

Up-scaling to stand transpiration of an Asian temperate mixed-deciduous forest from single tree sapflow measurements

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Abstract Species diversity in mixed forest stands is one of the factors that complicate up-scaling of transpiration from individual trees to stand level, since tree species are architecturally and functionally different. In this study, thermal dissipation probes were used to measure sap flow in five different tree species in a mixed-deciduous mountain forest in South Korea. Easily measurable tree characteristics that could serve to define individual tree water use among the different species were employed to scale up transpiration from single trees to stand level. Tree water use (TWU) was derived from sap flux density (SFD) and sapwood area (SA). Canopy transpiration (E) was scaled from TWU while canopy conductance (g_c) was computed from E and VPD. SFD, TWU and g_c were correlated with tree diameter at breast height

(DBH) for all the five measured species (SFD: $R^2 = 0.21$, $P = 0.036$; TWU: $R^2 = 0.83$, $P < 0.001$; g_c : $R^2 = 0.63$, $P < 0.001$). Maximum stand transpiration (E) during June, before the onset of the Asian monsoon rains, was estimated at 0.97 ± 0.12 mm per day. There was a good ($R^2 = 0.94$, $P < 0.0001$) agreement between measured and estimated E using the relationship between TWU and DBH. Our study shows that using functional models that employ converging traits among species could help in estimating water use in mixed forest stands. Compared to SA, DBH is a better scalar for water use of mixed forest stands since it is non-destructive and easily obtainable.

Keywords Allometric scaling · Sap flow · Temperate deciduous forest · Thermal · Dissipation probes · Tree water use

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Introduction

Understanding of water use by forest stands is critical in order to build a sustainable water resource management scheme. Previous attempts have been made to estimate transpiration in diverse tree species using sap flow measurement techniques, which can measure water use at tree level (Granier 1987; Oren et al. 1998; Hubbard et al. 2004; Dierick and Hölscher 2009). In forest monocultures, the individual tree transpiration is then up-scaled to stand level using simple allometrics

(Alsheimer et al. 1998; Köstner et al. 2001). In mixed forest stands, however, species diversity may complicate the up-scaling procedure, due to variations in species structure and function that influence water use by the individual tree species (O'Grady et al. 2009). In cases where species vary in growth forms, for example, those with shorter crowns remain in the sub-canopy where light levels are reduced, the humidity is higher and more constant, with little direct sunlight. Under such conditions, they are bound to experience lower transpiration rates compared to the canopy species, which are subjected to intense radiation, higher wind speeds, and lower humidity.

In cases where the forest is a mixture of deciduous and evergreen tree species, the evergreen species may have higher daily sap flow than the deciduous and semi-deciduous species because of their higher biomass and larger sapwood area involved in water transport (Dünisch and Morais 2002). Tree species may also differ in the way they respond to their abiotic environment, particularly during mild water stress that may occur during the day, and this could also determine the patterns of water use among co-occurring species (Bovard et al. 2005). Differences in transpiration have also been reported between diffuse-porous and ring-porous tree species, regardless of their position in the canopy as a result of differences in their wood structure and function (Oren and Pataki 2001). Structural and functional differences may, therefore, limit the application of simple allometric procedures for scaling up to stand transpiration from single trees.

On the other hand, Bucci et al. (2004) demonstrated that wood density, hydraulic architecture, and plant water relations are related and that wood density is age-dependent and not species-specific characteristic. Thus tree size, rather than species, is the main determinant of stand transpiration, as demonstrated in other more recent studies (Vertessy et al. 1995; Wullschlegel et al. 2001; Meinzer 2003; O'Brien et al. 2004; Meinzer et al. 2005; Zeppel and Eamus 2008). Significant correlation occurred between tree diameter and daily sap flux among 20 different rainforest species (Meinzer et al. 2005). Wullschlegel et al. (2001) derived daily stand transpiration from sap fluxes of five different deciduous tree species using sapwood area, and demonstrated that tree size and not species differences had overriding influence on stand transpiration. O'Brien et al. (2004), investigating 10

tree species in a wet tropical forest reported that structural characteristics such as tree height were the main determinants of tree sap flow. They concluded that the effect of species-specific differences was small and had less influence on stand transpiration. Similar conclusions were drawn by Dierick and Hölscher (2009) and Herbst et al. (2008), showing that maximum tree water use in forest stands is strongly related to tree diameter.

Competition for resources, particularly in resource-limited environments, is likely to compel the convergence of functional traits among diverse species, particularly those that relate to efficient resource acquisition, allowing species to functionally substitute each other (Meinzer 2003; Bucci et al. 2004; O'Grady et al. 2009). This suggests that differences in species may have limited influence on forest water use. In this article, we present results of tree water use from a mixed-deciduous temperate forest stand in South Korea. We hypothesize that stand transpiration is determined by tree structural characteristics, such as tree height, stem diameter etc., and is independent of species composition.

The objectives of the study were to (1) estimate water use in individual trees in a mixed, deciduous forest stand, (2) identify simple and easily measurable structural traits that universally define transpiration of single trees in a mixed temperate deciduous forest, and (3) find a general principle, based on simple functional relationships, which describes mixed stand transpiration.

Materials and methods

Study site

The study was conducted at the Long-term Ecological Research site in Mt. Gyebangsan, Gangwon-do (Province) in South Korea (37°44'41.3''N, 128°26'45.7''E, 960 m. a.s.l), which is located in the northern, cool temperate forest zone. The forest was ca. 40–50 years old and was a natural re-growth after the disturbance through massive logging of Korean forests that took place during and after the Korean War. Mean annual precipitation at Nae-myun (county) weather station, the nearest long-term site (1997–2009) weather recording station located 5.2 km away from the study site was $1,453 \pm 337$ mm (Fig. 1). Approximately

