

# A simple calibration improved the accuracy of the thermal dissipation technique for sap flow measurements in juvenile trees of six species

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**Abstract** The thermal dissipation technique is widely used to estimate transpiration of individual trees and forest stands, but there are conflicting reports regarding its accuracy. We compared the rate of water uptake by stems of six tree species in potometers with sap flow ( $F_S$ ) estimates derived from thermal dissipation sensors to evaluate the accuracy of the technique. To include the full range of xylem anatomies (i.e., diffuse-porous, ring-porous, and tracheid), we used saplings of sweetgum (*Liquidambar styraciflua*), eastern cottonwood (*Populus deltoides*), white oak (*Quercus alba*), American elm (*Ulmus americana*), shortleaf pine (*Pinus echinata*), and loblolly pine (*Pinus taeda*). In almost all instances, estimated  $F_S$  deviated substantially from actual  $F_S$ , with the discrepancy in cumulative  $F_S$  ranging from 9 to 55%. The thermal dissipation technique generally underestimated  $F_S$ . There were a number of potential causes of these errors, including species characteristics and probe construction and installation. Species with the same xylem anatomy generally did not show similar relationships between estimated and actual  $F_S$ , and the largest errors were in species with diffuse-porous (*Populus deltoides*, 34%) and tracheid (*Pinus taeda*, 55%) xylem anatomies, rather than ring-porous species *Quercus alba* (9%) and *Ulmus americana* (15%) as

we had predicted. New species-specific  $\alpha$  and  $\beta$  parameter values only modestly improved the accuracy of  $F_S$  estimates. However, the relationship between the estimated and actual  $F_S$  was linear in all cases and a simple calibration based on the slope of this relationship reduced the error to 1–4% in five of the species, and to 8% in *Liquidambar styraciflua*. Our calibration approach compensated simultaneously for variation in species characteristics and sensor construction and use. We conclude that species-specific calibrations can substantially increase the accuracy of the thermal dissipation technique.

**Keywords** Sap flux · Hydraulic conductivity · Xylem anatomy · Thermal dissipation technique

## Introduction

Accurately determining the quantity of water transpired by trees and forests is becoming increasingly important. However, the large size and complexity of trees makes direct measurement difficult. The measurement of stem sap flow ( $F_S$ ) is a widely used indirect approach for estimating tree and forest transpiration. Techniques to estimate  $F_S$  are based on the assumption that sap movement through the xylem is equivalent to transpiration (Smith and Allen 1996). A variety of stem  $F_S$  techniques have been developed, such as heat pulse velocity (Marshall 1958), heat balance (Čermák et al. 1973), thermal dissipation (Granier 1985), and heat field deformation (Nadezhkina et al. 1998), but all of these techniques are similar in that they rely on using heat as a tracer for  $F_S$  as introduced more than seven decades ago by Huber and Schmidt (1937). Each technique has advantages and disadvantages in terms of ease of use, cost, and size of the plant stems in which they can be used

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(Smith and Allen 1996; Wullschleger et al. 1998). Of these, the thermal dissipation technique is currently the most widely used to estimate transpiration of forests. The thermal dissipation technique has been used in boreal (Dursma et al. 2008), temperate (Herbst et al. 2007), and tropical forests (Chapotin et al. 2006), as well as savannas (Do et al. 2008), plantations (Samuelson et al. 2008), and orchards (Reis et al. 2006). The thermal dissipation technique has also been used recently to assess sap flow in monocots such as palm (Renninger and Phillips 2010) and bamboo (Kume et al. 2010). Thermal dissipation sensors are relatively inexpensive, easy to install, have low energy requirements (Andrade et al. 1998; Braun and Schmid 1999), and provide continuous long-term estimates of  $F_S$  (Saugier et al. 1997; Oliveras and Llorens 2001).

The thermal dissipation technique was first described by Granier (1985). Briefly, the thermal dissipation technique relies on the temperature difference between a continuously heated probe and a lower unheated probe inserted radially into the stem. Thermal dissipation increases and the temperature difference between the two probes decreases asymptotically with increasing  $F_S$  (Clearwater et al. 1999). Granier (1985) calibrated the thermal dissipation technique using three tree species (*Pseudotsuga menziesii*, *Pinus nigra*, and *Quercus pedunculata*) and developed an empirical relationship to determine sap flux density ( $F_d$ ,  $\text{g m}^{-2} \text{ s}^{-1}$ ):

$$F_d = \alpha K^\beta \quad (1)$$

where  $\alpha$  and  $\beta$  are parameter values, 119 and 1.231, respectively, and  $K$  is the dimensionless  $F_S$  index:

$$K = (\Delta T_{\max} - \Delta T) / \Delta T \quad (2)$$

where  $\Delta T_{\max}$  is the temperature difference between the heater and reference probe at zero flow (i.e., measured pre-dawn when  $F_S$  is assumed negligible) and  $\Delta T$  is the temperature difference at any given measurement point. The incorporation of sapwood area at the point of sensor insertion ( $SA$ ;  $\text{m}^2$ ) allows for the calculation of  $F_S$  ( $\text{g s}^{-1}$ ):

$$F_S = \alpha K^\beta \times SA \quad (3)$$

Multiplying  $F_S$  by 3.6 converts  $F_S$  units to  $\text{l h}^{-1}$ .

