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Apple tree water relations studied by means of the relative rate of water flow in the trunk xylem

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Abstract

The results of long-term investigations of variations of rates of water transport through the trunk xylem, its diameter, the leaf water potential and the transpiration rate of the apple tree showed that the daily rhythm of the relative rate of moisture flow in the trunk xylem is an obvious index of the state of the apple tree water exchange. This enables us to determine the period of its unbalance at intensive transpiration as well as the level of the forming water deficit with high accuracy and operativeness. Moreover, by the daily curve of the relative rate of xylem flow one can judge the role of contribution of the trunk reservoir to transpiration.

Introduction

An application of a thermal method of measuring rates of xylem moisture flows whose motive force are gradients of leaf water potential significantly increased operativeness and accuracy of determination of plant water exchange state. It enabled one to automatize this process. Various modifications of the method enable to record linear and relative rates of xylem flow of sap in the plant. The pulse method (*e.g.* Huber 1932, Tikhov 1979a) for measuring the linear rate of xylem flow is used significantly wider than that of stationary heating (*e.g.* Vieweg and Ziegler 1960, Tikhov 1979b) for recording the relative rate of sap flow in plant xylem pathways.. Short-term investigations of Ilnitskii *et al.* (1984), Tikhov (1975) as well as long-term experiments carried out by us under conditions of the commercial orchard showed an opportunity to use the relative rate of xylem moisture flow for ecological and physiological investigations and to apply it in practice with the view of optimizing plant water relations. Moreover, the method of stationary heating enables to automatize completely the process of measuring and to obtain not discrete, but continuous information during all the vegetational season. The equipment used in this connection is much simpler and more reliable in comparison with the pulse method.

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In the present work an attempt was made to estimate the water exchange state of the apple tree from the relative rate of moisture flow in the trunk xylem.

Material and methods

Investigations were carried out from 1983 till 1990 at the experimental farm of the Ukrainian Research Institute of Irrigated Horticulture on apple trees (*Malus domestica* Borkh. cv. Starcrimson) on M4 rootstock planted in 1978 at a spacing of 5 x 4 m.

We investigated such parameters of plant water relations as the rate of xylem water flow in the apple tree trunk (the linear rate V_l by means of the heat pulse method and the relative rate V_r by means of the stationary heating method) and the leaf water potential (by means of the pressure chamber). The relative rate of water flow V_r recorded automatically is an integral parameter depending on both V_l and the trunk water content (see Nadezhdina *et al.* 1988a, Nadezhdina *et al.* 1989 for details).

Variations of the trunk diameter (d) were measured with a micrometer, the transpiration rate, Q, was determined with the rapid weighing method. Relative air humidities, H, and air temperatures, T, were measured with an aspiration psychrometer *MB-4M* at the height of 2 m from the ground level. The soil moisture, W, was determined once a period of 7-10 d gravimetrically in every 10 cm layer at a depth of 0 - 50 cm where the bulk of roots were situated.

Results and discussion

It is noted in works published before (Nadezhdina 1989, Nadezhdina *et al.* 1989) that the representative daily rhythm of the relative rate of xylem moisture flow in the trunk has two pronounced maxima (in the morning and in the evening). The rate V_r in the day-time zone situated between these maxima correlates positively with the leaf water potential and negatively with the linear rate of sap flow in the trunk xylem. During the night period limited by the same maxima of V_r, the coefficient of correlation between the relative rate of xylem flow and the leaf water potential is as high as that in the day-time (of the order 0.7-0.9), but it changes its sign for the opposite one in comparison with day-time values of the same characteristics. It was also established that the definite constant value of the leaf water potential, $\psi_{threshold}$, corresponded to the maximum of V_r for every variety of plants.

Analysis of large quantity of synchronically measured values of relative and linear rates of xylem water flow, leaf water potential and fluctuations of the trunk diameter allowed to conclude that by the character of the curve of the daily rhythm of the relative rate of xylem moisture flow in the plant trunk one can judge the state of its water ex-change. The most representative daily rhythms of V_r characterizing different degrees of stress of this state are presented in Fig. 1. Here the first two rhythms indicate practically complete absence of water deficit in the plant (with the exception of a short period from 12.00 to 15.00 local time). The first rhythm is usually recorded on cool damp days of late autumn with the significantly shortened day length in comparison with a summer period. At this time instead of two maxima of V_r in the morning and in the evening one maximum is often observed at noon. In both presented cases the consumption of moisture by the plant does not exceed its supply from the soil. The characteristic signs of such a rhythm are zero or very low predawn flows and a single-peak maximum (in autumn) or a plateau at the level of the maximum (in summer) in the day-time. The leaf water potential does not decrease to the value lower than $\psi_{threshold}$ at such rhythms of V_r. In these cases the level of the maximum of V_r depends on the degree of approach of the leaf water potential value to $\psi_{threshold}$.

