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Variation in sap flux density and its effect on stand transpiration estimates of Korean pine stands

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Abstract Accurate estimates of stand transpiration (E) require the consideration of three types of variation in sap flux density (J_S) : radial, azimuthal, and tree-to-tree variation. In this study, the $J_{\rm S}$ variation of 50-year-old Korean pine (Pinus koraiensis) trees and its effect on E estimates was evaluated using Granier-type heat dissipation sensors. The value of $J_{\rm S}$ decreased exponentially with the radial depth from cambium to pith, and the coefficient of variation (CV) for radial variation was 124.3 %. Regarding the azimuthal variation, the value of $J_{\rm S}$ differed significantly among aspects and the average CV was 23.6 %. The average CV for tree-to-tree variation was 34.0 %, and the daily CV increased with increasing vapor pressure deficit (D). The error in the *E* estimates caused by ignoring the radial variation was the largest (109.2 %), followed by those caused by ignoring the tree-to-tree and azimuthal variations (24.3 and 12.6 %, respectively). While the contribution of the azimuthal variation to the E estimates was minimal in comparison to the other variations, the azimuthal variation among aspects was

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Research Institute for Agriculture and Life Sciences, 1 Gwanakro, Gwanak-gu, Seoul 151-921, Republic of Korea significant, and the usage of the north aspect measurement did not generate substantial error in the E estimates (0.6 %). Our results suggest that the variation, particularly the species- and site-specific radial variation, must be considered when accurately calculating E estimates.

Keywords Azimuthal variation · Radial variation · Sap flux · Stand transpiration · Tree-to-tree variation

Introduction

The transpiration rates of individual trees are commonly measured with various types of sap flux density (J_S) sensors [e.g., heat dissipation (Granier 1985), heat field deformation (Jiménez et al. 2000), and heat pulse velocity (Hatton et al. 1995)], and this tree-level estimation is subsequently scaled up to stand- or catchment-level transpiration. Sap flux sensors are particularly useful in complex terrain such as mountain regions, where they are employed in conjunction with data loggers to store continuously measured data (Granier et al. 1996; Köstner et al. 1998; Wilson et al. 2001; Kubota et al. 2005; Kume et al. 2010b).

However, the spatial variation of J_S within or among trees complicates the scaling from point measurements to tree- or stand-level transpiration rates (Phillips et al. 1996; Cermak and Nadezhdina 1998; Oren et al. 1998; Wilson et al. 2001; Ford et al. 2007; Tateishi et al. 2008; Kume et al. 2010a; 2012; Paudel et al. 2013), as the J_S sensor captures only a trivial proportion of the spatial variation in J_S throughout the entire xylem (Clearwater et al. 1999; Kumagai et al. 2005; Gebauer et al. 2008; Caylor and Dragoni 2009; Kume et al. 2010b; Barij et al. 2011; Alvarado-Barrientos et al. 2013; Paudel et al. 2013; Shinohara et al. 2013; Chang et al. 2014). Therefore, a large error may be introduced when J_S is scaled from a single point measurement to the whole tree without consideration of its spatial variation; that is, its radial, azimuthal, and tree-to-tree variations, which represent the J_S variation with xylem radial depth from the cambium, around the stem, and among trees within a stand, respectively.

Regarding radial variation, $J_{\rm S}$ normally decreases with radial depth from the cambium, especially in coniferous species (e.g., Phillips et al. 1996; Ford et al. 2004b; Fiora and Cescatti 2006). However, the radial profile of $J_{\rm S}$ differs between species and even among individual trees of the same species, and ignoring this variation can cause errors of up to 300 % in E estimates (Nadezhdina et al. 2002; Čermák et al. 2004; Kume et al. 2010b). Although azimuthal variation is commonly minimal compared to other variations, failing to consider it can also cause significant errors in E estimates. Tateishi et al. (2008) and Tsuruta et al. (2010) reported that the errors due to ignoring azimuthal variation reached 20 % in Quercus glauca and 30 % in Chamaecyparis obtuse based on tree-level estimation. Nevertheless, many studies still use one-directional measurement, usually of the north aspect, based on the assumption that azimuthal variation is trivial when a large number of sensors are used for scaling to the tree or stand level (e.g., Wilson et al. 2001; Poyatos et al. 2007; Alvarado-Barrientos et al. 2013). Finally, tree-to-tree variation is another key factor in accurate *E* estimates, as tree-to-tree variation within the same stand and species can vary considerably; therefore, disregarding tree-to-tree variation can also cause significant error in E estimates (Delzon et al. 2004; Kumagai et al. 2005; Kume et al. 2010b; Kume et al. 2012; Shinohara et al. 2013).