It has been argued that the thermal dissipation technique provides accurate estimates of  $F_S$  for all tree species, regardless of stem size or xylem anatomy, when the original empirically derived  $\alpha$  and  $\beta$  parameter values are employed (Eq. 1; Granier 1985, 1987; Granier et al. 1990). Results from some studies further support the accuracy of the thermal dissipation technique (Lu and Chacko 1998; Braun and Schmid 1999; McCulloh et al. 2007; Liu et al. 2008) while others do not (Gutiérrez and Santiago 2006; Bush et al. 2010; Steppe et al. 2010). Smith and Allen

(1996) argued that the original  $\alpha$  and  $\beta$  parameter values could not accurately estimate  $F_S$  in all species and all situations, and suggested that species-specific parameter values might be necessary. Although thermal dissipation sensors are commercially available, many experimentalists employ a variety of materials and construction techniques to fabricate their own sensors. Materials used to fabricate sensors, construction techniques, and the applied electrical power may affect the accuracy of parameter values derived from the original calibration (Lu et al. 2004). For example, Steppe et al. (2010) found that a commercially available sensor employing a different design than that originally described by Granier (1985) substantially underestimated actual  $F_S$  when using the original  $\alpha$  and  $\beta$  parameter values.

In this study, we inserted thermal dissipation probes in tree stems that were cut off from the roots and placed in water so that the rate of water uptake could be closely monitored. The purpose of the study was to compare the accuracy of the thermal dissipation technique in trees of ring-porous, diffuse-porous, and tracheid anatomies. Based on Smith and Allen (1996) and Clearwater et al. (1999), we expected that the technique would be more inaccurate in ring-porous than diffuse-porous or tracheid species. We made purpose-built sensors and, based on Lu et al. (2004) and Steppe et al. (2010), we expected that differences in probe construction from the original design (Granier 1985) would also contribute to inaccurately estimating  $F_S$ . However, we hypothesized that we could overcome these inaccuracies by performing calibrations to generate new  $\alpha$  and  $\beta$  parameter values that are specific to xylem anatomy or species. We further hypothesized that, if the new parameter values failed to substantially improve the estimates of  $F_S$ , we could improve the estimates by applying correction factors derived from the relationship between actual and estimated  $F_S$ .

## Materials and methods

### Study site and sample tree characteristics

The experiment was conducted between July 20 and September 4 2009 at Whitehall Forest, a warm temperate mixed pine–hardwood forest near Athens, Georgia, USA. Measurements were made on cut stems of five saplings from each of six species: sweetgum (*Liquidambar styraciflua* L.) (*Ls*), eastern cottonwood (*Populus deltoides* Bart.) (*Pd*), white oak (*Quercus alba* L.) (*Qa*), American elm (*Ulmus americana*, L.) (*Ua*), shortleaf pine (*Pinus echinata* Mill.) (*Pe*), and loblolly pine (*Pinus taeda* L.) (*Pt*). Species *Ls* and *Pd* have diffuse-porous xylem, *Qa* and *Ua* have ring-porous xylem, and *Pe* and *Pt* have tracheid xylem.

Stem sizes were similar among species, ranging from 65 to 90 mm in diameter (mean  $75 \pm \text{SE } 4$  mm) and  $22.14$  to  $42.63 \text{ cm}^2$  in sapwood area (mean  $29.3 \pm 3.1 \text{ cm}^2$ ) with sapwood radii ranging from 15 to 37 mm (mean  $26.0 \pm 1.0$  mm) at the thermal dissipation heater probe insertion point.

#### Thermal dissipation sensor construction and use

We used thermal dissipation sensors constructed in a manner similar to the original design described by Granier (1985). Each sensor consisted of two 20-mm-long 19-gauge stainless steel hypodermic needles, one needle a heated probe and the other, an unheated reference probe. The heated probe contained a constantan heating element (TFCC-005, Omega Engineering, Stamford, USA) tightly wrapped along the length of the needle resulting in a similar temperature throughout the length of the needle. Both the heated and reference probes contained a copper-constantan thermocouple (TFCC-005/TFCC-005, Omega Engineering, Stamford, USA) in the center of the probe's length (10 mm), which measured the temperature differential between the two probes. Both probes were sealed with low viscosity epoxy that when dried resulted in a solid waterproof sensor. Two thermal dissipation sensors were placed on opposite sides of each stem. Prior to drilling holes for sensor insertion, a 5-mm diameter circle of bark was removed down to the cambial layer where each probe was to be inserted. A battery-powered drill and a pre-drilled metal guide were used to ensure accurate spacing and parallel alignment of probes. Probe holes were drilled using appropriate sized drill bits to accommodate the diameter of reference (1.5 mm diameter) and heater probes (2.4 mm diameter). The heated probe was placed within a 2.4 mm aluminum tube to improve heat conductance along the length of the probe and coated with thermal conductive paste to improve thermal contact with the xylem.

