Theor. Appl. Climatol. 42, 215–221 (1990)

Theoretical and Applied Climatology

551.573

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Comparative Measurement of Stem Flow and Transpiration in Cotton

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With 7 Figures

Received January 16, 1989

Summary

Whole-plant transpiration (*T*) measurements have many applications, but appropriate methods have remained somewhat elusive. A new method using a constant power heat balance gauge, wherein the xylem mass flow rate is calculated from a balance of heat into and out of a stem, has been shown to provide accurate stem flow measurements. To evaluate the applicability of this promising method to field experiments, cotton (*Gossypium hirsutum* L. "GP 3774") stem flow measurements were compared with *T* measured from a weighing lysimeter. Initially to confirm method accuracy, stem flow values were compared in the glasshouse with *T* values determined by mass measurements of a potted plant. The root mean square error (*RMSE*) between the daylight losses from both ($n = 16$) was 8.6% of the mean measured *T* values. In the field, hourly stem flow and lysimeter *T* values were also similar, but there was a large variation in stem flow values among the different plants. To account for differences in plant size between the plants with gauges and all lysimeter plants, stem flow values were adjusted using a stem area ratio factor, which adjusted values, on the average for the season, by 25%. Before adjustment, daylight stem flow totals were consistently greater than lysimeter *T* values. After adjustment, the means differed by only 9%, and the *RMSE* was reduced from 129 to 69 g plant^{-1} d^{-1}. The coefficient of variation of daylight stem flow totals increased throughout the season. In the glasshouse, method accuracy was comparable (errors $< \pm 10\%$) to what has been previously determined. In the field, determining method accuracy was confounded by plant-to-plant variability and, possibly, by errors, unique to the gauge design used in this study, at high flow rates. Thus, this method can provide accurate flow measurements from individual herbaceous plants and is a valuable technique for many applications.

1. Introduction

Accurate transpiration (*T*) measurements from agronomic, range, and horticultural plants have many applications, but much of the existing instrumentation has limitations associated with its use. For example, mass water balances often have a low time resolution; micrometeorological techniques require, among other things, adequate fetch; lysimeters often disturb the soil/root system; and gas exchange measurements affect leaf boundary layers and need to be extrapolated over space and time.

One means of direct whole-plant *T* measurements is the heat pulse method (Cohen et al., 1981; Gray et al., 1985; Cohen et al., 1988; Green et al., 1988). The stem is invaded by a heater and thermocouples, and the stem temperature changes associated with a pulse of heat are measured. Sap mass flow rate calculations usually require knowledge of the active conducting xylem area and an empirical conversion factor which reflects the conversion of heat to sap velocity.

Recently, a constant power heat balance method, similar to a compensating heat balance method used on trees (Schulze et al., 1985), has been successfully used for stem flow measurements of herbaceous plants (Sakuratani, 1981; Sakuratani, 1984; Baker and van Bavel, 1987) and small shrubs (Steinberg et al., 1989; Heilman et al., 1989). The method uses a gauge which is noninvasive of the stem and does not require an empirical calibration. Mass flow is calculated by balancing the heat into and out of a stem. A small heat input is continuously provided from a flexible heater that encircles the stem. Heat losses include vertical and radial conduction and transport by the flow. There can be a time lag between flow initiation and gauge response, depending upon flow rate, and mass flow may not equal T (Steinberg et al., 1989), depending upon plant water capacitance and environmental conditions. For herbaceous plants the effects of both of these facors are usually insignificant with reasonable flow rates and sufficiently long periods. Ham and Heilman (1990) have shown, however, that with the gauge design described by Baker and van Bavel (1987), the method may overestimate flow at high flow rates, but minor design alterations (adjusting the heater width and/or the thermocouple placement) eliminate this problem.

Most of the work evaluating this method has been conducted under controlled environment conditions, using a small number of plants, and for a few days. To evaluate the utility of this method to field experiments, cotton (*Gossypium hirsutum* L. "GP 3774") stem flow measurements were compared with T measurements from a weighing lysimeter throughout a growing season.

2. Methods

Initially, to confirm method accuracy, cotton stem flow values were compared with T values calculated from successive mass measurements of potted plants in a glasshouse. In the field, cotton stem flow values were compared with T values measured by a weighing lysimeter. Comparisons were made for periods of 30 or 60 min; and of approximately 12.5 h [i.e., typically from 0630 to 1900 Central Standard Time (CST)].