As mentioned above, the variation in J_S consists of several different variations (i.e., the radial, azimuthal, and tree-to-tree variations). However, several studies have examined these separate components of the variation in J_S in order to compare their impacts on *E* estimates in tree stands (e.g., Kume et al. 2012; Shinohara et al. 2013). Kume et al. (2012) reported that the errors caused by azimuthal variation (16. and 21.6 %) were smaller than the errors caused by radial (33 and 44 %) and tree-to-tree (50 and 52 %) variations in *Robinia pseudoacacia* and *Quercus liaotungensis*, respectively. Shinohara et al. (2013), who studied a *Cryptomeria japonica* plantation, reported that the error caused by radial variation (15.1 %) was smaller than the errors caused by azimuthal and tree-to-tree variations (16.1 and 18.9 %, respectively).

Although these studies quantified the various variations and compared their effects on E estimates, their relative importance to E estimates was rather species- and sitedependent. Thus, these results have limited application for accurately estimating E in other species or sites. Therefore, in the present study, we evaluated the radial, azimuthal, and tree-to-tree variations in J_S for 50-year-old Korean pine trees in a plantation to obtain accurate *E* estimates using a heat dissipation sensor designed by Granier (1985). The purposes of the study were to (1) determine the levels of the three different types of J_S variation and (2) calculate the errors in *E* estimates when these spatial variations were not considered.

Materials and methods

Site description

Our study was conducted at a Korean pine plantation. This plantation was established approximately 180 m above sea level in 1963 at Mt. Taehwa, GyeongGi $(37^{\circ}18'15''N, 127^{\circ}19'00''E)$. In this area, the average air temperature is 11.5 °C, and the average precipitation is 1,471 mm. The bedrock of Mt. Taehwa is primarily composed of granite. Subcanopy species in the plantation include *Toxicodendron trichocarpum, Rhododendron yedoense, Magnolia kobus*, and *Zanthoxylum schinifolium*, and the average tree density and canopy height are approximately 450 tree ha⁻¹ and 18 m, respectively. The leaf area index (LAI) was developed from a site- and species-specific allometric equation by Ryu et al. (2014). The maximum and the minimum LAI during the growing season are approximately 5.40 m² m⁻², around early September, and 3.81 m² m⁻², around late March, respectively.

A study plot of 20×20 m for measuring radial and tree-to-tree variations was established in the plantation facing the northeast side in April 2011, and the slope angle is approximately 10°. Three trees located within 80 m of the plot were added for measurements of azimuthal variation in March 2012. These three trees were located within 10 m of each other.

Meteorological factors were measured at a tower located at the center of the plot. The air temperature (T) and relative humidity (RH) (HMP35C, Campbell Scientific, Logan, UT, USA), as well as the photosynthetically active radiation (Q, LI-190, LI-COR, Lincoln, NE, USA), were measured at the top of a tower 20 m high. These sensors were positioned slightly higher than the canopy height. The vapor pressure deficit (D) was calculated using T and RH. All of the measurements were taken every 30 s, and the 30 min average was stored on a data logger (CR1000, Campbell Scientific). Table 1 shows the meteorological variables during the study periods.

Sap flux density measurement

Granier-type heat dissipation sensors (Granier 1985; Granier 1987) were used for the J_S measurements. Each sensor

Table 1 Meteorological variables (T daily average air temperature,
Q daily average photosynthetically active radiation, D daily average
vapor pressure deficit)

Period	<i>T</i> (°C)	$\begin{array}{c} Q \ (\mu \mathrm{mol} \ \mathrm{m}^{-2} \ \mathrm{s}^{-1}) \end{array}$	D (kPa)
May 26–June 4, 2011	18.6 (15.9–21.8)	398 (189–609)	0.76 (0.18–1.47)
May 5–14, 2012	15.7 (12.8–17.0)	420 (79–584)	0.98 (0.20–1.57)

The *numbers in parentheses* represent the range of each variable for the given period

was composed of two different probes: an upper probe heated by a constant power (0.2 W) and a lower reference probe. The two probes were inserted radially into the stem at breast height and parted vertically from 13 to 15 cm to avoid thermal interference between them. The temperature difference between the probes was measured and converted into J_S as described by Granier (1987). Measurements were taken every 30 s, and the 30-min averages were stored in the data logger (CR1000, Campbell Scientific).

