

# Thermal dissipation sensors enter a new age: navigating frontiers in transpiration and hydrologic function

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## Abstract

Thermal dissipation (TD) sensors have been used extensively for a wide array of sap flow applications, and yet recently several limitations of this approach have been identified, including a tendency to underestimate absolute flows, especially in small stems with very high flows. However, when used properly, the TD method remains the most cost effective and reliable approach for determining relative flows in comparison studies. Major advantages of this method include the ability to replicate maximally within trees, across trees of different sizes, and across multiple species to capture the full range of natural variation in the study system. From early studies, such variation has been deemed a major challenge for representing stand-level dynamics. In a series of recent comparison studies, we determined mean sap flux density dynamics within and among groups of trees. These studies were conducted within temperate coniferous forest ( $n=46$ ), temperate oak savanna ( $n=36$ ), temperate pine forest ( $n=49$ ), temperate bottomland hardwood forest ( $n=23$ ), tropical premontane rainforest ( $n=43$ ), semiarid subtropical shrubland ( $n=25$ ), and tropical dry forest ( $n=15$ ), with a total of 237 sensors. Two study sites were also equipped with eddy covariance systems for determination of stand-level evapotranspiration. Sites subject to high background thermal gradients used the transient thermal dissipation method. Comparisons varied between studies but tended to focus on relative flow differences between species, between wetter and drier microsites, between understory and overstory components, or between wetter and drier periods of the growing season. Except for the shrubland sites, study trees tended to be at least 15-cm diameter and frequently exceeded 50-cm diameter. Results of this cross-site comparison highlight the inherent variation in natural stands and the importance of using large sample sizes. The TD approach remains a valuable and preferred method for the future determination of water use in trees. However, sensor replication can fundamentally impact a study's outcomes and should be more carefully considered in study design. Customized error mitigation strategies are best to address the sources of variation most problematic for a particular study. The development of "smart" calibration approaches that correct for fundamental effects of radial variation inherent in thermal dissipation studies is discussed.

**Keywords:** heat dissipation, relative flow, species comparison, heterogeneity, sampling errors, upscaling

## HISTORICAL CONTEXT

The original design for thermal dissipation (TD) sap flow sensors dates back nearly 40 years (Granier, 1985, 1987, 1996). Today, ~50% of sap flow studies use the TD method, compared to the second most common method, heat pulse (Burgess et al., 2001; Swanson, 1994) being used in ~27% of recent studies (Poyatos et al., 2016). The TD method is often preferred over other methods for comparative studies because it is relatively easy and inexpensive to replicate. Developments include commercialization [UP GmbH (Germany), Dynamax (USA), PlantSensors (Australia)], custom design modifications (e.g., Do and



Rocheteau, 2002b; Ford et al., 2004; James et al., 2002), new applications in a wide range of species (e.g., Sperling et al., 2012), and cross-calibrations among sensor types (e.g., Fuchs et al., 2017). Recently, sensor comparisons have demonstrated low performance of TD sensors relative to other methods (Flo et al., 2019). There is a strong need to resolve performance limitations inherent in the TD method and propose a new way forward.

### **CRITICAL NEEDS**

Accurate measurement of sap flow in trees and stands requires the ability to capture variation for that particular study system. Major advantages of the TD method include the ability to replicate maximally within trees, across trees of different sizes, and across multiple species to approach the capacity to capture the full range of natural variation. This is especially true for sensors built according to the original Granier design (Moore et al., 2004), since the materials are less expensive than commercially available brands. From early studies, accounting for within-tree and tree-to-tree variation in water use measurements has been deemed a major challenge for representing stand-level dynamics. Beyond the inherent differences between trees of different ages, sizes, and species, there are high degrees of variation due to local abiotic conditions (e.g., light, soil, nutrients). Even within a single tree, flow velocities vary with depth in the xylem, circumferentially around the tree, and vertically below the base of the live crown. Further, it is necessary to measure sap flow frequently throughout the day and for the entire growing season to adequately capture temporal variation. Even in monoculture plantations with evenly spaced trees of identical age, genetic traits, and resources, there will be non-uniform water use patterns within and among trees (Oren et al., 1998). Working in natural stands comprised of mixed species of varying ages warrants an optimized sampling design to adequately represent stand-level fluxes (Moore and Aparecido, 2018; Moore et al., 2018).

