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A New Method of Sap Flow Rate Determination in Trees

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Abstract. A new method of sap flow rate determination in stems of adult trees is described in which mass flow (the transpiration flux in the present case) is estimated from a heat-transfer measurement. The device used includes a couple of thermometers in a differential connection and plate electrodes, through which a controlled heat input flows into a defined studied segment of the xylem. The present method was tested first with a laboratory simulating system, then with the stem of a living adult tree *Prunus avium* L. The data are registered continually and automatically; continuous measurement of sap flow rate of long duration with a greater number of trees is thus made possible.

There are a number of techniques, based on various principles, that are used for sap flow rate determination in trunks of adult trees. The method of direct measurement of sap flow rate using a heat pulse is rather common; the first to use it was HUBER (1932) and among others were *e.g.* CLOSS (1957), LADEFOGED (1960, 1963), SWANSON (1962, 1967), SKAU and SWANSON 1963), REYNOLDS (1966), DOLEY and GRIEVE (1966). Even if the results obtained with the technique cannot be considered as absolutely accurate (MARSHALL 1958), they provide valuable information. For some purposes, the determination of the transpiration stream rate from the asymmetry of the temperature field appeared more feasible (VIEWEG and ZIEGLER 1960, LEYTON 1967, KARMANOV and RYABOVA 1968, ITTNER 1968 *etc.*). Mostly an active inflow of heat into the stem was used. A passive flow from the surroundings, on the other hand, was used by, *e.g.*, DAUM (1967). A special place among the methods of direct estimation of transpiration flow belongs to the use of radioisotopes (OWSTON and SMITH 1968), especially suitable for detailed studies. Individual methods suitable for the study of water relations of wood were compared by, *e.g.*, LANGE (1963, 1965), PENKA (1965), SLAVÍK and co-workers (1965), and others; with special reference to trees then by, *e.g.*, SWANSON and LEE (1966), LEYTON (1967), RUTTER (1968), and others.

Almost all the methods mentioned, serving for sap flow determination in stems of adult trees (with the exception of DAUM 1967; LEYTON 1967) give only relative values of the transpiration stream rate. Hence the aim of the present study was the development of a technique making it possible to obtain absolute data with some simpler equipment than that used above. The functional principle of the method was tested pirmarily.

Methods

From the above survey of principal methods used to determine the water relations of adult trees it may be seen that at present determinations of

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water flow in plants based on thermic principles appear to be most feasible. From their point of view the stem of a tree may be represented by a closed cylinder endowed with a capillary conductive medium, through which water flow takes place. In this connection differentiation is made between the hydroactive and hydropassive xylem. Hydroactive xylem is defined as that portion of the secondary xylem within which the transpiration stream occurs, its size approximating that of the sapwood (splint). Hydropassive xylem is defined as that portion of the secondary xylem within which there is no transpiration stream, its size approaching that of heartwood (duramen). In view of the fact that the flow of water through the hydropassive xylem is considered as quantitatively negligible, only the annual rings of hydroactive xylem are considered as conducting medium. This conducting medium may be divided in any definite height range into an arbitrary number of segments of known dimensions. In one of these segments (or in several of them, as the case may be) the transpiration flow rate is determined (Fig. 1).

A uniform and controlled heat input Q, measured in watts, is directed to the segment. Whenever a constant amount of water (M) flows through the segment, with a constant heat input its temperature will reach a definite steady value. The temperature will be inversely proportional to the water flow (Fig. 2). Validity of this relation presupposes that losses of heat from the segment by convection are negligible. The temperature of water flowing into the segment (T_1) is increased by the heat supplied to a value T_2. The difference between the two temperatures (ΔT) is related to the heat input Q and to the water flow rate according to

$$Q = M \,.\, \Delta T \,.\, \mathrm{c} \qquad [\mathrm{W}], \tag{1}$$

where Q = heat input directed to the segment,
M = transpiration flow rate [kg s^{-1}],
ΔT = difference of temperatures at the entry and the exit of the segment [K],
c = specific heat of water [J kg^{-1} K^{-1}].