The study plot contained twenty Korean pine trees. We used four of these trees to assess radial variation. Three J_{S} sensors were installed in each tree at different depths from the cambium to cover 0-60 mm of the xylem $(J_{S_0-20},$ $J_{S_{20-40}}$, and $J_{S_{40-60}}$, respectively). The outer sensors were installed at the north aspect to avoid direct radiation, and the $J_{S_{20-40}}$ and $J_{S_{40-60}}$ sensors were installed approximately 15 cm apart from the outer sensor to prevent thermal interference. To evaluate the azimuthal variation, six $J_{\rm S}$ sensors were installed at six aspects around the stem for each tree. All of the installed sensors were outer sensors, and each sensor was separated by 60°, starting from the north aspect. To gauge the tree-to-tree variation, fourteen outer sensors installed at fourteen trees in the plot were used for analysis. Table 2 shows the details of the studied trees, sensor installation, and measurement periods.

Stand transpiration calculation and error quantification

To quantify the errors in the *E* estimates caused by the radial, azimuthal, and tree-to-tree variations, we compared the reference *E* (E_R) estimates with estimates in which we ignored each source of variation. The E_R was calculated using 10 days of J_S data (i.e., March 26–June 4, 2011) from all of the outer sensors of the fourteen trees. First, the individual tree transpiration (E_T) was calculated as follows:

$$E_{\rm T} = \sum_{i=1}^{n} J_{\rm S_A_i} A_i, \tag{1}$$

where *n* is the number of the sapflux sensor depth along the xylem, A_i is the xylem area at depth *i*, and $J_{S_A_i}$ is the weighted J_S accounting for azimuthal variation. The

Table 2 Details of study trees, sensor installation, measurement periods, and the coefficient of variation (CV) for each variation type

Variations	No. of trees	Depth (mm) and aspect	DBH (cm)	Data periods	CV (%)
Radial	4	0–20, 20–40 and 40–60 at N	28.0 (21.7–31.7)	May 26– June 4, 2011	124.3
Azimuthal	3	N, NE, SE, S, SW and NW at 0–20	30.4 (26.0–36.8)	May 5– May 14, 2012	23.6
Tree-to- tree	14	0–20 at N	29.1 (21.5–36.4)	May 26– June 4, 2011	34.0

Sensors were installed at 0–20, 20–40, and 40–60 mm from the cambium

N, NE, SE, S, SW, and NW represent the aspects of the circumferentially installed sensors, and the sensors were sequentially installed 60° apart starting from the north aspect (*N* north, *NE* northeast, *SE* southeast, *S* south, *SW* southwest, *NW* northwest)

The average tree diameter at breast height (DBH) and its range are also represented for each variation type

sapwood depth was determined from the point where $J_{\rm S}$ reaches zero instead of from color distinction (e.g., Shinohara et al. 2013) or xylem water content (e.g., Fiora and Cescatti 2006). Similar to many studies which have claimed a discrepancy between the entire sapwood area and the hydroactive sapwood area (e.g., Cermak and Nadezhdina 1998; Poyatos et al. 2007), our study trees showed no clear distinction between sapwood and heartwood by color, and only a small part in the center of the xylem differed from the other part by color (Fig. 1). Therefore, in this study, we calculated E based on the assumption that the sapwood depth was the point at which $J_{\rm S}$ reaches zero. To assess the azimuthal variation of these trees, we assumed that all fourteen trees had the same average azimuthal variation as the three trees for which we measured the azimuthal variation (Kume et al. 2012; Shinohara et al. 2013). The radial variation was also evaluated using the average $J_{\rm S}$ ratios across the different depths observed in this study. In addition, we assumed that the $J_{\rm S}$ for parts of the xylem >60 mm from the cambium could be ignored, as these values were almost zero. Six of the twenty trees were not measured but were also accounted for in a similar way by assuming average outer $J_{\rm S}$ and ratio values for the radial and azimuthal variations. Consequently, the $E_{\rm R}$ was calculated using the following equation: $E_{\rm R} = \sum E_{\rm T}/A_{\rm G}$, where $A_{\rm G}$ is the study plot area.