2.1 Instrumentation and Theory

Gauges were fabricated locally or were purchased commercially (Models SGA10, SGA13, and SGA16, Dynamax, Inc., Houston, TX)[1]. The local gauges followed the design of Baker and van Bavel (1987), i.e., following the nomenclature of Ham and Heilman (1990), they were a "5-channel" gauge. The commercial gauges were of the "4-channel" design (Steinberg et al., 1990). Both types of gauges consisted of a 10-mm wide heater, an 8-junction thermopile mounted on both sides of high-density cork that encircled the heater, differentially-wired thermocouple junctions positioned above and below the heater on high-density cork, and foam insulation.

The xylem mass flow rate (F, $\mathrm{g\,s^{-1}}$) was calculated from the following (Baker and van Bavel, 1987)

$$F = [P - (K_{st} \cdot A \cdot (\mathrm{d}T_b + \mathrm{d}T_a)/\mathrm{d}x) - (K_g \cdot E)]/[C \cdot \mathrm{d}T_{ba}] \quad (1)$$

where P is the input power (W); K_{st} is the stem thermal conductivity ($\mathrm{W\,m^{-1}\,K^{-1}}$); A is the stem area ($\mathrm{m^2}$); $\mathrm{d}T_b$ and $\mathrm{d}T_a$ are the vertical temperature gradients below and above the heater (K), respectively; $\mathrm{d}x$ is the distance between the two junctions positioned both below and above the heater (m); K_g is the "gauge conductance" (see below), used for determining radial heat flow ($\mathrm{W\,V^{-1}}$); E is the thermopile voltage (V); C is the xylem sap heat capacity ($\mathrm{J\,g^{-1}\,K^{-1}}$); and $\mathrm{d}T_{ba}$ is the temperature gradient across the heater (K). The second and third terms inside the first set of brackets are the vertical and radial conductive heat losses, respectively.

A value of approximately 100 mW was used for P and a value of $0.54\,\mathrm{W\,m^{-1}\,K^{-1}}$ was used for K_{st} (Sakuratani, 1981, 1984; Baker and van Bavel, 1987). Signals were measured using a Model 7X Campbell Scientific, Inc., Logan, UT, data logger. The value of K_g, unique to each configuration (e.g., stem diameter and gauge), was calculated daily using Eq. (1) [assuming $F = 0$ (Steinberg et al., 1989) from approximately 0200 to 0600 CST].

2.2 Glasshouse

From day of year 23 through day 39, 1988, two mature cotton plants, each with a stem diameter of approximately 13 mm and a height of approximately 1 m, were placed in 10-L pots with the soil surface covered with plastic. The soil was a 1 : 1 mixture of vermiculite and a frio clay-loam (fine, montmorillonitic, thermic, Cumulic Haplustoll). Soil water levels were kept high. Pot mass was

[1] Mention of a trademark or a proprietary product does not constitute a guarantee or warranty of the product by the Texas Agricultural Experiment Station and does not imply its approval to the exclusion of other products that also may be suitable.

continuously measured with a 22-kg capacity load cell whose output was monitored by the data logger. The worst-case error for load cell measurements was approximately 5 g. The locally-fabricated gauges were covered with aluminum foil to minimize externally-induced temperature gradients. Gauge and load cell signals were averaged every 30 min. Heater voltage was provided by the data logger.

2.3 Lysimeter

Cotton was sown on day 95, 1988, at 15 plants m^{-2} in 0.67-m wide rows in a 5 ha field at the Blackland Research Center, Temple, TX, which included a 3 m^2 weighing lysimeter (Dugas et al., 1985) whose soil surface was covered with plastic. The soil in the lysimeter was a frio clay-loam (fine, montmorillontic, thermic, Cumulic Haplustoll). The three, 1.5-m long rows in the lysimeter were parallel with its 2-m long dimension. The lysimeter and a surrounding 1-ha area were irrigated to maintain high soil water levels. Ten-minute lysimeter T values were measured throughout the day. Lysimeter T values were converted to a per plant basis (e.g., g $plant^{-1} h^{-1}$ or g $plant^{-1} d^{-1}$) for comparison with stem flow values.

