

A comparison of daily water use estimates derived from constant-heat sap-flow probe values and gravimetric measurements in pot-grown saplings

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Summary Use of Granier-style heat dissipation sensors to measure sap flow is common in plant physiology, ecology and hydrology. There has been concern that any change to the original Granier design invalidates the empirical relationship between sap flux density and the temperature difference between the probes. Here, we compared daily water use estimates from gravimetric measurements with values from variable length heat dissipation sensors, which are a relatively new design. Values recorded during a one-week period were compared for three large pot-grown saplings of each of the tropical trees *Pseudobombax septenatum* (Jacq.) Dugand and *Calophyllum longifolium* Willd. For five of the six individuals, *P* values from paired *t*-tests comparing the two methods ranged from 0.12 to 0.43 and differences in estimates of total daily water use over the week of the experiment averaged < 3%. In one *P. septenatum* sapling, the sap flow sensors underestimated water use relative to the gravimetric measurements. This discrepancy could have been associated with naturally occurring gradients in temperature that reduced the difference in temperature between the probes, which would have caused the sensor method to underestimate water use. Our results indicate that substitution of variable length heat dissipation probes for probes of the original Granier design did not invalidate the empirical relationship determined by Granier between sap flux density and the temperature difference between probes.

Keywords: *Calophyllum longifolium*, Granier sensors, *Pseudobombax septenatum*, variable length probes, validation.

Introduction

Sap flow sensors have been used for over 70 years to estimate rates of water movement in plant stems (Huber and Schmidt 1936). Knowledge of the volume of water moved by plants is vital to understanding hydrologic cycles, community ecology

and the tradeoffs between water use and carbon acquisition. Recent examples in which sap flow techniques have been employed include assessing the impact of vegetation change from grasslands to woodlands on the hydraulic cycle of an aquifer (Roberts et al. 2005), determining differences in total water use by trees in riparian versus upland sites (O'Grady et al. 2006), scaling from leaf-level photosynthetic measurements to determine annual carbon gain differences between evergreen and broadleaf species based on sap flow (Catovsky et al. 2002) and assessing the effects of pathogens on physiology (Meinzer et al. 2004). The use of sap flow sensors has been crucial in characterizing hydraulic redistribution of soil water by roots (Burgess et al. 1998, 2000, 2001, Smith et al. 1999, Brooks et al. 2002, 2006, Scholz et al. 2002, Hultine et al. 2003a, 2003b, 2004, Moreira et al. 2003, Oliveira et al. 2005, Song et al. 2000) and nighttime transpiration (Benyon 1999, Bucci et al. 2004, Daley and Phillips 2006, Scholz et al. 2006). Various approaches have been used to assess sap flow rates, but all rely on measurement of changes in the temperature of the xylem induced by an external addition of heat.

One of the most commonly used techniques for measuring sap flow was developed by Granier (1985, 1987). This method uses two sensors, each containing a thermocouple inserted perpendicularly into the sapwood. The downstream sensor is heated and the measured difference in temperature between the sensors narrows as sap flux density ($\text{g m}^{-2} \text{s}^{-1}$) increases. Granier (1985) established the relationship between the temperature difference and sap flux density empirically by testing the system in detached stem segments through which water was allowed to flow at known rates.

There have been a number of previous tests of the original Granier sensors (Cabibel and Do 1991, Granier 1985, Lu and Chacko 1998, Clearwater et al. 1999, Lu et al. 2002), but the more recently developed variable length sensors (James et al. 2002) have not been tested as thoroughly. This new design dif-

fers from the original 20-mm-long sensors by having 10-mm-long sensors that can be installed at any depth because of variable length spacers of PEEK tubing between the sensor and the cable that runs to the data logger. The new probes also operate at slightly lower wattage to heat the downstream sensor. Lu et al. (2004) have raised doubts about the validity of Granier's empirical relationship when the sensor design deviates from the original. To evaluate this concern, we compared daily water use in large potted plants estimated gravimetrically and by the Granier method using variable length probes.