Under ideal conditions (when heat losses are negligible) it holds that the heat input carried out of the segment by transpiration flow is equal to the electrical output (P), hence $P = Q$. In reality, however, the amount of heat taken away by the transpiration flow is lower than the amount of heat supplied, a part of heat disappearing by convection to the surroundings. The thermal balance of the segment is then the following:

$$Q = P - \Sigma Q_{ii}$$

where Q_{ii} = the heat lost from the segment by convection. Heat losses in the segment considered occur both in the vertical and in the horizontal direction:

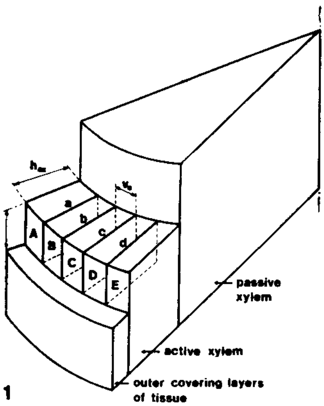
$$Q = P - (Q_{ap} + Q_{bas} + Q_{px} + Q_{fc} + Q_{t}) \tag{3}$$

where Q = heat input into the segment,
P = heat input corresponding to the electrical output.

In parentheses heat losses from the segment are collected:

Q_{ap} = heat lost by convection in the direction of the transpiration flow,
Q_{bas} = heat convected against the transpiration flow,
Q_{px} = heat transported into the passive xylem,
Q_{fc} = heat transported into layers outside the cambium (phloem, pericycle, primary and secondary cortex),
Q_t = heat transported into neighbouring segments of the hydroactive xylem.

The above equation is simplified, only the most important factors being included. Thus, *e.g.*, the loss of heat input in the medium is not considered,



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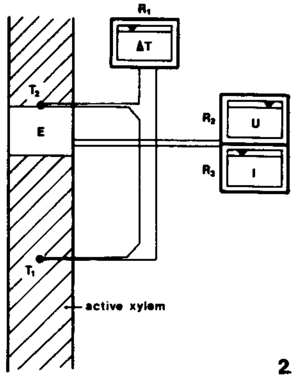

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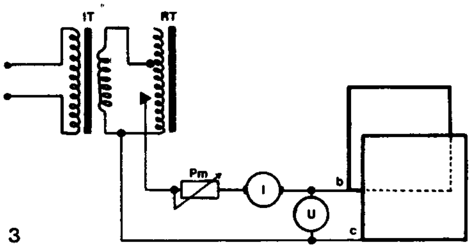
Fig. 1. The geometry of an active xylem segment chosen to determine the flow of water, schematically. Capital letters: individual segments of active xylem of the same width (v_e) corresponding to the distance between plate electrodes inserted. Small letters indicate individual plates, separating the segments. 1 = height of electrodes, h_{ax} = thickness of the active xylem.
Fig. 2. The circuit with plate electrodes and thermometers in the active xylem, schematically. R_1, R_2, R_3 recorders (for temperature difference ΔT, and current voltage U respectively, E = plate electrodes, T_1, T_2 = thermometers.

especially the fact that heat is dissipated not only in the space between the electrodes, the electrical field extending beyond this space. This loss of input, however, may be estimated with considerable accuracy as long as the material is homogeneous. Temperature changes resulting due to the thermal conductivity of the electrodes and temperature measuring probes were not taken into account either.

Heat losses in the vertical direction (Q_{ap} and Q_{bas}) must be considered when temperature measuring probes are being placed in the surroundings of the segment. The thermometer registering the temperature of xylem at the entry into the segment must be localized outside the influence of the temperature field near the segment. The thermometer registering the temperature at the exit of the segment, on the other hand, is to be placed at the maximum of the temperature field of the segment. With the transpiration flow rate higher than zero the maximum of the segment temperature belongs to the segment edge in the direction of the flow (Figs. 2 and 6). With higher rates of transpiration flow the heat losses in the vertical direction are of little significance. The situation is different with the losses of heat in the horizontal direction (*i.e.*, radial and tangential direction). The losses in the radial direction are less important than those in the tangential direction. The outer protecting layers and the hydropassive xylem contain a smaller fraction of mobile water than the hydroactive xylem and for this reason are more heat-stable. When the water flow is steady the two tissue systems act basically as passive thermal insulators which, on the one hand, reduce the