Stem flow measurements were made from day 174 through day 259. A total of 71 days were available for analyses. A total of fifteen different gauges was used; five were locally- and ten were commercially-fabricated. Two to ten gauges, usually more than seven, were attached below the first node of plants on the lysimeter, with one gauge per plant. The number of gauges used increased in the early part of the season due to an increase in the number of plants with appropriate stem diameters (typically >8 mm) for the gauges. Criteria for placing a gauge on a plant included the use of plants from all rows, if possible; use of plants with stem diameters of appropriate size; use of plants whose stem diameters averaged close to the average of all lysimeter plants; and exclusion of plants on the row ends. There were 1 to 4 gauges per row and each gauge was on 3 to 5 plants throughout the measurements period. Gauges were covered with aluminum foil and, for water protection, plastic wrap. Heater voltages were measured by the data logger and provided by a regulated DC power supply. Ten-minute stem flows were calculated using Eq. (1) for each plant with a gauge and were summed for daylight totals.

Because the plants upon which gauges were placed were not necessarily representative of all lysimeter plants, the stem flow data were adjusted. The average stem flow from all plants with gauges was adjusted by multiplying by a factor equal to the ratio of the mean stem area of all lysimeter plants to the area of the plants upon which gauges were placed. Daily stem diameters were linearly interpolated from diameter measurements made below the first node on all plants approximately every 4 weeks. For this adjustment, stem area was taken as a surrogate for other plant attributes (e.g., leaf area and root system development) and was presumed to reflect the effect these attributes had on T. The leaf area index on the lysimeter during this period, estimated from photosynthetically active irradiance measurements, Bougeur's Law, and an extinction coefficient, increased from approximately 1 to 3.

3. Results and Discussion

3.1 Glasshouse

Vertical and radial conductive heat fluxes were lowest during the midday (Fig. 1), reflecting the greater contribution of the xylem water in transporting heat. At night most of the flux loss was through vertical and, especially, radial conduction. Fluxes were constant during the early-morning hours when K_g was calculated.

On day 31, half-hour stem flow and T values were close (Fig. 2). These results are typical of other days. Nighttime T values were approxi-

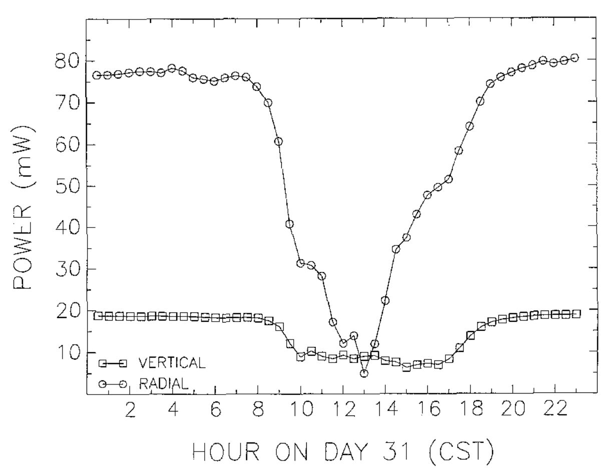

Fig. 1. Half-hour vertical and radial conductive heat fluxes associated with a stem flow gauge on a cotton plant. Input was 98 mW

mately 4 g plant^{-1} h^{-1}, while, for the calculation of K_g, it was assumed that $F=0$. This introduced a small error in the K_g calculation, but this affected daytime flow calculations by only a few grams. There was no evidence on this day or other days (results not shown) of significant plant water capacitance.

For the 16 days, daylight stem flow and load cell totals were close (Fig. 3). The root mean square error (*RMSE*) between the two values was 8.6% of the mean daily *T*. Results were comparable for both gauges. These results confirm previous studies (Sakuratani, 1981, 1984; Baker and van Bavel, 1987) regarding the method accuracy for herbaceous plants. Flow rates were always less than the values where Ham and Heilman (1990) found gauges of this design to overestimate flow.

Following the suggestion of Baker and van Bavel (1987), stem temperatures were calculated from an average of the temperature of the junction immediately below and above the heater. Half-hour averages of these temperatures, in conjunction with estimates of stem heat capacity and volume, were used to calculate the change in stem heat content. This additional term was included as a heat loss (or grain) in the numerator of Eq. (1). Including this term changed daytime flow rates approximately 1 g plant^{-1} h^{-1}, and, thus, this term was excluded. The diurnal range of stem temperature was approximately 20 K, a value probably typical of field conditions.