Material and methods

Plant material and site information

Three saplings each of *Pseudobombax septenatum* (Jacq.) Dugand and *Calophyllum longifolium* Willd. were grown at the Smithsonian Tropical Research Institute Santa Cruz Experimental Field Facility in Gamboa, Republic of Panama (9° N, 79° W, 35 m a.s.l.) (Winter et al. 2005, Cernusak et al. 2006). Plants were grown from seed in 378-l plastic containers (diameter 78 cm up to a height of 73 cm, total height 99 cm) filled with forest soil (Figure 1). The containers had a round, 38.5-cm-diameter opening at the top. A 5-cm hole at the base allowed drainage. Plants were fertilized with 30 g of Osmocote Plus (15,8,11 N,P,K) once per month. Soil containers

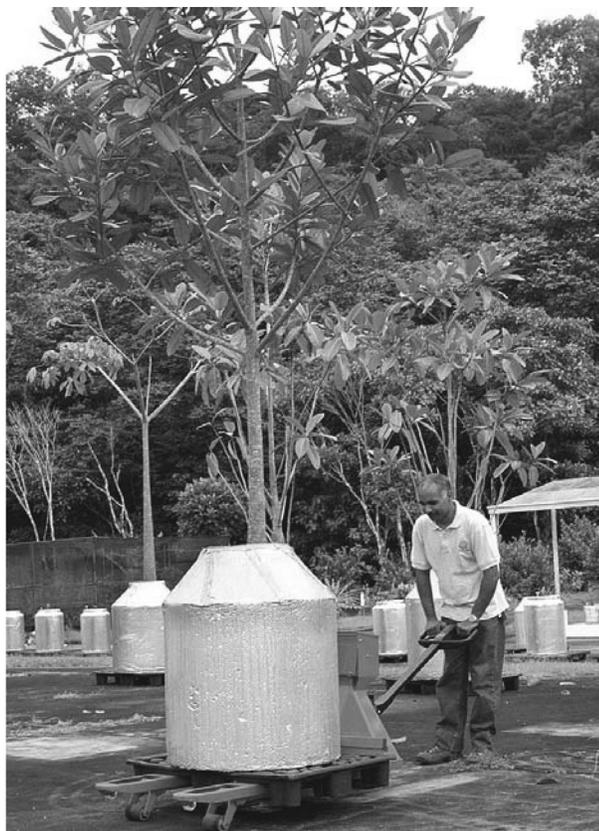


Figure 1. Weighing one of the *Calophyllum longifolium* saplings with the pallet truck scale.

were placed on polyethylene pallets (108 × 72 × 14 cm). Reflective insulation surrounded the soil containers and the base of the saplings, and loosely covered the tops of the containers. Experimental plants were aged about 36 (*P. septenatum*) and 40 (*C. longifolium*) months. Saplings were similar in size, but *Calophyllum* individuals had greater leaf areas (Table 1).

Sap flow measurements

Daily sapling water use was estimated by the heat dissipation technique. Two 10-mm-long probes (James et al. 2002) were inserted 15-mm deep in the sapwood of each sapling and 100-mm apart vertically so that the top probe was about 100 mm below the first branch junction. Sensors were coated with silicone heat sink compound before insertion to improve thermal contact with the xylem. The top probe was heated continually by the Joule effect with the power supply set to deliver 0.15 W per probe. The temperature difference between the probes was measured every minute and recorded by a data logger equipped with a 32-channel multiplexer and the mean was recorded every 10 min.

Sensors were installed on October 13, 2005 and data were collected through October 20, 2005. The recorded difference in the temperature (ΔT) between the sensors was converted to sap flux density, u ($\text{g m}^{-2} \text{s}^{-1}$), using Granier's (1985, 1987) empirical equation:

$$u = 119k^{1.231} \quad (1)$$

where the coefficient

$$k = \frac{\Delta T_m - \Delta T}{\Delta T} \quad (2)$$

and ΔT_m is the maximum daily temperature difference between the sensors, which is assumed to occur at night when sap flow has stopped. Sap flux density was scaled to sap flow (g s^{-1}) by multiplying by the cross-sectional area of the functional xylem, which was determined by dye staining. Specific-

Table 1. Leaf area, stem diameter and sapwood area of the experimental trees. Stem diameter and sapwood area were measured on the main stem between the two sensor probes. Standard deviations of the species' means are in parenthesis.

Individual	Total leaf area (m^2)	Stem diameter (cm)	Sapwood area (cm^2)
<i>Pseudobombax septenatum</i>			
1	6.2	6.3	18.0
2	6.7	6.3	17.0
3	4.4	6.7	19.4
Mean	5.8 (1.2)	6.4 (0.2)	18.1 (1.2)
<i>Calophyllum longifolium</i>			
1	8.9	6.2	23.4
2	8.4	6.2	22.5
3	10.5	5.7	18.1
Mean	9.3 (1.1)	6.0 (0.3)	21.3 (2.8)

cally, on October 20, 2005, the bole of each sapling was cut just above the soil surface, and the sapling was immediately transferred to a large water tank where the bole was recut under water just below the point of sensor installation. The cut end of the sapling was then placed in a bowl of 0.5% acid fuchsin for 10 min for dye perfusion. A segment of the bole between the sensors was collected and the cross-sectional face was scanned with a flat-bed scanner. The cross-sectional area of xylem that had been stained pink by the dye was measured with an image analysis program (Image J, NIH, USA, <http://rsb.info.nih.gov/ij/>). Only the central, nonconducting area of the stem was excluded from the area measurements. Sensors were entirely embedded within the stained area.

