

Including the heat storage term in sap flow measurements with the stem heat balance method

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Abstract

The importance of the change in stem temperature and therefore the heat storage term in the stem heat balance method of measuring sap flow is examined. Results from a range of measurements on a model stem, potted sunflower plants in a glasshouse, and *Guiera senegalensis* shrubs in the Sahel, Niger, are presented. A novel analysis of the heat balance in zero flow conditions allows the accurate determination of the gauge radial conductance and the stem segment heat capacity, both of which are required for accurate sap flow measurement with good dynamic resolution in low flow conditions. In high sap flow conditions the change in heat storage constitutes only a small component of the balance, and can be neglected, especially for small stems. The improved accuracy and dynamic resolution for stems of any size if heat storage is included allowed the measurement of low night-time flows during rehydration, and of redistribution of water between stems of *G. senegalensis* bushes in the field following rain.

1. Introduction

Sap flow measurement is an important technique for the study of plant water relations and water balances. The application of heat has been used to measure the movement of sap through intact plant stems since the pioneering work of Huber (1932). Although that early work led to the development of heat pulse velocity methods particularly suited for larger woody stems (for a review, see Jones et al. (1988)), other techniques have been developed using temperature profiles (Vieweg

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and Ziegler, 1960; Granier, 1985, 1987), or a stem heat balance. This last approach draws up a heat balance for a stem segment supplied with a known amount of heat, P :

$$C_{st} \frac{dT_{st}}{dt} = P - Q_r - Q_u - Q_d - Q_c \quad (1)$$

Heat (in W) is lost from the segment by conduction (radial heat loss, Q_r , and heat loss in downstream and upstream directions, Q_d and Q_u , respectively), and by convection in the sap stream, Q_c . The left-hand term in the equation represents the change in heat storage within the segment; C_{st} is the heat capacity ($J K^{-1}$) and T_{st} the average temperature of the stem segment (K). The heat transported by sap mass flow, Q_c , is given by

$$Q_c = c_w F (T_d - T_u) \quad (2)$$

where c_w is the specific heat of sap (taken as that of water), F is the mass flow rate of water ($mg s^{-1}$), and $T_d - T_u$ is the difference in temperature of water entering and leaving the heated segment. If Q_c can be evaluated, and $T_d - T_u$ measured, then the mass flow rate of water, F , through the stem can be calculated directly.

This approach has been applied in two different techniques. The first, where large heaters are implanted into the stem, was suggested by Daum (1967) and developed by Čermák and colleagues (Čermák et al., 1973, 1976, 1984), and is suitable only for larger stems. A second, non-invasive technique that is suited for both medium and small stems uses an insulated flexible heater wrapped around the stem, and temperature sensors to measure conductive fluxes. Two methods have been suggested using this latter approach. One uses a steady-state assumption (i.e. assuming the left-hand term in Eq. (1) is zero), with a constant power input through the heater, following the work of Sakuratani (1981, 1984) and the subsequent development by Baker and Van Bavel (1987) and Steinberg et al. (1989). The other method (technically more difficult) uses a variable power input to maintain the temperature difference between a reference point in the heated stem and the air constant (Kučera et al., 1977; Schulze et al., 1985; Fichtner and Schulze, 1990; Ishida et al., 1991). The advantage is that the dynamic response of the gauge is independent of the flow rate, and this method is therefore potentially more accurate.

Since gauges became commercially available in the late 1980s, the steady-state method has been used on a wide variety of both herbaceous (e.g. tomatoes, sunflower, cotton, maize, sugar cane) and tree (e.g. coffee, peach, pecan, hibiscus, roses, mesquite, vines) species. The magnitudes of the errors owing to gauge design and the measurement resolution have been analysed in detail elsewhere (Sakuratani, 1981, 1982; Baker and Nieber, 1989; Ham and Heilman, 1990; Groot and King, 1992). However, the basic assumption that steady-state conditions exist has not been considered in detail, except by Groot and King (1992), who considered in particular the low flow rate conditions in conifer seedlings. The importance of stem temperature changes will depend on sap flow rate, and on stem size. Groot and King (1992) noted that at low flow rates it was essential to include the heat storage term in the calculation. Dugas (1990), working with cotton, found the heat storage term insignificant, but Shackel et al. (1992), working with large-diameter peach, found it on occasion so large as to invalidate their estimates of flow. In particular, the stem

segment experiences fast changes in stem temperature in field conditions when transpiration changes rapidly at sunrise, partly because of large changes in ambient temperature, but also because of the movement up the stem of the heated water that was nearly stationary overnight, and the inflow of cold water from below. Are the large 'spikes' of sap flow often seen at these times of day real phenomena associated with the ready availability of water following overnight rehydration or re-equilibration, or are they artefacts? Further, sap flow changes rapidly in varying radiation conditions, which potentially causes large changes in stem temperature, and may invalidate the steady-state assumption. This paper considers the validity of the steady-state assumption, describes the magnitude of the errors that arise from it, and suggests improvements to the technique. Measurements from potted plants in controlled environments and from field conditions are used as illustrations. A companion paper (Grime et al., 1995) describes glasshouse and field comparisons of constant power with the variable power method.

2. Materials and methods

A series of experiments were carried out to evaluate the performance of gauges designed to measure sap flow using Eqs. (1) and (2) under a range of sap flow and ambient temperature conditions. A brief outline is given here; further details have been given by Grime (1992). The gauges used (Dynagauge Models SGB10, SGB13 and SGB19 and SGA16, Dynamax Inc, Houston, TX, USA) have been described by Steinberg et al. (1989). The installation and use of the gauges followed, in general, the recommendations of the manufacturer. The gauges were well insulated with closed-cell foam and shielded with a white PVC outer sheath and, in the field, with aluminium foil. The outputs from the gauges were monitored every 15 s with programmable data-loggers (Models 21X or CR7, Campbell Scientific, Ltd., Shepshed, UK). Additional thermocouples (copper–constantan, 42 SWG) for absolute temperature measurement were referenced to the logger panel thermistor (accuracy $\pm 0.2^\circ\text{C}$). The measured signals were averaged over periods of 10, 20 or 30 min and recorded for subsequent computation of flow rates. Power to the heaters was supplied from a 12 V d.c. source, and could be manually trimmed for the requirements of each gauge, but was otherwise constant.

In the greenhouse studies on potted plants sap flow data were compared with gravimetric measurements of transpiration recorded by either an electronic balance or a beam-deflection load cell, both with 1 g accuracy. Evaporation from the soil was eliminated by using plastic bags and foil.

2.1. Experiment 1

In the first experiment an SGA16 gauge was mounted on a 30 cm length of 16.5 mm diameter nylon rod. A thermocouple was inserted into an axial 1 mm diameter hole and positioned at the centre of the heated segment. Stem temperature was recorded during the ninth minute of each 10 min sap flow averaging interval. A

temperature-controlled incubator was used to give step changes in air temperature. The model stem was later moved to the laboratory bench, where ambient temperature varied more gradually.

2.2. Experiment 2

Eight-week-old sunflower plants in 7 l PVC cylinders were kept in a ventilated glasshouse at Reading during August 1991. Plants were kept well watered before the experiment. Sap flow in four plants was monitored for 5 days (Day of Year (DOY) 226–231, 14–19 August), during which time some of the plants were kept well watered, whereas others were left to dry out. Dynamax gauges mounted at the base of each stem recorded 20 min average sap flow rates, and the corresponding weight loss from each sealed pot was recorded using two load cells, and two manual balances (08:00–20:00 h only). A thermocouple was inserted 1–2 mm below the stem surface at the centre of the heater. Changes in stem temperature over each 20 min interval were calculated from the average of measurements made every 15 s over a 10 min period centred about each sap flow output time. After each experiment plants were rehydrated fully and the leaf area was measured destructively (AMS System, Delta-T Devices, Burwell, Cambridge, UK).

2.3. Experiment 3

Field measurements were made in fallow savannah on a sandy soil in August 1991 at the ICRISAT Sahelian Centre at Sadore, Niger (13°15'N; 2°17'E, altitude 230 m). Sap flow measurements were taken on stems of *Guiera senegalensis*, the dominant shrub in this vegetation (about 1000 bushes ha⁻¹), which grows up to 3 m tall. Dynamax sap flow gauges (Model SGB19) were mounted on two stems of the same *G. senegalensis* bush which joined a common root system. This was verified afterwards by partially excavating the root system. Fig. 1 shows the geometry of the bush used and gauge details for each stem. A thermocouple was placed inside each gauge at the centre of the heater to measure stem temperature. Two unventilated thermocouples with aluminium foil shields recorded ambient air temperature near each gauge. At 11:00 h on DOY 227, the leafy crown above the gauge on Stem A was covered for the rest of the experiment with two layers of polythene sheet and two large linen sacks to prevent transpiration. The second gauged stem, Stem B, was left uncovered throughout. Rainfall figures presented are those from the ICRISAT weather station located within 0.5 km.

