The  $R^2$ -values of  $D$ – $E_T$  were greater than those of  $R_s$ – $E_T$  for all individual trees. Although the  $R^2$ -values showed a subtle tendency to increase with DBH within each plot, when considering all individual trees in both plots, the  $R^2$ -values significantly increased with DBH ( $P < 0.0005$  and  $P < 0.005$  in Fig. 6a and b, respectively).



**Fig. 4 – Comparison between the mean stand sap flux densities ( $J_S$ ) in the UP and LP during DOY 139–340, 2005 (2005; closed circles), DOY 341, 2005 to DOY 79, 2006 (winter; crosses), and DOY 80–317, 2006 (2006; open circles). A 1:1 line is also shown.**

### 3.3. Environmental controls of $E$ in the UP and LP

For comparing  $J_S$  values in the UP and LP, it is more constructive to evaluate the effects of soil moisture on  $G_C$  that caused the difference in  $J_S$  values between the two plots



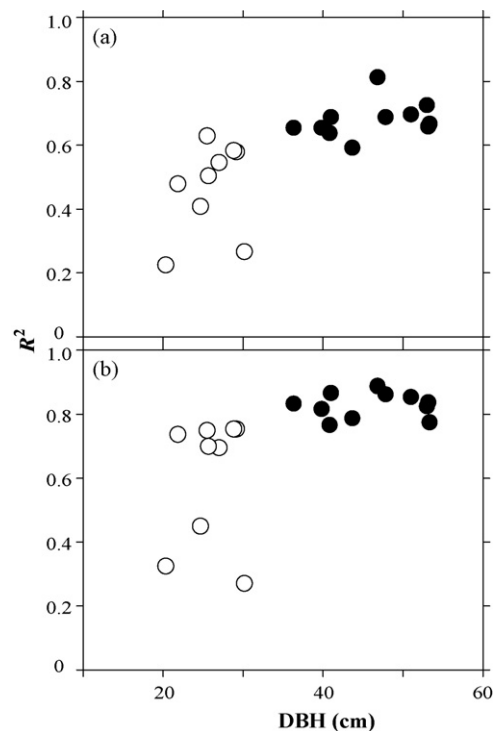
**Fig. 5** – Relationships between the mean stand sap flux density ( $J_s$ ) and (a) volumetric soil moisture content in the 0–50 cm soil layer ( $\theta_{0-50}$ ), (b) matric potential at 20 cm depth ( $\psi_{20}$ ), (c) solar radiation ( $R_s$ ) and (d) atmospheric humidity deficit ( $D$ ) averaged during daylight hours, in the UP (open circles) and LP (closed circles). The lines shown in (d) are  $y = 0.78 (1 - e^{-0.49x})$  ( $R^2 = 0.77$ ) for the UP (broken line) and  $y = 0.61 (1 - e^{-0.86x})$  ( $R^2 = 0.78$ ) for the LP (solid line).

(see Fig. 5). The general decline of  $G_C$  with decreasing soil moisture availability has been described many ways using a non-linear multiple regression model (e.g., Granier and Loustau, 1994; Granier and Bréda, 1996; Pataki and Oren, 2003). However, in this study, a clear relationship did not exist between the soil moisture condition (specific layers and whole profile) and  $G_C$  (daily mean and midday) in the UP or LP. Thus, according to the differences in  $J_s$  values between 2005 and 2006 (Fig. 4), parameters in Eq. (3) excluding that associated with the effect of  $\theta$  were estimated for the two studied periods.

Modeled midday  $G_C$  for both the UP and LP did not match measurements ( $R^2 < 0.1$ ). On the other hand, although modeled daily mean  $G_C$  values in both the UP and LP are moderately correlated with measured values in 2006 ( $R^2 = 0.57$  and 0.62, respectively), the  $R^2$  in the UP and LP reduce to 0.20 and 0.46, respectively, in 2005. The relationships between  $b$  and  $m$  (discussed later) derived from a boundary line analysis (e.g., Schäfer et al., 2000; Ewers et al., 2007) using midday  $G_C$  were similar to those from a parameterization using daily mean  $G_C$  despite larger values of  $b$  in the midday  $G_C$  analyses (data not shown). Therefore, we used the results only from the daily mean  $G_C$  analyses in this study.