Fig. 1 A cross-section of a Korean pine tree in Mt. Taehwa, Korea. *Black bars* mark various relative depths from the cambium, while the *red bar* represents the boundary line based on color distinction

Similar to the methods employed by Kume et al. (2012) and Shinohara et al. (2013), the *E* estimates that did not consider the radial variation were calculated assuming that the inner J_S values (J_{S_20-40} and J_{S_40-60}) were the same as the J_{S_20-20} . The *E* estimates obtained ignoring azimuthal variation were calculated using the J_S from each aspect. Similarly, the error caused by ignoring the tree-to-tree variation was calculated using the J_S from each tree.

In addition, we compared the E_R with the *E* estimates for multiple sample sizes (n = 1-13), using the same scaling

exercise to evaluate the effects of sample size on E estimates. Average E estimates from all possible combinations of sample trees for each sample size were calculated (Kume et al. 2012).

Statistical analysis

The coefficient of variation (CV) for each source of variation was calculated in order to compare the magnitudes of the variations in J_S . All curve fittings were performed with SigmaPlot 10.0 software and were based on the leastsquares method (Systat Software, San Jose, CA, USA). Statistical analysis was performed with the SAS version 9.3 software (SAS Institute, Cary, NC, USA).

Results

Spatial variations in J_S

Figure 2 shows the diurnal patterns of J_S (Fig. 2a) and meteorological variables (Fig. 2b) for ten consecutive days from each depth. In general, J_S followed the pattern of Q and D, and J_S showed nocturnal flow while the minimum night D was greater than 0.3 kPa. The average J_S values of J_{S_00-20} , J_{S_20-40} , and J_{S_40-60} were 10.7, 1.04, and 0.24 g m⁻² s⁻¹, respectively, indicating that J_S decreased sharply with increasing radial depth. Thus, the radial profile of Korean pine trees showed an exponential decrease with increasing radial depth, and the J_S values had almost



Fig. 2 a Diurnal patterns of sap flux densities (J_S) at each depth and **b** meteorological variables (photosynthetically active radiation (Q; *solid line*) and vapor pressure deficit (D; *dashed line*)) during the study period. Each symbol represents a different depth: outermost

(0–20; *filled circles*), second (20–40; *open squares*), and innermost (40–60; *filled triangles*). *Error bars* represent the standard error for four trees



Fig. 3 a Radial profile of sap flux density (J_S) and **b** daily average J_S at 0–20 mm (J_{S_0-20}) vs. 20–40 mm (J_{S_20-40}) and 0–20 mm (J_{S_0-20}) vs. 40–60 mm (J_{S_40-60}) . Symbols are the same as in Fig. 1. Linear regressions in **b** were forced through the origin. *Error bars* in **a** and **b** represent standard errors for ten days and four trees, respectively

reached zero at approximately 50 % relative depth from the cambium (Fig. 3a). Additionally, the daily average J_{S_20-40} and J_{S_40-60} values showed linear relationships with J_{S_00-20} , and the averages of J_{S_20-40} and J_{S_40-60} were 9.7 and 2.2 % of the average J_{S_00-20} , respectively (Fig. 3b). These results imply that, in Korean pine trees, the relative contribution from each depth is quite constant and presents substantial radial variation. The average CV of the radial variation for the four trees was 124.3 % (Table 2).

Figure 4a–c show the average diurnal patterns of J_S , and Fig. 4d–f show the average J_S of each aspect for three individual trees during ten days. Although the trends in azimuthal variation were not exactly the same for the individual trees, the J_S values of the eastern aspects were always statistically greater than or equal to those of the western aspects in all three trees (Fig. 4d–f). The average CV of azimuthal variation for the three trees was 23.6 % (Table 2).

Figure 5 shows the J_S diurnal patterns of all fourteen trees during the study period. The average J_S of the fourteen trees was 11.8 g m⁻² s⁻¹, and the range was

7.0–21.5 g m⁻² s⁻¹. The $J_{\rm S}$ variation among the different trees was higher when the $J_{\rm S}$ values were high, and the CV was correlated with meteorological variables (i.e., CV increased with increasing *D*), indicating that the differences in the relative contributions of individual trees to the *E* estimates were greater when *D* was high (Fig. 6). The CV of the tree-to-tree variation for the fourteen trees was 34.0 % (Table 2).