We used a 4 cm spacing between heater and reference probes because the experiments were conducted in an open area and large measurement errors associated with temperature gradients in the stem have been observed in open sites receiving high solar radiation (Do and Rocheteau 2002). This 4 cm spacing distance is similar to the 5 cm distance used by Granier (1985) to develop the original  $\alpha$  and  $\beta$  parameter values for the thermal dissipation technique. In a study of the effect of spacing on the accuracy of thermal dissipation measurements, Iida and Tanaka (2010) found that sensor spacing (4 or 15 cm) did not impact mean daily  $F_S$  during the growing season. If spacing between the heater and reference probe was to influence  $F_S$  estimates, it would likely do so by influencing  $\Delta T_{\text{max}}$  as heat should move upward when transpiration is occurring and only

influence the reference probe when transpiration is not occurring or is very low. Therefore, we tested the effect of probe spacing on  $\Delta T_{\text{max}}$  using spacing distances between heater and reference probes of 4, 8, and 12 cm in cut stems of each of the species used in the study that we had transported to the laboratory and kept at a constant temperature of  $23^\circ\text{C}$ . We found no statistically significant difference in  $\Delta T_{\text{max}}$  due to the spacing distance in any of the species (data not shown). Placing sensors on opposite sides of the stem could also influence  $\Delta T_{\text{max}}$  and  $F_S$  estimates if the heat from one sensor interfered with the other. Using a similar approach as described above, but with only two sets of sensors located on opposite sides of the cut stem, we calculated  $\Delta T_{\text{max}}$  without heating either sensor, with heating only one sensor, and with heating both sensors. We found that  $\Delta T_{\text{max}}$  was not statistically different when only one sensor was heated and when both sensors were heated (data not shown). The results of these preliminary experiments indicated our procedure was suitable for addressing questions related to the thermal dissipation technique.

After probe insertion, the distal 20 mm of each probe was wrapped in insulating foam, and the portion of the stem where the probes were inserted was shielded from solar radiation with reflective insulation. A constant voltage (V) of 1.8 V supplied 0.2 W to each heater probe. Sensor output was measured with a data logger (23X, Campbell Scientific, Logan Utah USA) every 30 s with means calculated every 5 min. The  $F_S$  values from the two sensors in each stem were averaged, and  $K$ ,  $F_d$ , and  $F_S$  were calculated for each individual tree using Eqs. 1–3.

#### Potometer experiment

At the beginning of each measurement period, five saplings from one of the six tree species used in the experiment were cut at ground level from natural forest stands and transferred to our experimental site within 10 min of being cut. The experiment was repeated over a 6 week period until all six tree species were sampled. All trees were harvested from the forest at dawn when transpiration was assumed to be negligible. We submerged the cut stems in a large container of water and cut off an additional 0.1 m section to remove vascular tissue that could potentially have experienced embolism from exposure to air while harvesting. Cut stems were then transitioned into plastic bags while still submerged and placed directly into separate 2 l plastic containers filled with water. In this way, the cut end of the stem remained in continuous contact with water during the remainder of the experiment. The plastic containers were placed on concrete platforms and trees were held upright by securing them to steel poles that were driven into the ground.

Water uptake was measured every 30 min over a 2 day period by adding and recording the amount of water required to return the water level in the container back to a pre-defined level. The quantity of water added every 30 min was considered to be the actual  $F_S$  of the stem over that time period. We used de-ionized water containing 40 mM KCL to decrease hydraulic resistance (Zwieniecki et al. 2001). The top of the plastic container was covered with parafilm (Pechiney Plastic Packaging, Menasha, Wisconsin) to prevent evaporation. Pre-dawn  $\Delta T_{\max}$  values (Eq. 2) on the second measurement day were used to calculate  $K$  throughout the 2 day measurement period. On the morning of the third day, stems were cut where the sensors were located and sapwood areas were determined. Due to the small diameter of the stems, the thermal dissipation probes spanned the radius of all, or most, of the sapwood; therefore, we did not develop or apply radial profiles when estimating  $F_S$ .

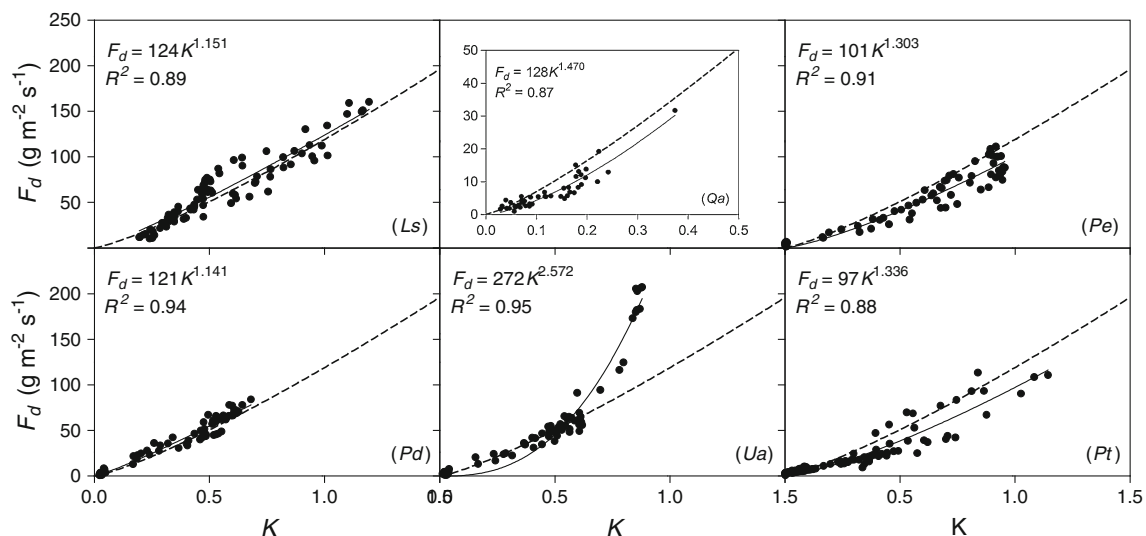
Of the five trees from each species, three were randomly selected to be used in each species-specific calibration of the thermal dissipation technique. Calibrations were performed using nonlinear regression of the form  $y = \alpha x^\beta$  to generate new  $\alpha$  and  $\beta$  parameter values to predict  $F_d$  as a function of  $K$ . We used actual water uptake as our measure of  $F_d$  in the calibration exercise and calculated  $K$  from the differential temperature and  $\Delta T_{\max}$  values obtained from the thermal dissipation sensors. Outlier data were identified by studentized residuals  $>|2|$  and were subsequently removed from the nonlinear regression. The coefficient of determination ( $R^2$ ) was calculated as  $1 - \text{SSE}/\text{CSS}$ , where SSE was the error sums of