Accordingly, the two most important considerations for an ideal sampling design are 1) adequate sample size, and 2) minimal sampling bias, given the fundamental problem of high natural variability in most studies. Failure to capture variance is likely common in many sap flow studies, but rarely is it acknowledged as a source of error. Other common sources of error exist in the TD measurement itself. Such errors have been well documented in the literature (Clearwater et al., 1999; Flo et al., 2019; Paudel et al., 2013; Peters et al., 2018). These include a susceptibility to natural thermal gradients, steep radial gradients from one end of the sensor to the other, sensors placed in partial non-conducting wood, inability to distinguish non-zero nighttime flows (i.e., baselining), bidirectional flows, wounding artifacts, and general noise in the signal due to low flows or improper heat regulation. Major advancements are needed in sap flux studies to improve accuracy and reduce errors. However, as the list of worrisome errors grows, there is also a critical need to understand which errors are most problematic in a given system of study.

Given the growing body of literature that demonstrates a need for custom calibrations and the mounting evidence that the original Granier design can underestimate flows by more than 25% (Flo et al., 2019), what is the future of the TD method? Calibrations require elaborate set ups to develop relationships between actual flows in a stem and the sensor output. The methods vary from intact tree lysimeters or similar weighing methods that include the root system (McCulloh et al., 2007; Sperling et al., 2012), to cut saplings placed in a water reservoir (Pasqualotto et al., 2019), to benchtop methods using cut segments of wood under either positive pressure (Bush et al., 2010; Paudel et al., 2013; Steppe et al., 2010; Reis et al., 2006) or vacuum (Ayuthaya et al., 2010; Bush et al., 2010; Fuchs et al., 2017; Hultine et al., 2010). There is a growing need to standardize calibration methodologies and optimize approaches that are less destructive and easier to carry out. Unfortunately, we still lack a fundamental understanding of the drivers of differences in calibrations between species, studies, and sensor types.

The objective of this paper is to discuss the future of TD sensors and recommend potential improvements, as we navigate frontiers in methodologies and strive for a higher standard of use. The three avenues for sensor advancement we propose include appropriate levels of sensor replication, customized error mitigation, and “smart” calibrations. In a series

of recent comparison studies (Table 1), we determined mean sap flux density within and among groups of trees. These studies were conducted within temperate coniferous forest ( $n=46$ ), temperate oak savanna ( $n=36$ ), temperate pine forest ( $n=49$ ), temperate bottomland hardwood forest ( $n=23$ ), tropical premontane rainforest ( $n=43$ ), semiarid subtropical shrubland ( $n=25$ ), and tropical dry forest ( $n=15$ ), with a total of 237 sensors. Two study sites were also equipped with eddy covariance systems for determination of stand-level evapotranspiration. Comparisons tended to focus on relative flow differences between species, between wetter and drier microsites, between understory and overstory components, or between wetter and drier periods of the growing season. Except for the shrubland sites, study trees tended to be >15-cm diameter and frequently in excess of 50-cm.

## NEW FRONTIERS

### Sensor replication

In our set of eight case studies, we found that mean sap flux density varied by an order of magnitude, from  $\sim 250$  to  $\sim 2000$   $\text{kg m}^{-2} \text{d}^{-1}$  (or 25 to 200  $\text{mm d}^{-1}$ , Figure 1). In general, higher flows were associated with greater sensor-to-sensor variance. Standard deviations were as much as 166% of mean values in honey mesquite (Figure 1g) and frequently above 100% of mean estimates in other studies. As expected, replication improved mean estimates by lowering standard errors, which ranged between 12 and 55% of mean values. Over all studies combined, standard errors averaged 137  $\text{kg m}^{-2} \text{d}^{-1}$ , an indicator of general precision in estimating mean fluxes in natural systems with moderate sensor replication ( $\sim 10$  to 20 per group).