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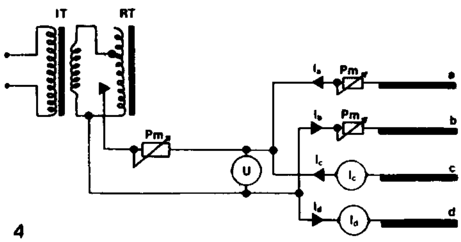

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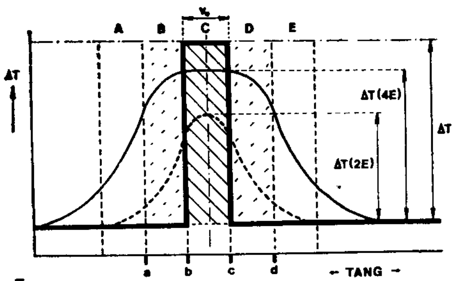
Figs 3 and 4. Circuit diagram when two Fig. (3) or four Fig. (4) plates are used. *IT* = isolating transformer, *RT* = regulating autotransformer, *Pm* = potentiometer, *I*, *U* = current and voltage meters, *a*, *b*, *c*, *d* = individual plate electrodes, I_a, I_b, I_c, I_d = individual currents towards corresponding electrodes.

heat loss from the segment, but on the other limit the influence of temperature changes in the proximity of the tree trunk. The situation is somewhat complicated by the presence of basipetal assimilation flow. Its rate, however, is so low when compared with the transpiration flow rate that it was neglected in the present study. Quite different is the situation with heat losses in the tangential direction, occuring in the system which contains a relatively great fraction of mobile water and hence is considerably more hest-labile. The heat losses in the tangential direction are higher than those in the radial direction. The magnitude of these losses depends on the segment width and changes with the rate of the transpiration flow. The importance of all heat losses considered and hence also the positive systematic error in the determination of the transpiration flow rate in the hydroactive xylem decreases when the transpiration flow rate increases. As may be seen from relationship (1), the accuracy of the determination depends also on the specific heat of water in the transpiration flow. Its value for distilled water (15 °C) is 4 186.8 J kg^{-1} K^{-1}. Under the given conditions, however, it is somewhat different due to the presence of salts and other substances and changes following the dynamics of these values. However, in view of the present accuracy of the method the absolute value of this deviation is relatively small and hence was neglected.

The device for transpiration flow measurement in the active xylem is composed firstly of plate electrodes through which a controlled heat input is injected into the segment, secondly of thermometers registering temperature inside and outside the segment. To measure the electrical output, supplying heat to the segment, the circuit shown in Fig. 3 was used as a fundamental two-electrode variant. The electrical output together with correction for losses due to measuring instruments equals



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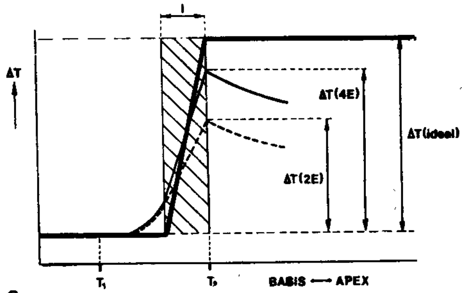

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Fig. 5. Temperature relations near to the measured segment of active xylem in horizontal direction. Segments and electrodes indicated in the same way as in Fig. 1. Abscissa corresponds to the plane tangential to tree trunk at the site of measurement and distances between individual electrodes are shown. Ordinate shows the temperature measured inside the active xylem (actually, the difference of temperatures measured in the plane of upper electrode edges, *i.e.* between the maximum temperature and that under the heated layer of the active xylem). In the striped segment the flow is measured, dotted parts correspond to neighbouring heated segments. Dash-and-dot line indicates the maximum level that may be reached by the temperature at a given heat input and a given constant flow. Thick solid line represents the ideal temperature pattern, corresponding to the situation in which no heat losses due to thermal conductivity occur. Dashed line shows the thermal relations in xylem when two electrodes (*2E*) are used according to the scheme in Fig. 3. The values of $\Delta T(2E)$ are then recorded. Solid line shows the same relations when four electrodes (*4E*) are used according to the scheme in Fig. 4; the values of $\Delta T(4E)$ are recorded. The difference $\Delta T(4E) - \Delta T(2E)$ represents the tangential losses of heat eliminated by the active thermal insulation of the segment. The ideal state corresponds to ΔT(ideal).
Fig. 6. Thermal relations in vertical direction near the active xylem segment measured.

