# Heat balance measurements—to quantify sap flow in thin stems only?

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## Abstract

Two methods were used to measure the flow of sap through the xylem of a mature Norway spruce by balancing heat. One, the tissue heat balance (THB), had been designed for tree stems of large diameter and is based on the balance of heat within an internal compartment of tissue conducting the sap. The other, the stem heat balance (SHB), is applicable for stems of small diameter. It follows the principle of balancing heat within a section of the entire stem. Both methods were tested in the laboratory using simple experimental simulators of flow. In the field, comparative measurements were made within the crown of a mature Norway spruce. The THB was inaccurate mainly because (1) it failed to consider the dissipation of heat appropriately during measurements, and (2) assessing the temperature within the tissue of the stem in such a way that it represented the entire heated compartment was not practicable. The SHB yielded more realistic results. A procedure obtaining approximate results also by THB is proposed. It is a fundamental requirement of balancing heat that all its fluxes can be completely assessed. This is unlikely to be achieved for a compartment inside a stem as intended by THB. There the dissipation of heat is not traceable and varies as the flow of sap changes. An insulated section of an entire stem, however, is a compartment, which allows one to measure the SHB including all its major components. Thus, balancing heat appears to be suitable for quantifying the flow of sap in thin stems by SHB rather than in thick stems as intended by THB, unless complex calibrations are made.

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## 1. Introduction

Attempts to quantify the flow of sap through the xylem of plants in response to transpiration, dehydration, rehydration or water translocation have led to the development of non-invasive techniques of tagging the moving sap without affecting its conducting tissue. A possible tag for such applications is heat, used to indicate the flow of sap in two general ways. In one a pulse of heat is injected into the xylem, and its passage is detected at a point further along the flow direction (e.g. Barrett et al., 1995; Hatton et al., 1995). The travel time of the pulse allows the velocity of the flow to be estimated. In the other procedure, which is the subject of this study, heat is balanced within the xylem; the convection of the heat and implicitly the flow of sap is found in the difference between the input of heat and its loss by conduction.

The disadvantage of using heat to quantify the flow in stems is its diffuse dissipation. In contrast to other techniques, e.g. imaging the flow of sap by nuclear magnetic resonance (Xia et al., 1993), tagging it by heat is unspecific. Depending on the thermal conductance of the surroundings, the heat in stems usually dissipates quickly, which may be crucial for both the heat pulse (see Marshall, 1958) and the heat balance techniques.

Heat can be balanced either inside the stems in xylem adjacent to inserted heating elements (Huber and Schmidt, 1937; Vieweg and Ziegler, 1960; Čermák et al., 1973; Granier, 1985, Granier, 1987; Pearcy et al., 1989) or in an entire section of stems using an external source of heat (Sakuratani, 1984; Baker and Van Bavel, 1987; Fichtner and Schulze, 1990; Ishida et al., 1991; Grime et al., 1995a). The latter is applicable for many species with stems of small diameter. In the case of trees, however, the sap is preferably heated inside stems because of their considerable size.

Balancing heat in thin stems has been facilitated by insulating entire sections of them and by determining the dissipation that still continues axially and radially (Sakuratani, 1981). However, the problem of determining the dissipation of heat has not yet been resolved for balances made internally inside thick stems. In this case, the heated compartments can neither be exactly delineated nor insulated. As a consequence, balancing heat appropriately appears to be difficult. Granier (1985) avoided the problem by establishing an empirical relation between sap flow and its cooling effect on a heated thermocouple inserted into the stem (see Diawara et al., 1991).

We have tried to determine how accurately the flow of sap in a tree can be quantified by the approaches proposed by Čermák et al. (1973) for thick stems and Sakuratani (1981) for thin stems. Both methods were tested in the laboratory using simple simulation of flow and compared in the field by parallel measurements in the crown of a mature Norway spruce.

## 2. Material and methods

### 2.1. Tissue heat balance (THB)

Inside the stem we balanced the heat through controlled electric heating of tissue (Čermák et al., 1973; Kučera et al., 1977; Čermák and Kučera, 1981). The temperature

within the heated compartment of xylem was kept at a constant value above that of the surroundings. The heat lost from the compartment by convection, i.e. the portion taken up by the passing sap, together with that lost by dissipation equalled the input of heat (Kučera et al., 1977):

$$P_{\mathrm{contr}} = \Delta T_{\mathrm{ts}} \left( \frac{Q_{\mathrm{sap}} C_{\mathrm{sap}} A_{\mathrm{e}}}{A_{\mathrm{t}}} + \lambda \right) \tag{1}$$

where $P_{\mathrm{contr}}$ is the controlled input of heat needed to maintain the constant difference between the temperature within the heated compartment and that of the ambient (W), $\Delta T_{\mathrm{ts}}$ is that constant difference (K), $Q_{\mathrm{sap}}$ is the flow of the sap through the entire cross-section of the stem (kg s$^{-1}$), $A_e$ is the cross-sectional area of hydroactive xylem between the heating electrodes (m$^2$), $A_{\mathrm{t}}$ is the cross-sectional area of the total hydroactive xylem (m$^2$), $C_{\mathrm{sap}}$ is the specific heat capacity of sap (assumed as pure water) (J K$^{-1}$ kg$^{-1}$), and $\lambda$ is the coefficient of the dissipation of heat (J K$^{-1}$ s$^{-1}$).

The dissipative portion of the balance was assumed to be constant and independent of any flow through the compartment. It was proposed, therefore, that the dissipative loss of heat could be determined when no heat is convected by flowing sap and it is equal to the input of heat.

By the rearrangement of Eq. (1) we obtain Eq. (2) (Kučera et al., 1977), which is the practical form for calculating the flow. The term $\dfrac{\lambda A_{\mathrm{t}}}{C_{\mathrm{sap}} A_{\mathrm{e}}}$ can be replaced by $Q_{\mathrm{c}}^0$, which is the fictitious 'sap flow' attributed to the dissipation of heat:

$$Q_{\mathrm{sap}} = \frac{P_{\mathrm{contr}} A_{\mathrm{t}}}{\Delta T_{\mathrm{ts}} C_{\mathrm{sap}} A_{\mathrm{e}}} - Q_{\mathrm{c}}^0 \tag{2}$$

For the heated compartment of xylem the balance may also be expressed in terms of fluxes of heat:

$$q_{\mathrm{sap}} = P_{\mathrm{contr}} - q_{\mathrm{c}}^0 \tag{3}$$

where $q_{\mathrm{sap}}$ is the convective loss of heat owing to the flow (W), and $q_{\mathrm{c}}^0$ is the loss of heat by dissipation determined at no flow (W).