There was no obvious relationship between  $G_C$  and the soil moisture condition. Nevertheless, dry soil moisture conditions, which occurred frequently in 2005, might have been another factor that controlled  $G_C$  in the UP and LP. It should be noted that absolute values of residuals of the  $G_C$  model using  $R_s$  and  $D$  relationships significantly increased with  $\theta$  in the UP ( $P < 0.05$ ) but not in the LP ( $P = 0.30$ ) (data not shown).

Mean model parameters are given in Table 2. There were no significant differences in parameter  $a$  between the UP and LP and between 2005 and 2006. On the other hand, while no inter-



**Fig. 6** – Relationships between stem DBH of individual trees and  $R^2$ -values obtained from correlations of solar radiation (a) and atmospheric humidity deficit (b) averaged during daylight hours with daily mean water use of individual trees, in the UP (open circles) and LP (closed circles).

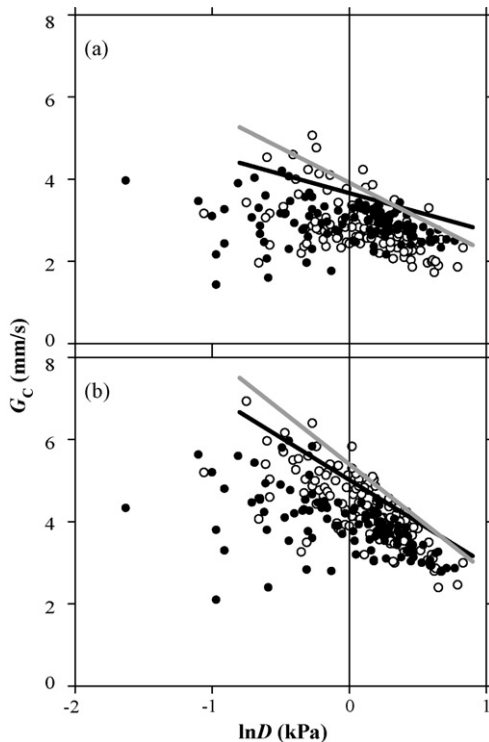
**Table 2 – Mean model parameters ( $\pm$ standard error) describing canopy stomatal conductance in response to solar radiation and vapor pressure deficit (see Eq. (3)) in the UP and LP in 2005 and 2006 (see Fig. 4 and text)**

Slope plot/studied period	<i>a</i>	<i>b</i>	<i>m</i>
UP/2005	89.3 <sup>a</sup> $\pm$ 32.7	3.67 <sup>b</sup> $\pm$ 0.28	-0.93 <sup>d</sup> $\pm$ 0.26
UP/2006	135.3 <sup>a</sup> $\pm$ 50.2	3.92 <sup>b</sup> $\pm$ 0.37	-1.68 <sup>d</sup> $\pm$ 0.32
LP/2005	93.5 <sup>a</sup> $\pm$ 28.1	5.02 <sup>c</sup> $\pm$ 0.33	-2.06 <sup>e</sup> $\pm$ 0.36
LP/2006	79.7 <sup>a</sup> $\pm$ 25.2	5.39 <sup>c</sup> $\pm$ 0.29	-2.63 <sup>e</sup> $\pm$ 0.29

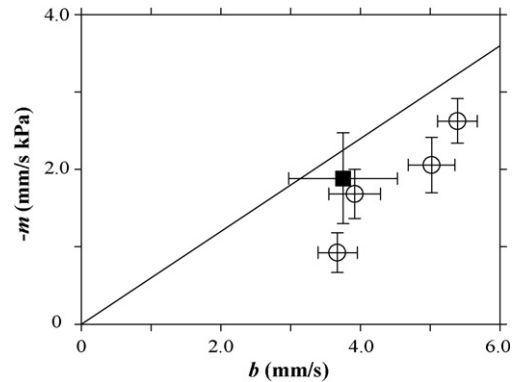
Superscripts denote slope position and study period differences from the Cochran-Cox test ( $P < 0.05$ ).

study period (i.e., 2005 and 2006) differences in parameters *b* and *m* were apparent, *b* and *m* in the UP were significantly different from those in the LP (Cochran-Cox test,  $P < 0.05$ ). In summary, the light response of  $G_C$  was similar for different slope positions and studied periods, while the reference value (at  $D = 1$  kPa) of  $G_C$  and the sensitivity of  $G_C$  to  $D$  were not significantly different for the different periods (which would have denoted differences in the soil moisture condition) but were affected by the slope positions (see Table 2).