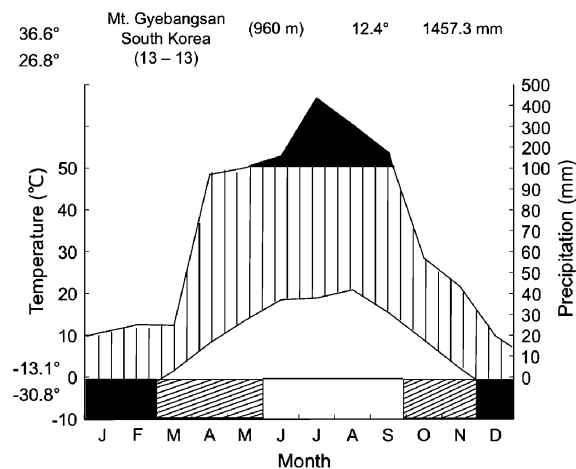


Fig. 1 Climate diagram according to Walter and Lieth (1967) for Mt. Gyeongsan, South Korea. Data was collected at the weather station between 1997 and 2009. Lined area indicates humid period and black area is when average monthly precipitation exceeds 100 mm (from May to September). The altitude of the site was 960 m a.s.l., mean annual temperature was 12.4° and mean annual amount of precipitation was 1,457 mm

45% of the total annual rainfall occurred between June and July, associated with the Asian monsoon. The period between March and April was relatively dry. Mean annual temperature was around 7.8°C with maximum and minimum daily mean air temperatures of 29.3 and -22.5°C occurring in August and January, respectively. The relative humidity within the forest canopy ranged between 52 and 86% most of the year, with July to September being the most humid months. Soils at the study site were classified as brown forest soils (B3) originating from metamorphic bedrock (Kim 2003; Lee et al. 2006).

Vegetation

Long-term vegetation survey has been conducted by the Korea Forest Research Institute (KFRI) at this site since the last 14 years. We demarcated a study plot measuring 40 m × 50 m (0.2 ha) during 2008–2009 to measure tree transpiration using sap flow techniques. A total of 24 different tree species were identified at the study site. Sap flow measurements were carried out on five dominant tree species, including *Tilia amurensis*, *Ulmus davidiana*, *Quercus mongolica*, *Acer mono*, and *Cornus controversa*. A total of 205 trees with DBH > 5 cm were identified within the study plot.

Tree density was 1,025 trees ha⁻¹, with a mean canopy height of 10 m. Mean tree diameter at breast height (DBH) was 15.9 cm with a total basal area of 21.2 m² ha⁻¹. The basal area of the trees was calculated from DBH and included the bark. The selected trees for sap flux measurement covered 70% of the total basal area within the demarcated study plot.

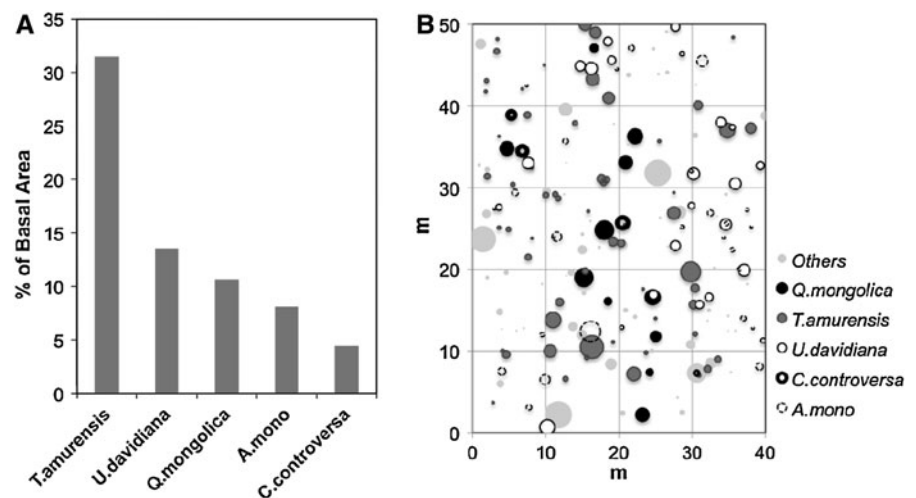
Micrometeorology

Micrometeorology measurements were carried out on the site using automated instruments installed at different locations within the plot in June and July 2008 and repeated over the same period in 2009, concurrently with sap flow measurements. Measurements were conducted inside and above the canopy, the latter using a 20 m scaffolding tower constructed on the site. Weather parameters included: light intensity (UA-002-08, Onset, USA) at 1 m (below the canopy) and at 20 m height (above the canopy), Photosynthetic Active Radiation (PAR) (LI-190, LI-COR, USA) at 20 m, air temperature and humidity (HMP35C, Campbell Scientific Inc., USA) at 5, 10, and 20 m height below, within and above the canopy, and soil water content and temperature (5TE, Decagon Devices, USA) at -5, -15, and -30 cm. These parameters were measured continuously during the experimental period. Data were averaged and logged every 30 min, either with loggers built into the sensors (light intensity) or a central data logger (DL2e, Delta-T Devices, UK). Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity. Precipitation data were obtained from an automated weather station built by the Korea meteorological administration located 5.2 km away from our study site.

Tree allometrics

The sample trees were selected according to species and tree size distribution in the plot (Fig. 2). *T. amurensis* was the dominant species in the plot, occupying 31.5% of the total basal area. *U. davidiana*, *Q. mongolica*, *A. mono*, and *C. controversa* were co-dominant and occupied 13.6, 10.7, 8.1, and 4.4% of the total basal area of the plot, respectively. Thus, these dominant and co-dominant species covered almost 70% of the total basal area of the study plot. We chose five trees each from *Q. mongolica*, *T. amurensis*, and *U. davidiana* and three trees

Fig. 2 a Percentage of basal area of sample tree species in the study plot. The basal area for the five measured species occupied 70% of all trees in the plot. **b** Study site with specific location and relative size of trees. Total plot size was 2,000 m²



each from *C. controversa* and *A. mono*, respectively, for the sap flow measurements. DBH ranges of 13.2–38.2 cm were considered (Table 1).