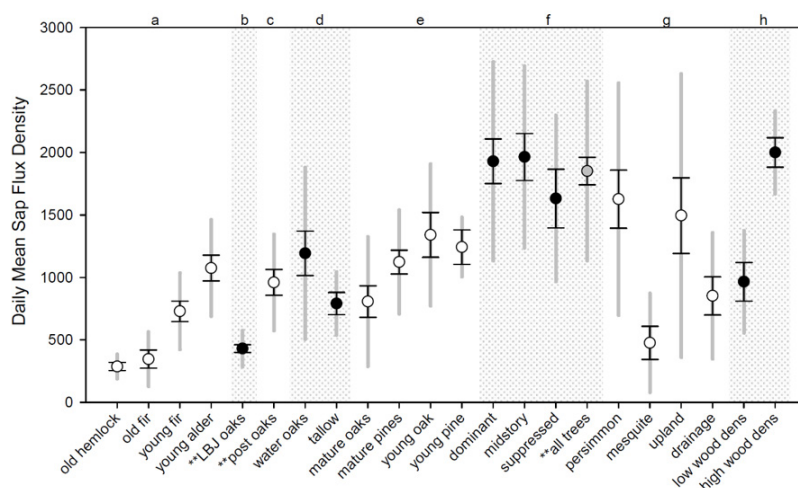


Figure 1. Daily mean sap flux density ( $\text{kg m}^{-2} \text{d}^{-1}$ ) for each study and tree category with standard errors (black) and standard deviations (gray). From left to right, alternating fill colors: a) temperate coniferous forest with three species (Western hemlock, Douglas-fir, red alder) and age categories (old-growth and young); b) temperate post oak savanna at the LBJ grassland; c) temperate post oak savanna; d) bottomland hardwood forest with two species (water oaks and Chinese tallows); e) temperate pine forest with two species (post oak, loblolly pine) and age categories (mature and young); f) tropical montane rainforest with three canopy categories (dominant, midstory, suppressed), as well as all trees combined (gray circle); g) semiarid subtropical shrubland with two species (persimmon and honey mesquite) and landscape positions (upland and drainage); and h) tropical dry forest with two species differing in wood density. \*\*Denotes studies where mean values for a single category were targeted. Citations for published studies are included in Table 1.

Table 1. Study site descriptions including location, species, number of trees, number of sensors, and sensor requirements (from statistical power test for sample size determination) for each comparison study reported in Figures 1 and 2. Number of sensors required is based on a 95% confidence interval and observed variance between sensors. Percent measured reflects the proportion of sensors deployed in that study relative to the number required to reach 95% confidence in the mean comparison.

Ecosystem type & comparison	Species	Number of trees	Number of sensors deployed	Number of sensors required	Percentage Measured (%)
a) Temperate Coniferous Forest, Oregon USA (Moore et al., 2004)					
Old hemlock	<i>Tsuga heterophylla</i>	3	9	112	8
Old fir	<i>Pseudotsuga menziesii</i>	3	9	8-112 <sup>a</sup>	8-113 <sup>a</sup>
Young fir	<i>Pseudotsuga menziesii</i>	7	14	8-16 <sup>a</sup>	88-175 <sup>a</sup>
Young alder	<i>Alnus rubra</i>	7	14	16	88
b) Temperate Oak Savanna, North Texas USA (unpublished data)					
LBJ oaks	<i>Quercus marilandica</i> , <i>Quercus stellata</i>	11	22	50	44
c) Temperate Oak Savanna, Southeast Texas USA (unpublished data)					
Post oaks	<i>Quercus stellata</i>	5	14	32	44
d) Temperate Bottomland Hardwood Forest, Texas USA (unpublished data)					
Water oaks	<i>Quercus nigra</i>	8	15	27	56
Chinese tallow	<i>Triadica sebifera</i>	6	8	27	30
e) Temperate Pine Forest, Texas USA (Cooper et al., 2019)					
Mature oaks	<i>Quercus stellata</i>	10	17	29	59
Mature pines	<i>Pinus taeda</i>	10	19	29	66
Young oaks	<i>Q. stellata</i> , <i>Q. marilandica</i>	10	10	273	4
Young pines	<i>Pinus taeda</i>	3	3	273	1
All oaks	<i>Q. stellata</i> , <i>Q. marilandica</i>	20	27	231	12
All pines	<i>Pinus taeda</i>	13	22	231	10
f) Tropical Montane Rain Forest, Costa Rica (Aparecido, 2017; Aparecido et al., 2016)					
Dominant	Various (see citations)	8	20	59-4255 <sup>a</sup>	0.5-34 <sup>a</sup>
Midstory	Various (see citations)	10	15	49-4255 <sup>a</sup>	0.4-31 <sup>a</sup>
Suppressed	Various (see citations)	8	8	49-59	14-16 <sup>a</sup>
All trees	Various (see citations)	26	43	41	105
g) Semiarid Subtropical Shrubland, Texas USA (unpublished data)					
Texas persimmon	<i>Diospyros texana</i>	8	16	9	178
Honey mesquite	<i>Prosopis glandulosa</i>	5	9	9	100
Upland	<i>D. texana</i> , <i>P. glandulosa</i>	7	14	26	54
Drainage	<i>D. texana</i> , <i>P. glandulosa</i>	6	11	26	42
h) Tropical Dry Forest, Brazil (unpublished data)					
Low wood density	<i>Commiphora leptophloeos</i>	5	7	4	175
High wood density	<i>Cenostigma pyramidale</i>	5	8	4	200

<sup>a</sup>Two comparisons were made, generating sensor requirement estimates for each, i.e.