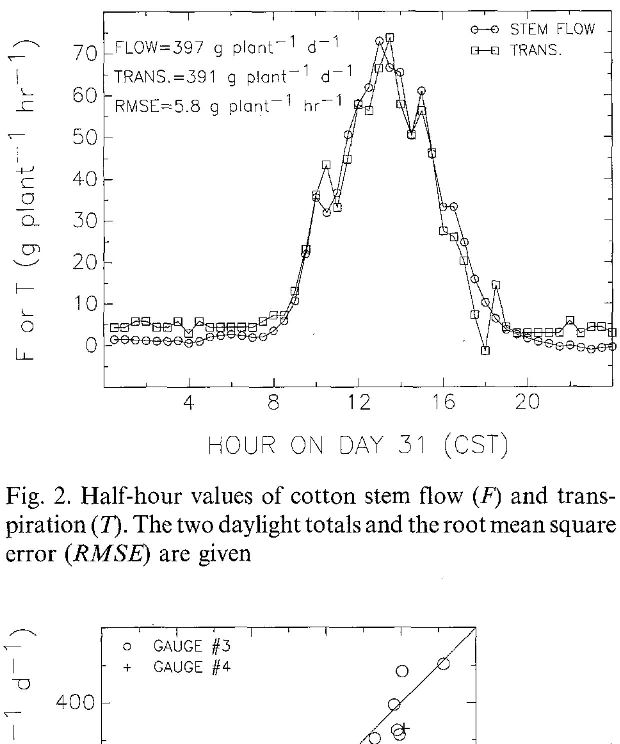

Fig. 2. Half-hour values of cotton stem flow (*F*) and transpiration (*T*). The two daylight totals and the root mean square error (*RMSE*) are given

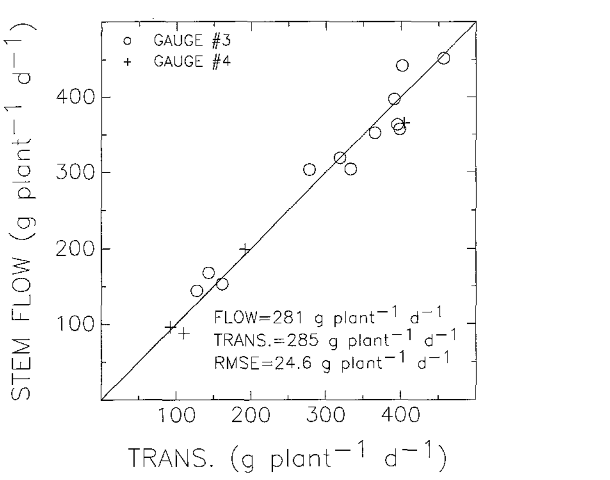

Fig. 3. Daylight totals of cotton stem flow (from two gauges) and transpiration. The mean totals and the root mean square error (*RMSE*) are given

3.2 Lysimeter

On day 208, hourly stem flow values, calculated from 10 min values, were consistently greater than those from the lysimeter (Fig. 4). The daylight stem flow total was 10% greater than the lysimeter value. On this day, the plants upon which gauges were placed had an average stem area that was 16% greater than the average of all lysimeter plants. After adjustment for stem areas (see above), daylight totals differed by only approximately 5%. There was a large standard deviation of hourly stem flow values. Midday hourly values from individual plants ranged from 30 to 100 g plant^{-1} h^{-1}.

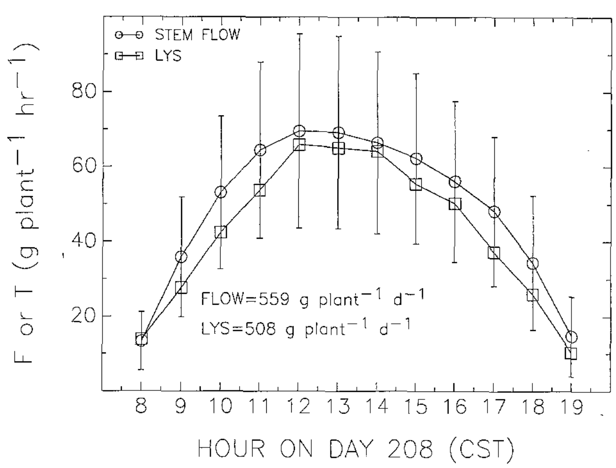

Fig. 4. Hourly values of cotton stem flow (*F*) and lysimeter transpiration (*T*). The population standard deviation of each hourly stem flow value ($n=10$) and the two daylight totals are given. For perspective, an average of 60 g plant^{-1} h^{-1} for all lysimeter plants is equal to 0.9 mm h^{-1}