squares for the fitted curve, and CSS was the total sums of squares corrected for the mean.

The two remaining trees from each species were used to examine the relationship between actual and estimated  $F_S$ , where estimated  $F_S$  was calculated from both the original and the new  $\alpha$  and  $\beta$  parameter values obtained in the calibration. We performed linear regression to determine line equations representing the relationship between actual and estimated  $F_S$ . Line equations were generated following the form: (1)  $y = mx + b$ , where  $y$  represents the dependent variable (estimated  $F_S$ ),  $x$  represents the independent variable (actual  $F_S$ ),  $m$  represents the slope of the regression line, and  $b$  represents the y-intercept; and (2)  $y = mx$ , where the intercept term,  $b$ , is set to zero by forcing the regression line through the origin. We calculated regression lines with and without the y-intercept to determine which approach provided the most accurate correction. All regression analyses, both linear and nonlinear, were performed using SAS (Version 9.1.3, SAS Inc., Cary, NC, USA).

## Results

Our calibration yielded  $\alpha$  and  $\beta$  parameter values that differed from the original values developed by Granier (1985) (Fig. 1). In some instances, the new parameter values were similar to the original values; in other instances, they were distinctly different (Fig. 1). Regardless of tree species, coefficients of determination indicated that the relationships between actual  $F_d$  and  $K$  were relatively strong.



**Fig. 1** Nonlinear regression of the form  $y = \alpha x^\beta$  where  $F_d$  (sap flux density) is the dependent variable,  $y$ , and  $K$  (the dimensionless sap flow index) is the independent variable,  $x$ , for *L. styraciflua* (*Ls*), *P. deltoides* (*Pd*), *U. americana* (*Ua*), *Q. alba* (*Qa*), *P. echinata* (*Pe*), and *P. taeda* (*Pt*). The dashed line shows the curve defined by the

original parameter values (i.e.,  $\alpha = 119$ ,  $\beta = 1.231$ ) and the solid line shows the curve obtained with  $F_d$  and  $K$  from this study. The coefficient of determination ( $R^2$ ) was calculated as  $1 - \text{SSE}/\text{CSS}$ , where SSE is the error sums of squares for the fitted curve and CSS is the total sums of squares corrected for the mean

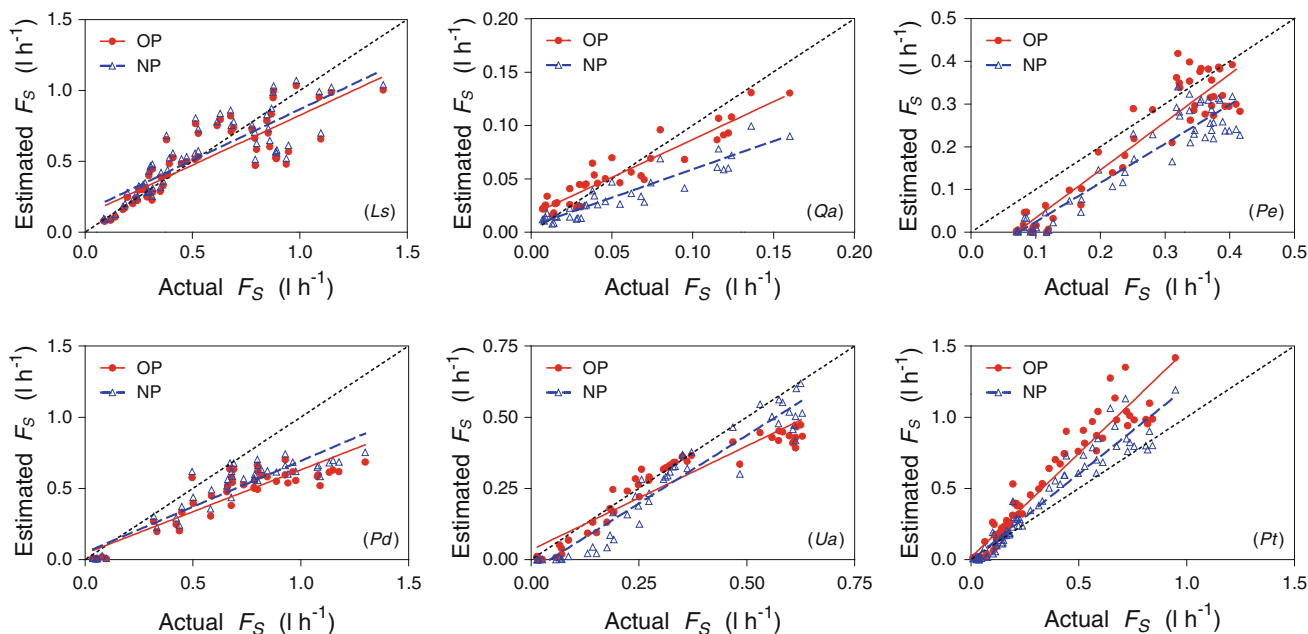
Regardless of which  $\alpha$  and  $\beta$  parameter values were used, thermal dissipation estimates of  $F_S$  did not correspond to actual  $F_S$  (Fig. 2). The thermal dissipation technique underestimated actual  $F_S$  in five species, but overestimated  $F_S$  in *Pt*. The relationship between estimated and actual  $F_S$  was linear in all species, but the magnitude of error varied among species and generally became larger as  $F_S$  increased. Estimating  $F_S$  with the new parameter values resulted in only a modest improvement in the correspondence between estimated and actual  $F_S$  in four of the species, and a poorer agreement in *Qa* and *Pe* (Fig. 2).