The upper boundaries of the data clouds were computed by letting  $R_s$  equal infinity in Eq. (3), indicating the  $G_C$  sensitivity to  $D$  under a non-limiting light condition (Fig. 7).  $G_C$  in the LP was apparently more sensitive to  $D$  than that in the UP, which corresponds to its greater reference value at  $D = 1$  kPa (see Oren et al., 1999b). The proportionality  $-m/b \approx 0.6$  results from the regulation of the minimum leaf water potential ( $\psi_L$ ) to prevent excessive xylem cavitation, and a value less than 0.6 denotes less strict regulation of  $\psi_L$  (Oren et al., 1999b; Ewers



**Fig. 7 – Relationships between canopy stomatal conductance ( $G_C$ ) and atmospheric humidity deficit ( $D$ ) in the UP (a) and LP (b) in 2005 (closed circles) and 2006 (open circles) (see Fig. 4 and text). Black and gray lines denote  $G_C$  under non-limiting light conditions for 2005 and 2006, respectively (see Eq. (3)).**



**Fig. 8 – Relationship between parameters *b* and  $-m$  in Eq. (3) (open circles; see Table 2). The parameter calculated from Oren et al. (2001) is also shown (closed squares). The oblique line is the theoretical relationship between the two parameters (Oren et al., 1999b). Vertical and horizontal bars represent one standard error.**

et al., 2005, 2007). Given the even-sized trees within each study plot, we could compare the proportionalities obtained in this study and other studies, even though the proportionalities are usually estimated for individual trees. As a result, *C. japonica* trees in this study had a proportionality significantly lower than 0.6 (Fig. 8;  $-m/b = 0.25-0.49$ ), implying these trees allow the minimum  $\psi_L$  to drop with increasing  $D$ .

## 4. Discussion

### 4.1. Seasonal patterns of *E* in the UP and LP

For the experimental site, a unique seasonal pattern of net photosynthetic flux was simulated (Watanabe et al., 2004): a low flux rate in winter, maximum in late spring, and a decreased rate in summer followed by a slight recovery in autumn. The lower  $G_C$  values observed during the growing seasons (Fig. 2c) seem to support this bimodal seasonal pattern of net photosynthetic flux.

Han and Mukai (1999) observed that Japanese cedar requires cold acclimation to prevent severe damage to the photosynthetic materials from low temperature stress and this is accompanied by needle color changes during the winter. Apparently, the canopy color in the UP and LP differs in the winter and hence the slope position difference might cause the higher  $J_s$ ,  $E_c$ , and  $G_C$  in the UP during this period (Fig. 2).



It should be noted the greater  $E_C$  and  $G_C$  reflected a larger  $A_{S\_stand}$  in the LP (Fig. 2), implying  $A_{S\_stand}$  was a strong determinant of water use in this forest watershed (e.g., Dunn and Connor, 1993; Vertessy et al., 1995, 1997; Roberts et al., 2001).

#### 4.2. $E_T$ in the UP and LP

McDowell et al. (2002) observed an increase in the sapwood to leaf area ratio ( $A_S:A_L$ ) with increasing tree size, and attributed it to a homeostatic mechanism that partially compensates for a decrease in hydraulic conductance as trees grow in height. On the other hand, Ewers et al. (2005) explained the effects of tree height and age on  $E_C$  and  $G_C$  via hydraulic properties for some contrasting tree species; some had an increasing  $A_S:A_L$  ratio, a constant minimum  $\psi_L$  and constant  $-m/b$  with increasing size and age, whereas some had decreasing  $A_S:A_L$  ratio, minimum  $\psi_L$  and  $-m/b$  with increasing size and age. As in many studies (e.g., Ryan and Yoder, 1997), the effect of tree height (via the slope position in this study; see Table 1) on the environmental control of  $E_T$  is expected also in this study (see Fig. 3).