$$P = U \,.\, I - \frac{U^2}{R_v} \tag{4}$$

(Units: W, V, A; R_v = voltmeter input resistance [Ω]).

When of four-electrode system is used (Fig. 4), the following relations apply

$$I_a + I_c = I_b + I_d \tag{5}$$

$$I_{bc} = I_b - I_a = I_c - I_d \tag{6}$$

As it is necessary to estimate the losses of input in the segment (Fig. 1, segment *C*) from the current passing through the segment (I_{bc}), measurement of currents I_c and I_d was used for the purpose. The electrical output

$$P_c = U(I_c - I)_d - R_c I_c (I_c - I_d) \tag{7}$$

where R_c = resistance of the ammeter measuring I_c. (The second term on the right-hand side represents losses in the measuring instruments.)

The above circuitry complies almost perfectly with the condition of Daum (1967) which postulates absolutely uniform distribution of heat on the segment surface. Moreover, there is the advantage of an active heat supply, due to which the sensitivity of the method is independent of thermal conditions outside the tree trunk, provided that the segment measured is thermally well insulated from the outside. The segment is thus heated directly by an ohmic resistance (Joulean heat), as a result of current passage between two electrodes, separated from earth and limiting the segment. The advantage of the method used rests in a uniform heating of the whole mass of the segment and in the possibility of a more accurate heat balance with heated space more accurately defined. Disturbances due to electrolytic processes were eliminated using alternating current (50 Hz).

The mass flow (water of the transpiration flow) is determined from equation (1) which, in view of the circuits used and of the instrument characteristics [*cf.* equations (4) to (7)], as well as of the dimensions of the segment studies is of the form

$$m_{id} = \frac{60P_c}{\Delta T_a k_d c_j S_s} \tag{8}$$

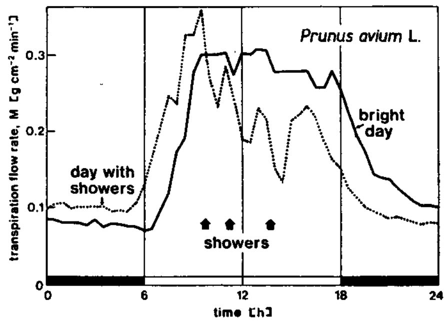
where m_{id} = specific transpiration flow through the active xylem assuming no heat losses from the segment [g cm^{-2} min^{-1}],
P_c = heat input supplied to the segment [see equation (7)],
ΔT_d = the difference of temperatures in the active xylem, measured at the point of the temperature field maximum and outside the field, estimated with a defined temperature probe (in scale units of the recorder used at a given sensitivity),
k_d = coefficient transforming the above units to kelvins, K (or degrees Celsius, °C),
c_j = specific heat of water [J kg^{-1} K^{-1}],
S_s = segment area exposed to the flow [cm^2].

The relationship derived is valid under steady conditions and in steady state (*i.e.*, no value changes, in theory for unlimited time. Under real conditions, espcially when water flow or input supplied changes, transient phenomena will occur, influencing temperature stability of the medium. No heat losses are included in the relationship. These losses are limited by using special technical equipment. Heat losses in the radial direction are limited due to a passive thermal insulation of the trunk and screening against the radiation heat, which eliminates also disturbances originating in the bottom parts of the trunk, leading to anomalies in records when flow is suddenly enhanced, especially in morning hours. Losses in the tangential direction are eliminated using an active thermal insulation. The two lateral sides of the segment in which the flow is determined are heated to the same temperature which prevails in its centre. The temperature gradient between the measured segment of xylem and the neighbouring xylem and hence also heat losses in this direction are annulled (Figs. 5 and 6). The above limitation of heat losses from the segment makes the determination of the transpiration flow considerably more accurate. Still, the results include errors resulting from residual heat losses, which were neither eliminated technically, nor included in the calculation [equation (3)].