(a) old fir is compared with old hemlock and young fir; young fir is compared with old fir and young alder.

(f) Dominant trees are compared with midstory and suppressed; suppressed trees are compared with dominant.

Our comparison indicates that sensor replication is critical to compare water use characteristics between coexisting groups of trees. Sample size or sensor requirements for

each comparison were determined using a statistical power test (Sullivan, 2018). Estimated number of sensors required was based on observed ranges between minimum and maximum observations using a 95% confidence interval. For comparisons between two groups, we used a two-sample comparison test with continuous outcome and 80% power. To determine the confidence in a mean value for a single species, we used a one-sample test with continuous outcome and 80% power. In temperate coniferous forests (Figure 1a), available data were insufficient to discern differences in average sap flux density over the entire study period between old western hemlock and old Douglas-fir. But mean differences between young Douglas-fir and young red alder were larger and more easily detected with the available data. In the semiarid shrubland study (Figure 1g), mean differences between species were larger than between the two landscape positions. In other cases, such as the tropical dry forest (Figure 1h), mean differences between the high and low wood density species were quite large and easily distinguishable.

The study located in an ultra-diverse tropical rainforest (Figure 1f) demonstrates the importance of high sensor replication and systematic sampling of groups. The diversity of trees in this study prevented replication within species, but rather replication focused on canopy position (dominant, midstory, and suppressed; see Aparecido et al. (2016) for sampling details). Differences due to canopy position were not large enough to be detected, but the equal allocation of sensors to each group likely reduced bias in the overall site mean estimate (Figure 1f gray).

Actual number of replicate sensors deployed in each case study are reported in Table 1 and averaged 14 per group, up to 27, which is typical or even considered above normal for similar TD studies. However, this amount of replication nearly always lacked sufficient statistical power to capture mean differences between groups or overall means for a given study due to the high variance inherent in these forests (Figure 1). Only the tropical rainforest study and dry tropical forest study had deployed enough sensors to accurately estimate site-level mean values (Table 1f, All Trees) or differences between groups (Table 1h), respectively.

However, some comparisons such as mesquite and persimmon required only a few sensors to detect species differences (Table 1g). In the temperate coniferous forest, modest replication ( $n=7$  trees each) was sufficient to compare young Douglas-fir to young red alder (88% of required), as well as young and old Douglas-fir (>100% of required), but not old western hemlock and old Douglas-fir ( $n=3$  trees each, only 8% of required), which needed an estimated 112 replicates according to the statistical power test (Table 1a). Both the temperate oak savannas (Table 1b, c) required about twice as many sensors than deployed to adequately capture mean sap flux density to within 95% confidence. Following a severe wildfire, post-fire recovery led to high variance (Figure 1e) that made it very difficult to compare young regenerating pines ( $n=3$ ) to resprouting oaks ( $n=10$ ) in the severely burned site (Table 1e), which needed an impractical 273 sensors per group according to the statistical power test. More replication would affect the power test inputs, so the actual number of sensors needed may be lower.

In the tropical rainforest (Table 1f), enormous numbers of sensors (4255) would be required to detect differences between dominant and midstory canopy positions, and an estimated 49 and 59 sensors are needed to differentiate between suppressed and midstory, or between suppressed and dominant, respectively. However, the total number of 43 sensors across all canopy positions was sufficient for estimating stand-level means. The statistical power test indicated that only 41 sensors were required in that case. Nevertheless, having accounted for potential bias between categories in this diverse system is arguably more robust than simple random selection of trees.