Before adjustment, daylight stem flow totals for the measurement period were consistently greater than lysimeter T totals (Fig. 5). The consistent overestimation was, in part, a result of the larger plants with gauges as compared to the lysimeter plant size average. After adjustment, the two means differed by only 9%, and the *RMSE* was reduced from 129 to 69 g $plant^{-1} d^{-1}$. These errors are larger than those measured in the glasshouse in this study and those previously published. The larger errors was likely because of the assumption of T being directly proportioned to stem area and because some plants occasionally had high flux rates (e.g., >130 g $plant^{-1} h^{-1}$) which may have been in error (Ham and Heilman, 1990). The errors would have been reduced if a different gauge design had been used (Ham and Heilman, 1990) and if the adjustment of flow had been based upon leaf areas (Heilman et al., 1990). The measurement of leaf area may require more work than measuring stem diameters, but it may reduce the number of devices required to represent adequately a population and thus be worth the effort.

On days with totals from locally- and commercially-fabricated gauges ($N=61$), the mean value from the lysimeter and from the locally- and commercially-fabricated gauges was 451, 712, and 464 g $plant^{-1} d^{-1}$, respectively. For adjusted flows, the means for the two gauge types were 513 and 768 g $plant^{-1} d^{-1}$ and the two *RMSE*s were 97 and 105 g $plant^{-1} d^{-1}$, respectively. Because of the larger size of the locally-fabricated gauges and, thus, larger plants, flow values from plants with these gauges were more often in the range of high flow values where this gauge design has been shown to be in error.

To account for this possible error at high flow rates, daily totals from individual plants were eliminated from the analyses if any 10-minute F value from that plants was >130 g $plant^{-1} h^{-1}$. This value was selected because it is in the middle of the range where Ham and Heilman (1990) found gauges of this design to be in error. This resulted in 59 daily totals being eliminated out of a total of 563 for all plants throughout the season. the mean unadjusted daily total for the lysimeter and the gauges was 447 and 480 g $plant^{-1} d^{-1}$ and the *RMSE* was 70 g $plant^{-1} d^{-1}$ ($n=59$). Thus, elimination of these high flow rate data decreased the mean to a value close to the lysimeter and resulted in a *RMSE* that was equal to that from the adjusted totals using all data. Adjusting the data for stem area, with high flow rates excluded, did not reduce the *RMSE*.

The plant-to-plant variability of flow rates increased throughout the season (Fig. 6). The seasonal average of the coefficient of variation (*CV*) was 44%. When data from plants with high flow rates were excluded (see above), the mean *CV* was reduced to only 38%. This large variabiality has implications for ensuring representative samples when making physiological measurements in the field (e.g., water potentials, stomatal conductances, and gas exchange rates), especially considering the additional variation that likely exists

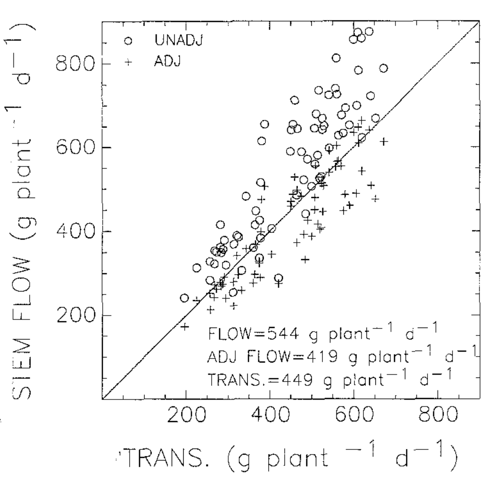

Fig. 5. Daylight totals of cotton stem flow, adjusted (ADJ) and not adjusted (UNADJ) for stem area differences, and of lysimeter transpiration. The mean totals are given. For perspective, an average of 600 g $plant^{-1} d^{-1}$ for all lysimeter plants is equal to 9 mm d^{-1}