Sources of error for *E* estimates

To analyze the error in the *E* estimates caused by ignoring spatial variation, the differences between the $E_{\rm R}$ and the E values calculated by ignoring the radial, azimuthal, and tree-to-tree variations were compared (Table 3). On average, the largest error in the E estimates occurred when the radial variation was ignored (109.2 %). Ignoring the azimuthal variation caused the smallest error on average with a normal distribution (12.6 \pm 8.4 %). However, E was underestimated by up to 23.6 % when only sensors installed on the southwest aspects of the trees were considered. E was also overestimated by up to 20.3 % when only northeast-aspect sensors were considered. The E estimates from the north-aspect measurements, which are commonly used for J_{S} measurements to avoid direct solar radiation, had the smallest error (0.6 % compared to the $E_{\rm R}$). Ignoring the tree-to-tree variation caused a higher error than ignoring azimuthal variation did, and a lower error than omitting radial variation. The errors also showed normal distributions among the trees, as did the azimuthal variation. The largest error in the E estimates due to ignoring tree-to-tree variation was 65.1 %, and the average error was $24.3 \pm 17.9 \%$.

The effect of sample size on the *E* estimates compared to the $E_{\rm R}$ is represented in Fig. 7. The differences in the *E* estimate ($E_{\rm D}$) decreased as the number of samples grew. The average $E_{\rm D}$ caused by a sample size of 1 was $56.3 \pm 45.0 \%$, and the maximum $E_{\rm D}$ was 167 %. $E_{\rm D}$ was <10 % when the sample size was >10.

Discussion

Spatial variations in J_S

The radial profile of $J_{\rm S}$ usually exhibits the highest rate slightly inside of the cambium and then decreases with increasing radial depth (Nadezhdina et al. 2002; Ford et al. 2004b). However, the shape of this profile varies with species (e.g., Phillips et al. 1996; Jiménez et al. 2000) and sometimes even among individuals of the same species (e.g., Fiora and Cescatti 2006; Poyatos et al. 2007). These different radial profiles could result from factors including



Fig. 4 a–c Average diurnal patterns of sap flux densities (J_S) and **d–f** average J_S from each aspect during the study period (north (N), northwest (NW), southwest (SW), south (S), southeast (SE), and northeast (NE) aspects) in individual trees. **a** and **d**, **b** and **e**, and **c** and

f represent the sizes of trees in diameter at breast height (26.0, 28.4, and 36.8 cm, respectively). *Different letters* in **d**–**f** indicate differences for which P < 0.05. *Error bars* represent the standard error for ten days



Fig. 5 Diurnal patterns of sap flux densities (J_S) for 14 trees during the study period

the radial variation in the hydraulic conductivity due to differences in tracheid diameter with depth (Tateishi et al. 2008), the proportion of malfunctioning xylem (Paudel et al. 2013), the anatomical connection between the vertical distribution of foliage and the sapwood (Dye et al. 1991), and stand age and tree social position (Fiora and Cescatti 2006). In our study, the average CV of the radial variation was 124.3 % (Table 2), which indicated that transpiration

from the outer xylem made a large contribution to J_S when compared to other species (e.g., Phillips et al. 1996; Fiora and Cescatti 2006; Shinohara et al. 2013). In addition, this large contribution of J_S from the outer xylem is speciesspecific rather than dependent on tree size because the CVs of different size trees will be similar due to the strong relationship between relative depth and normalized J_S (Fig. 3a).



Fig. 6 Relationship between the coefficients of variation (CV) for tree-to-tree variation and daily average vapor pressure deficit (*D*). Regression line: y = 6.6x + 27.8. The data were normally distributed without outliers

Table 3 Differences between the reference stand transpiration (E_R) and the *E* values calculated by ignoring the radial, azimuthal, and tree-to-tree variations in sap flux densities

Errors	Radial (%)	Azimuthal (%)	Tree-to-tree (%)
Average	109.2	12.6	24.3
Maximum	_	23.6	65.1
Minimum	-	0.6	2.1



Fig. 7 Effect of increasing the number of sample trees on stand transpiration (*E*) estimates. The differences in $E(E_D)$ were derived from the differences between the reference $E(E_R)$ and the *E* derived for each sample size