### Customized Error Mitigation

While many types of errors occur, they do not affect all studies equally. Custom, site-specific provisions to minimize errors associated with the use of TD sensors are recommended as the most efficient and effective approach. Sites with older, larger trees should mitigate errors associated with non-uniform flows across deep sapwood and/or circumferential variation (Aparecido et al., 2019). Installing additional sensors at multiple

depths and multiple locations around the tree, appropriate for their size, is necessary to capture the expected greater variation within trees, or else there will be increased risk of sampling bias. Most likely, flows are overestimated for large trees with deep sapwood when only the outer 2-mm sapwood is used to represent whole-tree water fluxes (Berry et al., 2018). These strategies were utilized in the temperate coniferous forest study in old-growth Douglas-fir and western hemlock (Moore et al., 2004), as well as in the tropical rainforest with old-growth trees in excess of 60-cm diameter (Aparecido et al., 2016). Younger trees, such as in plantations or orchards are associated with more uniform flows and, therefore should require fewer sensors to minimize errors associated with sampling bias.

In drier environments, there are several potential errors that require careful study design to mitigate. Natural temperature gradients (i.e., background temperature differences induced between the reference and the heater probes) can interfere with TD measurements in stands with a sparse density of trees (which allows for greater exposure to radiative heating of wood), or where asymmetric heating of wood or temperature differences between soil water and wood occur (Cermak and Kucera, 1981). Do and Rocheteau (2002a) found that natural temperature gradients, in a desert woodland, were as high 1°C (during day) to -2°C (during night) and could significantly overestimate sap flux rates.

To mitigate errors induced by natural temperature gradients, the Transient Thermal Dissipation (TTD) method has been shown to be quite effective (Do and Rocheteau, 2002a, b). In TTD, instead of the continuous heating applied through the heater probe, non-continuous heating is applied. For example, the TTD method used at our semiarid site utilized a 5 min heating cycle followed by a 25 min cooling cycle. Raw temperature differences recorded throughout the heating-cooling cycle enable corrections for 'drifts' induced by natural temperature gradients. This corrected temperature signal is used for calibrating against the actual sap flow rates. It should be noted, however, that the challenges of calibrations are not overcome by TTD and the method needs further testing and custom calibration before application. Paudel et al. (2013) used TTD on cut stems as opposed to sawdust-based calibrations by Do and Rocheteau (2002b) and noted a considerable improvement in flow estimates achieved by TTD relative to the continuous heating method.

Semiarid sites are also more likely to have dry nighttime conditions that prevent flows from reaching zero at night. While it is recommended that all sites check their zero flow baselines for errors, it is especially critical to note any moving baseline patterns that are caused by high vapor pressure deficits (VPD) at night. Baseline corrections for non-zero nighttime flows (see Fisher et al., 2007; Hoelscher et al., 2018) were implemented for the temperate pine forest (data not shown) and the temperate post oak savanna at the LBJ grassland (Figure 2). A threshold minimum value of 0.1 kPa VPD was used to find nights where zero flows were highly likely to occur (Figure 2a). The maximum differences in temperature observed for zero flow nights (known baselines) were then used to interpolate values for interim nights when non-zero flows were apparent (Figure 2b). Note that baselines drifted over the course of longer intervals of ten or more days (Figure 2b), so this method assumes that longer-term deviations from baseline are due to measurement drift, rather than progressively higher nighttime flows through the season. For more information about baseline corrections using VPD, see Hoelscher et al. (2018).

### **“Smart” Calibrations**

The TD approach relies on uniform flow velocities across the full length of the sensor. The perils of installing sensors in a combination of conducting and non-conducting wood were the topic of Clearwater et al. (1999), who described the physics of heat dissipation across non-uniform flows, as well as provided a mathematical approach to correct for errors associated with partial installation in inactive sapwood. This has led to extensive use of Clearwater's methodology in subsequent studies. Less attention was paid, however, to the consequences of steep flow gradients across sensors that were in otherwise functioning sapwood. Using the calculations in Clearwater et al. (1999), we demonstrate that anything other than 100% uniform flow can lead to an underestimation of sap flow (Figure 3). For a 2-cm probe, a difference of only 20% from one end of the probe to the other can result in an underestimation



of 13-16%. If the gradient were 40%, the underestimation rises to 26-30%. This is somewhat intuitive, given that a probe in 50% active sapwood and 50% inactive sapwood is expected to have a 48% underestimation of actual velocities of the active xylem. Given the average radial flow profiles of angiosperms and gymnosperms (Pataki et al., 2011), trees with 2 cm of active xylem with those gradients across the sensor would be expected to produce underestimations of 42 to 53%, respectively (Figure 3).

