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Improved Thermal Method of Continual Recording the Transpiration Flow Rate Dynamics

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Abstract. The analysis of the dynamic properties of thermal methods of transpiration flow measurement was performed and the measuring system developed, capable of quantitative measurements of fast flow changes (in minutes). The system is specified with a constant automatically maintained temperature difference between the heated and reference points in the measured part of the plant. System's output signal related to measured quantity is linear. The system has been under longterm testing in full grown trees using the method of heat balance with direct electric heating of the xylem. The results obtained so far may be considered very good.

In studying the plant-water relations in more detail, problems are of necessity encountered at a certain stage of work, which are associated with the dynamics of measurement — response of the measuring system's output signal to fast changes in the transpiration flow rate. In the thermal methods which permit continual measurement of the flow the variations in temperature due to the water flow in the heated part of a plant are largely taken as a basis for the flow rate calculation. However, the speed of temperature changes becomes limited owing to the heat inertia of the plant tissue and its contained water. This phenomenon becomes of special importance when the measurements are made in large trunks of full-grown trees. The problem has been discussed in more detail on the example of the heat balance method with direct electric heating of the xylem, initially developed by us for the transpiration flow rate measurement in full-grown trees (Čermák *et al.* 1973, 1976, Penka *et al.* 1973, Čermák and Deml 1972–74). (In that case the transpiration flow was measured in the segment of hydroactive xylem. The size of the segment was delimited by plate electrodes connected to a source of electric current.)

Theoretical

On the assumption of a homogenous heat field in the measured segment the fundamental differential equation for heat balance at the measuring block may be written

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$$P - Q_w c_w (T_s - T_e) = (m_w c_w + m_x c_x) \frac{dT}{dt} + \lambda (T_s - T_e) \tag{1}$$

where P = heat input to measured segment of xylem, [W]
Q_w = sap flow rate, [kg s^{-1}]
c_w = specific heat of sap, taken as water, [W s $grad^{-1}$ kg^{-1}]
c_x = specific heat of xylem, [W s $grad^{-1}$ kg^{-1}]
m_w = mass of water in measured segment, [kg]
m_x = mass of dry xylem in measured segment, [kg]
λ = coefficient of heat transfer from measured segment to its environment, [W s $grad^{-1}$]
T_s = temperature of water in measured segment, [K]
T_e = temperature of environment and of water entering the measured point, [K]
t = time, [s]

Solution of the differential equation (1) gives the temperature difference relation of $\Delta T = T_s - T_e$, in the form of

$$\Delta T = \frac{P}{Q_w c_w + \lambda} \left[1 - exp\left(-\frac{t(Q_w c_w + \lambda)}{m_w c_w + m_x c_x}\right)\right] \tag{2}$$

Assuming the heat input P and the flow rate Q_w to be constants, diagrammatic representation of the above equation will be exponential and, under condition of a steady state, limiting to a value of

$$\Delta T_0 = \frac{P}{Q_w c_w + \lambda} \tag{3}$$

with a time constant of

$$\tau = \frac{m_w c_w + m_x c_x}{Q_w c_w + \lambda} \tag{4}$$

From equation (3) we can derive the basic relation for the calculation of transpiration flow rate, in the form of

$$Q_w = \frac{1}{\Delta T_0} \cdot \frac{P}{c_w} - \frac{\lambda}{c_w} \tag{5}$$

On the assumption of a constant heat input, hyperbolic dependence of the measured temperature difference on the flow rate is clearly evident from this relation. In practice, this means that, with existing arrangements, the maximum flow rate coincides with the minimum value of temperature difference, which is not very convenient in view of the sensitivity of the measuring apparatuses used, especially so when a maximum value of the ΔT is to be kept within physiologically acceptable limits.