The tissue was heated by alternating current using five parallel plate electrodes of stainless steel (60 mm × 25 mm × 1.3 mm) inserted 20 mm apart. The heating was controlled by WAFL1 flow meters (Gröger S.E.P., Bayreuth, Germany) with $\Delta T_{\mathrm{ts}}$ kept constant at 1 K.

Instead of the usual sensors with metallic sheathings (Gröger S.E.P.) we used copper–constantan thermocouples coated with plastic. Sheathings of plastic ensured a more reliable electrical insulation around the thermocouples than metal ones. At the same time, they reduced the large thermal conductivity ($K$) of the sensors which caused enhanced conduction of heat along their own axes ($K_{\mathrm{steel}} > 14\,\mathrm{W\,m^{-1}\,K^{-1}}$; $K_{\mathrm{plastic}} \approx 0.3\,\mathrm{W\,m^{-1}\,K^{-1}}$ (Weast et al., 1985)). The response time of our sensors was not significantly different from that of metallic sensors.

## 2.1.1. Test in the laboratory

For simulating the flow through xylem a cuboid box of acrylic glass (490 mm ×
290 mm × 60 mm) was constructed and homogeneously filled with sawdust. The cuboid
shape was preferred to a cylinder because the heated compartments of xylem inside the
stems also are nearly cuboid. The sawdust was ponded with water to obtain a continuous
flow through it. When the water initially seeped into the dry sawdust it moved as a front,
indicating a fairly homogeneous flow. The flow was varied by levelling the water at
different heights above the sawdust. The water had been equilibrated to ambient
temperature before being supplied by a peristaltic pump. The heat sensors and the
electrodes were sealed into holes in the front wall of the box. The electrodes were placed
40 mm deep in the sawdust, whereas the thermocouples were inserted with their
junctions at only half that depth (20 mm). The whole box was insulated with a 40 mm
Styrofoam layer against the nearly constant air temperature in the laboratory. The $q_c^0$
was determined as the input of heat at no flow after the outlet of the box had been
closed. The flow of water calculated from the THB was compared with that measured
volumetrically.

## 2.1.2. Measurement in the field

The flow of sap was measured in the crown of a Norway spruce (*Picea abies* (L.)
Karst.) during the growing season of 1992. The tree was about 220 years old and 25 m
tall. It had a diameter at breast height of 0.36 m, an estimated total surface area of the
needles of 447 m$^2$ (Häsler et al., 1991), and was growing at the subalpine research
station Seehornwald, 1639 m above sea level near Davos, Switzerland. The living crown
extended from the top of the tree down to 3.5 m above ground. The flow through the
main stem was measured simultaneously at different heights in the crown.

The zone of xylem in which sap is conducted ($\Delta r_h$ in Fig. 1) was examined in three
stem discs cut from different levels of the lower half of a neighbouring tree. Maxima
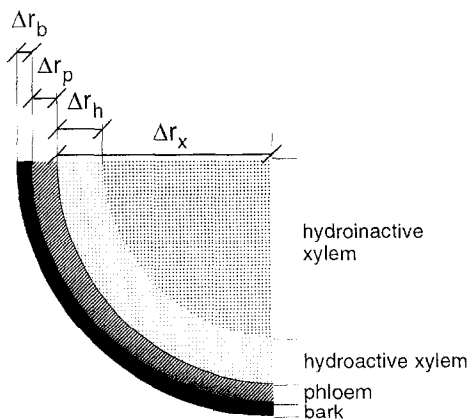and minima of $\Delta r_h$ within the individual discs differed by up to a factor of 3. On



Fig. 1. Illustration of the various tissues in the cross-section of a trunk: $\Delta r_b$ and $\Delta r_p$, thickness of the bark
and the phloem; $\Delta r_x$, radius of the xylem of which $\Delta r_h$ describes the hydroactive zone.

Table 1
Tissue heat balance: positions of the flow meters in the main stem with corresponding estimates of the cross-sectional areas of hydroactive xylem and the heated parts of them

| Flow meter positions | | | Characteristics of the hydroactive xylem [a] | | | |
|---|---|---|---|---|---|---|
| Stem height (m) | Stem diameter (m) | Exposure | Radial thickness $(\Delta r_h)$ (mm) | Total cross-section $(mm^2)$ | Measured cross-section | |
| | | | | | $(mm^2)$ | (% of total area) |
| 15.6 [b] | 0.198 | W | 11 | 5810 | 440 | 7.5 |
| 3.3 [c] | 0.346 | W | 19 | 17650 | 760 | 4.3 |

[a] Estimates are based on the examination of stem discs of a neighbouring tree and drill shavings obtained during the installation of the flow meters.
[b] The position divides the surface area of all needles of the tree into an almost equal upper and lower part of $218 m^2$ and $229 m^2$, respectively (Häsler et al., 1991).
[c] Basal position below the lowest branch.

average, $\Delta r_h$ made up 11% of the disc radii. The bark and the phloem $(\Delta r_b + \Delta r_p)$ on average extended over 9% of the radii. These data served to estimate $\Delta r_b + \Delta r_p$ and $\Delta r_h$ at the positions in the experimental crown where flow meters were installed. These estimates were checked while the sensors of the flow meters were being installed. The different layers of tissues below stem surface (see Fig. 1) could be localised by examining shavings as the drill penetrated them progressively. The shavings turned from brown to almost white when the drill entered the hydroactive zone, and they turned to pale yellow on reaching the hydroinactive xylem. Installing the flow meters required eight holes to be drilled within an area of 220 mm by 100 mm of stem surface (Čermák and Kučera, 1981). Two holes were located within the heated region of the stem, which corresponds to a surface area of 80 mm by 25 mm. The comparison of $\Delta r_b + \Delta r_p$ and $\Delta r_h$ within the heated region with the values measured outside of it was our basis for deciding whether the chosen measuring positions were taken as representative for the entire cross-section or not. The estimates of cross-sectional areas of hydroactive xylem and the heated parts of them, on which the presented data are based, are listed in Table 1.