To estimate the sapwood area (SA) of the sample trees, an increment borer was used to extract cores of sapwood at the sensor installation height (about

Table 1 Studied sample trees at Mt. Gyeongsan, June and July in 2008 and 2009

Species	Sample trees	DBH (cm)	Tree height (m)	Sapwood depth (cm)	Canopy area (m ²)	Mean SFD (g m ² s ⁻¹)	Max SFD (g m ² s ⁻¹)
<i>Q. mongolica</i>	Q1 ^a	27.6	14	2.9	16.0	21.9 ± 3.4	27.7
	Q2 ^a	28.4	14	3.1	37.8	15.9 ± 3.9	23.8
	Q3	20.3	13	2.0	19.8	21.8 ± 3.9	30.8
	Q4	13.3	12	1.4	9.1	4.3 ± 2.6	11.7
	Q5 ^a	38.2	15	4.9	46.5	24.4 ± 4.0	34.6
<i>T. amurensis</i>	T1	29.2	17	1.5	18.8	38.9 ± 9.3	54.5
	T2	18.9	14	0.8	9.0	7.7 ± 2.8	13.5
	T3	26.8	15	1.3	14.7	38.7 ± 8.9	53.2
	T4	13.2	12	0.6	16.8	21.4 ± 7.8	33.9
	T5	17.8	13	0.8	18.5	18.6 ± 7.7	32.7
<i>U. davidiana</i>	U1	23.1	15	1.6	11.2	22.9 ± 5.4	32.0
	U2	23.4	14	1.7	37.2	14.3 ± 2.4	18.3
	U3	28.6	16	2.2	22.7	23.3 ± 3.9	30.4
	U4	26.1	15	1.9	37.1	21.3 ± 4.9	30.1
	U5	18.7	15	1.3	18.5	28.9 ± 4.1	35.4
<i>C. controversa</i>	C1	25.3	15	1.2	62.5	34.0 ± 7.6	48.8
	C2	22.3	15	1.0	41.9	33.4 ± 7.0	49.3
	C3	17.6	15	0.7	28.8	15.7 ± 5.7	27.9
<i>A. mono</i>	A1	15.0	13	0.3	13.3	15.7 ± 5.7	27.0
	A2	22.0	14	0.5	38.7	30.7 ± 12.4	50.2
	A3	13.8	11	0.3	12.1	31.9 ± 13.9	57.8

Diameter at breast height (DBH) was measured at the beginning of sensor installation. Tree height was measured in 2007 and sapwood depth was estimated by empirical regression models of DBH (see Fig. 5). Projected canopy area was measured in late fall, 2008 and sap flux density (SFD) was measured during June 2008 and 2009

^a Trees with a sapwood depth larger than 20 mm had two sensors in different depth

1.3 m height) on same species, but different trees from those installed with the sap flow sensors. Sapwood depth was determined visually on those cores since sapwood and heartwood were clearly distinguishable. Sapwood area was determined from sapwood depth and tree DBH based on the equation (Vertessy et al. 1995, Meinzer et al. 2005):

$$SA = \alpha \times DBH^\beta \quad (1)$$

where α is a constant and β is the allometric scaling exponent, and both are species-specific coefficients. Coefficients of the regression models for each measured species, number of samples and R^2 are provided in the legend of Fig. 5.

The ground-projected crown area (A_{cp} , m^2) of sample trees was measured in eight horizontal directions using a compass, crown mirror, and measuring tape. The octagonal area was calculated as the sum of eight triangles (Schmidt 2007). These results were used to compute canopy conductance (g_c , $mm\ s^{-1}$).

Tree sap flow

Sap flux density (SFD) was measured in the tree stems of five trees per species using the thermal dissipation method (Granier 1987) during June and July 2008 and repeated during the same period in 2009. This period was chosen as it was considered the most active period in the context of plant water use, just before the onset of the Monsoon rains. All sensor installations were made on the north-facing side of the trees to avoid exposure to the sun and minimize direct short-wave radiation (Wilson et al. 2001; Wullschlegel et al. 2001). In addition, the sensors were covered with a radiation shield (Styrofoam sheets with aluminum foil) to further minimize the direct thermal load. Power for heating the sensors was provided by lead-acid batteries that were recharged with solar panels via a charge controller. Each sensor consisted of a pair of 2 mm diameter probes vertically aligned ca. 15 cm apart. Each probe included a 0.2 mm diameter copper–constantan thermocouple. The two thermocouples were joined at the constantan leads, so that the voltage measured across the copper leads provided the temperature difference between the heated upper probe and the lower reference. Heating across the entire length of the 20 mm upper probe was achieved with a constant

current of 120 mA supplied to a constantan heating wire, resulting in a heating power of 200 mW (Granier 1987).

Sensors were placed in the outer 20 mm of the sapwood (annulus 1, 0–20 mm radial sapwood depth). In cases where the tree trunk was large with a sapwood radius greater than 20 mm (Table 1), a second sensor was implanted 20 to 40 mm into the sapwood. Sensors were spaced 10–15 cm circumferentially, away from the first sensor pair, on the same side of the stem to avoid azimuth differences. Temperature differences were measured every 5 min and a 30-min mean value was logged (DL2e with LAC-1 in single ended mode, Delta-T Devices, England). Sap flux density (SFD, $g\ m^{-2}\ s^{-1}$) for each sensor was calculated from ΔT in accordance with Granier (1987), assuming zero SFD (i.e. ΔT_{max}) at night and VPD near zero:

$$SFD = 119K^{1.231} \quad (2)$$

where,

$$K = \frac{(\Delta T_{max} - \Delta T)}{\Delta T} \quad (3)$$

Tree water use (TWU, $kg\ h^{-1}$) was obtained by multiplying SFD by sapwood cross-sectional area (SA, m^2):

$$TWU = \sum_{i=1}^n (SFD_i \times SA_i) \quad (4)$$

where, SFD_i is sap flux density of the annulus i ($g\ m^{-2}\ s^{-1}$) and SA_i is sapwood area of the annulus i (m^2). This took into account the second annulus ring, in case a second sensor was installed into the tree. For example, $i = 1$ was annulus ring 0–20 mm sapwood depth, $i = 2$ was annulus ring 20–40 mm sapwood depth.

Stand transpiration (E , mm per day) was computed by summing the contributions from all the trees in the study plot:

$$E = \sum_{j=1}^n TWU_j \times A_{plot}^{-1} \quad (5)$$

where, TWU_j is tree water use of tree j ($kg\ h^{-1}$) and A_{plot} is plot area (m^2). TWU of the trees on which sensors were not installed was estimated from the relationship between SFD and the computed SA of each species (Eq. 1).

Estimation of canopy conductance

Canopy conductance was calculated from the sap flow measurements or stand/canopy transpiration, in relation to climate variables: half hourly averaged air temperature, VPD, and canopy transpiration as described by Köstner et al. (1992):

$$g_c = (\rho_w \cdot G_v \cdot T_k) \cdot \frac{E_c}{D} \quad (6)$$

where, ρ_w is density of water (998 kg m^{-3}) and G_v is gas constant of water vapor ($0.462 \text{ m}^3 \text{ kPa kg}^{-1} \text{ K}^{-1}$), T_k is air temperature (K), D is VPD of the air (kPa), E_c is canopy transpiration (mm s^{-1}) (Schmidt 2007). To estimate g_c based on this model, data from measurements between 10 and 15 h, when half hourly rates of E_c were highest, were used. This model assumed that tree canopies were well coupled to the atmosphere, so that aerodynamic conductance (g_a) was larger than g_c (Köstner et al. 1992; Phillips and Oren 1998).