2.4. Calculation methods

The calculation methods of Baker and Van Bavel (1987) and Steinberg et al. (1989) are repeated briefly here to clarify the analysis below. The usual assumption is that the heated stem segment is in thermal equilibrium, and therefore that the dT_{st}/dt term (Eq. (1)) is zero (Baker and Van Bavel, 1987; Manufacturer's Manual, Dynamax Inc.). The power in, P , is calculated from the heater resistance and the measured

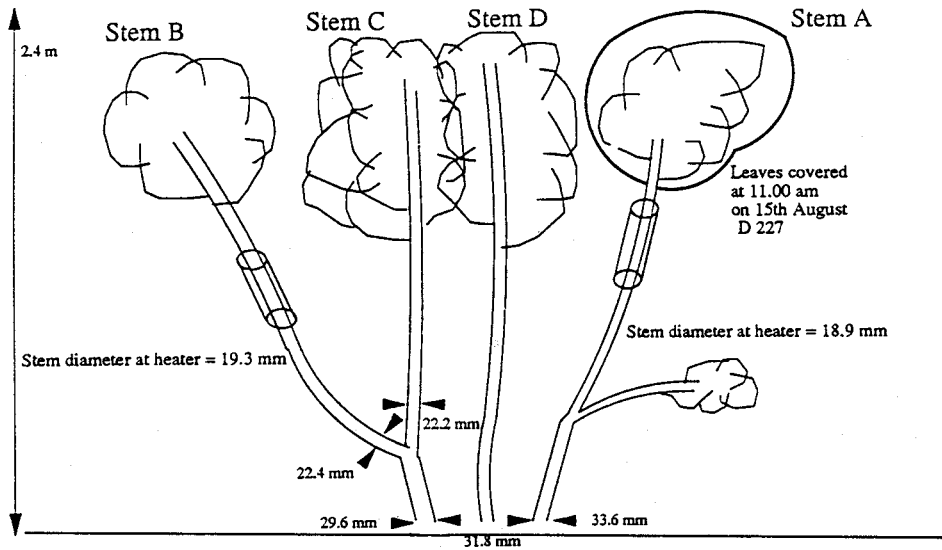


Fig. 1. Diagram of multistemmed *Guiera senegalensis* bush used for field tests in Niger. Gauges were attached to Stems A and B. Numbers indicate stem widths.

supply voltage. The vertical conductive heat fluxes Q_u and Q_d are calculated (assuming one-dimensional heat flow along the axis of the stem) from temperatures measured above and below the heater:

$$Q = K_{st} A \frac{dT}{dx} \quad (3)$$

where K_{st} is the thermal conductivity of the stem ($W m^{-1} K^{-1}$) and A is the cross-sectional area of the heated segment. dT/dx is approximated by $\Delta T/\Delta x$, in which ΔT is the temperature difference over the separation Δx . Heat loss by conduction upstream and downstream from the heated segment then becomes

$$Q_v = Q_u + Q_d = K_{st} A \frac{(\Delta T_u + \Delta T_d)}{\Delta x} \quad (4)$$

Sakuratani (1984) suggested that because F is not very sensitive to the value of K_{st} except at very low flow rates, an average value of $0.54 W m^{-1} K^{-1}$ may be used for most crop plants with a high water content. For woody stems a value of $0.42 W m^{-1} K^{-1}$ is more appropriate (Steinberg et al., 1989). The radial heat flux is assumed to be proportional to the voltage output (E) of the radial thermopile:

$$Q_r = K_r E \quad (5)$$

The value of K_r , the gauge radial conductance ($W mV^{-1}$), is determined by measurements when there is no flow (i.e. $Q_c = 0$, for example by covering the stem leaves with a plastic bag, or assuming no flow at night or, more drastically, by stem excision), so

that

$$K_r = \frac{(P - Q_v)}{E} \quad (6)$$

If an appropriate value for K_r can be determined then the heat flux owing to sap flow is given by difference and the sap flow rate calculated from Eq. (2). The main difficulty in the technique is that both flow and dT_{st}/dt must be zero for correct determination of K_r . The first condition is well recognised. For example, if there is even a small flow at night, caused by rehydration of the downstream parts of the plant, then the minimum apparent K_r ($= K_a$) occurs just before dawn, when the water flow is at a minimum. However, in most night-time situations the stem will be cooling, and therefore K_a determined at night will be an underestimate of the true value, resulting in the overestimation of sap flow at night. The extent of this overestimation depends on the rate of cooling. As an example of this effect in zero flow conditions, typically K_a shows a minimum early in the night when heat loss from the segment is maximum. However, if the stem segment temperature is measured then a heat storage term, Q_s , can be calculated and added to the heat balance equation:

$$Q_s = c_v V_e \frac{dT_{st}}{dt} = C_{st} \frac{dT_{st}}{dt} \quad (7)$$

where c_v is the volumetric heat capacity of the stem, and V_e is the effective segment volume.

3. Results

3.1. Estimating heat storage: test with an artificial stem

A nylon rod in which Q_c is zero provides a test of the influence of the assumption of steady-state stem temperature on calculations of F in a fluctuating temperature environment. The thermal conductivity of nylon was taken as $0.25 \text{ W m}^{-1} \text{ K}^{-1}$ (Crawford, 1981). The value for K_r was chosen such that the calculated sap flow rate oscillated about a mean of zero. This value should correspond to the true value of K_r under steady-state temperature conditions within the segment, assuming that there was no net gain or loss of heat by the rod over the period of the experiment.

Figs. 2(A) and 2(B) show the changes in rod temperature that were imposed and the calculated flows over a 7 day period. Rod temperature was approximately 4 K higher than the air owing to the heater. Although the rod surface temperature was only measured at a point, we made the same assumption as in the basic stem heat balance method, i.e. that there was negligible radial variation. During periods of steady temperature within the stem, the calculated sap flow was very close to zero ($\pm 3 \text{ g h}^{-1}$). However, during transition periods there were large spikes, indicating discrepancies of up to 20 g h^{-1} . During stem warming, net heat gain by the stem caused an overestimate of sap flow, and the converse occurred during stem cooling.

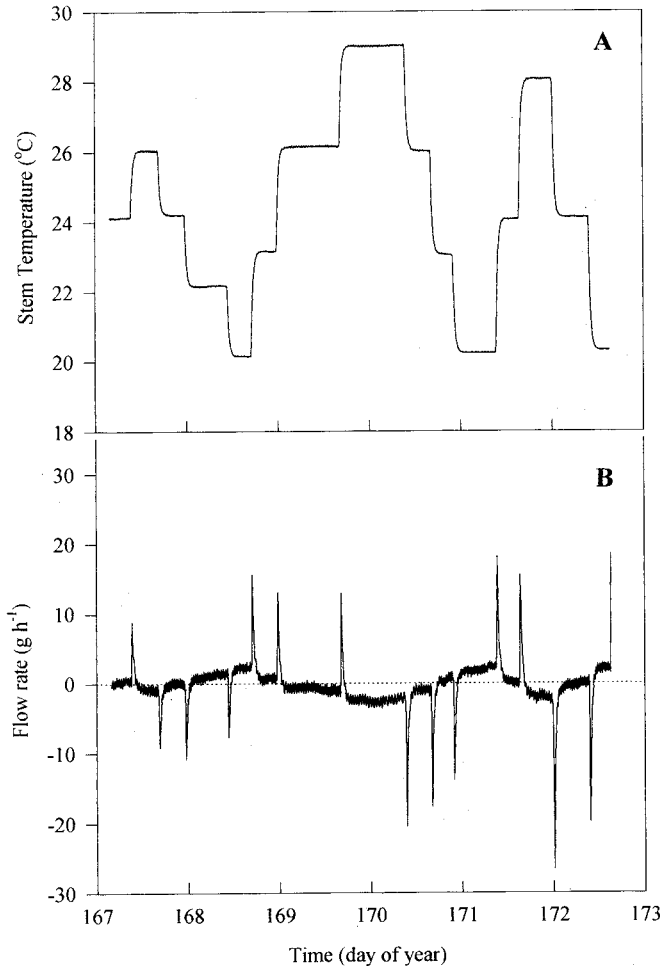


Fig. 2. (A) Time course of stem segment temperature for a range of incubator temperature settings; (B) effect of changes in ambient temperature on the calculated sap flow rate for a nylon rod 'stem'. $d_h = 16.5$ mm, $K_{st} = 0.25$ W m⁻¹ K⁻¹ and $K_r = 0.925$ W mV⁻¹. For clarity, only a few days are shown.