Materials

The present method was originally tested using an artificial dendrosimulator in a laboratory, in which the active xylem was modelled by glass beads or balsa wood and only after confirming the theoretical assumptions applied to a living tree. Measurement with simulators was concentrated on the range of small flows near the limits of the sensitivity of the method 0.00 to 0.15 g cm^{-2} min^{-1}). The flow through a simulator was determined both by the calculation from

Fig. 7. A circadian record of water flow through the active xylem in the adult *Prunus avium* L. (Continuous record of the data as evaluated for half-hour intervals.) The given values of the transpiration flow rate calculated according to equation (*8*) asm ideal include the error resulting from the temperature difference ΔT (ideal) $\Delta t(4E)$, according to Figs. 5a and 6.



measured temperature values and volumetrically. Temperature was measured using thermocouples of copper-constantan (Cu-Cst), placed in waterproof envelopes in holes of 1 mm diameter. Electrical data were registered using the potentiometric recorder EZ-4 (Laboratorní přístroje, Praha) and the three-channel device ZiRg-320 (Metra, Blansko). Electrodes were prepared from stainless steel plates 0.9 mm thick.

An adult tree *Prunus avium* L., growing in the arboretum of Agricultural University in Brno, 6 m high and 20 cm ($d_{1,3m}$) thick was chosen for field measurement. Detectors (four plate electrodes and two thermometers) were placed 1.3 m high on the north side of the tree. The whole basis of the trunk to the detectors was screened with aluminium foil and, near the probes, it was insulated with a 50 mm thick layer of polyurethane foam. The recorders were placed in a field laboratory about 10 m away from the tree.

Results

When measuring with a simulator, a high correlation between the actual and the calculated flow was found ($r = 0.980$). The response time of the recorder to greater changes in flow was about 10 s. The limit of sensitivity with the simulator described was found to be at the specific flow of 0.03 g cm^{-2} min^{-1}.

Measurements carried out with the living tree showed that in the main respects the tree and the simulator are comparable. Results of transpiration flow rate measurements (carried out for about 1 000 h) are represented by an example of the record, prepared during a bright day and during a day with showers (Fig. 7). The flow during the bright day was at its minimum in the early morning hours; after sunrise (illumination of the tree top) it increased rapidly and after some three hours it reached a relatively stable diurnal value. Smaller fluctuation of the flow may be explained due to short periods of shade due to a sporadic presence of clouds. Transpiration flow rate at the height of 1.3 m from the ground (about 0.5 m from the base of the tree crown) was relatively steady during the whole period of the bright part of the day (when the tree crown was illuminated). During the whole time in which the observations were carried out neither noon depression nor another pronounced fluctuation in the flow rate were observed, with the exception of a morning rise and an evening fall. The fall in the rate of the transpiration flow starts continually after sunset. It is, however, less rapid than the morning increase and continues during the night till the morning minimum. There are interesting changes in the transpiration flow rate which occur in the midst of a hot summer day, during which showers repeatedly took place. Each of these showers was followed by a rapid fall in the intensity of the transpiration flow and by another increase when the rain stopped. A general decrease in the transpiration flow rate, however, persists, obviously due to increased air humidity.

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Byla navržena nová metoda stanovení vedení vody v kmeni adultních stromů, založená na principu měření hmotného toku (transpiračního proudu) na základě přenosu tepla. Zařízení se skládá z dvojice diferenciálně zapojených teploměrů a deskových elektrod, kterými je přiváděn kontrolovaný tepelný výkon do zkoumané části aktivního xylemu (definovaného segmentu). Navržená metoda byla vyzkoušena na simulátoru v laboratorních podmínkách a na kmeni živého adultního stromu *Prunus avium* L. Data jsou plně automaticky a kontinuálně registrována: to umožňuje kontinuální sledování intensity transpiračního proudu po dlouhá časová údobí simultáně u většího počtu stromů.