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The effect of environmentally induced stem temperature gradients on transpiration estimates from the heat balance method in two tropical woody species

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Summary

Commercially available sap flow gauges were used to evaluate the performance of the stem heat balance (SHB) technique for measuring sap flow in coffee (*Coffea arabica* L. cv. Yellow Catuai) and koa (*Acacia koa* Gray) plants under greenhouse and field conditions. Transpiration rates measured gravimetrically and with the SHB technique were similar in greenhouse tests, provided that insulation in addition to that supplied by the gauge manufacturer was applied to reduce radiant heating in the vicinity of the sap flow gauges. Unrealistic estimates of transpiration rates were sometimes obtained under both field and greenhouse conditions as a result of negative stem temperature differentials from below to above the gauge heater, even in the absence of power applied to the heaters. It was possible to correct this environmentally induced bias by means of additional stem insulation that minimized the rate of change in stem temperature, or by applying simple corrections using the ΔT values for unheated gauges operated as blanks. In the field, where dense canopies reduced the radiant energy load on stems, temperature corrections were unnecessary, because ΔT values in unheated gauges were near zero.

Keywords: Acacia koa, Coffea arabica, coffee, koa, sap flow, stem heat balance technique.

Introduction

The need for improved irrigation management and a better understanding of plant water relations has led to the development of several methods for estimating water flow through plant stems. The stem heat balance (SHB) technique (Vieweg and Ziegler 1960, Čermák et al. 1973, Sakuratani 1981, Baker and Van Bavel 1987) has the advantage of being non-intrusive, does not require calibration, responds rapidly to changes in water flow, and can be used over long periods without damage to the plant.

The theoretical basis for the SHB method has been discussed in detail elsewhere (Sakuratani 1981, Baker and Van Bavel 1987, Ham and Heilman 1990). Briefly, the technique involves measuring the energy balance of a stem segment to which a known amount of heat is applied through a heating element.

Thermocouples are used to measure the partitioning of heat loss between vertical and radial conduction, two of the three major components of the heat balance. Heat removed by convection in the rising sap (Q_f) is then calculated as a residual:

$$Q_f = (Q - Q_v - Q_r) , \quad (1)$$

where Q is the total heat applied to the stem segment, Q_v is the vertical conductive heat loss, and Q_r is the radial conductive heat loss. Mass flow rate (F) is calculated from Q_f with the heat capacity of water (c) and the temperature increase of the sap:

$$F = Q_f / c(\Delta T) , \quad (2)$$

where ΔT is the difference between stem temperatures measured above and below the heater.

Two critical assumptions implicit in the relationship described by Equation 1 are that: (i) heat storage in the stem segment is negligible in relation to the heat applied, and (ii) the term ΔT is solely a consequence of the heat applied to the stem through the gauge heater.

Several studies have reported a high degree of accuracy of the SHB method when compared with gravimetric measurements (Baker and Van Bavel 1987, Ham and Heilman 1990), or when subjected to mathematical analysis (Baker and Nieber 1989, Groot and King 1992). Nevertheless, at least one study reported serious errors in direction and magnitude of the SHB estimates of sap flow when compared to those obtained with a lysimeter (Shackel et al. 1992). Disagreement between the two methods was attributed to a violation of the critical assumption that the stem temperature differentials from below to above the gauge heater (ΔT) originate solely from the energy applied to the heater. This conclusion was based on measurements of substantial negative ΔT values even when power was not applied to the gauge heater. Large temperature differentials in the environment, and conditions leading to a high radiation load on an exposed stem, may adversely affect the accuracy of the SHB technique, particularly if the gauge is not appropriately insulated and shielded. Although transient, anomalous or unrealistic estimates of sap flow may have little influence on the validity of cumulative daily totals, diurnal patterns of flow, rather than daily totals, are often of greater interest in physiological studies. It is, therefore, desirable to determine the extent to which diurnal patterns are subject to error resulting from environmentally induced variation in ΔT.

In this study, we used two tropical woody species to evaluate the effects of different types of insulation, radiation shielding, and canopy cover on the reliability of sap flow estimates by the SHB technique. Our objectives were to assess the impact of environmentally induced stem temperature differentials on the accuracy of sap flow estimates and to develop procedures for minimizing this measurement bias.