Gravimetric measurements

To determine whole-plant transpiration, the soil was saturated with water, the soil surface covered with a 5-cm layer of gravel to reduce evaporation, the drainage hole closed and containers plus plant plus pallet were weighed using a PW800 pallet truck scale (A and A Scales LLC, Prospect Park, NJ; capacity 2500 kg, graduation 0.5 kg) before sunrise and after sunset. Total mass ranged from 620 to 700 kg, and mass readings were fully reproducible. Two iron pallets (90 kg combined mass) were used as a standard to further check output stability and temperature sensitivity of the balance; the balance output was constant throughout the experiment. Water lost through transpiration was replenished following mass determination after sunset. Evaporation of water from the soil surface, measured in containers without plants, was below the resolution of the pallet truck scale. Evaporation from 40-l pots with a similar soil surface (0.11 m^2) as the 378-l pots was determined with a Sartorius QS64B balance (Thomas, Swedesboro, NJ; capacity 64 kg, graduation 5 g) and ranged from 25 to 50 g during the day and 5 to 10 g at night.

Meteorological data collection

Microclimate was measured at 15-min intervals with a LI-190SA quantum sensor (Li-Cor, Lincoln, NE), HMP45C temperature and relative humidity probe (Campbell Scientific, Logan, UT) and a fine-wire thermocouple with Model ASPTC aspirated shield (Campbell Scientific), all connected to a Campbell Scientific CR10X data logger

Data analysis

Total daily water use (kg day^{-1}) was estimated by the sap flow method by summing the total sap flow for each sapling between 0700 and 1800 h. For the scale method, total daily water use was estimated from the difference in container mass measured before dawn and after sunset. Sap flow data for a sapling were used only when a 24-h cycle was measured without interruption. Faulty sensors resulted in the elimination of data for one day for one sapling and two days for another sapling. Data recorded for all individuals during the first two days after probe installation were also excluded because the ΔT_m was much higher than later in the week, indicating that some time was required to establish good thermal contact between the

sensors and the surrounding sapwood. Although ΔT_m continued to decline in one *P. septenatum* individual until the fourth day, these data were not discarded because the daily ΔT also declined, resulting in consistent values of k after two days. To determine if gravimetric and sap flow measurements resulted in similar estimates of daily water use, paired *t*-tests were performed for each individual.

Results

Sap flow measurements were conducted over a series of sunny days in October 2005 (Figure 2A). Figure 2B shows the sap flow rate in all six saplings over three consecutive days. On Days 291 and 292, the sensors indicated a steep increase in sap flow after dawn, then a relatively steady period of flow, followed by a decline in the afternoon. On Day 290, following a brief rain shower, all saplings exhibited an afternoon depression in sap flow followed by a partial recovery. For all individuals, the sensors showed negligible nighttime sap flow.

The dye perfusions indicated that the sensors were entirely surrounded by functional xylem. Where the stem segment was stained, the concentration of the dye was uniform, suggesting there were no areas with markedly different sap flow rates. In the *P. septenatum* saplings, the entire xylem cross-sectional area was functional, but the thick bark and wide pith limited