Statistical analyses

SFD and environmental variables were recorded as half hourly averaged values. These variables, including TWU and g_c estimated from SFD were converted into daily averages. Data are presented as mean \pm standard deviation (SD). SFD, TWU, and g_c were compared between years and also among tree species using one-way ANOVA. Where differences were found among species, a post-hoc Kruskal–Wallis test was carried out. Normality of samples was established by testing the residuals obtained from the ANOVA. Measured and estimated E by the relationship between TWU and DBH were compared with t -test. Regression analysis was tested with Pearson correlation test. All statistical analyses including regression models were based on a 0.05 significance level and performed with R version 2.6.2 (R Development Core Team 2009).

Results

Micrometeorological and soil moisture measurements

Daily mean air temperatures over the measurement period of June and July were about 19.3°C in 2008

and 18.3°C in 2009. Averaged daily VPD were 0.34 kPa in 2008 and 0.28 kPa in 2009, while the summed daily PAR were $32.6 \text{ mol m}^{-2} \text{ day}^{-1}$ in 2008 and $25.9 \text{ mol m}^{-2} \text{ day}^{-1}$ in 2009, respectively (Fig. 3a). The total amount of precipitation recorded during the measurement period was 89 mm in 2008, and 178.5 mm in 2009. Mean SWC within the 30 cm soil profile was $0.24 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$ in 2008 and $0.21 \pm 0.05 \text{ m}^3 \text{ m}^{-3}$ in 2009 (Fig. 3b). Before the onset of our experiments 2009 was comparatively drier than 2008, as demonstrated by lower SWC at the beginning of measurements. A rainstorm event on June 3, 2009 amounting to 73 mm , however, significantly raised the SWC (from 0.11 to $0.29 \text{ m}^3 \text{ m}^{-3}$), and SWC thereafter was comparable to 2008.

Transpiration rate and canopy conductance

Mean maximum sap flux density (SFD_{max}) for the 21 trees measured was $247.5 \pm 93.1 \text{ kg m}^{-2} \text{ h}^{-1}$ in 2008 and $271.5 \pm 97.1 \text{ kg m}^{-2} \text{ h}^{-1}$ in 2009 (Table 2). There was no significant ($F = 0.88$, $P = 0.35$) difference in SFD between the 2 years. And also, mean maximum tree water use (TWU_{max}) was $21.0 \pm 21.8 \text{ kg day}^{-1}$ in 2008 and $32.9 \pm 22.0 \text{ kg day}^{-1}$ in 2009 (Table 2). A comparison of maximum TWU from different years showed same results ($F = 1.00$, $P = 0.33$). Mean daily SFD of *Q. mongolica*, *T. amurensis*, *U. davidiana*, *C. controversa*, and *A. mono* were $40.9 \pm 17.8 \text{ kg m}^{-2} \text{ h}^{-1}$ ($n = 5$), $49.5 \pm 26.1 \text{ kg m}^{-2} \text{ h}^{-1}$ ($n = 5$), $49.2 \pm 8.4 \text{ kg m}^{-2} \text{ h}^{-1}$ ($n = 5$), $59.5 \pm 24.5 \text{ kg m}^{-2} \text{ h}^{-1}$ ($n = 3$), and $55.4 \pm 17.8 \text{ kg m}^{-2} \text{ h}^{-1}$ ($n = 3$). Tree water use (TWU) and g_c averaged over the measurement period are shown in Table 3. The mean daily TWU ranged from 1.2 kg day^{-1} for *A. mono* with DBH of 15.0 cm to 70.1 kg day^{-1} for *Q. mongolica* with DBH of 38.2 cm . And mean g_c amounted from 0.7 mm s^{-1} for *Q. mongolica* with DBH of 13.3 cm to 16.1 mm s^{-1} for *T. amurensis* with 29.2 cm . Mean maximum g_c of the stand was $5.6 \pm 4.8 \text{ mm s}^{-1}$.

The averaged E was $0.64 \pm 0.26 \text{ mm day}^{-1}$ in 2008 and $0.70 \pm 0.30 \text{ mm day}^{-1}$ in 2009. The maximum E occurred around day 177 in 2009 (June 26, 0.97 mm day^{-1} , Fig. 4), coinciding with the highest daily total PAR and VPD. There were no significant ($F = 0.31$, $P = 0.73$) differences in daily transpiration among *Q. mongolica*, *T. amurensis*, and