The junctions of thermocouples were placed radially in the centre of hydroactive xylem where sap was assumed to flow fastest (see Čermák et al., 1992). The plate electrodes were inserted 45 mm deep into the stem to ensure that the whole radial profile of hydroactive xylem was heated. Stems were insulated for a length of 1 m around the flow meters with an inner 10 mm layer of Styrofoam and an outer 60 mm layer of glass wool with a reflecting surface of aluminium. An additional 0.8 m of the bole below this was covered with a reflecting radiation shield. This prevented the sap from being heated by solar radiation before entering the flow meters. The $q_c^0$ was determined each night as the mean input of heat between 02:00 h and 04:00 h. Parameters for the heating controller were empirically adjusted to the local range and kinetics of flow. The power of the heating was logged at 5 min intervals.

## 2.2. Stem heat balance (SHB)

In thin stems we balanced the heat by constant heating and continuously measuring its dissipation (Sakuratani, 1984; Baker and Van Bavel, 1987). Two gauges (SGB 16 and SGB 25, Dynamax Inc, Houston, TX, USA) were used; these fit stems of diameters reaching from 15 mm to 19 mm and from 24 mm to 32 mm, respectively. An insulated section of stem was constantly heated by a strip surrounding it. The heat lost from the section, in addition to the portion measured as dissipating through the insulation and along the stem, was taken up by the flowing sap. The energy of this heat, divided by the heat capacity of sap and the difference of temperature across the heater, yielded the flow:

$$Q_{sap} = \frac{P_{contr} - \left( K_{ax} A_s \dfrac{\Delta T_b - \Delta T_a}{\Delta x} + G_{ra} E \right)}{C_{sap} \Delta T_{ab}} \tag{4}$$

where $P_{const}$ is the constant input of heat into the stem (W), $K_{ax}$ is the axial thermal conductivity along the stem (W m$^{-1}$ K$^{-1}$), $A_s$ is the cross-sectional area of the stem (m$^2$), $\Delta T_b$ is the temperature difference of the axial gradient below the heater (K), $\Delta T_a$ is the temperature difference of the axial gradient above the heater (K), $\Delta x$ is the distance between each two thermocouples measuring axial gradients below and above the heater (m), $G_{ra}$ is the gauge factor representing the radial conductance of heat (W mV$^{-1}$), $E$ is the voltage of the thermopile within the insulation (mV), and $\Delta T_{ab}$ is the difference between stem temperatures above and below the heater (K).

The term in parentheses in Eq. (4) corresponds to $q_c^0 \dfrac{A_t}{A_e}$ of the THB (see Eq. (2) and Eq. (3)). In contrast to the expression for the THB, which represents the dissipation of heat at no flow only, the term in parentheses here may vary during measurements and considers dissipation also while sap flows.

To minimise bias in SHB owing to changing temperatures of the stem, foam insulations provided by the manufacturer of the gauges were placed below and above the gauges. The constant power of heating for both gauges was within the range of 4–4.5 V. It was measured using separate cables leading from the logger directly to the heater strip. Signals of the gauges were logged every 15 s and averaged over 10 min before being recorded.

### 2.2.1. Test in the laboratory

The flow of sap through thin stems was simulated in tubes of acrylic glass 15 mm and 32 mm in diameter and packed with cotton wool. The choice of cotton wool and not sawdust, as used for the THB, was made for practical reasons. Although the flow through the tubes could be finely adjusted by raising or lowering the water source, i.e. the hydraulic head, relative to them, it nevertheless was primarily determined by the saturated hydraulic conductivity of the material. By using cotton wool pressed gently into the tubes we could achieve flows similar to those found in stems. This was not practicable using sawdust. The thermal conductivity of cotton wool is nearly the same as

that of sawdust ($K_{cot. wool} = 0.04\,\mathrm{W\,m^{-1}\,K^{-1}}$, $K_{sawdust} = 0.06\,\mathrm{W\,m^{-1}\,K^{-1}}$ (Weast et al., 1985)). The $K_{ax}$ of our flow simulators was estimated to be $0.29\,\mathrm{W\,m^{-1}\,K^{-1}}$. This value was obtained from a saturated simulator with no flow through it, using the $G_{ra}$ which had been determined on a woody stem for which we assumed $K_{ax}$ to be $0.42\,\mathrm{W\,m^{-1}\,K^{-1}}$ (Van Bavel and Van Bavel, 1990). Water did not condense inside the gauges under laboratory conditions. There was good contact between the thermocouples of the gauges and the smooth tube surfaces, and it was not necessary to seal the gauges with grease (see below). The flows through the tubes measured by SHB were compared with those determined volumetrically.

In addition to the simulation experiment the flow of sap was measured in 5-year-old potted saplings of Norway spruce. They were selected so that their basal stem fitted into the gauge SGB 25. Their pots were sealed with plastic and covered with aluminium foil before being placed on an electronic balance (PM30-K, Mettler, Switzerland) which automatically recorded the loss of weight owing to transpiration while the flow of sap was determined by SHB. This was done in the same way as described for the measurement in the field (see below), except that $G_{ra}$ was determined at the end of measurement after saplings had been cut above the gauge, and not during the night because saplings then transpired under the conditions in the laboratory. The flows measured by SHB were compared with the transpiration determined gravimetrically.

### 2.2.2. Measurement in the field

The use of SHB in the experimental tree was practically restricted to straight sections of branches. We applied a thin film of silicone grease (G4, Dynamax Inc., Houston, TX, USA) before we attached a gauge. This improved the thermal contact between the heater and thermocouples of the gauge and the surface of the stem. Gauge and insulation were covered with a reflective shield of aluminium and clear plastic foil. The axial thermal conductivity of woody stems used to calculate the flow of the sap was taken from Van Bavel and Van Bavel (1990) ($K_{ax} = 0.42\,\mathrm{W\,m^{-1}\,K^{-1}}$). The factor of radial conductance $G_{ra}$ was determined each night as the mean apparent $G_{ra}$ between 02:00 h and 04:00 h when there was to be assumed no flow of sap. Table 2 describes the position and some further characteristics of the branch where the flow of sap was measured simultaneously with that lower in the crown measured by THB (see Fig. 2).