As nearly all heat exchange during transition periods occurred in the radial direction (data not shown), and as $Q_r \gg Q_v$, errors in calculation of K_r from the minimum value of K_a will be the main explanation for the discrepancies.

On the laboratory bench the stem temperature changed at a slower rate (Fig. 3(A)) than in the incubator. The rate of change in heat storage within the segment (Q_s) could be calculated as in Eq. (7), provided C_{st} or its components c_v and V_e are known, but these parameters are not known precisely. To avoid this problem, a novel non-destructive approach was adopted here for the estimation of C_{st} . A major benefit of this approach is that it leads to an estimate of the true value of K_r requiring only a zero sap flow ($Q_c = 0$) condition, and making no assumption about dT_{st}/dt . The heat

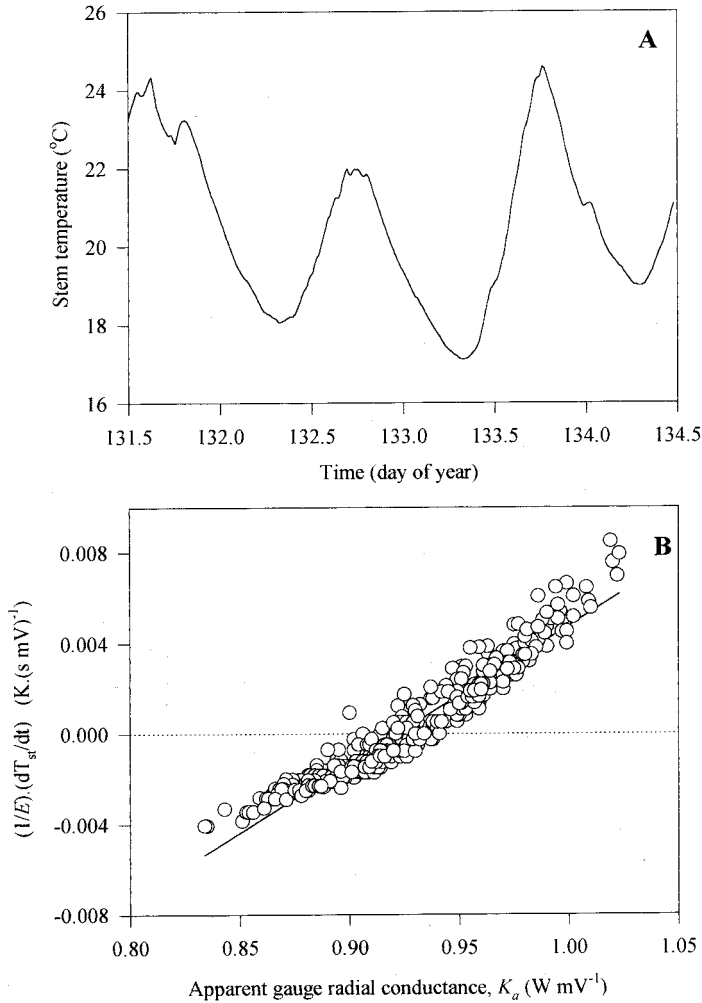


Fig. 3. (A) Time course of stem temperature under a natural, diurnal ambient temperature environment; (B) plot of $1/E(dT_{st}/dt)$ against apparent gauge radial conductance, K_a , for a sap flow gauge mounted on the nylon rod stem; 576 observations over 96 h. Linear regression shown is $y = 0.061x - 0.056$, $R^2 = 0.927$.

balance (Eq. (1)) can be written in the form

$$C_{st} \frac{\Delta T_{st}}{\Delta t} = P - Q_v - K_r E \quad (8)$$

where $K_r E$ is substituted for Q_r , and dT_{st}/dt is approximated by $\Delta T_{st}/\Delta t$, the change in stem temperature over period t . Dividing through by E gives

$$\frac{C_{st}}{E} \frac{\Delta T_{st}}{\Delta t} = \frac{P - Q_v}{E} - K_r \quad (9)$$

The first term on the right-hand side of the equation represents K_a , (see Eq. (6)), which is equal to K_r when $\Delta T_{st}/\Delta t$ is zero. Dividing through by C_{st} , gives

$$\frac{1}{E} \frac{\Delta T_{st}}{\Delta t} = \frac{K_a}{C_{st}} - \frac{K_r}{C_{st}} \quad (10)$$

Therefore a plot of $1/E(\Delta T_{st}/\Delta t)$ against K_a should be a straight line, with slope $1/C_{st}$ and intercept $-K_r/C_{st}$. Fig. 3(B) shows the above analysis for the nylon rod data in the laboratory test. There was a strong linear relationship ($R^2 = 0.927$), and from the slope and the intercept, $C_{st} = 16.37(\pm 0.36) \text{ J K}^{-1}$ and $K_r = 0.920(\pm 0.011) \text{ W mV}^{-1}$, where the figures in parentheses refer to the 95% confidence limits. The value calculated for K_r by this method was the same as that chosen originally to force calculated sap flow to oscillate diurnally about a mean of zero. This is encouraging with respect to both the analysis used and the accuracy of the measurement of small changes in stem temperature with time. However, there is evidence of curvature in Fig. 3(B). A tentative explanation is that the value of C_{st} decreases as $\Delta T_{st}/\Delta t$ increases; this is expected if an increase in ambient temperature effectively decreases the length of the portion of stem that is being heated above ambient.

Fig. 4(A) shows the time course of Q_s calculated from Eq. (7) using the value of C_{st} determined from the regression. There is a clear diurnal trend as stem temperature lags behind air temperature. The maximum value of Q_s (0.006 W) corresponds to only 6% of the power supplied by the heater (0.1 W). However, temperature changes in the laboratory are slower than those in the field.

Neglecting the storage term in the heat balance equation resulted in calculated sap flows of $\pm 12 \text{ g h}^{-1}$ (Fig. 4(B)), bearing in mind that the true sap flow was zero. Inclusion of the storage term greatly reduced over- and under-estimates of sap flow rate during the course of a day to $\pm 3 \text{ g h}^{-1}$. However, over 24 h, the heat storage errors were found to be self-compensating: cumulative sap flow for the 4 days was calculated to be 9.2 g only.

3.2. Heat storage in sunflowers in glasshouse conditions

Experiment 2 with potted sunflower plants studied plants exposed to a large variation in irradiance, and hence large changes in both stem temperature and sap flow rate. Results from two contrasting plants are presented here: a well-watered plant with small leaf area (0.129 m^2) and low sap flow rate, and a leafier plant (0.301 m^2) with high flow rates, but subjected to water stress.

3.2.1. Low sap flow rates and plant well supplied with water

In well-watered plants, where rehydration was likely to be minimal, and therefore night time sap flow negligible, K_a changed by as much as 20% within and between nights, because of changes in stem temperature. As a first approximation, K_r was initially set subjectively as an approximate average value of the night-time K_a . Although this is not ideal, the time course of K_a during the night varied with conditions, rising from an early minimum when the stem was cooling, or falling to a dawn