Materials and methods

Plant material

Experiments were conducted with two woody species, coffee (*Coffea arabica* L. cv. Yellow Catuai) and koa (*Acacia koa* Gray) (Mimosoideae), a valuable evergreen hardwood tree endemic to Hawaii and one of the dominant rain forest tree species. For the greenhouse experiments, 2-year-old coffee seedlings were planted in 18-liter pots filled with potting mix, and 6-month-old koa seedlings were planted in 7.5-liter pots.

Sap flow measurements

Commercially available sap flow gauges (Dynamax, Inc., Houston, TX) were used for all measurements. These gauges, which have been described in detail elsewhere (Steinberg et al. 1990*a*), consist of a flexible heating element that surrounds the stem, a thermopile to evaluate radial heat loss, and thermocouples above and below the heater to evaluate vertical conductive heat loss. Although the gauge components were surrounded by foam insulation supplied by the manufacturer, additional insulation was installed. The heating elements were operated at constant power using a voltage regulator (model AVR3, Dynamax). A datalogger (model CR21X or CR10, Campbell Sci., Logan, UT) equipped with a 32-channel multiplexer (AM416, Campbell Sci.) permitted up to eight gauges to be operated simultaneously. Data were recorded at 15-s intervals and either 20-min (coffee) or 15-min (koa) averages were stored in a solid state storage module (SM196, Campbell Sci.). The temperature gradient associated with vertical conductive heat loss was converted to power by multiplying by the thermal conductivity of wood (0.42 W m^{-1} $°C^{-1}$; Steinberg et al. 1989). Sheath conductivity (K_{sh}), necessary for the calculation of radial heat loss, was estimated when sap flow was likely to be zero. For coffee plants, K_{sh} was computed as the average of the apparent K_{sh} values measured between 2400 and 0500 h for each day. For koa plants, the lowest K_{sh} value registered during the night period was used.

Greenhouse experiments

Experiments on coffee were conducted in greenhouses at the Hawaiian Sugar Planters' Experiment Stations in Kunia and Aiea, Oahu. The plants were thoroughly irrigated at the beginning of each series of experiments. The sap flow gauges (Models SGB19 and SGB25, Dynamax) were installed between two foam extension rings near the base of the stem, approximately 10 to 15 cm above the soil. Stem diameter at the point of attachment of the gauges ranged from 19.6 to 28.2 mm. Before installation of a gauge, the stem surface was smoothed with a coarse cloth and coated with silicone-based waterproofing grease (Dow Corning 64, Dow Corning, Midland, MI). Additional insulation consisted of two layers of flexible thin foam (0.5 cm), surrounded by one layer of thick (2.5 cm) foam. String was used to wrap the foam tightly around the gauge and stem. An outer layer of heavy duty aluminum foil was wrapped around the whole installation. A cone-shaped shield constructed out of a reflective automobile windshield liner, was attached to the stem just above the gauge insulation. Open slits facilitated air circulation. The pots were sealed in plastic bags from the bottom of the gauge insulation to avoid evaporation of soil water and then covered completely with aluminum foil. Transpiration was determined by recording weight loss at 20-min intervals with an electronic balance, accurate to 0.1 g.

Two sap flow gauges installed on separate plants were typically operated simultaneously on six different days. One gauge was operated in the absence of heating power to assess the influence of ambient conditions on the stem temperature differential across the heater (ΔT, Equation 2). On several occasions, both gauges were operated with the heaters on and gravimetric data were collected for the two plants simultaneously. In these cases, a third plant with an unheated gauge was monitored at the same time.

Greenhouse experiments on koa were conducted at the Department of Agronomy and Soil Science, University of Hawaii at Manoa, Oahu. Five sap flow gauges (Model SGA10, Dynamax) were installed on five separate stems approximately 15 cm above the soil, and insulated following the procedure described for coffee. Stem diameter at the point of attachment of the gauges ranged from 9.5 to 11 mm. The plants were thoroughly irrigated each morning. A switchbox was installed to selectively interrupt power to individual gauge heaters, to allow heated and unheated gauges to be run simultaneously. Four sap flow gauges, two heated and two unheated, were run for several days. Transpiration was determined gravimetrically at 15-min intervals as described for coffee.

Field experiments

Field experiments with coffee were conducted in commercial fields at McBryde Sugar Co., Eleele, Kauai. Three large fields with the plants grown in a hedgerow configuration were selected. Spacing was 3.60 m between rows and 0.71 m between plants. Each plant had four to five vertical stems, one of which usually became dominant and occupied the upper plant canopy. The leaf area index (LAI) values for the three fields were 0.7, 3.4 and 4.2. In the field with the lowest LAI, the plants were small (0.5-m tall) and did not form a continuous hedgerow. In the two other fields, the plants formed a dense canopy that fully shaded the bases of the stems. Estimation of radiation below the coffee canopies, using Beer's Law and assuming an extinction coefficient of 0.3 to 0.6 (Jaramillo-Robledo and Marden dos Santos 1980), indicated that radiation under the hedgerows was 30 to 80% lower than radiation above the canopy at LAI = 4.2, and 10 to 30% lower at LAI = 0.7.