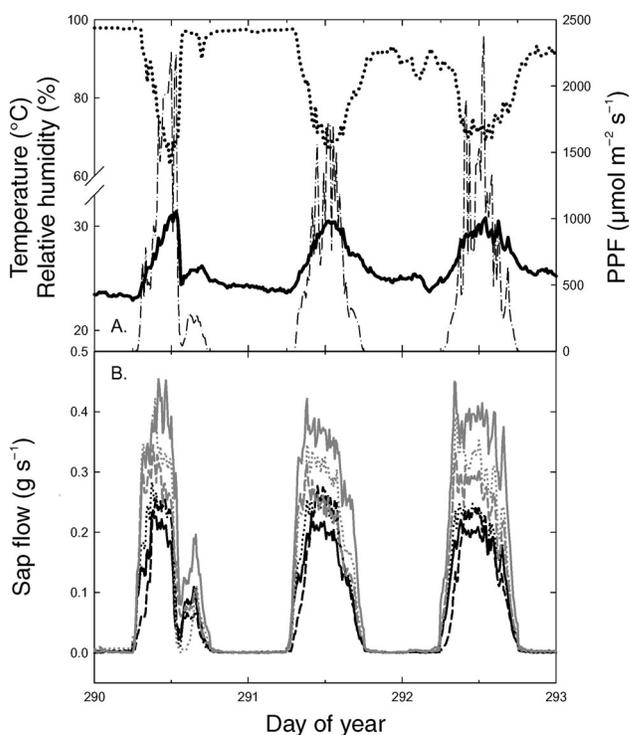


Figure 2 A. Temperature (solid line), relative humidity (dotted line), and photosynthetic photon flux (PPF; dash-dotted line) for the three consecutive days of the experiment during which sensors functioned in all six saplings. B. Sap flow in individual saplings of *Pseudobombax septenatum* (black lines) and *Calophyllum longifolium* (gray lines).

the total conductive area. In the *C. longifolium* saplings, there was an area of unstained non-functional wood near the center of the stem, but the sensors did not reach this area.

Estimates of daily water use measured gravimetrically and with sap flow sensors showed general agreement (Figure 3). For all but one *P. septenatum* sapling, the values from the two methods were not significantly different ($0.12 \leq P \leq 0.43$, Table 2). In the sapling that showed differences between the estimates ($P < 0.05$), the sap flow sensors underestimated water use compared with the gravimetric measurements. For *P. septenatum* individuals, sap flow sensors estimated daily water use values between 4.6 and 8.7 kg day⁻¹, and gravimetric measurements ranged from 4.1 to 10 kg day⁻¹. In *C. longifolium* saplings, daily water use estimates by the sensor were between 7.2 and 14.3 kg day⁻¹, and gravimetric daily totals were from 6.3 to 14.0 kg day⁻¹.

Discussion

Recently, there has been concern that changes from Granier's original sensor design might invalidate Granier's empirically derived relationship between sap flux density and differences in temperature between the probes (Equation 1; Lu et al. 2004). For the current study, the variable length sensors described by James et al. (2002) were tested in intact container-grown saplings of two species that had not previously been measured. The sensors showed the expected patterns of sap flow with a sharp increase in the morning to a value maintained until mid-afternoon when water flow declined steadily (Figure 2B). The maximum nighttime temperature difference between sensors ranged from 13 to 18 °C, resulting in localized maximum xylem temperatures of 37 to 43 °C.

Previous tests by James et al. (2002) suggest that variable length sensors perform reliably in both angiosperm and conif-

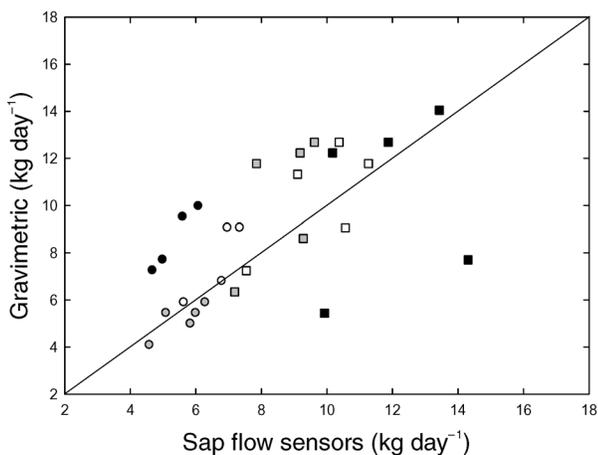


Figure 3. Daily water use estimates for individuals measured gravimetrically and with sap flow sensors. Symbols represent individuals 1, 2 and 3 of *Pseudobombax septenatum* (○, ●, ●) and *Calophyllum longifolium* (■, □, ■), respectively. Only the *P. septenatum* individual designated by ● deviated significantly from the 1:1 relationship indicated by the solid line.

Table 2. Mean water use estimates by the sap flow and gravimetric methods for the three individuals of each species, and *P* values from paired *t*-tests comparing sap flow and gravimetric estimates of water use. Mean daytime sap flux (g m⁻² s⁻¹) was calculated from 0700 to 1800 h over the course of the sap flow measurements. Standard errors are given in parentheses.