Fig. 5a and b suggests that trees growing in the UP (fine soils) used water retained by stronger capillary forces in pore spaces smaller than those for trees in the LP (coarse soils). For this reason, trees in the UP may require less water potential to exhaust their water supply compared to trees in the LP (see Hacke et al., 2000), where *C. japonica* was approaching its maximum height, and therefore the tree height in the UP might be lower to control the minimum  $\psi_L$  (see Ryan and Yoder, 1997; Hubbard et al., 1999).

Furthermore, it is interesting to focus on the insensitivity of  $J_S$  in the UP to soil water content because soil moisture conditions were consistently drier in the UP than in the LP during the study period. Tromp-van Meerveld and McDonnell (2006) reported that in the upper slope position, which has shallower soils,  $E_T$  was limited by soil moisture whereas in the lower slope position with deeper soils,  $E_T$  was not limited by soil moisture, because spatial variation in soil depth was responsible for differences in total water availability in the slope. Unlike Tromp-van Meerveld and McDonnell (2006), we did not find a clear relationship between  $J_S$  and the soil moisture condition for either the whole profile or specific soil layers. In addition, Bréda et al. (1995) found that stand water uptake occurred from progressively deeper soil horizons as the length of a drought increased, and that limited rooting depth resulted in a negative  $E$  response even under moist soil conditions. Therefore, a likely reason for the insensitivity to drought of UP trees is that water uptake occurred from deeper soil horizons for UP trees than for LP trees. Furthermore, this might have increased the root to tree ratio for UP trees resulting in a reduction in tree size (see Sperry et al., 1998; Magnani et al., 2000).

In addition, Wullschleger et al. (2000) reported linear relationships between daily canopy  $E$  for individual trees and daily average radiative energy and between  $E$  and daily average  $D$ , with their scatters increasing for small trees. Also in this study,  $D$  and  $R_s$  could better explain  $E_T$  for larger trees, which were located in the LP (Fig. 6), partly because  $E_T$  for larger trees saturated at higher levels of the environmental

factors than did smaller trees. This results in decreases in the  $R^2$  values between  $J_S$  and the environmental factors in the UP (Figs. 5c and d).

#### 4.3. $J_S$ in the UP and LP

The lines regressed against  $D - J_S$  data in the UP and LP indicated that around  $D = 1-1.5$  kPa,  $J_S$  was greater in the LP (Fig. 5d). In fact, the probability density functions of  $D$  in 2005 and 2006 confirmed the frequency at  $D = 1-1.5$  kPa was much higher in 2006 than in 2005 (data not shown) and thus, the large discrepancy between  $J_S$  values in the UP and LP in 2006 (Figs. 2 and 4).

For estimation of watershed-scale  $E$ , predicting  $J_S$  from  $F_d$  measurements in a partial stand (e.g., in only the LP) using the similarity in  $J_S$  values between partial stands (e.g., between the UP and LP) (Fig. 4) would be practical. Although the mean difference in  $J_S$  values for the UP between the measured values and predicted values from the  $D - J_S$  relationship in Fig. 5d was 0.01%, it should be noted that even if  $J_S$  in the LP is substituted, the mean difference was only 6.6%. This implies that  $J_S$  measured in a partial stand is a reasonable estimate for other stands in the watershed. Again, note that  $A_{S\_stand}$  is a strong determinant of water use in forest stands. For example, measurements of a spatial variation in  $E_T$  across a topographically controlled soil moisture gradient suggested quantifying spatial pattern of  $A_{S\_tree}$  is important for understanding spatial estimates of  $E$  (Adelman et al., 2008; Loranty et al., 2008). Furthermore, Ewers et al. (1999) found  $J_S$  did not differ among stands with treatments such as irrigation and fertilization, and differences in  $E_C$  reflected differences in  $A_{S\_stand}$ .