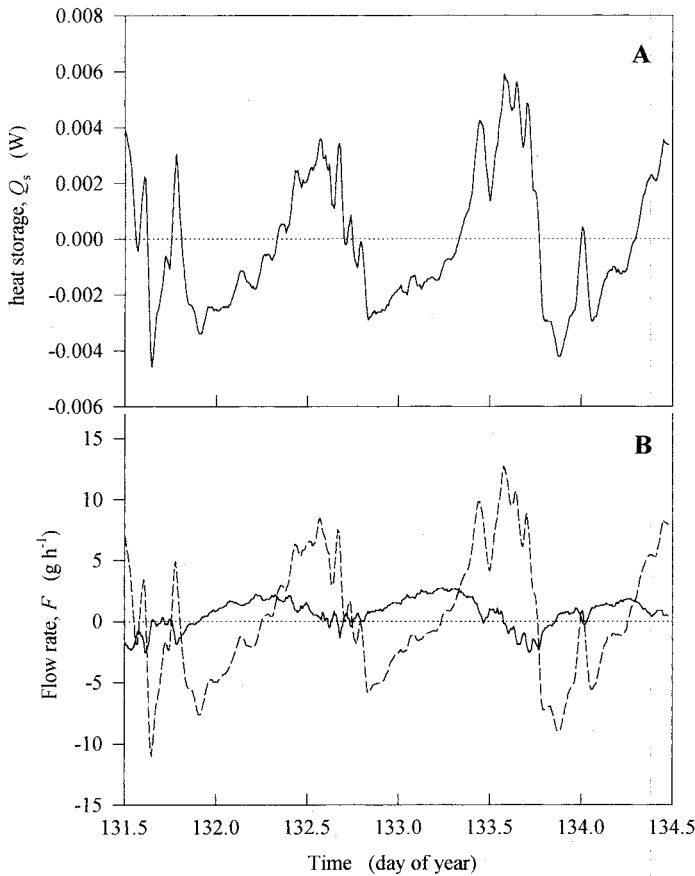


Fig. 4. (A) Time course of the change in heat storage, Q_s ; (B) calculated sap flow rates neglecting Q_s (dashed line, large fluctuations) and including Q_s (continuous line, small fluctuations) for a nylon rod stem in the laboratory. $C_{st} = 16.4 \text{ J K}^{-1}$ and $K_r = 0.920 \text{ W mV}^{-1}$.

minimum when there was sap flow at night, or following a pattern combined from these two conditions. There was intermittent cloud cover on all days, and the variation in Q_c followed closely that of irradiance, which had peak values of $1200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ on DOY 227 and lower peaks of $900 \mu\text{mol m}^{-2} \text{ s}^{-1}$ on the other days. The power supplied to the heater was suitably set for maximum gauge sensitivity: Q_c/P at midday sap flow rates was around 0.8, with $T_d - T_u$ around 1.5 K at midday (see Dynamax Manual). Stem temperature (T_{st}), lagged behind changes in ambient air temperature, T_a , by up to 1 h. Heat exchange was predominantly from the stem to the air, but early in the morning $T_{st} - T_a$ decreased rapidly from approximately +6 K (Fig. 5(A)), becoming negative temporarily because water taken up by the roots was at a lower temperature than the air while the pots were shaded.

Making the assumption that, for a well-watered plant, there was no sap flow at night, the same analysis was used to determine C_{st} and the true value of K_r as for the

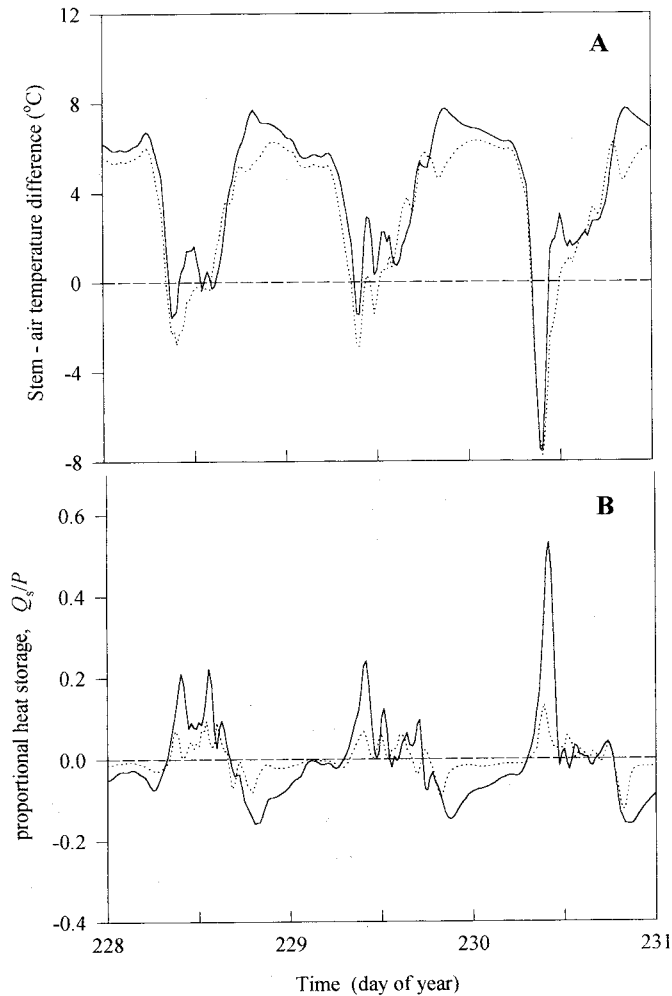


Fig. 5. Time courses of (A) the difference between stem and ambient air temperature and (B) change in heat storage, Q_s , within the stem segment as a proportion of power supply to the heater (P), for a small well-watered sunflower ($C_{st} = 27.99 \text{ J K}^{-1}$; continuous line) or a larger sunflower undergoing a water stress cycle ($C_{st} = 11.85 \text{ J K}^{-1}$; dotted line).

nylon rod. Regression analysis was performed on data from 21:30 h to 04:30 h for each night of the experiment, and is summarised in Table 1. For each night there was a strong linear relationship between $1/E(\Delta T_{st}/\Delta t)$ and K_a , as indicated by the high values of R^2 . The mean values for C_{st} and the true K_r for the five nights were 27.99 J K^{-1} ($\sigma_{n-1} = 2.15$) and 1.27 W mV^{-1} ($\sigma_{n-1} = 0.01$), respectively.

The true value of K_r exceeded that set by eye by about 9%. The K_a value equalled K_r for only a very brief period in the early morning when T_{st} was at a minimum value, i.e. dT_{st}/dt and Q_s equalled zero. This occurred after the time of minimum T_a , such

Table 1

Summary of regression analysis to determine C_{st} and the true K_r from night-time measurements for well-watered sunflower

	DOY				
	225	226	227	228	229
Intercept	0.0523	0.0436	0.0466	0.0430	0.0433
S.E. intercept	0.0002	0.0001	0.0002	0.0001	0.0001
R^2	0.9889	0.9966	0.9649	0.9949	0.9951
Slope	-0.0406	-0.0341	-0.0370	-0.040	-0.0338
S.E. slope	0.00093	0.00043	0.0015	0.0005	0.0005
C_{st} (J K^{-1})	24.64	29.28	27.01	29.44	29.58
K_r (W mV^{-1})	1.290	1.276	1.259	1.267	1.281

No. of observations — 23.

that both $T_{st} - T_a$ and Q_s had begun to change rapidly. Consequently, K_a changed rapidly and interpolation of K_r from the time of minimum T_{st} would be subject to large errors. Determination of K_r from regression analysis provided a better estimate.

The above mean value of C_{st} was used to calculate the rate of change of stem heat content, Q_s , which is shown in Fig. 5(B) as a proportion of the heater power. There were net heat losses from the stem during the night and heat gains during the day. Generally, Q_s represented 5–20% of the power supplied to the heater (0.1 W) but rose to 40–60% during rapid changes of either sap flow or ambient temperature. Ignoring Q_s resulted in large early morning spikes in the estimates of sap flow (Fig. 6(A)), which are largely removed by taking account of Q_s . The time course of gravimetric transpiration was indistinguishable from the Q_s corrected sap flow.

Improvement in the temporal resolution of stem heat balance gauges by including heat storage is clearly illustrated in Fig. 7, which shows sap flow rate (F) calculated both excluding (open symbols) and including (filled symbols) Q_s against gravimetric transpiration for DOY 229. Inclusion of heat storage results in less scatter, with points falling closer to the 1:1 line. Cumulative daytime sap flow amounts are shown in Table 2 for three different calculation methods and are compared with

Table 2

Daytime (07:00–19:00 h) totals of sap flow and gravimetric transpiration (g) for well-watered sunflower with low flow rates

DOY	Gravimetric	Flow ^a	Corrected ^b	Corrected ^c
226	288	422	430	317
227	^d			
228	332	408	367	334
229	296	342	302	267
230	285	391	327	298

^a Gauge radial conductance, $K_r = 1.17 \text{ W mV}^{-1}$, excluding heat storage, Q_s . ^b $K_r = 1.17 \text{ W mV}^{-1}$, including Q_s . ^c $K_r = 1.27 \text{ W mV}^{-1}$, including Q_s . ^d Gravimetric data missing.