When using the original  $\alpha$  and  $\beta$  parameter values (OP,  $\alpha = 119$ ,  $\beta = 1.231$ ), the discrepancy between the estimated and actual cumulative  $F_S$  ranged from an overestimate of 55% in *Pt* to an underestimate of 34% in *Pd* (Fig. 3a, Table 1). Calculating cumulative  $F_S$  with the new  $\alpha$  and  $\beta$  parameter values (NP) reduced the error in some species, increased it in others, and had little effect on the remainder (Fig. 3a, Table 1). Attempting to correct  $F_S$  estimates derived from the original parameter values by multiplying  $F_S$  by the inverse of the slope and adding the y-intercept (OP + S + I) produced an improvement in the accuracy of the estimated cumulative  $F_S$  for *Pd* and *Pt*, but it produced a larger error in the other four species (Fig. 3b, Table 1). Similarly, correcting  $F_S$  estimates derived from the new parameter values with the slope and y-intercept (NP + S + I) did not necessarily improve cumulative  $F_S$

estimates (Fig. 3b, Table 1). However, substantial improvements in the correspondence between estimated and actual cumulative  $F_S$  were realized when  $F_S$  estimates were corrected by multiplying them by the inverse of the slope when the y-intercept was zero (OP + S and NP + S; Fig. 3c, Table 1). Through this correction procedure, we reduced the error between estimated and actual cumulative  $F_S$  to <6% in five of the species and <12% in *Ls*. The same correction procedure applied to  $F_S$  estimates derived from the new parameter values reduced the error from 1 to 4% in five of the species and 8% in *Ls*.

### Discussion

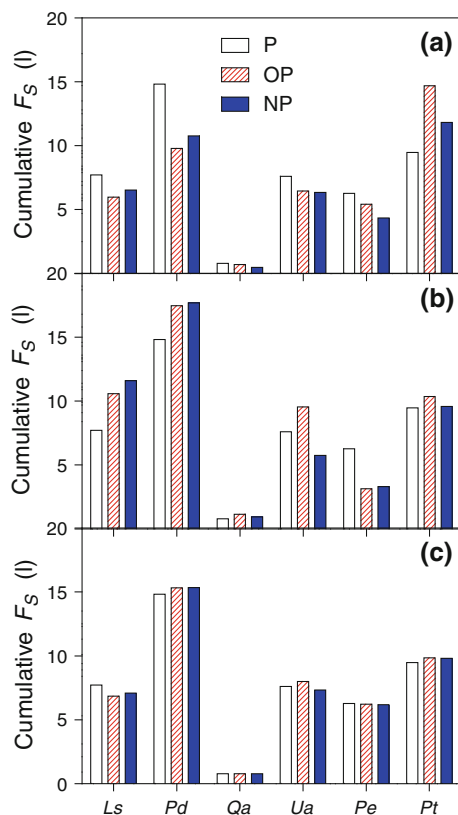
Our experiments demonstrated that the thermal dissipation technique produced  $F_S$  estimates that deviated substantially from actual  $F_S$ . There have been a number of studies evaluating the accuracy and sensitivity of the thermal dissipation technique. Comparisons of gravimetric or volumetric water loss with thermal dissipation  $F_S$  estimates have yielded both agreement and disagreement with the original calibration of Granier (1985, 1987). For example, McCulloh et al. (2007) measured water loss from sapling-sized *Pseudobombax septenatum* and *Calophyllum longifolium* trees in large pots and found good agreement between estimated and actual  $F_S$  when averaged over a