#### 4.4. $G_C$ in the UP and LP

The greater sensitivity and reference value in the LP caused the higher  $G_C$  in the LP around  $D = 1-1.5$  kPa (Fig. 7), resulting in the higher  $J_S$  in the LP around  $D = 1-1.5$  kPa (Fig. 5d) and in 2006 (Fig. 4). In general, an associated decline in stomatal conductance ( $g_s$ ) with tree height can be expected to maintain a balance between water supply and demand (Oren et al., 1999b; Schäfer et al., 2000; Delzon et al., 2004a; Ryan et al., 2006). Schäfer et al. (2000) and Delzon et al. (2004a) reported that mean canopy  $g_s$  of individual tree crowns decreases with tree height, and that its sensitivity to  $D$  also decreases according to Oren's hypothesis (Oren et al., 1999b;  $-m/b \approx 0.6$ ). Since we could assume the LP canopy to be more closed than UP (Table 1), the leaf-specific  $G_C$  ( $\approx$  the mean canopy  $g_s$ ) in the LP is thought to be smaller than in the UP. This may result in the smaller  $g_s$  and the lessened sensitivity to  $D$  with increasing tree height found in our studied site. It is also possible that, despite the shorter trees in the UP, the  $g_s$  and its sensitivity to  $D$  of trees were less than those in the LP due to their growth in fine soils (see Hacke et al., 2000).

Furthermore, Oren et al. (1999b) reported drought-tolerant desert species had a significantly lower proportionality than 0.6, and these species have xylem morphology adapted to withstand lower water potential under high atmospheric demand without excessive and catastrophic cavitation (Ewers et al., 2005). In addition, Ewers et al. (2005) insisted such a trait

would allow these species to continue to take up carbon when other species had to decrease stomatal conductance to prevent excessive cavitation. Although *C. japonica* trees are suited to moist soil conditions, which are found in the LP, they also had a proportionality significantly lower than 0.6 (Fig. 8;  $-m/b = 0.25\text{--}0.49$ ). *C. japonica* is the major plantation species in Japan, and has traditionally been planted in valleys or on lower slopes for a long time. It has been observed that *C. japonica* trees planted in a riparian zone have extremely full growth while the mortality of the trees under a dry soil condition such as on a ridge is high. This corresponds with the observation that  $G_C$  in this study did not respond to the soil moisture condition. Hence, we hypothesized that proportionality  $<0.6$  would confer a carbon uptake advantage to tree species suitable for moist soil condition as  $g_s$  would not have to decrease with increasing atmospheric demand. Note that a flood-tolerant species under flooded conditions (Oren et al., 2001) had a proportionality estimated as 0.50 (see Fig. 8), which supports our hypothesis, while a wetland tree species had a value near 0.6 across a changing water table (Ewers et al., 2007).

#### 4.5. E in the UP and LP

The above findings are suggested as the reasons for the similarity between  $J_S$  in the UP and LP and for the occasional deviation. However, it should be noted that even though the bias or the occasional difference are taken into consideration, the potential error in estimation of stand  $E$  from a partial stand (e.g., only the LP) is comparable to a sap flux-measurement error. Rather, this study confirms “conservativeness” of  $J_S$  along a slope. Roberts (1983) claimed variations in soil moisture status, in most circumstances, have negligible effects on  $E$  rate. Although his result was from site-to-site comparisons, his theory is applicable to stand-to-stand comparisons within a site. Furthermore, previous studies have suggested that, in forests,  $E$  is a “conservative process” because differences in forest stand status mainly affect partitioning of the components of canopy  $E$  but not its magnitude (Roberts, 1983; Oren et al., 1998; Delzon and Loustau, 2005). Understory trees were apparently larger in the UP, and thus higher  $E$  rates of understory trees might compensate for the difference in  $E$  between the UP and LP.

## 5. Conclusion

In this study, we compared  $E$  at two plots along a slope and found the similarity in  $J_S$  between the UP and LP. Despite only two plots observation, it is believed that this finding is the first-step for allowing a simple and straightforward treatment of watershed-scale  $E$ . Further investigation, e.g., measurements for other slope aspects, is required for watershed-scale  $E$  estimates based on  $J_S$  from  $F_d$  measurements of a partial stand.