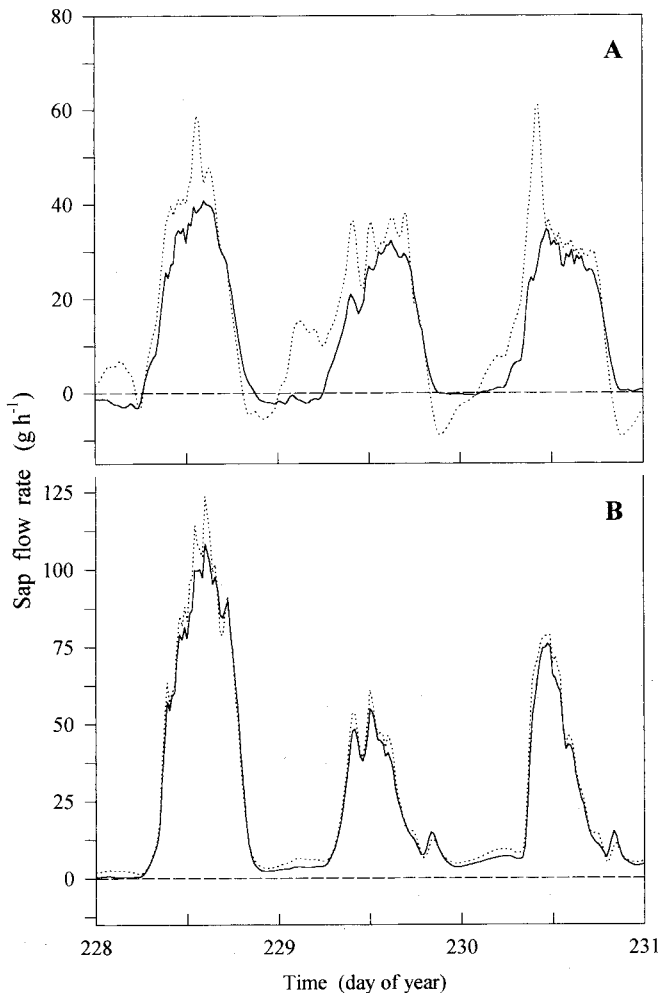


Fig. 6. Sap flow rates calculated neglecting (dotted line) and including (continuous line) the heat storage component in the heat balance equation, for (A) a small well-watered sunflower or (B) a larger sunflower undergoing a water stress cycle. Other details as in Fig. 5. (Note difference in sap flow scales in (A) and (B).)

corresponding gravimetric estimates of transpiration. Using the value of K_r set by eye and ignoring Q_s consistently overestimated cumulative sap flow by up to 40%. If K_r was set by eye, and Q_s was included in the heat balance, there was a large improvement, but the best agreement (within 8%) was found using the true K_r and including Q_s .

3.2.2. Medium to high sap flow rates (plant experienced water stress at end of experiment)

Initially, when the plants were well watered, F was close to zero at night (Fig. 6(A)). As the plants became increasingly water stressed, F increased above zero at night,

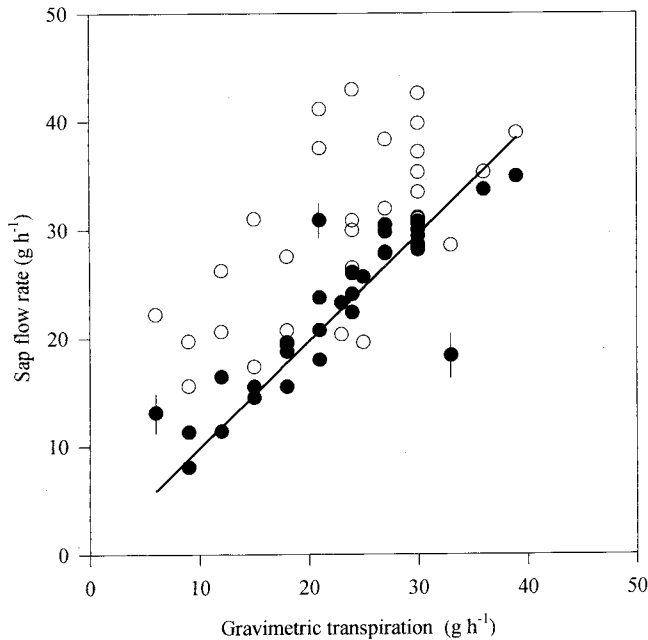


Fig. 7. Relationship between sap flow, calculated neglecting stem heat storage, Q_s (○), or including Q_s (●), and gravimetric transpiration for well-watered sunflower on DOY 229. $K_r = 1.17 \text{ W mV}^{-1}$ when Q_s is neglected and $K_r = 1.27 \text{ W mV}^{-1}$ when Q_s is included, and $C_{st} = 27.99 \text{ J K}^{-1}$ in both cases. Line shown is $y = x$. (For an explanation of marked points, see the Discussion).

suggesting that plants continued to take up water at night to replace that taken from storage during the day. There are two other indications that this is not an artefact. First, large positive spikes of F on the evenings of DOY 229 and DOY 230 occurred almost immediately after rewatering. Before watering, the plants were very limp with drooping flower heads; following watering there was a visible increase in turgidity as the flower heads began to straighten up. Second, $T_d - T_u$ was low (0.5 K) during the night of DOY 225–226, when the plant was well watered, whereas on other nights, $T_d - T_u$ was considerably higher (1.0–1.5 K; data not shown). If there is sap flow at night, K_a will overestimate K_r . However, the results with the well-watered plant, given above, show that K_a at night tends to underestimate K_r if changes in stem heat content are not considered. These opposing influences on K_r may be self-compensating to some extent for small night-time sap flows.

As a first estimate, the value of K_r used to calculate Q_r was taken to be the average K_a for the first three nights, where sap flow was presumed to be negligible. Alternatively, the regression analysis procedure described above was used to estimate C_{st} and the true K_r using data from 21:30 h to 04:30 h on the night of DOY 225–226. The analysis showed a good linear relationship ($R^2 = 0.944$) and gave values for C_{st} and K_r of 11.85 J K^{-1} and 1.021 W mV^{-1} , respectively. The value for K_r agreed well (+4%) with that set by eye (0.98 W mV^{-1}), suggesting that the zero flow assumption made was reasonable for this night. Using this value for C_{st} , the rate of change in stem

Table 3

Daytime (07:00–19:00 h) and 24 h totals of sap flow and gravimetric transpiration (g) for partly water stressed sunflower with high flow rates

DOY	Daytime			24 h		
	Gravimetric	Flow ^a	Corrected ^b	Gravimetric	Flow ^a	Corrected ^b
226	714	805	738	762	838	758
227	967	951	903	1009	974	914
228	1000	908	868	1048	949	894
229	435	394	368	479	477	433
230	570	485	450	595	814	521

^a $K_r = 0.98 \text{ W m V}^{-1}$, excluding Q_s .

^b $K_r = 1.02 \text{ W m V}^{-1}$, excluding Q_s .

heat content was calculated, and is shown in Fig. 5(B). Q_s rarely exceeded 13% of the power input during the day or 3% at night. As Q_s was a much smaller component of the heat budget than in the low flow case, its inclusion in the calculation of sap flow did not make a marked difference (Fig. 6(B)), but detailed inspection of the data showed that it did improve the dynamic response of the gauge.

At these high sap flow rates, accumulated sap flow over 24 h was consistently within $\pm 10\%$ of accumulated transpiration irrespective of the procedure used to calculate sap flow (Table 3). The difference between 12 h and 24 h accumulated sap flow totals represents the amount of water taken from storage within the plant tissue. For DOY 229 and 230 this represented as much as 20% of the total water lost from the leaves (24 h gravimetric totals).

3.2.3. Quantification of heat storage effect in the field

A field test of the importance of Q_s was carried out by comparing gauges on two stems of the multistemmed *G. senegalensis* bush (shown in Fig. 1) during the rainy season. Fig. 8(A) shows the course of K_a before and after covering Stem A on DOY 227. Before covering, the K_a at night varied approximately $\pm 6\%$ about 1.2 W m V^{-1} , with a downward trend that indicated sap flow. After covering, there were large negative and positive changes at sunset and at sunrise, respectively, and heavy rainfall events also caused K_a to decrease rapidly as the stem cooled. Between the spikes, the apparent K_r changed slowly, averaging around 1.2 W m V^{-1} . The similarity between the average apparent K_r at night before and after covering suggests that sap flow during darkness was small, but the existence of night-time flow was confirmed from observation of $T_d - T_u$ (data not shown), which was around 2–3 K at night before covering, but decreased to around 0.3 K after covering. Given the hyperbolic dependence of $T_d - T_u$ on the flow rate, flow rates as low as $5\text{--}10 \text{ g h}^{-1}$ would be sufficient to cause the values of $T_d - T_u$ observed before covering.