Table 2
Stem heat balance: position and characterisation of the analysed branch

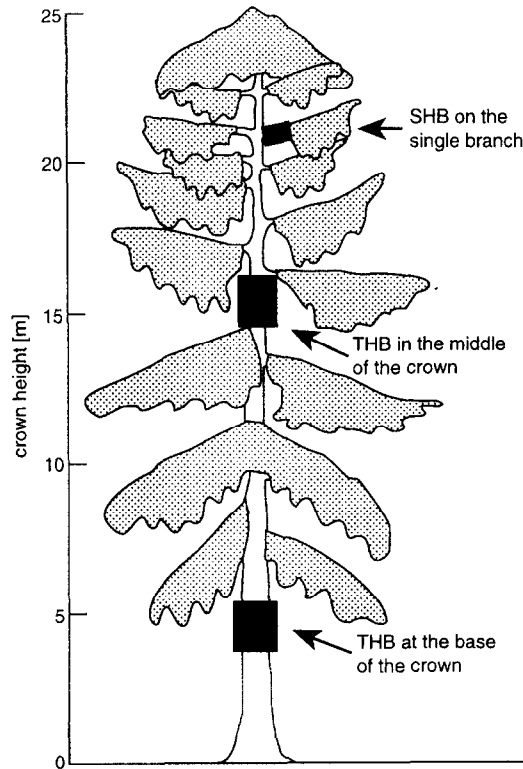| Position of measured branch | | | Branch characteristics | | | |
|---|---|---|---|---|---|---|
| Stem height (m) | Stem diameter (m) | Exposure | Branch diameter 1 m from trunk (mm) | Length of branch (m) | Needle surface area [a] | |
| | | | | | (m²) | (% of upper crown half) |
| 20.6 | 0.1 | SSW | 10 | 2 | 3.2 | 1.5 |

[a] Häsler et al. (1991).

Fig. 2. Schematic diagram of positions at which tissue heat balance (THB) and stem heat balance (SHB) were measured. (For details see Table 1 and Table 2.)

## 2.3. Gas exchange, dendrographical and environmental measurements

Stomatal conductance ($g_s$) was measured in 21 needle samples of variable age in the north- and south-facing part of the upper crown between 18 and 20 m above the ground. A gas exchange system LI-6200 (Li-Cor, Lincoln, NE, USA) which had been specially adapted for enclosing individual age classes of needles was used. Vapour flux density ($E$) was estimated using the Penman–Monteith equation (Eq. (5); Jones, 1992) under the assumptions that (1) the global radiation ($R$) measured horizontally above the tree was representative of that incident upon the needles, and (2) a constant boundary-layer conductance of needles ($g_b$) determined at the wind velocity of $1.6\,\mathrm{m\,s^{-1}}$ on a twig replica of filter paper existed:

$$E = \frac{sR + \rho_a c_p g_b \delta e}{\lambda \left[ s + \gamma \left( 1 + \dfrac{g_b}{g_s} \right) \right]} \tag{5}$$

where $s$ is the slope of saturation vapour pressure vs. temperature ($\mathrm{kPa\,K^{-1}}$), $\rho_a$ is the air density ($\mathrm{kg\,m^{-3}}$), $c_p$ is the specific heat of air ($\mathrm{J\,kg^{-1}\,K^{-1}}$), $\delta e$ is the vapour

pressure deficit (kPa), $\lambda$ is the latent heat of vaporisation ($J\,kg^{-1}$), and $\gamma$ is the psychrometer constant ($kPa\,K^{-1}$).

The continuous variation in water content of the stem was measured using a dendrograph mounted 11.8 m above the ground. The dendrograph consisted of a precision displacement transducer (TRANS-TEK, Ellington, CT, USA) on a metallic frame which was anchored 50 mm deep in the hydroinactive xylem. The measuring point contacting the stem was placed 5 mm below the bark surface to avoid bias caused by hygroscopic bark swelling or shrinking. The method has been described by Herzog et al. (1995).

Matric potentials of soil water were measured with 42 tensiometers arranged at depths of 0.1, 0.35 and 0.8 m along two transects across the rooted area. The weather was recorded at the top of a 35 m tower 15 m south of the experimental tree.

# 3. Results

## 3.1. Tissue heat balance

The results of the THB conducted within the box filled with sawdust are presented in Fig. 3, which shows the three balanced fluxes of the heat: its input, its dissipation, and the portion convected by flowing water, all in relation to that portion of heat which should have been convected according to volumetric measurements. Within the range of the measured densities of flow, the convection of heat determined by THB was at most 25% of that obtained volumetrically. This underestimation became more pronounced as flow densities approached zero.
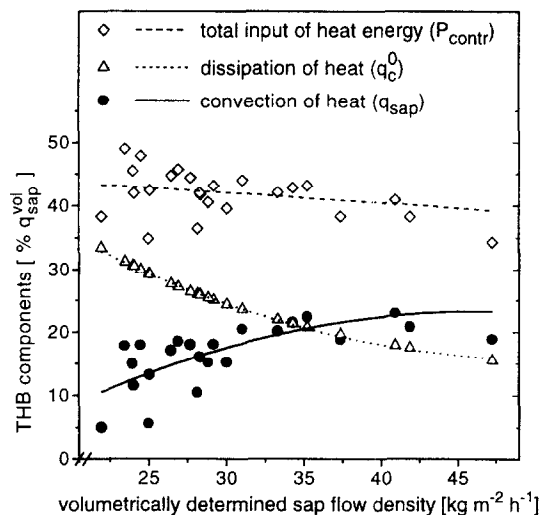