## Acknowledgments

The maintenance of the KHEW is supported by the Kyushu Research Center of the Forestry and Forest Products Research

Institute (FFPRI) and the National Forests in Kyushu Office. This work was supported by Grants-in-Aid for Scientific Research (Nos. 17380096 and 17510011) from the Ministry of Education, Science and Culture, Japan. This study is part of “The Long-Term CO<sub>2</sub> Flux Observation Project (#200303)” supported by the FFPRI. We are grateful to Sayaka Aoki for help with fieldwork. Tomo’omi Kumagai wishes to thank Hikaru Komatsu for his useful critique.

## REFERENCES

- Adelman, J.D., Ewers, B.E., Mackay, D.S., 2008. Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration. *Tree Physiol.* 28, 647–658.
- Bladon, K.D., Silins, U., Landhäusser, S.M., Lieffers, V.J., 2006. Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting. *Agric. For. Meteorol.* 138, 104–119.
- Bréda, N., Granier, A., Barataud, F., Moyne, C., 1995. Soil water dynamics in an oak stand. I. Soil moisture, water potentials and water uptake by roots. *Plant Soil* 172, 17–27.
- Cienciala, E., Kučera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. *J. Hydrol.* 236, 109–120.
- Delzon, S., Loustau, D., 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agric. For. Meteorol.* 129, 105–119.
- Delzon, S., Sartore, M., Burrell, R., Dewar, R., Loustau, D., 2004a. Hydraulic responses to height growth in maritime pine trees. *Plant Cell Environ.* 27, 1077–1087.
- Delzon, S., Sartore, M., Granier, A., Loustau, D., 2004b. Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiol.* 24, 1285–1293.
- Dunn, G.M., Connor, D.J., 1993. An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiol.* 13, 321–336.
- Ewers, B.E., Gower, S.T., Bond-Lamberty, B., Wang, C.K., 2005. Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell Environ.* 28, 660–678.
- Ewers, B.E., Mackay, D.S., Gower, S.T., Ahl, D.E., Burrows, S.N., 2002. Tree species effects on stand transpiration in northern Wisconsin. *Water Resour. Res.* 38, 1103, doi:10.1029/2001WR000830.
- Ewers, B.E., Mackay, D.S., Samanta, S., 2007. Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. *Tree Physiol.* 27, 11–24.
- Ewers, B.E., Oren, R., 2000. Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. *Tree Physiol.* 20, 579–589.
- Ewers, B.E., Oren, R., Albaugh, T.J., Dougherty, P.M., 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. *Ecol. Appl.* 9, 513–525.
- Ford, C.R., Hubbard, R.M., Kloeppel, B.D., Vose, J.M., 2007. A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance. *Agric. For. Meteorol.* 145, 176–185.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3, 309–320.
- Granier, A., Biron, P., Bréda, N., Pontailier, J.-Y., Saugier, B., 1996a. Transpiration of trees and forest stands: short and