Making the assumption that after covering there was negligible sap flow through Stem A, regression analysis was performed on all data for DOY 230–236 (432 observations) for Stem A (Fig. 8(B)). The linear relationship was not as strong ($R^2 = 0.74$) as it was for the glasshouse experiments, but C_{st} and K_r ($\pm 95\%$

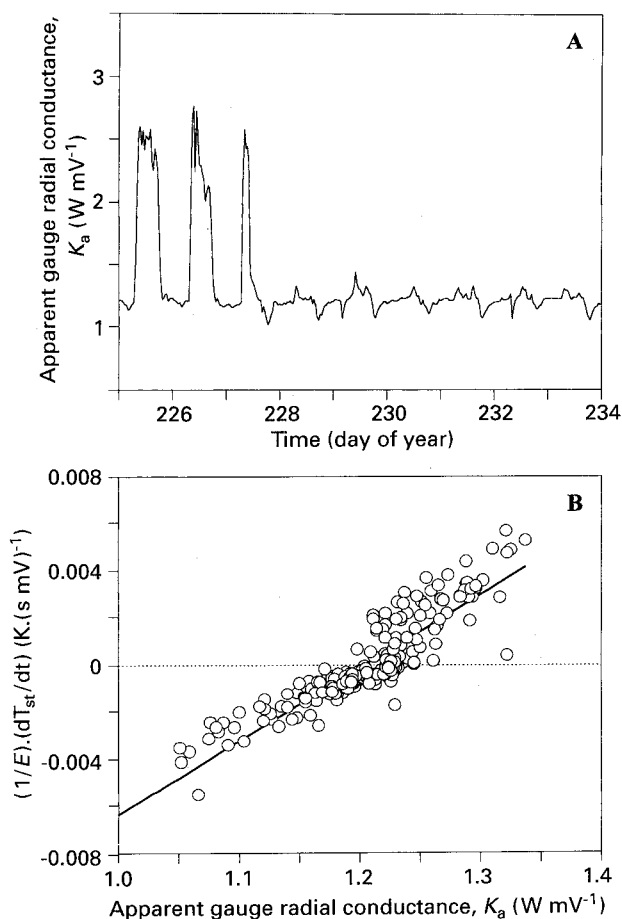


Fig. 8. (A) Time course of apparent gauge radial conductance, K_a ; (B) plot of $1/E(dT_{st}/dt)$ against apparent K_r in a *G. senegalensis* bush before and after covering stem to prevent transpiration; 432 observations during DOY 230–236.

confidence limits) were $32.44(\pm 1.95) \text{ J K}^{-1}$ and $1.204(\pm 0.065) \text{ W mV}^{-1}$, respectively. There was no significant difference between the value of K_r and the average set by eye for the period after covering (1.20 W mV^{-1}). The value calculated for C_{st} was used to estimate Q_s both after and before covering (Figs. 9(A) and 9(B)). After covering, under assumed zero sap flow conditions, Q_s represented around 30% (0.04 W) of the power (P) supplied by the heater (0.13 W). Neglect of Q_s in the heat balance resulted in large positive values of sap flow around sunrise ($50\text{--}80 \text{ g h}^{-1}$) and negative sap flow of $10\text{--}20 \text{ g h}^{-1}$ around sunset. Inclusion of Q_s reversed these patterns of calculated sap flow, resulting in negative values of $30\text{--}60 \text{ g h}^{-1}$ at sunrise followed by slowly increasing sap flow (maximum 10 g h^{-1}) during the rest of the day and night.

Before covering, F calculated excluding Q_s generally exceeded that calculated including Q_s until around 15:30 h, after which F remained very slightly less

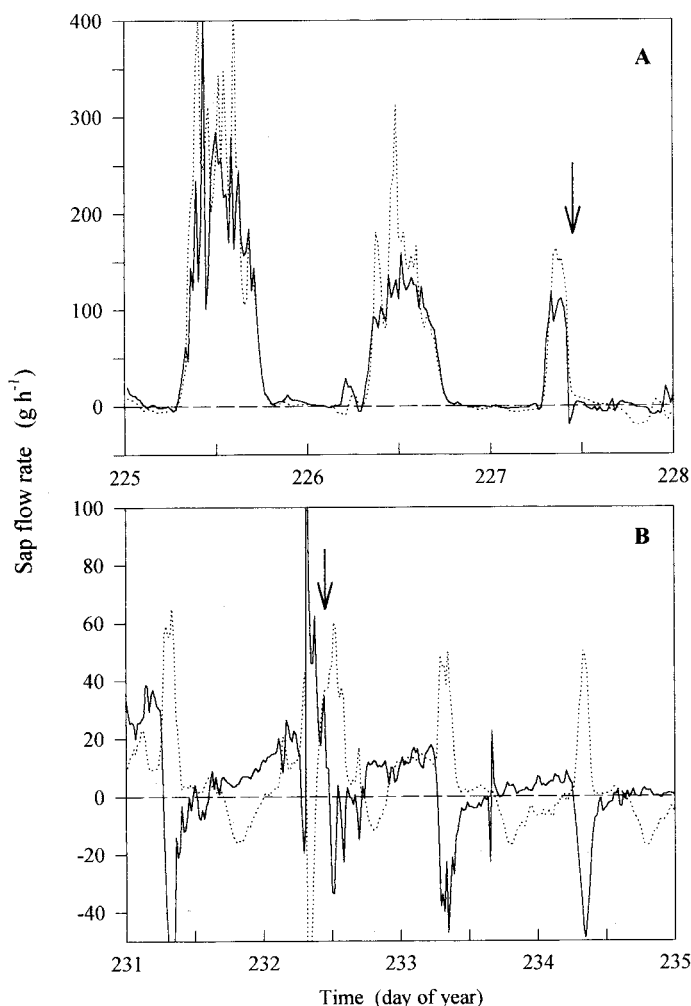


Fig. 9. Calculated sap flow in a *G. senegalensis* bush before (A) and after (B) covering leaves to prevent transpiration. Sap flow was calculated neglecting (dotted line) and including (continuous line) heat storage, Q_s . Arrow in (A) indicates time of covering, and in (B) indicates occurrence of 36 mm rainfall. (Note different sap flow scales in (A) and (B); for clarity, data for only some days are shown.)

throughout the night. For short periods, instantaneous values disagreed by up to 58%. The effect on daily totals of sap flow was much smaller (approximately 20%).

For the second gauged stem (Stem B) there was strong evidence of significant sap flow at night (high $T_d - T_u$). Consequently, the regression approach could not be applied to determine C_{st} . If c_v is constant for a particular species under similar water status, then C_{st} is governed solely by V_e ; because both gauges were the same model (i.e. of the same geometry), C_{st} for Stem B was estimated by multiplying C_{st} for Stem A by 1.043, the ratio of the stem cross-sectional areas (measured at the heater). Using