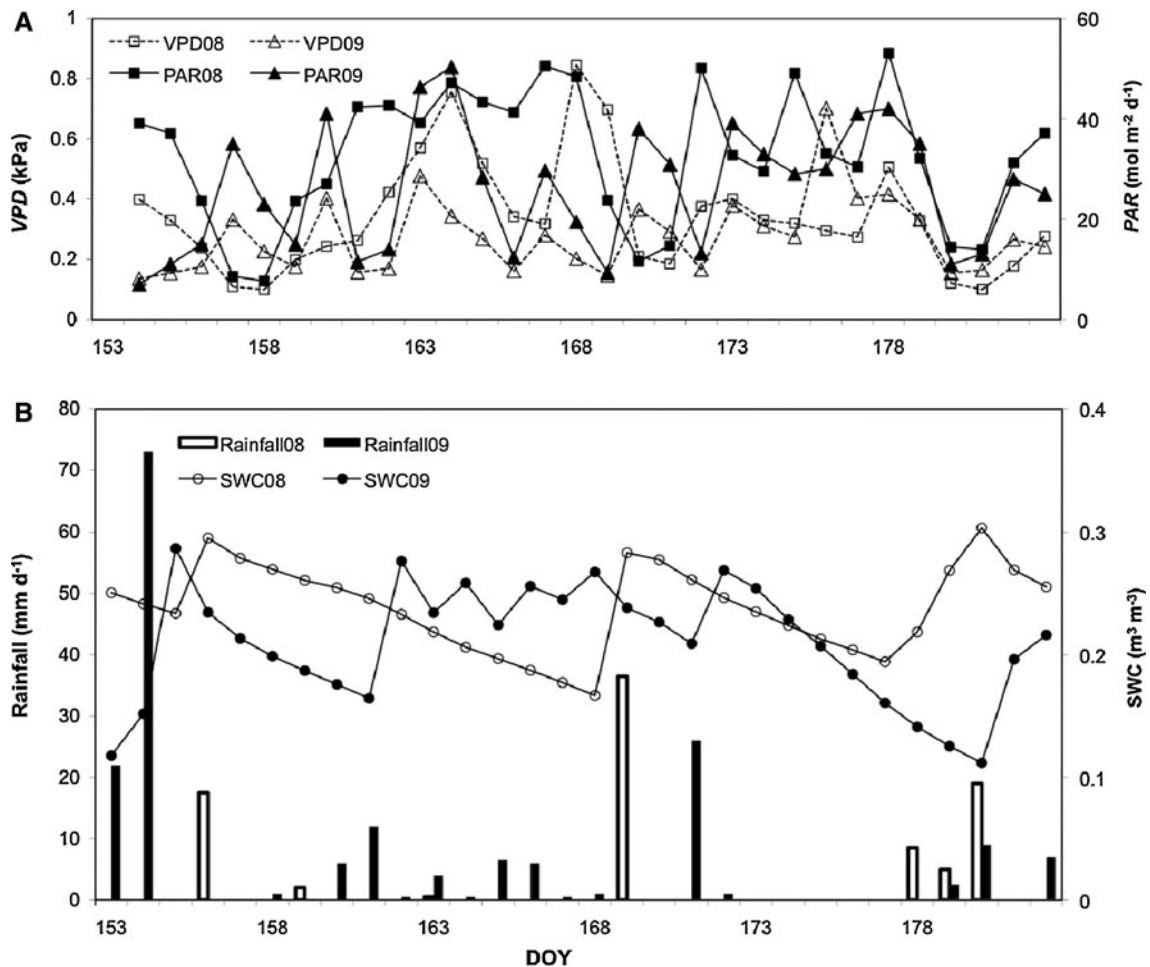


Fig. 3 **a** Daily mean vapor pressure deficit (VPD, kPa) and daily amounts of photosynthetically active radiation (PAR, mol m⁻² day⁻¹), **b** rainfall (mm day⁻¹) and soil water content

(m³ m⁻³) recorded at the study site during June 2008 and 2009 when sap flow measurements were conducted

Table 2 Maximum sap flux density (SFD_{max}) and maximum tree water use (TWU_{max}) averaged over 21 measured trees from June 2008 and June 2009

	June 2008	June 2009	<i>F</i> value	<i>P</i> value
Max. SFD (kg m ⁻² h ⁻¹)	247.48	271.46	0.8834	0.3529
SD	93.13	97.14		
Max. TWU (kg d ⁻¹)	21.02	32.91	0.9971	0.3264
SD	21.77	22.02		

U. davidiana. The percentage mean contribution of the three species was about 30% each, while *Cornus controversa* and *A. mono* each accounted for about 4% of the total transpiration. There was no significant

influence of species on SFD ($P = 0.82$), TWU ($P = 0.19$), and g_c ($P = 0.23$).

Relationship between tree water use and tree size

Parameters derived from the allometric equation (Eq. 1) relating SA and DBH of the five different species are shown in Fig. 5. The converged regression model inverted from the five different species showed a strong relationship ($n = 35$, $R^2 = 0.81$, $P < 0.001$) between SA and DBH. This model was used to compute SA of non-measured species to arrive at SA for the whole study plot. *Q. mongolica* (0.15 m² ha⁻¹), *T. amurensis* (0.29 m² ha⁻¹), *U. davidiana* (0.16 m² ha⁻¹), *C. controversa* (0.03 m² ha⁻¹),

Table 3 Mean tree water use (TWU, kg day⁻¹) and canopy conductance (g_c , mm s⁻¹) of individual tree species

Species	Sample trees	Mean TWU (kg day ⁻¹)	Mean g_c (mm s ⁻¹)
<i>Q. mongolica</i>	Q1	27.8 ± 11.6	13.1 ± 4.3
	Q2	20.1 ± 9.1	3.4 ± 0.9
	Q3	14.2 ± 6.4	4.3 ± 1.7
	Q4	1.3 ± 0.7	0.7 ± 0.2
	Q5	70.1 ± 23.4	9.7 ± 4.1
<i>T. amurensis</i>	T1	20.4 ± 9.7	16.1 ± 4.3
	T2	1.9 ± 0.9	2.0 ± 0.8
	T3	17.2 ± 5.2	6.7 ± 2.2
	T4	2.6 ± 1.3	2.1 ± 0.6
	T5	3.7 ± 2.0	2.4 ± 0.6
<i>U. davidiana</i>	U1	13.7 ± 5.7	13.4 ± 2.9
	U2	9.2 ± 2.9	7.0 ± 1.2
	U3	22.3 ± 7.7	9.2 ± 2.9
	U4	17.3 ± 5.5	5.4 ± 2.3
	U5	9.1 ± 3.7	2.9 ± 0.8
<i>C. controversa</i>	C1	14.7 ± 5.4	4.2 ± 1.8
	C2	10.8 ± 4.0	2.8 ± 0.9
	C3	2.8 ± 1.3	1.5 ± 0.4
<i>A. mono</i>	A1	1.2 ± 0.6	2.3 ± 0.6
	A2	5.4 ± 3.1	2.6 ± 0.7
	A3	2.0 ± 1.0	1.6 ± 0.5

and *A. mono* (0.06 m² ha⁻¹), accounted for 79.3% of total SA which was 0.87 m² ha⁻¹ (study plot = 0.2 ha).