- long-term monitoring using sapflow methods. *Global Change Biol.* 2, 265–274.
- Granier, A., Biron, P., Köstner, B., Gay, L.W., Najjar, G., 1996b. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. *Theoret. Appl. Climat.* 53, 115–122.
- Granier, A., Bréda, N., 1996. Modeling canopy conductance and stand transpiration of an oak forest from sap flow measurements. *Ann. Sci. For.* 53, 537–546.
- Granier, A., Loustau, D., 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71, 61–81.
- Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R., Oren, R., 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495–505.
- Han, Q., Mukai, Y., 1999. Color acclimation and photoinhibition of photosynthesis accompanied by needle color changes in *Cryptomeria japonica* during the winter. *J. For. Res.* 4, 229–234.
- Hanba, Y.T., Noma, N., Umeki, K., 2000. Relationship between leaf characteristics, tree sizes and species distribution along a slope in a warm temperate forest. *Ecol. Res.* 15, 393–403.
- Hubbard, R.M., Bond, B.J., Ryan, M.J., 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19, 165–172.
- Japan Forestry Agency, 2002. Forestry Agency Business Papers. Available online at: <http://www.rinya.maff.go.jp/toukei/toukei.html> (in Japanese).
- Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. Lond., Ser. B* 273, 593–610.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.
- Komatsu, H., Kang, Y., Kume, T., Yoshifuji, N., Hotta, N., 2006a. Transpiration from a *Cryptomeria japonica* plantation, part 1: aerodynamic control of transpiration. *Hydrol. Process.* 20, 1309–1320.
- Komatsu, H., Kang, Y., Kume, T., Yoshifuji, N., Hotta, N., 2006b. Transpiration from a *Cryptomeria japonica* plantation, part 2: responses of canopy conductance to meteorological factors. *Hydrol. Process.* 20, 1321–1334.
- Kosugi, K., 1994. Three-parameter lognormal distribution model for soil water retention. *Water Resour. Res.* 30, 891–901.
- Kubler, H., 1991. Function of spiral grain in trees. *Trees* 5, 125–135.
- Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y., Otsuki, K., 2005a. Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agric. For. Meteorol.* 135, 110–116.
- Kumagai, T., Aoki, S., Shimizu, T., Otsuki, K., 2007. Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiol.* 27, 161–168.
- Kumagai, T., Aoki, S., Otsuki, K., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y. 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. *Trees*, submitted for publication.
- Kumagai, T., Nagasawa, H., Mabuchi, T., Ohsaki, S., Kubota, K., Kogi, K., Utsumi, Y., Koga, S., Otsuki, K., 2005b. Sources of error in estimating stand transpiration using allometric relationships between stem diameter and sapwood area for *Cryptomeria japonica* and *Chamaecyparis obtusa*. *For. Ecol. Manage.* 206, 191–195.
- Kumagai, T., Saitoh, T.M., Sato, Y., Morooka, T., Manfroi, O.J., Kuraji, K., Suzuki, M., 2004. Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects. *J. Hydrol.* 287, 237–251.
- Loranty, M.M., Mackay, D.S., Ewers, B.E., Adelman, J.D., Kruger, E.L., 2008. Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient. *Water Resour. Res.* 44, W02441, doi:10.1029/2007WR006272.
- Lu, P., Müller, W.J., Chacko, E.K., 2000. Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. *Tree Physiol.* 20, 683–692.
- Luizao, R.C.C., Luizao, F.J., Paiva, R.Q., Monteiro, T.F., Sousa, L.S., Kruijt, B., 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Global Change Biol.* 10, 592–600.
- Mackay, D.S., Ahl, D.E., Ewers, B.E., Gower, S.T., Burrows, S.N., Samanta, S., Davis, K.J., 2002. Effects of aggregated classifications of forest composition on estimates of evapotranspiration in a northern Wisconsin forest. *Global Change Biol.* 8, 1253–1265.
- Magnani, F., Mencuccini, M., Grace, J., 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant Cell Environ.* 23, 251–263.
- Martin, T.A., Brown, K.J., Cermák, J., Ceulemans, R., Kucera, J., Meinzer, F.C., Rombold, J.S., Sprugel, D.G., Hinckley, T.M., 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. *Can. J. For. Res.* 27, 797–808.
- McDowell, N., Barnard, H., Bond, B.J., Hinckley, T., Hubbard, R.M., Ishii, H., Köstner, B., Magnani, F., Marshall, J.D., Meinzer, F.C., Phillips, N., Ryan, M.G., Whitehead, D., 2002. The relationship between tree height and leaf area: sapwood area ratio. *Oecologia* 132, 12–20.
- Meinzer, F.C., Grantz, D.A., 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13, 383–388.
- Monteith, J.L., Unsworth, M.H., 1990. Principles of Environmental Physics, 2nd edition. Edward Arnold, London.
- Nakada, R., Fujisawa, Y., Hirakawa, Y., 1999. Soft X-ray observation of water distribution in the stem of *Cryptomeria japonica* D. Don I: general description of water distribution. *J. Wood Sci.* 45, 188–193.
- Nobuchi, T., Harada, H., 1983. Physiological features of the “white zone” of sugi (*Cryptomeria japonica* D. Don)—cytological structure and moisture content. *Mokuzai Gakkaishi* 29, 824–832.
- Oren, R., Ewers, B.E., Todd, P., Phillips, N., Katul, G., 1998. Water balance delineates the soil layer in which moisture affects canopy conductance. *Ecol. Appl.* 8, 990–1002.
- Oren, R., Phillips, N., Ewers, B.E., Pataki, D.E., Megonigal, J.P., 1999a. Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree Physiol.* 19, 337–347.
- Oren, R., Sperry, J.S., Ewers, B.E., Pataki, D.E., Phillips, N., Megonigal, J.P., 2001. Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded *Taxodium distichum* L. forest: hydraulic and non-hydraulic effects. *Oecologia* 126, 21–29.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999b. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.* 22, 1515–1526.
- Pataki, D.E., Oren, R., 2003. Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest. *Adv. Water Res.* 26, 1267–1278.
- Phillips, N., Oren, R., 1998. A comparison of daily representations of canopy conductance based on two conditional time averaging methods and the dependence of daily conductance on environmental factors. *Ann. Sci. For.* 55, 217–235.