Experiments with coffee were designed to test the effect of canopy cover on gauge performance. Eight sap flow gauges (Models SGB13, SGB16, SGB19 and SGB25, Dynamax) were installed on dominant branches approximately 10 to 20 cm above the soil surface and operated in every field according to the procedure described for the greenhouse experiments. Stem diameter at the location of the gauges ranged from 13.4 to 28.8 mm. Four of the gauges were operated without power applied to the heaters, to provide an estimate of environmentally induced fluctuations in ΔT. Environmental variables (solar radiation, air temperature, relative humidity and wind speed) were monitored from an instrument tower erected in each field.

Field experiments with koa were conducted in an 18-month-old plantation, with an LAI of 0.47, at Waiawa, Oahu. Experiments with koa were designed to explore the effect of reflective trunk shielding on gauge performance. Four sap flow gauges (Model SGB25, Dynamax) were installed on two 18-month-old koa trees that bifurcated approximately 0.3 m above the ground. Trunk diameter at the point of attachment of the gauges ranged from 28 to 31 mm. On each of the two trees, one gauge was installed at the base of each of the two main branches, approximately 15 cm above the bifurcation. One gauge on each tree was operated with power applied to the heater while the other was unheated. The gauges were insulated differently to assess if the ΔT values for unheated gauges were being affected by the presence or absence of additional trunk shielding. The base of one tree was covered with aluminum foil from the base of each gauge to the soil surface for a distance of approximately 30 cm. The trunk of the other tree was not covered. After two days, the foil was removed from the trunk of the first tree and transferred to the second tree, and the sap flow gauges were operated again for two consecutive days.

Results and discussion

The average SHB and gravimetric estimates of transpiration were similar in the greenhouse tests performed on potted coffee and koa (Figure 1). In coffee, differences in transpiration estimated by the two techniques were less than 10%. Despite substantial air temperature fluctuations inside the greenhouse (Figure 2), ΔT values inside unheated gauges installed on different plants remained close to zero throughout the day (Figure 2). The slight overestimate of transpiration rate, as measured by the SHB technique before 1000 h, was associated with the small, negative ΔT values recorded for the unheated gauge. This suggests that, in the greenhouse experiments with coffee, the gauge and stem insulation were adequate to minimize the bias in stem ΔT values caused by the fluctuating environmental conditions.

For koa in the greenhouse, the daily course of transpiration estimated by the SHB technique was consistently lower than, but generally within 10%, of that determined by weight loss (Figure 3). The underestimated transpiration, as measured by the SHB method, was associated with the positive stem ΔT values recorded for the unheated

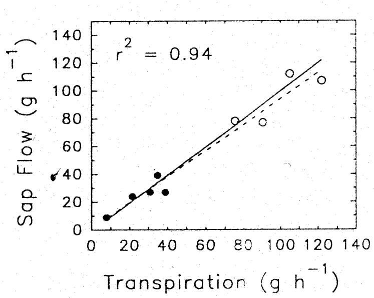

Figure 1. Comparison of average transpiration rates measured gravimetrically and by the SHB technique in five koa (●) and four coffee (O) plants grown in the greenhouse. The solid line represents the 1/1 relationship.

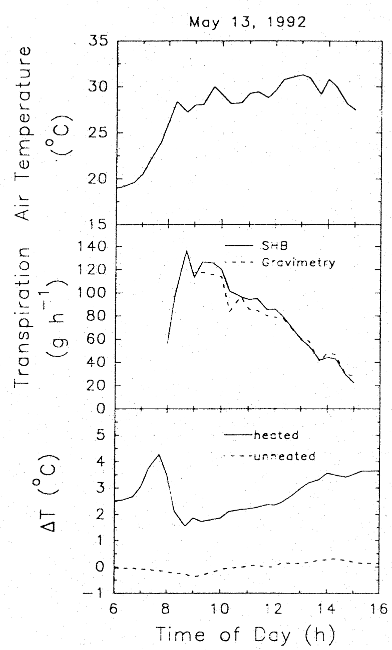

Figure 2. Comparison of transpiration rates estimated gravimetrically and by the SHB technique in a coffee plant growing in the greenhouse. Air temperature and diurnal courses of stem ΔT for the heated and unheated gauges were measured concurrently.