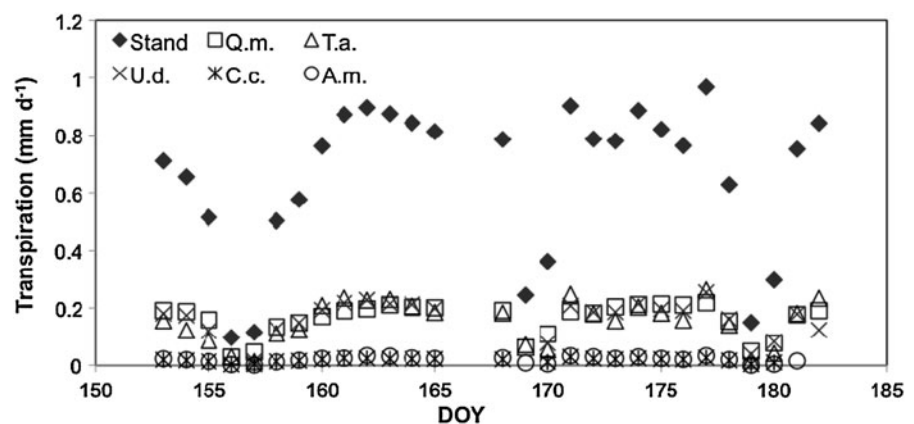
Observed SFD, TWU and g_c were dependent on tree size, determined by DBH and SA. SFD and TWU had a stronger dependency on DBH than on SA. For example, a regression of SFD in individual trees

against SA did not show any relationship ($n = 21$, $R^2 = 0.03$, $P > 0.44$), but a regression between SFD and DBH showed that DBH could explain 21% of the observed variability ($n = 21$, $R^2 = 0.21$, $P = 0.036$) in SFD among the studied trees (Fig. 6a). Moreover, the relationship between mean daily TWU and DBH was stronger ($n = 21$, $R^2 = 0.87$, $P < 0.001$) for all measured species (Fig. 6b). SA was also significantly correlated with TWU, but less than DBH ($n = 21$, $R^2 = 0.83$, $P < 0.001$). g_c had significant relationship with both DBH and SA, and also like other relations g_c was correlated better with DBH ($n = 17$, $R^2 = 0.63$, $P < 0.001$) (Fig. 6c) than SA ($n = 17$, $R^2 = 0.48$, $P = 0.002$). E estimated from measured TWU was compared with E^* estimated from modeled TWU based on the relationship of DBH and TWU (Fig. 6b). In this study, the empirical model was $TWU = 0.0002 \times DBH^{3.4302}$ for mean daily TWU over the measurement period ($P < 0.001$). There was a strong agreement ($n = 22$, $R^2 = 0.94$, $P < 0.0001$) between the measured and modeled E^* .

Relationship between tree water use and climate factors

Both VPD ($R^2 = 0.78$ and $P < 0.0001$) and PAR ($R^2 = 0.91$, $P < 0.0001$) (Fig. 7) could explain most of the daily fluctuations in E . E increased with increasing VPD, attaining a maximum at VPD = 0.5 kPa, but later dropped at higher VPD (Fig. 7a). On days when VPD was high, E increased during morning hours with increasing PAR and reached a maximum at around midday, when PAR was $>1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 7b). Canopy conductance (g_c) of the stand corresponding to the light conditions more than

Fig. 4 Estimated stand transpiration (E , mm day⁻¹) and transpiration of measured species, *Quercus mongolica* (Q.m.), *Tilia amurensis* (T.a.), *Ulmus davidiana* (U.d.), *Cornus controversa* (C.c.), and *Acer mono* (A.m.)



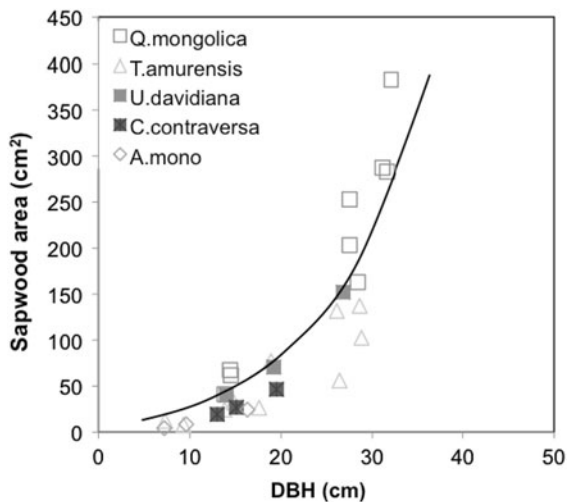


Fig. 5 Relationship between sapwood area (SA, cm²) determined from increment core extracted from more than five samples per species and their respective DBH ($n = 35$, $R^2 = 0.81$, P value < 0.001). The regression equation for *Quercus mongolica* was $SA = 0.2067 \text{ DBH}^{2.1}$ ($n = 9$, $R^2 = 0.94$), for *Tilia amurensis* was $SA = 0.1846 \text{ DBH}^{2.0}$ ($n = 10$, $R^2 = 0.85$), for *Ulmus davidiana* was $SA = 0.1745 \text{ DBH}^{2.1}$ ($n = 3$, $R^2 = 0.98$), for *Cornus controversa* was $SA = 0.0757 \text{ DBH}^{2.2}$ ($n = 3$, $R^2 = 0.98$), for *Acer mono* was $SA = 0.0215 \text{ DBH}^{2.4}$ ($n = 3$, $R^2 = 0.98$), and for all the studied species was $SA = 0.053 \text{ DBH}^{2.4}$ ($n = 35$, $R^2 = 0.81$)

20 mol m⁻² day⁻¹ of PAR, was plotted against VPD (Fig. 7c). The selected data showed a log-linear relationship between g_c and VPD ($R^2 = 0.69$, $P < 0.0001$). This regression model agreed with the simplified model of Lohammer et al. (1980):

$$g_c = b - c \times (\ln \text{VPD}) \quad (7)$$

where, b is g_c at a reference VPD = 1 kPa.

Discussion

Tree water use and environmental factors

Five phylogenetically diverse temperate forest tree species were studied to identify any shared characteristics in their water use and whether these shared characteristics could aid in upscaling of transpiration in mixed-deciduous forest stands. We examined the relationship between tree size and the area of hydraulically active xylem and used this functional relationship to scale up tree water use from single trees to stand level, based on simple and easily measurable