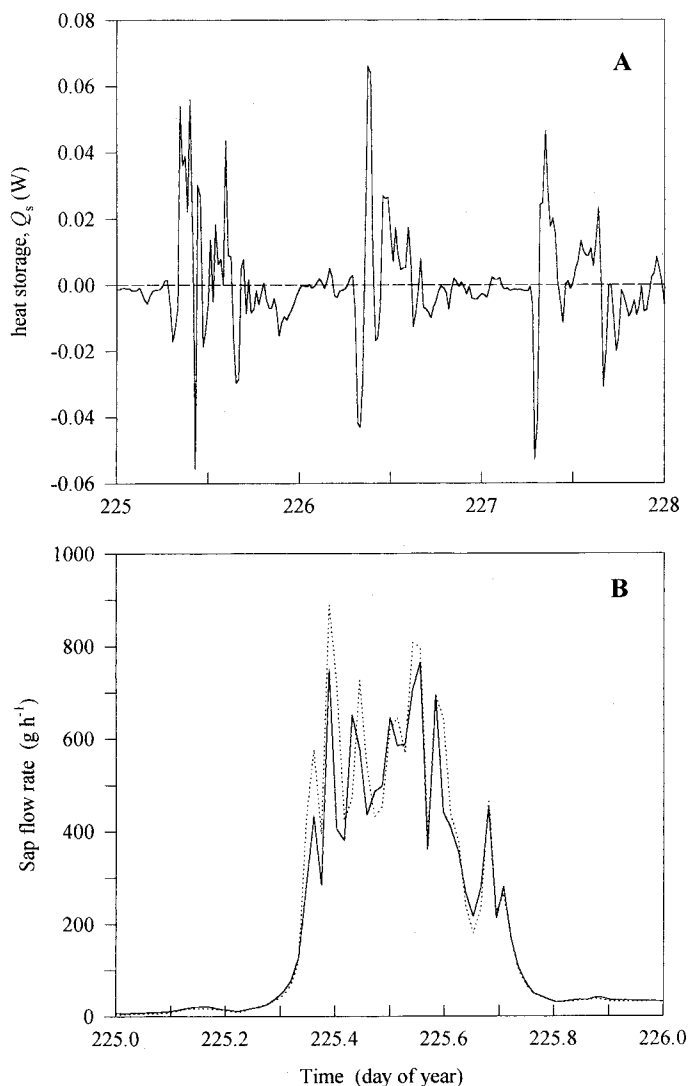


Fig. 10. (A) Time course of heat storage calculated using an estimated value of the stem heat capacitance, $C_{st} = 33.8 \text{ J K}^{-1}$; (B) sap flow rate calculated neglecting (dotted line) and including (continuous line) the heat storage component in the heat balance equation, for a transpiring stem of a *G. senegalensis* bush. In (B), for clarity, only data for DOY 225 are shown.

this value, Q_s was calculated, and is shown in Fig. 10(A). Apart from the large positive and negative spikes ($\pm 0.08 \text{ W}$, or 57% of P) that occur around sunrise and sunset, when changes in both sap flow rate and ambient air temperature are rapid, Q_s was generally less than $\pm 0.03 \text{ W}$ (21% of P) during the day, and around $\pm 0.01 \text{ W}$ (7% of P) during the night. The diurnal course of Q_s was much more variable than in the greenhouse experiments, being not so obviously positive during the day, and negative

Table 4

Daily totals (midnight to midnight) of sap flow (g) in an uncovered stem of *G. senegalensis* calculated excluding and including heat storage (Q_s)

DOY	Flow excluding Q_s	Flow including Q_s	% Difference
225	5039	4677	–7.7
226	3436	2894	–18.7
227	2485	2319	–7.2
228	2695	2510	–7.4
229	3021	2819	–7.1
230	2038	1935	–5.4
231	3485	3140	–11.0
232	957	938	–2.0
233	3585	3373	–6.3
234	3780	3559	–6.2
235	1437	1410	–1.9

The percent difference is calculated as $[(i - e) \times 100/i]$, where i is including and e is excluding Q_s .

at night. In this respect, neglect of Q_s in the heat balance equation is more likely to be self-compensating than under greenhouse conditions. This difference between field and glasshouse is probably not related to the flow rates per se but to the different phasing of the diurnal patterns of temperature and radiation.

Sap flow rates in Stem B for one selected day (DOY 225) calculated either neglecting or including Q_s in the heat balance equation are shown in Fig. 10(B). After sudden changes in sap flow rate during the day, there was a consistent lag of F calculated excluding Q_s behind that calculated including Q_s . At night, because Q_s was low and there was some sap flow, there was very good agreement between the two calculated values of sap flow rate. Under such conditions, the correct setting of K_r is more important than quantifying Q_s . In the case of Stem B, K_r was set from the minimum K_a observed on DOY 230–231 (1.26 W mV^{-1}). This was the lowest night-time minimum K_a observed during the period of the experiment, and occurred just after the soil had received 48 mm of rainfall during the previous two nights, thereby reducing large changes in tissue water status and subsequent sap flow at night.

Inclusion of Q_s at least partially eliminated the large spikes in sap flow calculated in the early morning. However, the influence of Q_s on the calculation of daily totals of sap flow was small (Table 4), where daily totals calculated without Q_s overestimated by an average of 7.4% over the 11 days, although for some days the overestimates were substantially higher.

4. Discussion

Tests with a model stem with zero sap flow showed that the influence of Q_s could be appreciable, though self-compensating in the calculation of 24 h totals of sap flow (Fig. 4(B)). In real situations, where there is a large diurnal change in sap flow, error in

daily totals owing to neglect of Q_s will depend upon the phase relationship between sap flow and Q_s , which in turn depends upon the extent to which stem temperature lags behind ambient air temperature. If there was no phase lag between stem and air temperature, only a difference in amplitude, then neglect of Q_s would be self-compensating if the diurnal course of sap flow was symmetrical about the time of maximum T_{st} and T_a . In fact, there is typically a phase lag between T_{st} and T_a , such that Q_s is roughly in phase with the diurnal course of sap flow (Fig. 5(B)). Consequently, and as a result of the change in sign of Q_s (positive during periods of sap flow, and negative when there is no sap flow), neglect of Q_s in the heat balance is not self-compensating over 24 h (Tables 2–4). These findings are contrary to previous suggestions, including those in the gauge manufacturer's manual.

The experiments with two contrasting sunflower plants in UK glasshouse conditions showed that Q_s can represent a larger component of the heat balance at low than at high sap flow rates (Fig. 5(B)). However, it should be noted that the stem diameter for the higher flow rate plant was smaller than for the low sap flow plant (14 mm vs. 16 mm), and that this 30% difference in stem area (and therefore V_c) will account for some of the reduction in the heat storage component. Results from the well-watered, low sap flow rate case showed that Q_s may represent up to 60% of the power supplied to the heater, i.e. a significant component of the heat balance under rapidly changing conditions, and is generally around 5–20% under typical glasshouse conditions. This echoes the findings of Groot and King (1992) on conifer seedlings. As proposed in the calculation section, neglect of Q_s at night results in K_a underestimating K_r by as much as 16%, thereby overestimating sap flow both at night and during the day. If the true value of K_r is used and Q_s is included, then agreement with gravimetric transpiration to within 10% is possible under strong diurnal changes in radiation, even under these low sap flow rate conditions.

With higher flow rates and varying degrees of water stress, the situation is more complicated, but may be more representative of many field situations. Fluctuations in tissue water content may cause sap flow at night leading to substantial overestimation of K_r . If a zero or negligible sap flow situation is achieved (Baker and Van Bavel, 1987; Steinberg et al., 1989), then K_r can be estimated from the night-time minimum of K_a without causing significant errors in sap flow calculated ignoring changes in Q_s . However, overestimate of K_r owing to sap flow may be partly or totally offset by the underestimation of K_r when changes in Q_s are not considered. In this situation, inclusion of Q_s can improve the dynamic response of gauges, but is not essential with respect to estimating daily totals of sap flow. Furthermore, because there are changes in tissue water status downstream of the sap flow gauge, then instantaneous values of sap flow at the base of a stem are not a good estimate of water lost from the leaves as transpiration. This is exemplified by Fig. 7, where some of the scatter even after correction for Q_s is attributable to changes in tissue water. In particular, the points marked correspond to periods of sudden change in transpiration rate where there is most likely to be discrepancy between transpiration and sap flow.

The appropriate division of sap flow rates into 'low' and 'high' classes to determine the magnitude of the error needs consideration. Sap velocity (mm s^{-1}) is arguably the most appropriate criterion. In the sunflower experiments, the low and high flow cases

showed daily peaks of about 0.07 (Q_s significant) and 0.22 mm s^{-1} (small Q_s effects), respectively. Shackel et al. (1992) reported large errors in sap flow measurements in a peach tree of about 60 mm diameter, where the peak sap velocity was between 0.07 and 0.08 mm s^{-1} . In contrast, Dugas (1990) found no significant heat storage effects in 9 mm diameter cotton stems, with peak sap velocity exceeding 0.3 mm s^{-1} , corresponding to our high flow condition.

The field test on *G. senegalensis* confirmed many of the points found in the glasshouse. First, significant night-time sap flow was observed, especially after rainfall altered the soil water potential. However, K_r could be estimated reliably from the minimum value of K_a even though sap flow was not zero. The rate of change of the stem segment heat content could be estimated using the regression approach, provided that a zero sap flow situation could be assumed at some time. Inclusion of this term in the heat balance equation improved the temporal resolution of gauges, and would have been important in a study of the dynamics of plant water relations (Figs. 9(A), 9(B) and 10(B)). However, large changes in tissue water status during the day made sap flow measurement unsuitable for estimating instantaneous values of transpiration, rather than sap flow. In principle, this might be rectified if changes in plant water content were measured over the same interval. Errors in daily totals of sap flow attributable to Q_s were not self-compensating, and caused an overestimate of up to 10%, although as this was in low flow conditions the absolute errors were small. However, it must be noted that there was no independent measure of transpiration in the field, and daily totals of accumulated sap flow may not be a good estimate of daily accumulated transpiration, when there is a net change in plant water status over 24 h.