Fig. 3. Relative fluxes of heat (THB) balanced within the box of acrylic glass filled with sawdust with water flowing through it at various experimentally controlled rates. The fluxes are expressed as percentage of that convection of heat ($q_{sap}^{vol}$) which would correspond to the volumetric flow measurement.
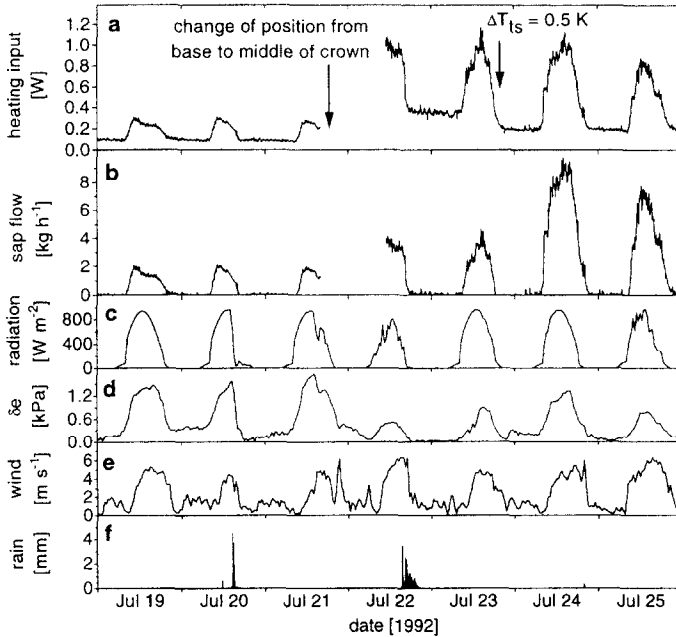
Fig. 4. (a) The input of heat into tissue heat balance measured in the tree crown at its base from 19 to 21 July and its middle from 22 to 25 July. In the late afternoon of 23 July, $\Delta T_{ts}$ was reduced from 1 to 0.5 K. (b) Diurnal variation of sap flow calculated from input of heat and $\Delta T_{ts}$. (c)–(f) Diurnal variation in global radiation, vapour pressure deficit ($\delta e$), wind velocity and rain for the same period.

Fig. 4 shows two subsequent measurements, where THB was conducted at different heights in the crown. The initial signal of heat input was measured from 19 to 21 July at the base of the crown (Fig. 4(a)). On 21 July the measuring position was changed to the middle of the crown. After the thermal steady-state at the new position had been established the measurement continued in the afternoon of 22 July. The input of heat measured in the middle of the crown was significantly larger than that measured at its
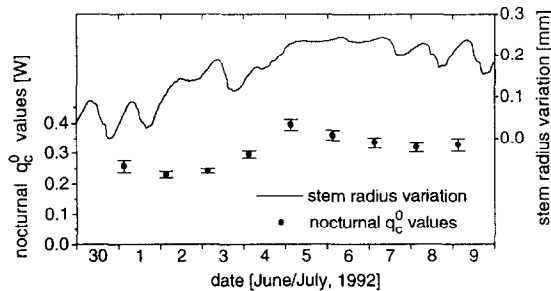


Fig. 5. Changes in $q_c^0$ (averages $\pm$ SD of 5 min readings taken between 02:00 h and 04:00 h) as the trunk resaturated after a period of dry weather. Tissue heat balance and trunk radius were measured in the middle of the crown.

Table 3
Stem heat balance: measurements of the flow of water through tubes of acrylic glass filled with cotton wool (abbreviations are explained in the text)

| Gauge type | Diameter of tube (mm) | $K_{ax}$ (W m$^{-1}$ K$^{-1}$) | Duration (h) | Mean sap flow rate $\pm$ SD [a] (kg h$^{-1}$) | Deviation from volumetric measurement (%) |
|---|---|---|---|---|---|
| SGB 16 | 15 | 0.29 | 3.2 | $0.068 \pm 0.0023$ | +6.5 |
| $G_{ra} = 0.64$ W m V$^{-1}$ | | | 7.2 | $0.056 \pm 0.0030$ | +5.0 |
| | | | 7.2 | $0.053 \pm 0.0043$ | +2.8 |
| SGB 25 | 32 | 0.29 | 4.8 | $0.161 \pm 0.0264$ | +12.6 |
| $G_{ra} = 1.57$ W m V$^{-1}$ | | | 4.7 | $0.138 \pm 0.0194$ | +11.0 |
| | | | 8.0 | $0.116 \pm 0.0308$ | +8.0 |
| | | | 7.3 | $0.102 \pm 0.0103$ | +9.8 |

[a] Measured by heat balance.

base. In the late afternoon of 23 July, $\Delta T_{ts}$ was reduced from 1 to 0.5 K. Subsequently, the nocturnal input of the heat, representing its dissipation ($q_c^0$) in absence of flow, dropped to about half of its value. The peaks of the heating at daytime, however, showed little response to the reduction of $\Delta T_{ts}$. Fig. 4(b) shows the flows of sap resulting from the measured signals of heat input given above. About twice as much flow was measured in the middle of the crown than at its base. This is not realistic for a period of several days. Further, the reduction of $\Delta T_{ts}$ caused an increase in the measured flow which cannot be explained by the weather (Fig. 4(c)–(f)).

The fluctuation of $q_c^0$ together with that of the radius of the stem is shown in Fig. 5. The data represent a period during which the weather changed from dry to wet. The resaturation of the stem was indicated by its swelling. At the same time, the nocturnal input of heat increased as a result of enhanced dissipation of it within the stem.
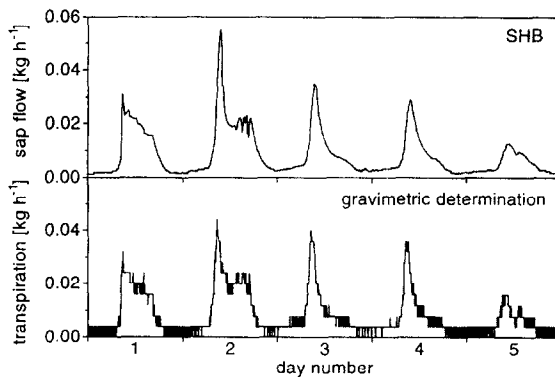


Fig. 6. Sap flow through the stem and transpiration of a potted Norway spruce sapling derived from stem heat balance (SHB) and weight respectively.
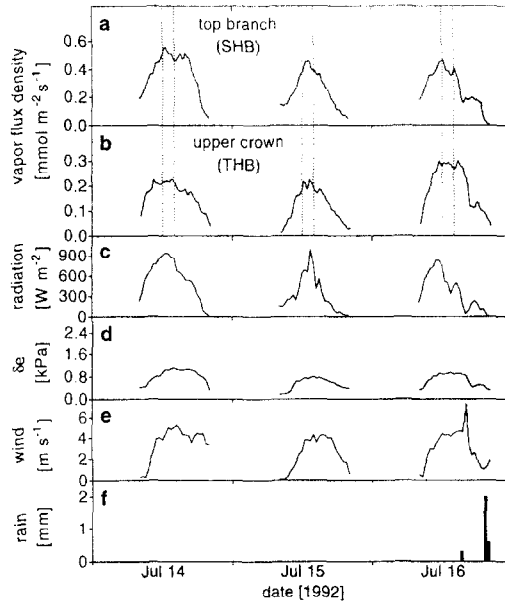
Fig. 7. Water vapour fluxes from (a) a single branch, and (b) the entire upper half of the crown for the daytime periods of 14–16 July derived from the tissue heat balance (THB) and the stem heat balance (SHB) respectively. (c)–(f) Diurnal variation in global radiation, vapour pressure deficit $(\delta e)$, wind velocity and rain for the same periods. Matric potentials of soil water were 20 kPa or greater.