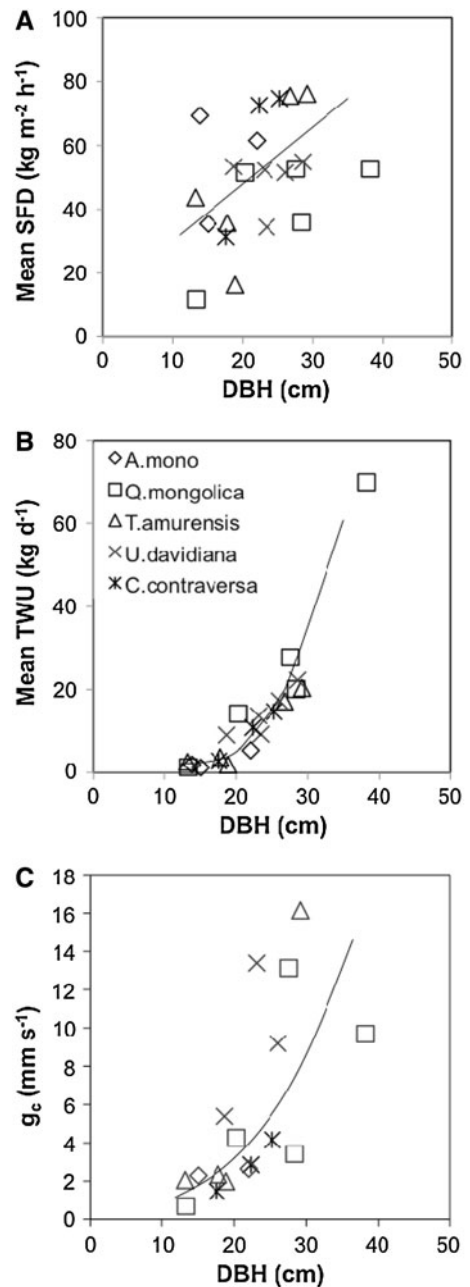


Fig. 6 Relationship between DBH and **a** mean sap flux density (SFD, kg m⁻² h⁻¹) ($n = 21$, $R^2 = 0.21$, P value = 0.036), **b** mean tree water use (TWU, kg day⁻¹) ($n = 21$, $R^2 = 0.87$, P value < 0.001) and **c** canopy conductance (g_c , mm s⁻¹) significant ($n = 17$, $R^2 = 0.63$, P value < 0.001), of all the measured trees

allometry. We provide the first estimates of tree water use in this region and report the first study in which sap flux measurements have been concurrently carried out

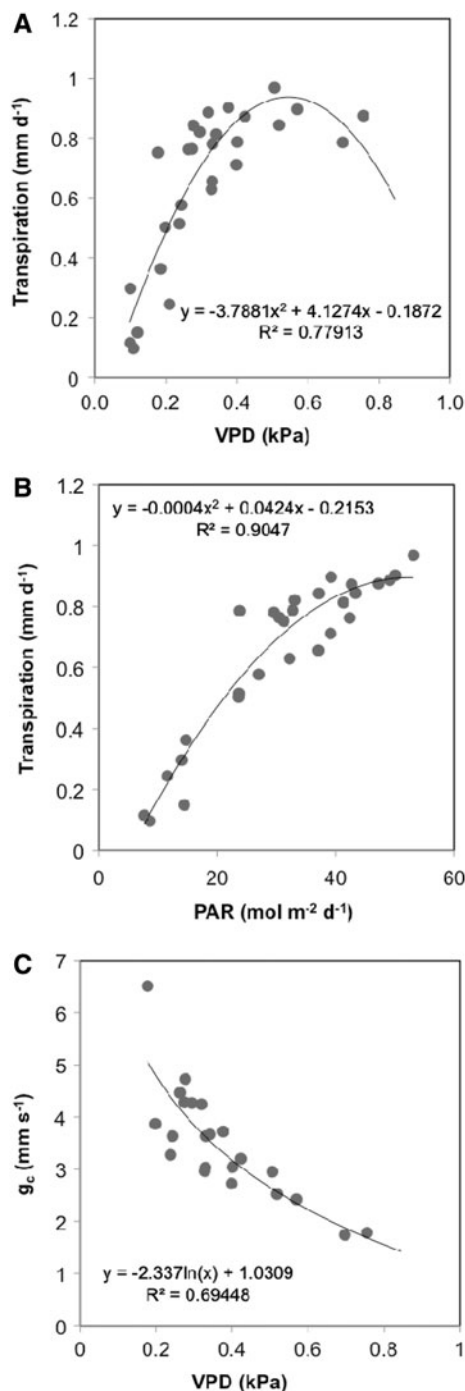


Fig. 7 **a** Relation between vapor pressure deficit (VPD, kPa) and stand transpiration (E) ($n = 28$, $R^2 = 0.78$, P value < 0.0001). **b** Tree transpiration (E , mmol day^{-1}) and photosynthetically active radiation (PAR, $\text{mol m}^{-2} \text{day}^{-1}$) ($n = 28$, $R^2 = 0.91$, P value < 0.0001) and **c** Canopy conductance of the stand (g_c , mm s^{-1}) under non-limiting light condition decreased and VPD ($n = 22$, $R^2 = 0.69$, P value < 0.0001)

on several species in mixed-deciduous forests of South Korea. Han and Kim (1996) measured SFD of *Q. mongolica* during a growing season in S. Korea using heat pulse methodology and reported maximum SFD values of $40 \text{ kg m}^{-2} \text{h}^{-1}$, occurring in May. These rates are comparable with the maximum SFD of $40.9 \pm 17.8 \text{ kg m}^{-2} \text{h}^{-1}$ observed for *Q. mongolica* in our study.

The maximum E was 0.97 mm day^{-1} when daily sum VPD was 24.2 kPa , daytime mean VPD was 0.67 kPa and the daily sum PAR was $53.1 \text{ mol m}^{-2} \text{day}^{-1}$. These rates are lower compared to those reported in other studies on temperate deciduous stands (Oren and Pataki 2001; Wullschlegler et al. 2001). For example, peak stand transpiration of upland oak forest of east Tennessee, USA was 2.2 mm day^{-1} in May prior to canopy closure when the maximum daily sum VPD was 35 kPa (Wullschlegler et al. 2001). Maximum daily stand transpiration of the Duke forest, North Carolina, dominated by *Quercus* and *Acer* species reached 2 mm day^{-1} when daytime mean VPD was almost 2.2 kPa (Oren and Pataki 2001). Under conditions of sufficient soil water availability, light and VPD control the canopy conductance and hence transpiration (Granier and Bréda 1996). Mean daily maximum VPD at our study site was between 0.3 and 0.6 kPa during most of the days. This VPD range was lower compared to a range of 0.5 – 2.2 kPa reported for the above studies and may account for the lower E measured at this study site.