**Fig. 2** Linear regression of estimated versus actual sap flow ( $F_S$ ) rate for *L. styraciflua* (*Ls*), *P. deltooides* (*Pd*), *U. americana* (*Ua*), *Q. alba* (*Qa*), *P. echinata* (*Pe*), and *P. taeda* (*Pt*). Estimated  $F_S$  was calculated by applying both the original thermal dissipation parameter values (OP;  $\alpha = 119$ ,  $\beta = 1.231$ ) and new parameter values derived from

this study (NP; see Fig. 1). The dotted line extending from the origin represents a 1:1 relationship between the dependent and independent variables. Line equations and coefficients of determination ( $R^2$ ) for these relationships are presented in Table 2





**Fig. 3** Estimated (OP and NP) and actual (P) cumulative sap flow ( $F_S$ ) for *L. styraciflua* (Ls), *P. deltooides* (Pd), *U. americana* (Ua), *Q. alba* (Qa), *P. echinata* (Pe), and *P. taeda* (Pt). Estimated  $F_S$  was calculated by applying both the original thermal dissipation parameter values (OP;  $\alpha = 119$ ,  $\beta = 1.231$ ) and new parameter values derived from this study (NP; see Fig. 1). The different panels present  $F_S$  estimates **a** without applying a correction factor, **b** corrected by multiplying estimates by the inverse of the slope and adding the y-intercept, **c** corrected by multiplying estimates by the inverse of the slope when the regression line was forced through the origin

7 day period. However, they also observed a large amount of variation between estimated and actual  $F_S$ , as we did, among individual days. Lu et al. (2002) observed a 1:1 relationship, and less daily variation than McCulloh et al.

(2007) between thermal dissipation  $F_S$  estimates and gravimetric measurements of water loss in 2.5 m tall potted banana plants. Using both gravimetric and cut stem/potometry approaches, Lu and Chacko (1998) found that the thermal dissipation technique underestimated cumulative daily  $F_S$  by 6–10% in two 4-year-old *Mangifera indica* trees. Gutiérrez and Santiago (2006) used large (15–18 m tall) *Ochroma lagopus* and *Hyeronima alchorneoides* trees as potometers to calibrate the thermal dissipation technique and found that the technique underestimated  $F_S$  to different degrees in the two species. On the first day of the test when transpiration rates were high, the discrepancy between actual and estimated cumulative daily  $F_S$  was 14% in *Hyeronima alchorneoides* but only 2% in *Ochroma lagopus*. On the second day when transpiration rates were moderate, the discrepancy increased to 52 and 28% in the two species, respectively. That different species exhibited different degrees of error between estimated and actual  $F_S$  suggests that the original  $\alpha$  and  $\beta$  parameter values may not be appropriate for all species.

Our calibrations yielded  $\alpha$  and  $\beta$  parameter values that differed from those originally described by Granier (1985). Using the original  $\alpha$  and  $\beta$  parameter values, the thermal dissipation technique substantially underestimated  $F_S$  in *Eucalyptus grandis*  $\times$  *urophylla* clones compared to other sap flow techniques (Almeida et al. 2007), prompting Hubbard et al. (2010) to perform a calibration using pressure to push water through cut stems at known flow rates. This calibration produced substantially different  $\alpha$  (845.6) and  $\beta$  (1.606) parameter values than those originally reported by Granier (1985, 1987). Bush et al. (2010) also used pressure to push water through branch segments of four ring-porous species and obtained  $\alpha$  parameter values exceeding original parameter values by nearly three orders of magnitude. Reis et al. (2006) used a similar testing procedure for papaya (*Carica papaya*) stems and found that changing  $\alpha$  and  $\beta$  parameter values to 1530.8 and 1.9104, respectively, was necessary for accurate  $F_S$  estimates. Steppe et al. (2010) also used a hydraulic head to test the

**Table 1** Percent difference between actual and estimated  $F_S$  for *L. styraciflua* (Ls), *P. deltooides* (Pd), *U. americana* (Ua), *Q. alba* (Qa), *P. echinata* (Pe), and *P. taeda* (Pt)

Species	OP	NP	OP + S + I	NP + S + I	OP + S	NP + S
Ls	−23	−15	+37	+50	−11	−8
Pd	−34	−27	+18	+19	+3	+4
Ua	−15	−17	+26	−24	+5	−3
Qa	−9	−39	+46	+21	+2	+1
Pe	−14	−31	−50	−47	−1	+1
Pt	+55	+25	+9	+1	+4	+4

Estimated  $F_S$  was calculated using both the original (OP) and new  $\alpha$  and  $\beta$  parameter values (NP). Estimated  $F_S$  was corrected by: multiplying  $F_S$  by the inverse of the slope and adding the y-intercept (OP + S+I and NP + S+I), and multiplying  $F_S$  by the inverse of the slope when the y-intercept was zero (OP + S and NP + S)

**Table 2** Line equations derived from linear regression of estimated versus actual sap flow ( $F_S$ ) rate (Fig. 2) for *L. styraciflua* (*Ls*), *P. deltooides* (*Pd*), *U. americana* (*Ua*), *Q. alba* (*Qa*), *P. echinata* (*Pe*), and *P. taeda* (*Pt*)