The azimuthal variation in $J_{\rm S}$ may result from differences in crown sun exposure (Oren et al. 1999), soil water distribution (Lu et al. 2000), vessel lumen diameter in the xylem (Tateishi et al. 2008), and the direction of the stand

side (Shinohara et al. 2013). The smaller J_S associated with the west aspects than with the east aspects in our study may be attributed to our northeast-facing study site, which could have caused large differences in crown sun exposure (Fig. 4). In our study, although the azimuthal variation in J_S was smaller than the other spatial variations, the average CV value of 23.6 % was comparable to those reported for other studies, for which the CV ranges from 21 to 27 % for *Mangifera indica* (Lu et al. 2000), from 15 to 25 % for *Cryptomeria japonica* (Tsuruta et al. 2010), from 23 to 45 % for *Robinia pseudoacacia*, from 22 to 45 % for *Quercus liaotungensis* (Kume et al. 2012), and from 7 to 38 % for *Cryptomeria japonica* (Shinohara et al. 2013).

Tree-to-tree variation may be caused by water-use competition among trees within a stand (Oren et al. 1998; Jimenez et al. 2010). Lagergren and Lindroth (2004) found a correlation between sap flow and competition index that depends on the distance and DBH of neighboring trees, and several studies have reported significant relationships between the water use of trees and tree size (i.e., tree height or DBH) (e.g., Delzon et al. 2004; Shinohara et al. 2013). Although we did not examine the relationship between the water use of an individual tree and its size, our results show that the relative variation in J_S (i.e., CV) among the trees increased with increasing D (Fig. 6). These results indicate that tree-to-tree variation increased with increasing D.

Sources of error in E estimates

In our study, the largest error was caused by radial variation, followed by tree-to-tree and azimuthal variations (Table 3). Kume et al. (2012) and Shinohara et al. (2013) reported that tree-to-tree variation was greater than radial variation in their study sites, although the amount of error caused by ignoring tree-to-tree variation in the present study was comparable to that seen in their results (24 vs. 19-52 %). This difference resulted from the large radial variation in our study, namely, the exponential decrease in $J_{\rm S}$ with increasing radial depth; however, the related error was well within the range previously reported by other studies (e.g., Nadezhdina et al. 2002; Ford et al. 2004a). In addition, Kume et al. (2012) concluded that azimuthal variation was a minor source of error for E estimates in comparison to other variations, and Shinohara et al. (2013) also reported that the error caused by azimuthal variation was smaller than that of tree-to-tree variation. Our results were in agreement with these findings.

Although greater numbers of sensors provide more accurate *E* estimates, many studies have been conducted to calculate an ideal minimum sample size in light of limited resources (e.g., Kumagai et al. 2005; Kume et al. 2010b). Similar to the method of Kume et al. (2010b), which determined the minimum sample size with a marginal CV (= dCV/dn) of greater than -0.5, we applied a marginal

error in E estimates (= dE_D/dn) of greater than -0.5 as the minimum sample size. Based on this criterion, the appropriate minimum sample size at our study site was eight, which was similar to the output of the Kume et al. (2010b) method (which ranged from 7 to 9 depending on the simulation). Our minimum sample size created an average 13.9 % error compared to the $E_{\rm R}$. Although our minimum sample size is smaller than the 10–15 found by the previous study to be needed for accurate estimations of stand sapwood area and average stand $J_{\rm S}$, respectively, in a 20×20 m plot, we believe that these differences in minimum sample size can be attributed to differences in stand densities (1,900 vs. 450 trees ha^{-1}). Despite the fact the number was smaller than that recommended by the previous experiment, the ratio of the minimum sample size to the total number of trees was greater in our study (8/20 vs. 15/58), suggesting that the proportion of sample trees needed for accurate E estimates should increase as the total number of trees in a stand decreases.

Conclusions

We examined the radial, azimuthal, and tree-to-tree variations in $J_{\rm S}$ and their effects on E estimates in a Korean pine stand using Granier-type heat dissipation sensors. Our results clarified the importance of accounting for the spatial variation of $J_{\rm S}$, with radial, tree-to-tree, and azimuthal variations being progressively less important. These findings differed from those found in studies by Kume et al. (2012) and Shinohara et al. (2013). Our observations suggest that species- and site-specific consideration of the spatial variation is necessary in order to obtain accurate *E* estimates—especially the radial variation, which decreased exponentially with increasing radial depth. The azimuthal variation among aspects was significant, but its contribution to the E estimate was minimal in comparison to those of the other variations. Tree-to-tree variation also led to considerable error in the estimated E, and this variation should therefore be accounted for along with the radial variation when attempting to accurately estimate E.

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