## 3.2. Stem heat balance

The results of the SHB conducted within the glass tubes are listed in Table 3. Both gauges systematically overestimated the flow of water. Gauge SGB 16 measured within
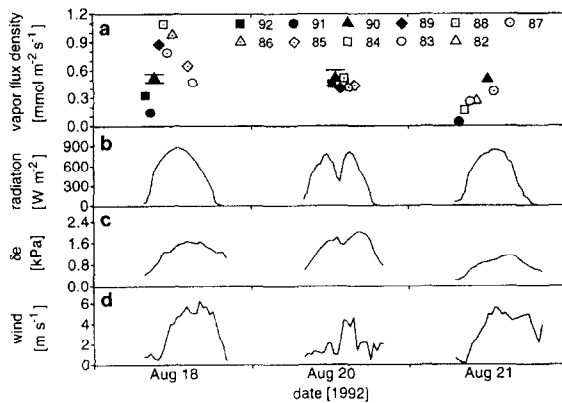


Fig. 8. (a) Water vapour fluxes from 0–10-year-old needles estimated by gas exchange in the upper half of the crown on 18, 20 and 21 August. Symbols indicate the year of needle origin. SD is shown where it is larger than the symbol. (b)–(d) Diurnal variation in global radiation, vapour pressure deficit $(\delta e)$ and wind velocity. There was no rain during these 3 days, and matric potentials of soil water were 25 kPa or greater.

an error of $+6.5\%$, whereas the other one, SGB 25, deviated by $+12.6\%$. The scatter of the results of both gauges was within $\pm 2.5\%$. The flow of sap measured at the base of the potted sapling is shown in Fig. 6. Although it is in a low range between 0 and $0.06 \, kg \, h^{-1}$, it is in good agreement with the transpiration determined gravimetrically.

In the field, SHB yielded diurnal courses of sap flow through branches which had similar kinetics to those obtained through the THB. An example is shown in Fig. 7, where for better comparability the flows of sap are expressed as fluxes of vapour through the corresponding leaf surfaces. The fluxes derived from SHB around noon reached values in the range of $0.4–0.6 \, mmol \, m^{-2} \, s^{-1}$. Those estimated by THB were about half as much. SHB results agreed better with estimates of vapour flux by gas exchange shown in Fig. 8. These reached values in the range of $0.5 \, mmol \, m^{-2} \, s^{-1}$ on 21 August when the weather was similar to that on 14–16 July, and up to $1.1 \, mmol \, m^{-2} \, s^{-1}$ when the air was drier. The different age classes of needles thus seemed to transpire fairly equally.

## 4. Discussion

### 4.1. Measurements by THB

#### 4.1.1. Non-representative measurement of $\Delta T_{ts}$

The entire heat injected into the box simulating the flow of sap was smaller than that portion of heat which should have been convected by the flow (Fig. 3). Even without the subtraction of $q_c^0$, flows would have been underestimated. Measurements made in the stem of the tree were similarly problematic. The signal of heat input measured at the base of the crown from 19 to 21 July (Fig. 4) yielded a flow which was too small to be reasonably explained. The signal from 22 to 25 July, obtained in the middle of the crown, was greater in contrast to the preceding one. Such discrepancies frequently happened and indicate the failure to measure $\Delta T_{ts}$ correctly. This may arise from a misrepresentation of the average temperature in the heated compartment by the selective measurement made by only two thermocouples.

As the flow meters were limited in their power for heating, $\Delta T_{ts}$ was kept at 1 K and was not increased. Although measurements using $\Delta T_{ts} > 1 \, K$ (e.g. Köstner et al., 1992) cannot be expected to be less prone to errors in the determination of $\Delta T_{ts}$, they might still provide a better resolution than those using $\Delta T_{ts} = 1 \, K$. However, the large deviations in our results raise questions about the temporal evolution and the distribution of the temperature within the electrically heated balancing compartment. In our approach we attributed great importance to the proper assessment of the temperature within this compartment. For this reason, we coated thermocouples leading from the tissue inside the stem to its surface with sheathings of plastic. This should have precluded the bias resulting from enhanced dissipation of heat along the sensors which would have occurred if they were metallic. Plastic covered sensors measure the temperature locally around the junction of the thermocouple. Hence, selective measurements by them depend much on the distribution of temperature. On account of the considerable thermal conductivity of wet tissue ( $K_{tissue} \approx 0.4–0.6 \, W \, m^{-1} \, K^{-1}$ (Siau, 1984)) the temperature

within the range of the sensors could be expected to be fairly evenly distributed. Nevertheless, assessing its average over the entire balancing compartment which cannot be insulated inside the stem and includes tissues of different density and thickness (Swanson, 1994) seems not to be sufficient with only two sensors. In addition, inserting the sensors causes damage of these tissues which may affect the geometry of sap flow and thus the spatial distribution of heat (see Dugas et al., 1993).

### 4.1.2. Incomplete balance of the heat

The deviation in the results from THB conducted in the simulator increased as the flow of water decreased (Fig. 3). Fig. 9 illustrates a possible mechanism. It describes the transition in the fluxes of the heat during the start of its convection by flowing water. As long as there is no flow, the input of heat is equal to its dissipation $q_c^0$. When water starts flowing the dissipation of heat, independent of the flow, would have to remain at $q_c^0$ to obtain the required linearity between the input of heat and that portion of it which is really convected by sap flow. The situation is described by the top line of the triangle in the background. If, however, the dissipation of heat decreases as its convection increases, as it is indicated by the line from $q_c^0$ to $q_c^{0\prime}$, the input of heat becomes a complicated function of both the convection and the dissipation of it. This situation is described by the top line of the curved triangle in the foreground. It means that the flow $q_{sap}^{real\prime}$, indicated in the illustration, would be underestimated by an amount corresponding to $P_{contr}^{\prime\prime} - P_{contr}^{\prime}$. The described change in dissipation would explain some of the underestimation in our result and also why this was more pronounced as the flow decreased.