Limitation of the dynamics of measurement owing to heat inertia can be estimated from equation (4) for the time constant of the plant's measured part. According to that equation and following the physical concept, the time constant increases with increasing mass of the plant's heated part and conversely, it decreases with the flow rate Q_w. The results of measurement obtained so far using this method of heat balance have indicated the time constant value, τ, at zero flow rate (night time for instance) to be about 45 min. This value decreases with the flow rate increasing at the same rate as the ΔT_0 does; thus, under favourable weather conditions in the day time, it is some 5–10 min. Having accepted the assumption that the measuring system is capable of transferring the harmonic input signal whose period is 5 times as much as the system's time constant at a sufficient level of reliability, *i.e.* at 2% amplitude error and 3% phase error, it will mean that the ΔT quantity will not follow differential variations in the flow rate within the zone of its maximum values without any noticeable distortion until the periods have attained about half an hour, while within the zone of its minimum values — until the period has reached 4 h. A striking example of the time constant influence is seen in the ΔT response to the jump change in transpiration flow rate from a maximum to values approximating zero (for instance a thunderstorm at noon time in summer). In this instance the temperature difference will be decreasing exponentially according to equation (2), and the value corresponding to zero flow rate will not be approximated, with an error of 3 per cent, until after a time lag of 2.5 h. Since data reported in the literature (Sheriff 1972, 1974, a.o.) suggest that the changes in transpiration flow rate are substantially faster even in tree trunks than the dynamic parameters indicated by the method discussed above permit, it should be stated that the method in question presumably involves distortion of the record of fast changes in the transpiration flow rate.

Some improvement might be expected from reduction of the mass (m) to be heated, according to equation (4), which would result in diminishing the time constant magnitude, τ. However, this is possible solely by reducing the size of the measured xylem segment whose minimum dimensions are limited. When the mentioned method of heat balance is employed, specifically, depth is limited by the requirement of covering all of the inflow active profile; thickness is limited by ratio of the xylem segment profile portion damaged by the electrodes to the segment volume; and height is limited by the requirement of a maximum homogeneity attainable in the heat field necessary for accurate calculations according to equation (1).

Similar conclusions could be drawn from analyses of the greater part of methods hitherto reported in which continual measurement of the transpiration flow rate has been based on thermal principles (Zinsmeister and Dixon 1966, Daum 1967, Pickard and Puccia 1972, a.o.).

An efficient way of eliminating the influence of heat inertia in heated masses follows from equation (2). Formal simplification of the equation is possible by substituting equations (3, 4) into the form of

$$\Delta T = \Delta T_0 \left[1 - exp\left(-\frac{t}{\tau}\right)\right] \qquad (6)$$

From this expression it is evident that the member in square brackets becomes operative more expressly solely during a transition action, *i.e.* immediately following the ΔT_0 change when $t \leq \tau$. For $t \gg \tau$ this member tends to converge, and it holds that

$$\Delta T = \Delta T_0 .$$

In other words, with the temperature difference value remaining unchanged, the time constant τ fails to operate, too. Thus, the condition for eliminating influence of the time constant τ may be formulated as follows:

$$\Delta T_0 = \frac{P}{Q_w c_w + \lambda} = \text{constant} \tag{7}$$

The requirement for satisfying this condition invariably determines the relation between the independent variable — flow rate — and the heat input, in the form of

$$P = \Delta T_0(Q_w c_w + \lambda) \tag{8}$$

If the heat input P is controlled so that equation (7) is satisfied with any value of the flow rate Q_w, the heat input will be a linear function of the flow rate even with its arbitrarily fast changes. It therefore follows that the measurement requires the incorporation of a special regulating circuit to automatically control the input for heating, to the end that the temperature difference in the measured block remains constant.

Practical

A special regulating circuit has been developed and constructed to realize the condition of constant temperature difference. Its block-schematic diagram is shown in Fig. 1.

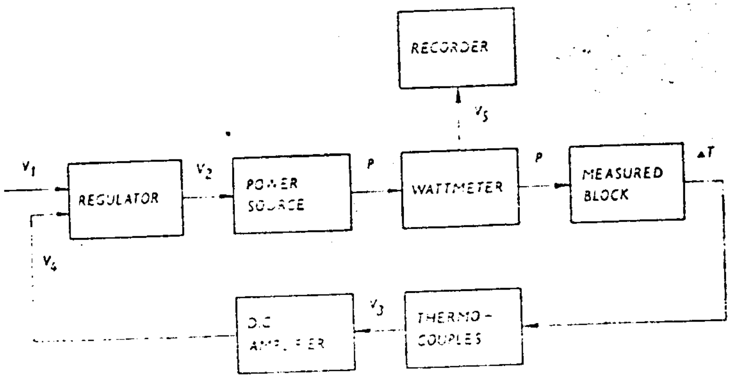


Fig. 1. The block-diagram of the regulating circuit. U_1 = voltage corresponding to required ΔT value, U_2 = output voltage of the regulator, P = electric input to heat the measured block, U_5 = output voltage of the W-meter, ΔT = temperature difference, U_3 = voltage of the thermocouples, U_4 = amplified voltage of the thermocouples.