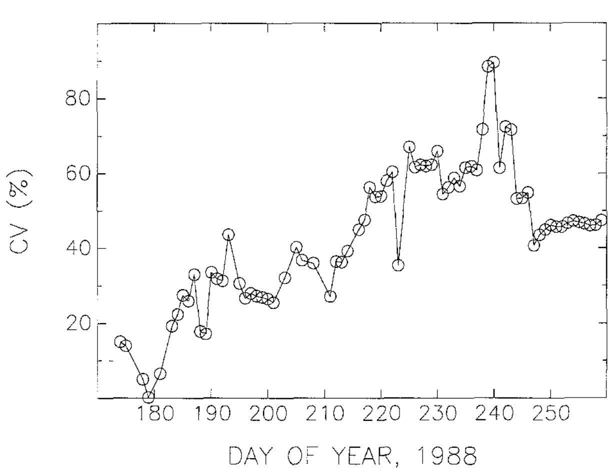

Fig. 6. Coefficient of variation (*CV*) of daylight cotton stem flow totals

within a plant. This high variability is supported by other data. During the summer of 1987, ten heat pulse gauges (Cohen et al., 1988) were placed on soybean plants (leaf area index approximately 4) on the lysimeter at Temple, Texas, and daily T was measured from each plant for 7 days. The CV of these T values averaged 33% (Unpublished data, Y. Cohen, 1987).

The K_g values varied both while a gauge was on a plant and when it was moved to a new plant (Fig. 7). The difference in K_g between the locally- and commercially-fabricated gauges was primarily a result of different heater resistances (90 vs. 127 ohms) and gauge materials. The variation in K_g while on a plant reflected the effect of changing stem/gauge contact associated with stem growth. Most of these changes were gradual and small, and the effect of these small changes in K_g on daytime stem flow values was minimal. There were, however, large changes occasionally associated with movement to a new plant. These large changes reflected the effect of a different stem/gauge contact and gauge radius (Baker and van Bavel, 1987). There was a high variability in K_g when a gauge was removed and re-applied to a stem and when the same gauge was mounted on stems of comparable diameter (results not shown). These results confirm that, when the flow is low, the use of early-morning outputs for calculation of K_g (Steinberg et al., 1989) is an appropriate procedure.

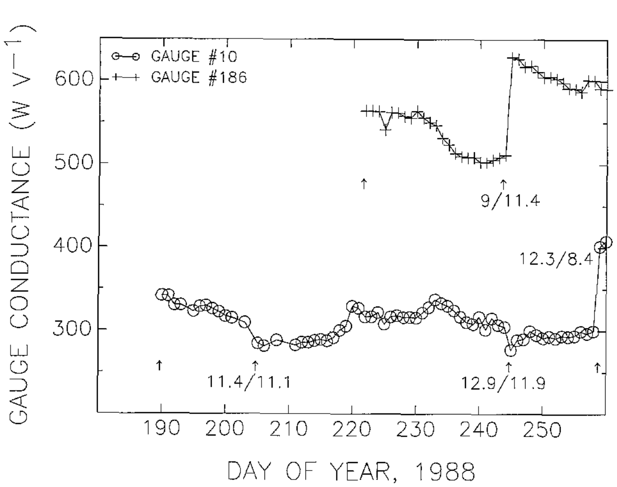

Fig. 7. Daily gauge conductance (see text) for a locally (#10) and a commercially (#186) fabricated stem flow gauge. Arrows denote placement on a plant or movement to a new plant and numbers, separated by a slash, denote the stem diameter (mm) of plant from which gauge was removed and upon which it was placed

4. Conclusions

The accuracy of stem flow measurements in the glasshouse from a method using constant power stem flow gauges was comparable (errors $< \pm 10\%$) to what has been previously determined. Errors in the field were larger, but interpretation of this was confounded by the likely inability to select a representative sample of plants and the possible error at high flow values from the gauges used in this study. Since the latter problem is easily resolved by a simple change in gauge design, this method offers the potential for accurate stem flow measurements from individual plants for many physiological and ecological problems. However, it is likely that a large number of devices will be required to describe adequately field plant-to-plant variability.

Acknowledgement

The author acknowledges M. Heuer and A. Mantanona for assistance in field measurements and data analyses.

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