Heat put into an uninsulated compartment of xylem will escape all around. When the flow of sap starts and increases, the diffuse heated volume changes its shape from a
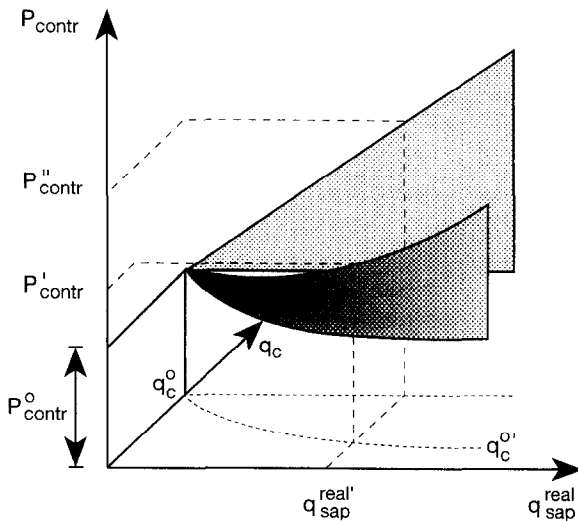


Fig. 9. Theoretical variation in balanced fluxes determined by the tissue heat balance method, showing the variation of $q_c^0$ and its effect on $P_{contr}$.

rotation- to a mirror-symmetry and is increasingly deformed towards the direction of flow. In this process the dissipation of heat, e.g. towards the base of the stem, is reduced in favour of that portion which is convected by sap. Thus, $q_c^0$ determined at no flow is not representative of the dissipation of heat during flow. Despite the constant $\Delta T_{ts}$, the dissipation—if a constant thermal conductance is assumed—would remain constant only if temperature gradients around the heated compartment were to remain so. These gradients, however, may undergo marked changes depending on flow (see Grime et al., 1995b). Accordingly, the dissipation may change also.

### 4.1.3. Vaguely defined balancing compartment

The gradients of temperature at the tangential borders of the heated compartment will become steeper as the flow of sap increases. An increasing amount of unheated sap then passes outside the heated compartment and removes heat dissipating tangentially. The resulting increase in dissipation is compensated by additional input of heat to keep $\Delta T_{ts}$ constant. Thus, heating electrodes, although their arrangement may exactly define a compartment of the cross-section $A_e$, contribute heat to sap passing in xylem adjacent to the compartment. This mechanism, illustrated in Fig. 10, might substantially affect the THB. It would help to explain the signal measured from 23 to 25 July (Fig. 4). There the nocturnal $q_c^0$ decreased to half of its value in response to halving $\Delta T_{ts}$, whereas the peaks of heating during daytime reacted little, which seems not to be explicable only by different daily transpiration owing to the weather.

### 4.1.4. Impracticable determination of $q_c^0$

A reliable value of $q_c^0$, representing the dissipation of heat at no flow, cannot be obtained at the bases of large trees. Because of the considerable capacity of adult trees to store water internally, sap within the bases of their stems keeps moving during the night. Stores from which water has been withdrawn by transpiration at daytime are then recharged (Jarvis, 1975; Herzog et al., 1994). Further, trees may also transpire at night (Herzog, 1995). To prevent the determination of $q_c^0$ from being affected by such flows, the value was determined during nights with fog when the tree did not transpire and was probably saturated with water (e.g. Köstner et al., 1992). Under such conditions, however, $q_c^0$ may drift considerably in response to a change in the conductance of heat through the stem (Fig. 5). Changes in $q_c^0$ occurred over longer periods also for no apparent reason. Factors such as the seasonal fluctuation in water content of the stem and the production of resin around the electrodes might have been involved.

### 4.2. Measurements by SHB

SHB conducted in glass tubes yielded results with slight systematic deviations. These were unlikely to have resulted from the estimated $K_{ax}$ of the simulators of sap flow $(0.29 \, W \, m^{-1} \, K^{-1})$. Although calculations reacted more sensitively to changes in $K_{ax}$ with data originating from a simulator than they did with those from a stem, in both cases a 10% uncertainty in $K_{ax}$ yielded less than 1% uncertainty in results. The calculation of the flow generally seemed to react rather insensitively to $K_{ax}$ (see Ishida et al., 1991; Dugas et al., 1993). The most probable reason for the systematic deviations
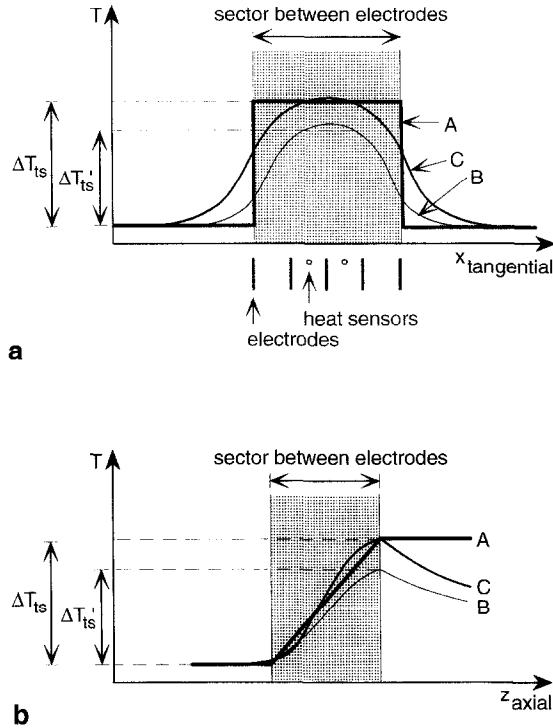
Fig. 10. Theoretical variation of temperature across the trunk compartment heated by tissue heat balance. (a) Horizontal–tangential to the trunk in correspondence to heating electrodes and thermocouples. (b) Axial up the trunk. Profile A shows the ideal case with no horizontal dissipation of heat. Profile B shows the decrease in $\Delta T_{ts}$, if the dissipation in the real case were not compensated for. Profile C shows the situation where the heating has been adjusted to ensure $\Delta T_{ts}$ remains constant.

seems to be the small thermal conductivity of acrylic glass ($K_{acrylic\ glass}$ = 0.19 W m$^{-1}$ K$^{-1}$ (Weast et al., 1985)). The walls of the tubes might therefore have hindered the heat from spreading homogeneously over the whole cross-section of the simulators. This would be substantiated by the finding that the gauge with the larger diameter showed more pronounced overestimations than that with the smaller diameter. Cohen et al. (1993) argued that an uneven distribution of the temperature might also occur across the stems of plants. However, errors resulting from this problem for thin stems seem to be tolerable in range (see also Baker and Nieber, 1989). A dependence in the deviations on flow rates cannot be detected in the results.