- Roberts, J., 1983. Forest transpiration: a conservative hydrological process? *J. Hydrol.* 66, 133–141.
- Roberts, S., Vertessy, R., Grayson, R., 2001. Transpiration from *Eucalyptus sieberi* (L. Johnson) forests of different age. *For. Ecol. Manage.* 143, 153–161.
- Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. *Plant Cell Environ.* 29, 367–381.
- Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth: what keeps trees from growing beyond a certain height. *Bioscience* 47, 235–242.
- Sabate, S., Sala, A., Gracia, C.A., 1995. Nutrient content in *Quercus-ilex* canopies—seasonal and spatial variation within a catchment. *Plant Soil* 169, 297–304.
- Sawano, S., Komatsu, H., Suzuki, M., 2005. Differences in annual precipitation amounts between forested area, agricultural area, and urban area in Japan. *J. Jpn. Soc. Hydrol. Water Resour.* 18, 435–440 (in Japanese with English summary).
- Schäfer, K.V.R., Oren, R., Tenhunen, J.D., 2000. The effect of tree height on crown level stomatal conductance. *Plant Cell Environ.* 23, 365–375.
- Schäfer, K.V.R., Oren, R., Lai, C.-T., Katul, G.G., 2002. Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO<sub>2</sub> concentration. *Global Change Biol.* 8, 895–911.
- Sperry, J.S., Alder, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitations to plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell Environ.* 21, 347–359.
- Tateno, R., Hishi, T., Takeda, H., 2004. Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. *For. Ecol. Manage.* 193, 297–306.
- Tokuchi, N., Takeda, H., Yoshida, K., Iwatsubo, G., 1999. Topographical variations in a plant–soil system along a slope on Mt Ryuoh, Japan. *Ecol. Res.* 14, 361–369.
- Tromp-van Meerveld, H.J., McDonnell, J.J., 2006. On the interrelationships between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale. *Adv. Water Res.* 29, 293–310.
- Vertessy, R.A., Benyon, R.G., O’Sullivan, S.K., Gribben, P.R., 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiol.* 15, 559–567.
- Vertessy, R.A., Hatton, T.J., Reece, P., O’Sullivan, S.K., Benyon, R.G., 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiol.* 17, 747–756.
- Watanabe, T., Yokozawa, M., Emori, S., Takata, K., Sumida, A., Hara, T., 2004. Developing a multilayered integrated numerical model of surface physics—growing plants interaction (MINoSGI). *Global Change Biol.* 9, 1378–1400.
- Wilson, K.B., Hanson, P.J., Mulholland, P.J., Baldocchi, D.D., Wullschlegel, S.D., 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agric. For. Meteorol.* 106, 153–168.
- World Resources Institute, 2004. EarthTrends 2003. Available online at: <http://earthtrends.wri.org>.
- Wullschlegel, S.D., Hanson, P.J., Todd, D.E., 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. *For. Ecol. Manage.* 143, 205–213.
- Wullschlegel, S.D., King, A.W., 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in a yellow-poplar trees. *Tree Physiol.* 20, 511–518.
- Wullschlegel, S.D., Wilson, K.B., Hanson, P.J., 2000. Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. *Agric. For. Meteorol.* 104, 157–168.
- Zang, D., Beadle, C.L., White, D.A., 1996. Variation of sapflow velocity in *Eucalyptus globulus* with position in sapwood and use of a correction coefficient. *Tree Physiol.* 16, 697–703.