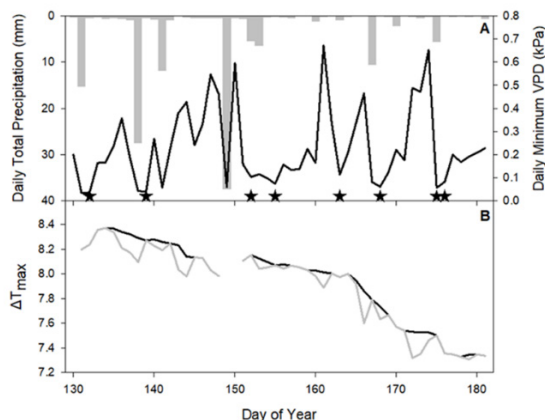


Figure 2. Temporal trends in (A) daily precipitation (in mm; gray bars) and minimum daily vapor pressure deficit (in kPa; solid black line) were associated with variations in maximum daily temperature differences ( $\Delta T_{max}$ , °C) between the heated and unheated probes (B) in oaks at the LBJ grassland. Stars indicate days when minimum VPD approached zero and nighttime transpiration was assumed to equal zero. The corrected  $\Delta T_{max}$  are indicated by the black line in (B), and the gray line shows the original baseline values.

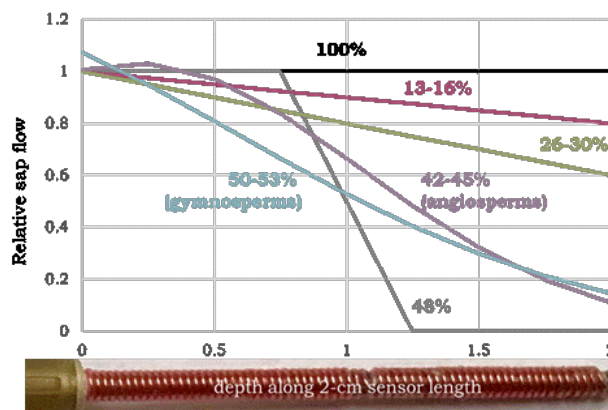


Figure 3. Considering a typical TD sensor with a length of 2 cm, relative flow is not always 100% across the full length of the probe (black line), as is theoretically assumed for TD probes. Clearwater et al. (1999) provides a mathematical basis for predicting and correcting for underestimated flows in non-conducting wood. The gray line describes a sensor in 1-cm-deep sapwood (50% active, 50% inactive) that would result in a 48% underestimation in flows using the original Granier equation. The pink and green lines describe linear reductions in relative flow of 20% and 40%, respectively. The purple and blue lines describe average velocity profiles for angiosperms and gymnosperms as reported by Pataki et al. (2011). Associated underestimations in flows as computed using equations in Clearwater et al. (1999) are given for each scenario.

It is reasonable to project that issues with using TD probes in non-uniform flow profiles common among many (if not most) trees, could be a major factor to explain the systematic underestimation reported for sap flow calibrations in TD studies (Fuchs et al., 2017). This “smart” approach to calibrations that accounts for gradients in velocity has the potential to open new opportunities for using profiles to customize calibration for each individual tree using their own unique profile. If actual velocity profiles are known, then the Clearwater et al. (1999) correction is an ideal way to reduce bias caused by using calibrations in a very small subset of stems. We simply do not know that calibrations done on cut stems, in the laboratory, using induced (often excessive) flows are representative of responses for the entire species. Those stems used in calibration may not represent all trees of that species for several reasons. First, the stems selected for calibration tend to be smaller than mature trees. Second, the stems may undergo cavitation during handling prior to calibration, which would artificially alter their velocity profiles relative to in situ trees. Third, calibrations may be done using unnaturally strong tension to move water through the stem that artificially steepens the velocity profile relative to in situ trees. Therefore, “smart” calibrations pose an exciting future for improving the accuracy and precision of TD methods in the future.

## CONCLUSIONS

In conclusion, the TD approach remains a valuable and preferred method for the future determination of water use in trees. Sensor replication can fundamentally impact a study’s outcomes and should be more carefully considered in study design. Addressing the high variation (including both bias and error) inherent in most studies is best done by first identifying which sources of variation are most problematic for that particular study. This will allow for targeted approaches that best correct for bias and error. And finally, we propose the development of new “smart” calibration approaches that correct for fundamental effects of radial variation that could eventually lead to simpler and more accurate customized corrections for individual stems.

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