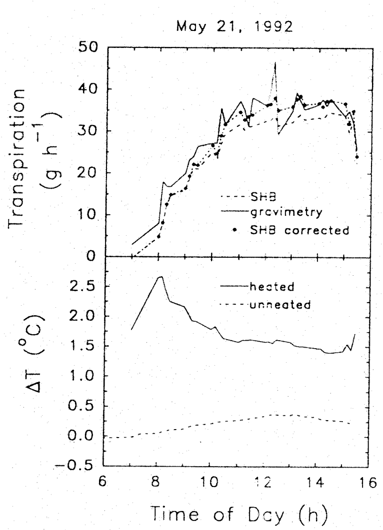

Figure 3. Comparison of transpiration rates estimated gravimetrically and by the SHB technique in a koa plant growing in the greenhouse. Corrected transpiration rates were calculated using the ΔT values for the blank, unheated gauge operated concurrently.

gauges installed on adjacent plants. A similar bias in the ΔT values for the heated gauges would lead to an underestimate of sap flow (Equation 2). To remove this potential bias from the ΔT values for heated gauges (Čermák et al. 1984), the average values of ΔT obtained for the two unheated gauges installed on nearby plants were subtracted from the ΔT values obtained for the heated gauges. Sap flow rates were then recalculated using the corrected ΔT values. In most cases, this correction substantially increased the similarity between transpiration estimated by the SHB and gravimetric methods (Figure 3). Examination of ΔT values obtained from the unheated gauges on consecutive days revealed substantial day-to-day variation in both the magnitude and diurnal course of ΔT among the gauges (Figure 4). These results suggest that for each new gauge installation, the effect of external conditions on ΔT values should be evaluated before assuming that SHB measurements of transpiration are reliable. If all gauges in a given installation yield similar values of ΔT in the absence of power applied to the heaters, then application of a ΔT correction factor obtained from one or more unheated gauges, operated concurrently, may be justifiable during subsequent SHB measurements.

Diurnal fluctuations in the ΔT values for unheated gauges on field-grown koa plants were invariably smaller when the stem was covered with aluminum foil from the base of the gauge to the soil surface than when the trunk was left fully exposed (Figures 5 and 6). Switching the foil from one tree to the other confirmed that this result was not caused by differences between trees, but by the presence or absence of additional trunk shielding. In contrast to the typically positive values of ΔT measured for unheated gauges in the greenhouse, stem ΔT measured for unheated gauges in the field was either positive or negative, depending on the time of day and external conditions (Figure 3). These results suggest that sap flow in the trees without additional aluminum foil shielding along the trunk would be substantially overestimated during some portions of the day and underestimated during others (Figures 5 and 6). For example, the abrupt peak in transpiration observed in the unshielded tree

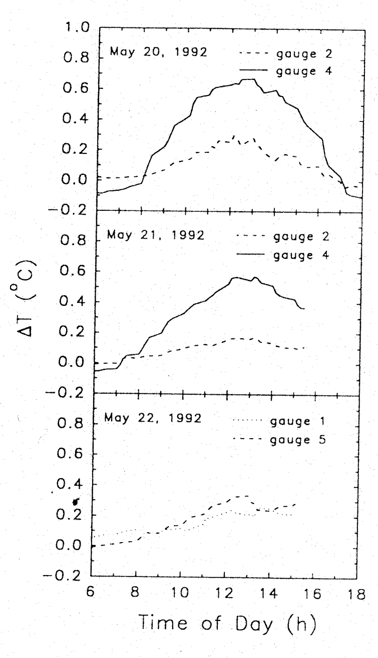

Figure 4. Diurnal courses of stem ΔT values for the unheated gauges operated on consecutive days in koa plants grown in the greenhouse. Two different gauges were used on May 22, 1992.