Species	OP	NP	OP ( $b = 0$ )	NP ( $b = 0$ )
<i>Ls</i>	$y = 0.702x + 0.123$ (0.72)	$y = 0.719x + 0.148$ (0.72)	$y = 0.870x$	$y = 0.921x$
<i>Pd</i>	$y = 0.588x + 0.043$ (0.83)	$y = 0.644x + 0.050$ (0.86)	$y = 0.639x$	$y = 0.703x$
<i>Ua</i>	$y = 0.730x + 0.034$ (0.90)	$y = 0.955x - 0.041$ (0.93)	$y = 0.807x$	$y = 0.862x$
<i>Qa</i>	$y = 0.708x + 0.016$ (0.89)	$y = 0.531x + 0.006$ (0.87)	$y = 0.892x$	$y = 0.597x$
<i>Pe</i>	$y = 1.122x - 0.079$ (0.88)	$y = 0.914x - 0.067$ (0.87)	$y = 0.872x$	$y = 0.700x$
<i>Pt</i>	$y = 1.462x + 0.016$ (0.93)	$y = 1.217x - 0.006$ (0.93)	$y = 1.491x$	$y = 1.205x$

Estimated  $F_S$  was calculated by applying both the original thermal dissipation parameters (OP;  $\alpha = 119$ ,  $\beta = 1.231$ ) and new parameters derived from this study (NP; see Fig. 1). Line equations were generated following the form: (1)  $y = mx + b$ , where  $y$  represents the dependent variable (estimated  $F_S$  rate),  $x$  represents the independent variable (actual  $F_S$  rate),  $m$  represents the slope of the line, and  $b$  represents the  $y$ -intercept; and (2)  $y = mx$ , where the intercept term,  $b$ , is set to zero by forcing the line through the origin. The coefficient of determination ( $R^2$ ) is included parenthetically after the intercept term

accuracy of the technique in cut stems of *Fagus grandifolia* and reported that  $F_S$  was underestimated by 60% when using the original  $\alpha$  and  $\beta$  parameter values. From these studies and our results, we conclude that the thermal dissipation technique should be calibrated for individual species and different thermal dissipation sensor types. In some instances, the original parameter values may be suitable, but in many situations, it is likely that the original parameter values (Granier 1985, 1987) will produce substantial errors in  $F_S$  estimates.

There are a number of possible reasons why there are discrepancies between calibrations performed in different studies. Wilson et al. (2001) and Gutiérrez and Santiago (2006) concluded that differences in construction between the original design of Granier (1985) and that of commercially available thermal dissipation sensors could lead to different estimates of stand transpiration. We have also observed differences in  $F_S$  estimates between thermal dissipation sensors of different design used in the same tree stem (personal observation). However, some studies have reported good agreement between sensors constructed in different ways. For example, McCulloh et al. (2007) found that the sensor design by James et al. (2002) compared favorably with the original Granier (1985) design in pot-grown saplings of *Pseudobombax septenatum* and *Calophyllum longifolium*.

The rate of water movement (i.e.,  $F_S$  or  $F_d$ ) could potentially influence the calibration results. For example, Gutiérrez and Santiago (2006) found poor relationships between estimated and actual  $F_S$  at low  $F_S$  but good relationships at high  $F_S$ . Similarly, Liu et al. (2008) found that measurement error increased as  $F_S$  decreased. However, both Bush et al. (2010) and Steppe et al. (2010) found that measurement error decreased as  $F_S$  decreased. We observed a similar relationship of increased error with increased  $F_S$ . We are unaware of any studies that have directly addressed the influence of  $F_S$  on calibrations.

Maximum  $F_d$  for individual trees in our study (19.98–179.27  $\text{g m}^{-2} \text{s}^{-1}$ ) were within the same general range as those reported in other sap flow calibration studies (e.g., Granier 1985; Braun and Schmid 1999; Gutiérrez and Santiago 2006; McCulloh et al. 2007) and field studies (see Lu et al. 2002). The range used in our calibration is consistent with the range observed in field studies suggest that our calibration should be relatively robust. Whenever possible, calibration efforts should include the full range of  $F_S$  observed in the field for a particular species.

Xylem anatomy may also influence calibration results performed in different studies. We had hypothesized that the thermal dissipation technique would be less accurate in ring-porous than diffuse-porous or tracheid species. However, we found no consistent relationship between xylem anatomy and accuracy of the thermal dissipation technique. The largest errors we observed were in diffuse-porous (*Pd*) and tracheid (*Pt*) xylem anatomies. Clearwater et al. (1999) reported that  $F_d$  would be substantially underestimated if the thermal dissipation probe was partially in heartwood. James et al. (2002) reported that a reduction in the length of the measuring tip of the probe from the widely used 20 mm to 10 mm reduced errors associated with abrupt changes in water uptake such as between sapwood and heartwood. In our study, we found that a few of the probes—but not the thermocouples themselves—extended slightly into the heartwood of the ring-porous species; however, they did not appear to under- or over-estimate  $F_S$  to a greater extent than the probes in the species with diffuse-porous and tracheid anatomies. Applying correction factors to account for sapwood depth (e.g., Clearwater et al. 1999) did not consistently improve  $F_S$  estimates in our study (data not presented). Depending on the individual tree, the application of a sapwood depth correction factor either modestly improved or drastically reduced the accuracy of  $F_S$  estimates.

Errors in  $F_S$  estimated by the thermal dissipation technique could also result from natural temperature gradients.