In the regulator of this measuring system the voltage proportional to the required ΔT value is compared to amplified voltage from the thermocouples located in the measured block. The power-source output to heat the measured block is controlled by amplified difference between the voltages. The power source is constructed as a sinus oscillator provided by a voltage-controlled amplitude, and a 10 W amplifier is added. The oscillator frequency selected in our case was 1.5 kHz, high enough to eliminate potential electrochemical action on the xylem. The power-source output supplied to the measured block is recorded using an electronic W-meter of our own design, and registration occurs in a line recorder. The regulation result is zero difference between the voltage of required value and the amplified voltage from the thermocouples, which is directly proportional to ΔT values. The electric input P into the segment displays automatic alterations, linear with the flow rate Q_w, which provides for direct gauging of the recorder scale with respect to the given measured block (for instance in kg.h^{-1}). When evaluating the record, it is of course, necessary to subtract the $\frac{\lambda}{c_w}$ value following equation (5). Equation (5) can also be transformed to the instructive form, more suitable for practical use

$$Q_w = Q_w^{\text{rec}} - Q_w^{\text{fic}} \tag{9}$$

where Q_w^{rec} = the recorded value of transpiration flow rate (without correction on heat losses from the segment),

Q_w^{fic} = the fictive value of transpiration flow rate, representing the heat losses from the segment when the flow rate is approximating zero — than $Q_w^{\text{fic}} \doteq Q_w^{\text{rec}}$. This value can be used as the index of segment water content, too.

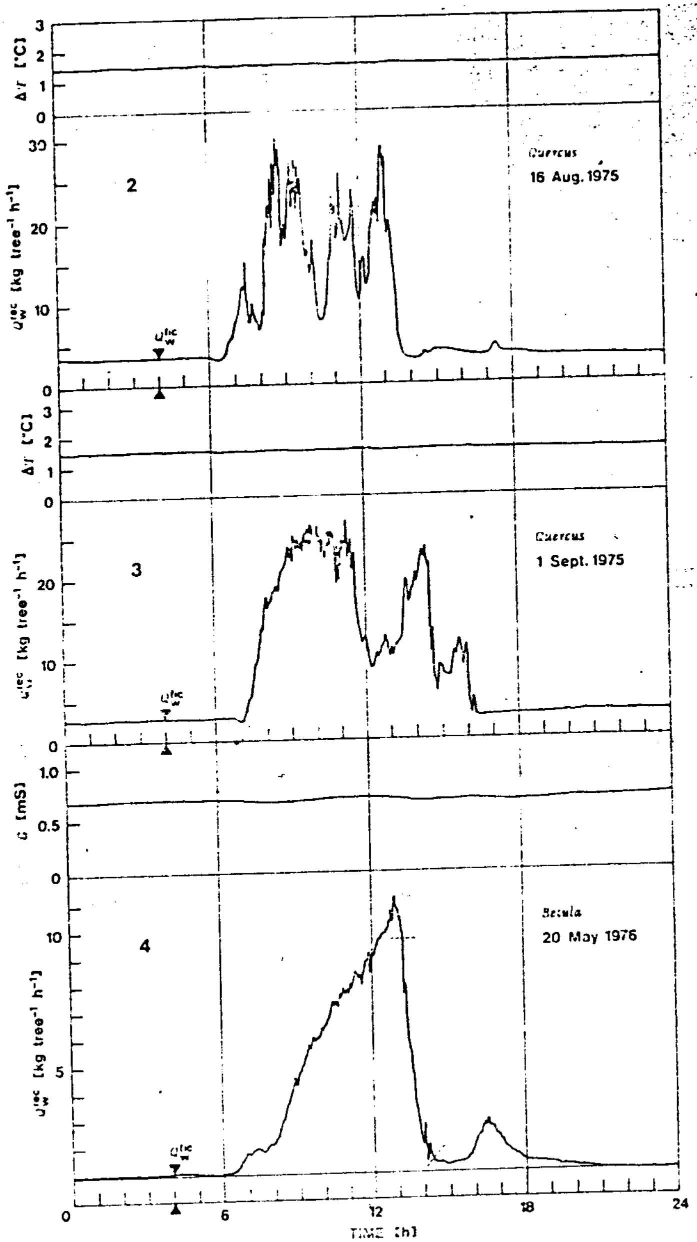
The measuring system described here has been tested in the field over two years on full-grown individuals of several tree species.