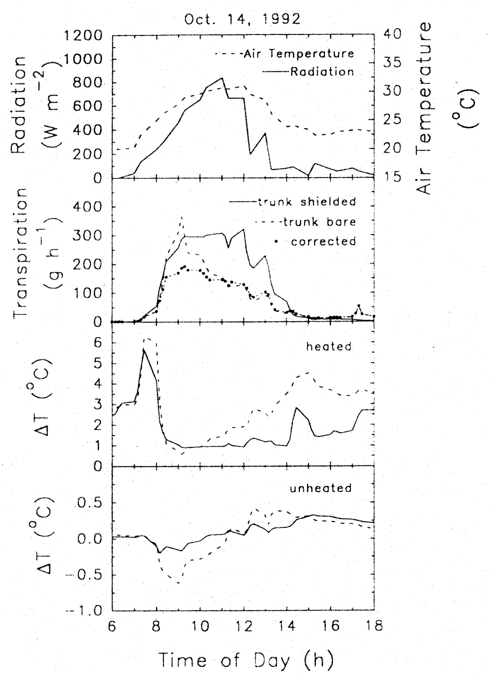

Figure 5. Diurnal courses of solar radiation, air temperature, transpiration rates estimated by the SHB technique, and stem ΔT values for the heated and unheated gauges installed on bare and shielded stems of koa trees growing in the field on October 14, 1992.

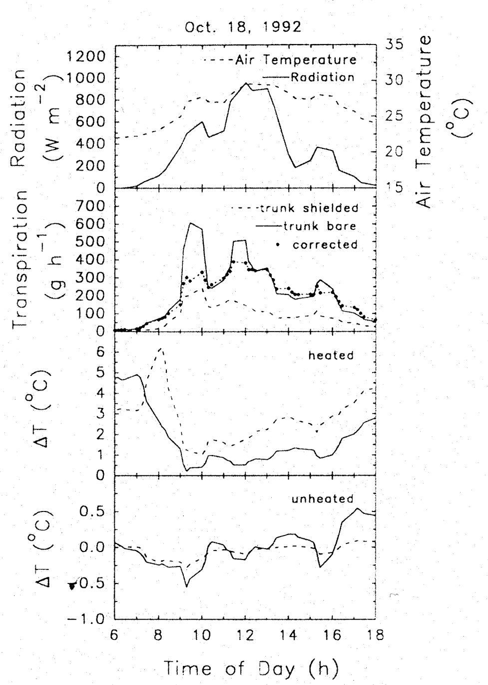

Figure 6. Diurnal courses of solar radiation, air temperature, transpiration rates estimated by the SHB technique, and stem ΔT values for the heated and unheated gauges installed on bare and shielded stems of koa trees growing in the field on October 18, 1992. The reflective foil was transferred from the shielded tree to the bare tree shown in Figure 5 on October 16, 1992.

in Figure 5 shows how an environmentally induced, negative ΔT can lead to large transient overestimates of sap flow (see Equation 2). When ΔT values obtained from the heated gauges installed on trees with unshielded trunks were corrected by subtracting ΔT measurements obtained from an unheated gauge on the same tree, the recalculated diurnal patterns of sap flow were similar to those obtained from gauges installed on trees with shielded trunks (Figures 5 and 6).

In coffee plants growing in the field in a hedgerow configuration, ΔT values for the unheated gauges were typically slightly positive and considerably smaller in magnitude than ΔT values for the heated gauges (Figures 7 and 8). These results indicated that the small bias in ΔT values caused by fluctuating ambient conditions (Table 1, Figures 7 and 8) had a negligible effect on gauge accuracy. Even at relatively low values of LAI (Figure 7), the coffee canopy was apparently dense enough to shade the stems and minimize externally induced temperature gradients.

Although water capacitance in the trunk could cause disagreement between transpiration measured gravimetrically and sap flow measured with the SHB technique (Waring and Running 1978, Kitano and Eguchi 1989), capacitance was unlikely to have played an important role in our study, given the small stem diameter of the plants selected (Jarvis 1975, Carlson and Lynn 1991). Furthermore, the virtually instantaneous response of transpiration to fluctuations in solar radiation (Figures 5–8) suggested that capacitance was minimal for both the coffee and koa trees.