Individual	Sap flux g m ⁻² s ⁻¹	Water use		<i>P</i> value
		Sap flow kg day ⁻¹	Gravimetric kg day ⁻¹	
<i>Pseudobombax septenatum</i>				
1	87.4 (9.9)	6.7 (0.7)	7.7 (1.6)	0.15
2	73.9 (9.1)	5.3 (0.6)	8.6 (1.3)	< 0.01
3	68.9 (8.9)	5.6 (0.7)	5.2 (0.7)	0.12
<i>Calophyllum longifolium</i>				
1	120.5 (16.5)	11.9 (1.9)	10.4 (3.7)	0.42
2	100.7 (15)	9.8 (1.5)	10.4 (2.2)	0.43
3	112.9 (12.9)	8.6 (1)	10.3 (2.7)	0.17

erous trees (Irvine et al. 2002, Meinzer et al. 2003, 2004). Thus, the general agreement of daily water use estimates from gravimetric measurements and sap flow sensors (Table 2, Figure 3) was expected. The design of the variable length sensors represents an improvement over the original sensors (Granier 1985) because the effective sensor length is shorter (10 versus 20 mm), allowing detailed measurement of radial profiles of sap flux when multiple sensors are inserted across the depth of the sapwood. Because radial variation in sap flux can be large (Phillips et al. 1996, Jimenez et al. 2000, James et al. 2002, Domec et al. 2005a, 2005b), measurement across the depth of sapwood may increase the accuracy of whole-tree sap flow estimates and improve water use predictions (James et al. 2002).

Both gravimetric and sap flow methods of estimating plant water use indicated that *C. longifolium* saplings transpired more water on a daily basis than *P. septenatum* saplings (Figures 2B and 3), which was consistent with the greater leaf area of *C. longifolium* individuals (Table 1). Although *P. septenatum* individuals had a slightly larger mean stem diameter, thicker bark and a larger pith area resulted in a smaller sapwood area than in *C. longifolium* (Table 1).

In the *P. septenatum* individual where the two methods yielded different estimates of daily water use, several explanations are possible. If the probes were positioned in a region that spanned both high and low or no sap flux density, the sensors would underestimate the true value because the relationship between ΔT and the coefficient *k* is nonlinear (Clearwater et al. 1999). This situation did not apply to the underestimation of water use by the sensor, because the dye perfusion indicated that the entire cross-sectional area of xylem was transporting water. A second possibility for the discrepancy is that the sensor was located in a pocket of wood that transported water more poorly than adjacent areas, such as caused by tension wood, unseen knots or other heterogeneities in the wood. This is unlikely, though, given the uniformity of the dye stain. A third possible cause is high nighttime transpiration, which would result in a lower ΔT_m (Equation 1) than would occur at

zero flow and which would result in an underestimate of sap flow by reducing the difference between ΔT_m and the ΔT measured throughout the day. However, the gravimetric measurements indicated nighttime water loss ranged from 0 to only 5% of the total daily water loss. A fourth possibility is that water evaporated from the pot during the hot days and not at night when humidity was high. The sensors could have been accurately measuring sap flux, whereas the scale may have been recording both transpiration and soil evaporation. However, this seems unlikely, given the small amount of water lost from the pots without plants.

A final explanation is that the sensor underestimated flow because a gradient in ambient temperature during the day caused a decrease in the measured ΔT by heating the lower probe without altering ΔT_m . This effect could have been checked by turning the power source to the heated sensors off and observing any consistent ambient temperature gradients. In this case, the problem could be corrected by subtracting these natural gradients from the ΔT induced by heated sensors (Do and Rocheteau 2002, Phillips et al. 2003).

Although only one sapling showed statistical differences between the tested methods, some other saplings showed considerable variation on certain days, with one method indicating, in some cases, twice the daily water use of the other method (Figure 3). Although the 0.5-kg graduation on the scale contributed to some of this variability, we do not know the source of the remaining variation. However, our results indicate that the methods agree over a period of a few days.

The general consistency of the daily water use values estimated by sap flow sensors and the gravimetric method revalidate the new sensor design (James et al. 2002). The variable length sensors are inexpensive to construct and robust for use in the field. They are also crucial for evaluating species with variable sap flux densities across the depth of their sapwood. Sap flow measurements are the only available method for investigating dynamic changes in daily water use at the whole organism level. The self-zeroing method of the Granier-type sensors makes the empirical relationship particularly impervious to minor changes in sensor design. The two sources most likely to cause deviation from the empirical calibration would be species-specific differences in the thermal properties of the functional sapwood, and changes in ΔT caused by conductive heat transfer because the upstream and downstream probes are installed too close to each other.

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