Lundblad et al. (2001) found that thermal gradients in stems of *Picea abies* and *Pinus sylvestris* trees caused errors of up to 30%. Do and Rocheteau (2002) reported that thermal gradients produced errors of over 100% in *Acacia tortilis* trees. It has been assumed that greater probe separation improved the accuracy of the thermal dissipation technique by preventing heating of the reference probe at night. However, a trade-off exists between minimizing errors associated with heating the reference probe at night and errors caused by thermal gradients (Lu et al. 2004). Iida and Tanaka (2010) reported no difference in  $F_S$  estimates made during the growing season on *Pinus densiflora* trees when probes were spaced 4 or 15 cm apart, suggesting that substantial probe separation is not necessary. Our calibration compensated for any potential interaction that might have occurred between the heater and reference probes, suggesting another reason why species-specific calibrations are important for improving accuracy.

Additional factors that are difficult to control but could also reduce the accuracy of the thermal dissipation technique include errors in estimating  $\Delta T_{\max}$  (Ewers and Oren 2000; Regalado and Ritter 2007), wounding responses (Hogg et al. 1997), as well as inherent within- and between-tree variation. For example, species that exhibit nighttime transpiration (Phillips et al. 2010) may never experience zero flow rates; thus,  $\Delta T_{\max}$  derived under nighttime transpiration would result in inaccurate  $F_S$  estimates. That the thermal dissipation technique currently lacks a wound correction factor similar to that developed for the heat pulse velocity technique (Swanson and Whitfield 1981) may also reduce accuracy (Hogg et al. 1997). Finally, it can be difficult to account for the potentially large within- and between-tree variation (Ewers and Oren 2000; Oliveras and Llorens 2001; Fiora and Cescatti 2006; Phillips et al. 2010).

Based on information derived from our calibrations, we applied a variety of correction factors to thermal dissipation estimates of  $F_S$  to determine which correction procedure yielded the most accurate estimate. Calibrations performed with either potometry or a hydraulic head provide data that can be used to generate new  $\alpha$  and  $\beta$  parameter values as well as correction factors based on the relationship between estimated and actual  $F_S$ . In our study, simply applying the new  $\alpha$  and  $\beta$  parameter values generated for each species through the calibration was clearly not enough to overcome the inaccuracies of the thermal dissipation technique (Fig. 3a, Table 1). In fact, the new parameter values were just as likely to decrease as they were to increase the accuracy of  $F_S$  estimates. Similarly, correcting  $F_S$  estimates by multiplying them by the inverse of the slope and adding the y-intercept of the relationship between estimated and actual  $F_S$  improved estimates in only a few instances (Fig. 3b, Table 1). Clearly, the best

correction was obtained by multiplying  $F_S$  estimates by the slope of the relationship between estimated and actual  $F_S$  when the y-intercept is zero (Fig. 3c, Table 1). Averaged across all of the species we investigated, the average percent difference between estimated and actual  $F_S$  using the original parameter values was 25%. We reduced the error to 4% by applying the simple correction factor derived from the relationship between estimated and actual  $F_S$  when the y-intercept is zero.

## Conclusions

Our experiments demonstrated that a relatively simple calibration can appreciably improve the accuracy of the thermal dissipation technique in saplings of six tree species representing the range of tree xylem anatomies. The same calibration simultaneously compensated for inaccuracies in estimates that may result from probe construction, installation, and spacing that differ from the original description of the thermal dissipation technique (Granier 1985). Our findings, in addition to reports of other calibrations, have led us to conclude that there is no universal set of  $\alpha$  and  $\beta$  parameter values suitable for accurately calculating  $F_S$  from thermal dissipation measurements. Rather, each species and sensor combination may require a unique calibration and unique parameter values. Our results complement those of Steppe et al. (2010) who used a similar calculation to correct the underestimation of  $F_S$  from a commercially available thermal dissipation sensor. Whereas the Steppe et al. (2010) calibration used a hydraulic head positioned over cut stem segments of *Fagus grandifolia* to simulate  $F_S$ , we used transpiration to pull water through the xylem under tension. In both studies, the relationships between actual and estimated  $F_S$  were linear; however, the relationships deviated from the 1:1 line. The inaccuracy of  $F_S$  estimates highlights the importance of performing species-specific (and sensor-specific) calibrations when there is a need to estimate the quantity of water transpired from trees or when rates of transpiration are being compared among species. If a comparison of relative changes in  $F_S$  is desired within a single species, then positive or negative bias in  $F_S$  estimates could be tolerated and calibrations are not essential.

Theoretically, a calibration using potometry, which relies on transpiration to pull water through the stem, should be more accurate than a calibration employing a hydraulic head to push water through the stem because a positive pressure could push water through channels in the stem in which water previously did not flow. Side by side calibrations performed using both approaches with similar sized tree stems would be instructive in determining which—if either—calibration approach is superior.



However, the choice of calibration procedure may partly depend on the size of stems, as potometry is limited to stems of relatively small size. In addition, it is likely that correction factors will only be valid for the stem size range used in the calibration. Caution should be applied for trees that are larger or smaller, or grown in different conditions than those used for the calibration. Regardless, both calibration approaches appear capable of improving the accuracy of the thermal dissipation technique.

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