We observed that, under some circumstances, the influence of ambient conditions

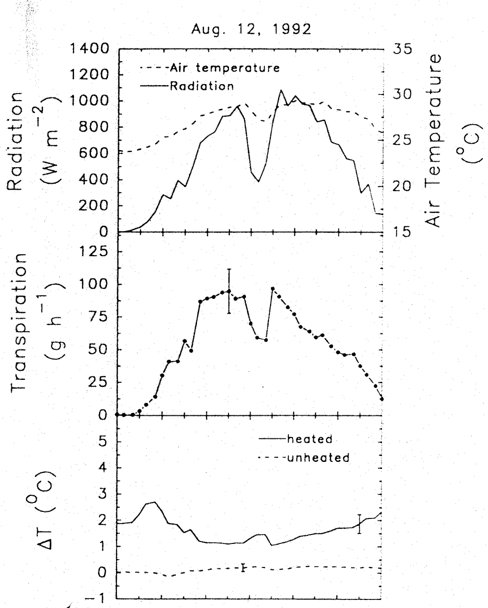

Figure 7. Diurnal trends of solar radiation, air temperature, transpiration rates estimated by the SHB technique, and stem ΔT values for four heated and four unheated gauges installed on eight coffee trees grown in the field in a hedgerow configuration (LAI = 0.7). Each value of transpiration and stem ΔT represents the average of four coffee plants. Vertical bars represent the largest SE.

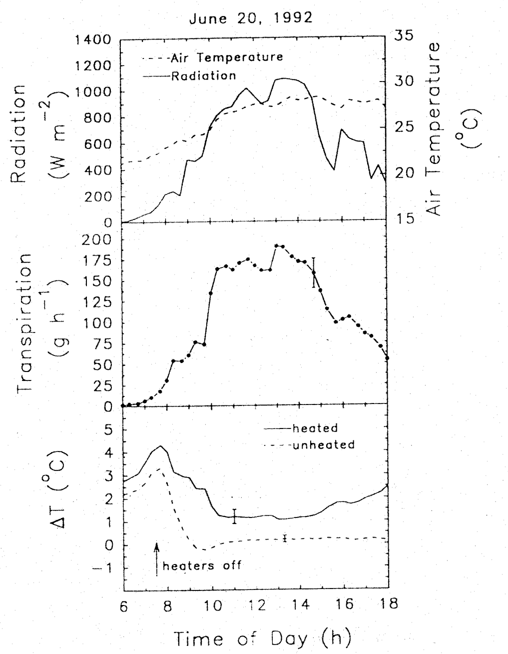

Figure 8. Diurnal courses of solar radiation, air temperature, transpiration rates estimated by the SHB technique, and stem ΔT values for four heated and four unheated gauges installed on eight coffee trees grown in the field in a hedgerow configuration (LAI = 4.2). Each value of transpiration and stem ΔT represents the average of four coffee plants. Vertical bars represent the largest SE.

Table 1. Environmental variables recorded during the field tests at McBryde Sugar Co., Kauai, and Waiawa Correctional Facility, Oahu.

Species	Date	Solar radiation ($W\ m^{-2}$)		Air temperature (°C)			Relative humidity (%)		Wind speed ($m\ s^{-1}$)
		Mean	Max	Min	Max	Mean	Min	Max	
Coffee	June 20	586	1086	22.5	28.5	26.7	60.2	80.4	1.85
	Aug 12	527	1062	23.9	29.2	27.5	58.4	75.5	2.29
Koa	Oct 14	295	839	19.8	31.6	23.2	57.8	73.7	0.58
	Oct 18	365	954	19.5	29.9	23.7	49.5	73.2	1.32

on ΔT led to serious errors in estimates of sap flow. In most earlier evaluations of the SHB technique using plants grown under field (Dugas 1990, Steinberg et al. 1990*a*, 1990*b*) or greenhouse conditions (Steinberg et al. 1989, Ham and Heilman 1990), serious errors associated with environmentally induced stem temperature gradients were not reported. In field-grown peach trees, however, anomalous stem temperature differentials caused by ambient conditions resulted in large errors in SHB estimates of transpiration (Shackel et al. 1992). This source of error has apparently gone unnoticed in at least one field study in which unusually high SHB estimates of sap flow were reported that were inconsistent with the low values of stomatal conductance observed (Zajicek and Heilman 1991).

Our results suggest that, for each new gauge installation, similarly installed heated and unheated gauges should be operated concurrently to evaluate the potential effect of environmentally induced stem temperature differentials on gauge accuracy. If necessary, insulation and shielding can then be modified to minimize the magnitude of ΔT values observed in unheated gauges. In cases where it is not possible to provide sufficient insulation and shielding, or when operating in environments with high energy load or rapid and large fluctuations in ambient temperature, or both, it may be necessary to operate gauges continuously with the heaters off as "blanks" and apply the resulting ΔT values as corrections. The accuracy of this procedure will be constrained by the degree of similarity in the configuration and environment of the heated and unheated gauges. Corrections are unnecessary under fully developed canopies that reduce the radiant energy load so that temperature fluctuations become small, because ΔT values for unheated gauges are likely to be near zero.

Acknowledgments

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