The experiments with sunflower plants in glasshouse conditions and *G. senegalensis* in the field showed that inclusion of Q_s in the heat balance equation can greatly improve the temporal resolution of the stem heat balance method. Further, there are several important details of sap flow that can now be resolved. In the second sunflower experiment the lag between sap flow and gravimetrically determined transpiration changed as the plant became water stressed. To emphasise these changes, the data from Fig. 6(B) are replotted in Fig. 11. It is clear that when the plant was well watered in the morning (Fig. 11, DOY 227), some of the water lost as transpiration came from storage within the plant tissue. In the afternoon, when atmospheric demand began to fall, sap flow exceeded transpiration, to replace the previous loss from storage. However, when the plant is water stressed (Fig. 11, DOY 229 and 230), sap flow matches gravimetric loss better, with a tendency for sap flow to be lower, and considerable 'recharge' sap flow at night. Porometer measurements confirmed that stomatal resistance was high during the stressed period, indicating that there is a limit to the amount of water that is available from the plant tissue store. For the sunflower plant in this experiment, Table 3 shows that as much as 20% of the daily transpirational water loss came from storage within the plant tissue. This represented up to 40% of the water contained in tissue above the gauge.

The experiment with *G. senegalensis* also shows the potential of sap flow gauges in understanding water relations. The negative flow in the covered, non-transpiring stem (Fig. 9(B)) is not an artefact, and shows that water stored within the plant tissue in

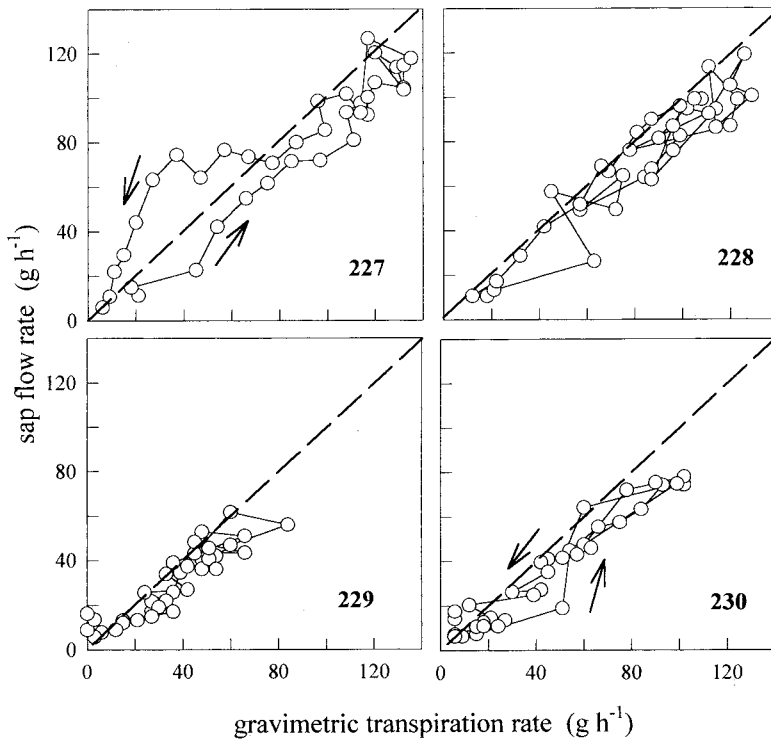


Fig. 11. Relationship between sap flow rate and gravimetric transpiration over 4 days of a drying cycle with sunflower. Arrows show time course of measurements where this is distinct, and number indicates day of year.

that stem (Stem A) moved down the stem in response to changes in water status of the uncovered, transpiring stems, via the common root system. Leaf water potential measurements were made using a pressure chamber, on three leaves of each stem, at 13:15 h GMT on DOY 228 (the day after Stem A had been covered). The mean leaf water potentials for each stem were -1.00 ± 0.03 MPa, -0.92 ± 0.03 MPa, -0.97 ± 0.04 MPa and -0.97 ± 0.06 MPa for Stems A, B, C and D, respectively; i.e. closely similar, as expected for stems with a common root system. Predawn measurement on the covered stem gave leaf water potentials of around -0.3 MPa, and therefore this diurnal change in tissue water status must be associated with redistribution of water within the plant, as no water was lost from the leaves. This redistribution of water is manifested as sap flow measured by the gauge on Stem A. Similar behaviour was reported by Daum (1967), where the direction of sap flow was reversed in a shaded branch to supply the sunlit crown. The occurrence of some, though generally low (± 20 g h⁻¹), sap flow owing to redistribution may explain the poorer correlation between $1/E(\Delta T_{st}/\Delta t)$ and the apparent K_r than was observed in the glasshouse experiments (Fig. 8(B)). It is also likely that the high, Q_s -corrected sap flow calculated after the rainfall event on DOY 232 (Fig. 9(B)), may also indicate real movement of sap as the stem rehydrated following wetting-up of the soil.

Table 5

Summary of experimental and literature values for the volumetric specific heat capacity ($\text{J cm}^{-3} \text{K}^{-1}$) of various species

Species	Heat capacity	No. of samples
<i>Guiera senegalensis</i>	2.96	1
<i>Helianthus annuus</i>	4.04	4
<i>Ficus benjamina</i>	3.40	3
Small fruit trees ^a	2.6–3.0	

^a Valancogne and Granier (1991).

Fig. 10(B) shows clearly how the dynamics of the gauge in the field change when Q_s is included. In these conditions of fluctuating insolation, the uncorrected flow was generally one measurement period behind the corrected flow, indicating that it takes about 20 min for the gauge to return to a steady state after a sudden change in sap flow rate and/or temperature. This lag is much longer than the time constant quoted by the manufacturer (values of 4 min and 1 min at flow rates of 100 g h^{-1} and 800 g h^{-1} , respectively, for an SGB19 gauge; Dynagauge Manual, and Baker and Van Bavel (1987)) for the effect of changing sap flow rate on the temperature distribution within the stem segment. The lag in Fig. 10(B) demonstrates the additional time required for the gauge and stem to return to thermal equilibrium under field conditions when a sudden change in sap flow rate is associated with changes in irradiance and temperature. Groot and King (1992) also noted the marked improvement in gauge dynamic response when Q_s was included.

The regression analysis used here allowed the estimation of the thermal capacitance (C_{st}) of the stem. The value of C_{st} depends upon two properties: the effective volume of the heated segment, V_e , which depends upon the gauge geometry and the stem diameter, and the volumetric specific heat capacity of the stem, c_v , which depends upon the volume fractions of air, water and cellulose making up the stem, and the wet bulk density of the stem. No measurements were made of these parameters, but by making the same assumption as Valancogne and Granier (1991), i.e. that the effective volume of the segment for which the heat balance is conducted is that bounded by the midpoints of the upper and lower thermojunction pairs, then a value for the volumetric specific heat capacity, c_v , can be estimated for each of the stems measured. This is shown in Table 5 for the plant species reported here, and for additional work on *Ficus benjamina*. Experimental results were encouraging. For the woody stemmed *G. senegalensis* and *F. benjamina*, c_v was lower than for the less woody *H. annuus*, and agreed well with values reported by Valancogne and Granier (1991) for small fruit trees. The value for *H. annuus* was very close to that of water, as expected for a non-woody stem. If the bulk density and volume fractions of the gas, liquid and solid matrix components of the stem are known, a value for c_v can be calculated (Edwards and Warwick, 1984) using the equation

$$C_v = 2.114F_m + 4.186F_l \quad (11)$$

where F_m and F_l are the volume fractions of solid matrix and liquid sap, respectively, and the values reported in Table 5 lie within the range predicted by this equation.

5. Summary

To date, no comprehensive study of the importance of including Q_s in the heat balance has been reported in the literature. To test the significance of deviations from steady-state stem heat balance theory on both instantaneous and accumulated daily totals of sap flow, experiments were conducted under a range of sap flow and ambient temperature regimes. From these findings, it is clear that Q_s should not be assumed to be negligible particularly under low rates of sap flow, and that under all conditions inclusion of the heat storage term improves the dynamic resolution of sap flow rates determined by the heat balance method.

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