We found that the gauges in the field often failed to work. Possible reasons for this have been discussed by Shackel et al. (1992). However, once they did run properly there were no indications of substantial deviations in their results. Vapour fluxes from the leaves of a branch estimated by SHB (Fig. 7) were in the range of values also estimated by gas exchange in the same crown (Fig. 8: 21 August compared with 14–16 July). They might have been slightly overestimated because the leaf area of the crown may have increased since its determination. On the other hand, estimates by gas exchange

might have been a little underestimated because they were based on a constant boundary-layer conductance of the needles determined at the wind velocity of $1.6\,\mathrm{m\,s}^{-1}$, whereas the wind actually blew at up to $6\,\mathrm{m\,s}^{-1}$ above the canopy. However, such underestimation might be compensated by neglecting the mutual shading of twigs.

### 4.3. Suggestion to improve measurements by THB

An approximate procedure for correcting the heating signals measured by THB is described in Fig. 11. Two examples, taken simultaneously at the base and in the middle of the crown (Fig. 11(a)), are calculated without correction (Fig. 11(b)–(d)) and with the proposed two-step correction steps (Fig. 11(e)–(h)). The first step consists of adjusting raw signals to a reference ($q_c^{0ref}$) which standardises the systematic error arising from the non-representative measurement of $\Delta T_{ts}$. In the second step, standardised signals are
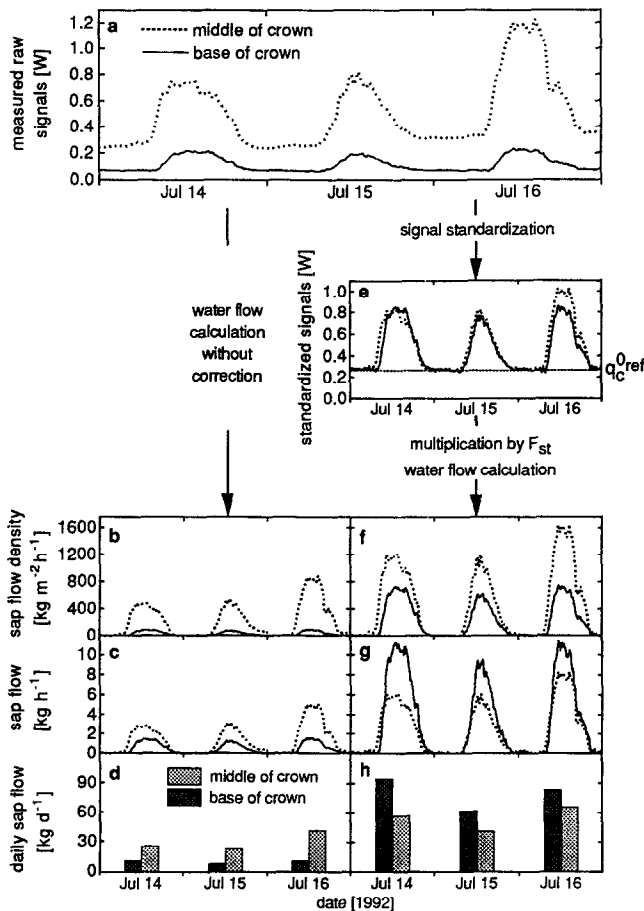


Fig. 11. Sequence of calculations of daily sap flow derived from the tissue heat balance method. (a)–(d) Using no corrections. (e)–(h) Using adjustments to $q_c^{0ref}$ and by $F_{st}$ corresponding to $q_c^{0ref}$.

multiplied by a correction factor ($F_{st}$). After these adjustments the signals allow flows of sap to be calculated according to Eq. (2).

$F_{st}$ is the factor required to obtain a proper value of the flow calculated from a signal with nocturnal input of heat $q_c^0 = q_c^{0ref}$. The $q_c^{0ref}$ thereby serves to standardise any other signal with respect to $F_{st}$. As we could not exactly determine $F_{st}$ for the measurements in the large crown, we estimated it by comparing the THB with the SHB within the crown. Densities of vapour fluxes from the entire upper half of the crown (THB) and from one major branch of it (SHB) were estimated for the days of our examples in Fig. 11 (Fig. 7). The upper part of the crown was chosen for the comparison so as to minimise errors resulting from the buffering of flows by internal stores and from the different transpiration of shaded and illuminated parts of the crown. $F_{st}$ was determined as the ratio of averaged fluxes between 12:00 h and 14:00 h of all 3 days (Fig. 7, periods marked by dotted lines). We found it to be 1.96 for $q_c^{0ref} = 0.28$ W, which is the average $q_c^0$ of the 3 days.

The correction parameters thus obtained were also used to adjust the basal signal, assuming that the thermal conductance of the stem at the base of the crown did not significantly differ from that in the middle. Flows of sap regularly resulting from adjusted signals were within a reasonable range in contrast to those calculated from raw signals (Fig. 11, bottom).

## 5. Conclusion

The quantification of the flow of sap through stems by balancing heat requires a precisely defined compartment. All conductive—and possibly also air-convective and radiative—fluxes of heat from and to this compartment must be measured. The change in temperature of the passing sap must be known and should occur homogeneously over the entire compartment. Balancing heat in an open compartment of xylem inside a stem cannot meet these requirements. Therefore, this approach yields inaccurate results unless the various errors happen to compensate each other. Although the measurements can be improved by adjusting the raw signals, an exact calibration seems impracticable because the unknown flow of the sap as well as the variable thermal conductance of the stem would have to be considered (see the approach proposed by Granier, 1985). Insulating an entire section of a thin stem (less than 25–35 mm in diameter (Swanson, 1994)) provides a compartment for which fluxes of heat can be assessed and successfully balanced. The quantification of the flow of sap then seems practicable, but only at this scale.

## Acknowledgements

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