Results and Discussion

The dynamic properties of measurement are now no more given by magnitude of the time constant τ, but rather by quality of the operation in the regulating circuit as the result of the design of transmission constants attained in the regulator used. However, the methodological aspects of this regulator-circuit system, and its design, are beyond the scope of our paper. An analytical determination of the limiting frequency of changes in the flow rate Q_w, at which correct results are still obtained in the measuring system output, is rather complicated when considered from the viewpoint of the theory of regulation, requiring modelling in the computer; this, for the time being, has not been undertaken. Nevertheless, from the frequency characteristic obtained for the proposed regulation circuit it may be concluded that the system is capable of responding to changes in the flow rate which occur within one-minute intervals.

The record of the transpiration flow rate as obtained by measurement in the trunk bases of full-grown trees, and of another record of ΔT values, both made during one day under unstable weather conditions (Figs. 2, 3, 4), can illustrate what fast changes in the transpiration flow rate the apparatus described here is able to cover. Thus, with the Q_w increasing or decreasing, the values of flow acceleration Q_w/dt recorded were approximately of about 3—4 kg.tree^{-1} h^{-1} min^{-1} in birch and of about 7—9 kg tree^{-1} h^{-1} min^{-1} in oak. It therefore follows that two independent measurements of the transpiration flow rate with one-minute differences in the time scale can differ in the Q_w values by as much as 25—35 per cent approximately in both species. Indeed, still higher factual maximum values may be attained.

In this connection the question arises, 'What factual rates of the transpiration flow change can actually be expected to occur in the various parts



Figs. 2 and 3. Diurnal records of the transpiration flow rate (Q_w) in a full-grown oak tree (*Quercus sessilis* EHRH.) over two days characterized by changeable cloudiness and occasional showers. Axis x — time [h] has been plotted; axis y — (bottom) flow values Q_w^{rec} [kg tree^{-1} h^{-1}]; (top) temperature difference values in the measured point, ΔT [K]. The time of recording and the value of so-called fictive flow, Q_w^{fic}, have been marked in the diagram, the latter corresponding to the heat loss from the tree trunk segment under measurement. When reading actual values of trees irrespective of the method of registration'. The determining parameters of environment (such as solar radiation temperature, humidity, wind force, and other factors) influence the movement of the transpiration flow rate largely through variations in the leaf water potential and leaf surface — air temperature difference. The fastest changes in the transpiration flow rate observed directly in the leaves or shoots of plants (whether produced by the given environmental conditions or by internal oscillations of the water-conducting system), provided the measurements are made with an apparatus in which inertia of the response rate may be assumed as zero (SHERIFF 1972, 1974, SHERIFF and SINCLAIR 1973), roughly cover minute intervals (corresponding to the order of about 10^{-2} Hz). Similar frequencies of changes have also been established for the resistance of plant leaves (FARQUHAR and COWAN 1974, MEDERSKI *et al.* 1975, a.o.); for leaf temperatures (PERTTU 1971, a.o.); for stomatal responses to variations in humidity (LANGE *et al.* 1971, a.o.). These data suggest that no faster changes in the transpiration flow rate than those indicated above practically occur in plants.

The question has not been discussed as yet in more detail of how the plant structure characteristics affect the behaviour of the *TFR* changes, particularly those occurring in the parts of plants that are distant from the leaves (for instance at the base of a full-grown tree). In such cases, inertia of the water-conducting system may be expected to become more operative, due to its pertinent resistances and capacities acting as a low-frequency valve. In addition to this inertia of the water-conducting system also the averaging influence of a larger number of the xylem's conducting elements will be involved, *i.e.* the mean flow rate will be measured in selected segment. It corresponds to the resultant behaviour of a large number of the leaves in the various parts of the tree-crown (under the conditions given by application of the above method, some 2 to 20 m² of leaf blade surface will be concerned). Analyses of these questions will become the object of our further studies.