In mixed forest stands, different species have different crown structures and characteristics that modify the crown environment. Different species and forest trees, therefore, have varying access to light above and within the canopy. The VPD below the canopy is modified since wind speed is reduced and air circulation lower compared to that above the canopy. Moreover, VPD below the canopy could be lower because of the transpiration of the understory and the lower canopy. Canopy trees, therefore, gain more access to direct solar radiation compared to suppressed ones, which grow below the canopy and have access only to diffuse light and light flecks (Köstner et al. 1992). Differences in crown exposure may, therefore, account for the differences in transpiration rates among the studied tree species. For example, *Q. mongolica*, *T. amurensis*, and *U. davidiana* were canopy trees, constituting more than 80%

of the total canopy cover in the study plot and accounted for approximately 75% of the total stand transpiration.

Tree water use and functional convergence

Despite their phylogenetic diversities, the five deciduous species studied showed a convergence in their water use and water use functions (Fig. 6b). These results support our hypothesis that trees of different species growing together in a common location tend to have converging water use strategies. This assumption was based on the fact that tree transpiration is regulated by the microclimate prevailing above the forest canopy and soil moisture condition (Hinckley et al. 1978). As long as soil water is not limiting, as was the case at our study site, tree transpiration will basically be influenced by the microclimate and the ability to transport water through the xylem (Oren and Pataki 2001). We established a strong relationship between the conducting surface area and TWU. It is, therefore, not surprising that water use by the different species is similar. Thus, water use by the different tree species in a mixed stand could be explained by the existing SA as long as the trees are exposed to similar environments.

Estimation of SA in forest trees is complex and destructive. Previous attempts have been made to identify easily measurable parameters that accurately describe sapwood area, and which can ultimately be employed as surrogates for SA. For example, Vertessy et al. (1995) compared stem DBH, SA, and leaf area as a scaling factor in tree water use from individual tree level to stand level and all three methods gave similar results. Although leaf area may potentially be estimated from remotely sensed data (Wessman et al. 1988), which require less manpower in the field, DBH is the more easily available and measurable scaling factor. Therefore, the revelation that DBH describes SA of this mixed forest could be a significant step toward quantifying forest water use in the species rich temperate forests, which occur in this complex mountainous terrain of S. Korea. In our study, a power function of the form $Y = \alpha \times X^\beta$ appeared to be an adequate model for estimating SA and TWU from DBH. Thus, in mixed native temperate stands, water use traits of diverse species could be generalized with tree size characteristics.

This relationship between water use traits and tree size was not influenced by the species under consideration. In our study, DBH accounted for 87% but SA accounted for 84% of the variation in total daily TWU among five different tree species. Köstner et al. (1992) suggested that TWU could be more closely related to tree circumference or diameter than SA. We also found that the relationship between mean TWU (kg day^{-1}) and DBH was somewhat stronger than SA. Both regressions were, however, significant with P values < 0.0001 . Our results resemble those of Zeppel and Eamus (2008), who observed that the relationship between daily total water use and DBH did not differ between broad-leaved and needle-leaved species, at any time in a native temperate stand in Australia.

The relationship between DBH and SFD was weak ($R^2 = 0.21$). We, however, established an increasing trend of SFD with increasing DBH ($P = 0.036$). Our results compared well with other previous studies conducted by Granier et al. (1996) and Oren et al. (1998). On the other hand, Meinzer et al. (2001) observed a negative correlation between maximum SFD and DBH from 23 species ($R^2 = 0.85$). Phillips et al. (1999) observed no relationship at all between DBH and SFD.

The relationship between SA and DBH in temperate forests may be different from other forest ecosystems. For example, the degree of increasing SA with DBH in tropical forest (Meinzer et al. 2001) is steeper than the result we found in this temperate forest. This is mainly because plants are differently adapted to different habitats and vary in their plant traits (Grime and Hunt 1975). The allometric model with tree transpiration rate reported here is not consistent with the predicted universal model suggested by Enquist et al. (1998), which considered 37 different species and growth forms, including herbaceous plants, shrubs, tree seedlings, and mature evergreen and deciduous trees. Even though the increasing pattern with DBH was same, the model we proposed here showed much less transpiration rates against DBH. We attribute these differences to the existing climate conditions, which regulate daily maximum transpiration rates. This result could be caused by different compositions of the samples and different DBH range of studied plants. Besides, their universal model covered a larger DBH range, from 0.2 to 100 cm, while in our study we considered DBH

range from 13 to 38 cm only. If we consider habitat effects, calibrations should be done for each measurement site and the environmental conditions of the calibration should represent the measurement period (Sevanto et al. 2008).

Although we found that for these five deciduous species, variation in water use was governed largely by tree size, during the course of the day, however, this capacity may be regulated by stomatal response to light and VPD. During the morning hours, transpiration increased with increasing light intensities but saturated or decreased when PAR levels rose above $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$. PAR above $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ in most cases coincided with VPD greater than 0.2 kPa at which stomatal closure was observed. Stomatal conductance in *Nothofagus* trees located near the top of the canopy decreased by 50% as VPD increased from 0.5 to 1.2 kPa (Köstner et al. 1992). We observed stomatal closure from a VPD of 0.2 kPa but it was only from a VPD of 0.6 kPa that a significant reduction in transpiration was observed (not shown). Our study site was located at an elevation of 960 m a.s.l and is influenced by cool climatic conditions and high precipitation such that VPD remains below 0.2 kPa most of the time. It is likely that long-term adaptations make trees more sensitive to VPD changes, and trees growing in cool and moist environments experience stomatal closure at lower VPD compared to their counterparts in warmer and drier locations. For example, Luis et al. (2005) showed stomata closing in the range of VPD from 0.1 to 1.5 kPa at 1650 m a.s.l. during the wet season. Kumagai et al. (2008) working under similar low VPD conditions reported stomatal closure starting at 0.25 kPa. These are very interesting findings that require further investigations and an extension to more species in order to derive general principles that explain water use by highly mixed forest stands.

Conclusion

Tree water use in the five deciduous species was effectively explained by tree size (DBH) irrespective of species. Thus, whole tree water use could be effectively estimated using a simple general model that relates TWU with DBH, for these five different deciduous species. Although there is need to extend these investigations onto other forest species, results from these five species showed that DBH is a good

scaling factor for estimating forest water use in the rugged terrain of S. Korea. The advantage of DBH is that it is easily obtainable and is also non-destructive compared to, for example, LAI and SA, respectively. Our findings are a significant contribution to the ongoing efforts to build hydrology budgets of S. Korea.

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