The new measuring system described in this paper, which has been tested under the conditions of a longterm operation, is a qualitative jump in the uses of thermal methods concerning the studies of fast (in min) Q_w changes. The simple mode of evaluating the measured values is another advantage not to be neglected; for after gauging the recorder scale (establishment of the constants) for a given measuring block, no further calculation of the data is required. Moreover, the reduction of heat action as exercised on plant tissues is the system's quality on the credit side, too. It is noteworthy that the initial method of ours and the one described here both give quantitatively

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of the transpiration flow rate, Q_w, from the record, this value is to be subtracted from recorded ones, Q_w^{rec}, according to relation $Q_w = Q_w^{rec} - Q_w^{fic}$. The latter value is utilizable also as the index of segment water content.

Fig. 4. Diurnal record of the transpiration flow rate (Q_w) in a full-grown birch tree (*Betula alba* L.) during the day characterized by heavy shower. For description see Figs. 2 and 3. The ΔT plot on axis y (top) has been replaced by the record of electric conductivity in the tree trunk segment, G [mS]. The shower initiation and termination points are designated by marking lines on the curve.

identical results when longer time intervals (for instance one day) are concerned.

It follows from practical applications of the results obtained so far that, among other things, caution is necessary in assessing ambulant measurement of similarly variable parameters in the plant-to-water relations where factual, comparable differences in the values found during the short term interval might be wrongly interpreted as an error due to the measuring.

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References

Čermák, J., Deml, M.: [Measuring water transport in woody plants, mainly in adult trees.] In Czech. — Czechoslovak Patent No. 155 622. Praha 1972—74.

Čermák, J., Deml, M., Penka, M.: A new method of sap flow rate determination in trees. — Biol. Plant. 15 : 171—178, 1973.

Čermák, J., Kučera, J., Penka, M.: Improvent of the method of sap flow rate determination in full-grown trees based on heat balance with direct electric heating of xylem. — Biol. Plant. 18 : 105—110, 1976.

Daum, C. R.: A method for determining water transport in trees. — Ecology 48 : 425—431, 1967.

Farquhar, G. D., Cowan, I. R.: Oscillations in stomatal conductance. The influence of environmental gain. — Plant Physiol. 54 : 769—772, 1974.

Lange, O. L., Lösch, R., Schulze, E. D., Kappen, L.: Response of stomata to changes in humidity. — Planta 100 : 76—86, 1971.

Maderski, H. J., Curry, R. B., Chen, L. H.: Effects of irradiance and leaf water deficit on net carbon dioxide assimilation and mesophyll and transport resistances. — Plant Physiol. 55 : 594—597, 1975.

Penka, M., Čermák, J., Deml, M.: Water transport estimates in adult trees based on measurements of heat transfer by mass flow. — Acta Univ. Agr. (Brno) Ser. C, 42 : 3—23, 1973.

Perttu, K.: Factors affecting needle and leaf temperatures. — Dep. of Reforest. Royal Coll. of Forestry, Res. Notes 25 : 1—33, 1971.

Pickard, W. F., Puccia, C. J.: A theory of the steady state heat step method of measuring water flux in woody plant stems. — Math. Biosci. 14 : 1—15, 1972.

Sheriff, D. W.: A new apparatus for the measurement of sap flux in small shoots with the magnetohydrodynamic technique. — J. exp. Bot. 23 : 1086—1095, 1972.

Sheriff, D. W.: A model of plant hydraulics under non-equilibrium conditions. — J. exp. Bot. 25 : 552—561, 1974.

Sheriff, D. W., Sinclair, R.: Fluctuations in leaf water balance with a period of 1 to 10 minutes. — Planta 113 : 215—229, 1973.

Zinsmeister, G. E., Dixon, J. R.: Thermal flowmeters: the effect of axial conduction. — Trans. Amer. Soc. Mech. Eng. J. Heat Transfer 8 : 64—68, 1966.