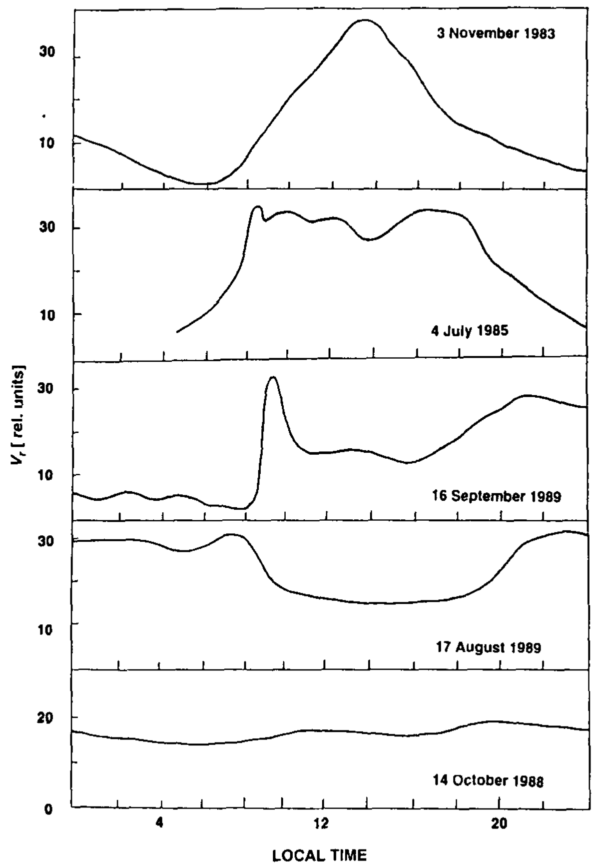

Fig. 1. Representative daily rhythms of the relative rate of water flow in the trunk xylem under different states of the water exchange of the apple tree.

It should be noted that rhythms of V_r, having a form similar to that shown on the plot for 16.09.89, are the most frequent for the vegetational season. This is a representative daily rhythm of V_r with a water deficit in the day-time when the consumption of moisture exceeds its supply from the soil owing to transpiration and water is consumed from the trunk reserves. The characteristic sign of such a rhythm is a double-peak shape of the curve of the rate of sap flow with maxima of V_r in the morning and in the evening and with depression in the day-time as well as the level of the flow in the predawn time which is lower than that in the day-time.

With increase in the water deficit the predawn relative rate of xylem increases, and the value of the ratio of the rate in the predawn time to that in the day-time equalling 1 or more suggests formation of the critical water deficit in the plant (Nadezhdina 1989). The higher the level of night flow, the deeper is the value of the negative water deficit in the plants. Such increase in V_r is observed to the level of the morning maximum. Moreover the value of the night leaf water potential corresponds to $\psi_{threshold}$. The example of such a daily rhythm of V_r on 17 August 1989 is shown in Fig. 1.

With subsequent increase in water stress, the night flow decreases simultaneously with the morning and evening maxima to the level of usual depression in the day-time. A kind of smoothing of the daily rhythm curve of V_r occurs. This suggests the deep water deficit in the tree. For 8 years of investigations we observed such rhythms only in autumn 1988 during severe dry winds (see Fig. 1, the rhythm on 14 November 1988). The consumption of moisture during several days similar to those presented on the plot was higher than its supply from the soil. The predawn leaf water potential was equal to -0.75 MPa, *i.e.* it was much lower than $\psi_{threshold}$; therefore, moisture reserves of the trunk did not replenish even at night. Hence an absence of characteristic bends in the rhythms of V_r follows.

Research of V_r variations is interesting not only in the aspect of observations of the plant water exchange state, but also in the aspect of the role of the trunk reservoir contribution to transpiration. In this connection we tried to represent obtained data as a model of transpiration flow proposed by Katerji and Hallaire (1984). Taking as an instance alfalfa, the authors showed an opportunity of division of transpiration flow, Q, into constituents - root absorption (a) and consumption from the reserves of the plant reservoir (q). Situated from left to right according to the degree of increasing stress of weather conditions, Figs. 2d,e,f,g,h,i represent daily rhythms of the leaf water potential, ψ, the transpiration rate, Q, and the relative rate of water flow, V_r, in the xylem of the apple tree trunk. On considered days the soil moisture was no limiting factor. Figures 2a,b,c also represent the relationship $\psi = f(Q)$ in the form of hysteresis loops. Unlike alfalfa in the apple tree, hysteresis is insignificant or even completely absent. This is apparently characteristic of fruit crops because analogous data were obtained for apple trees (*e.g.* Landsberg *et al.* 1976, Landsberg and Jones 1981) and citrus cultures (*e.g.* Cohen *et al.* 1983) before.

As in the case of alfalfa, in the sunny day, the leaf water potential changed linearly depending on transpiration (see Fig. 2a) from the sunrise (t_o) to time t_1 (to construct plots the point corresponding to zero transpiration flow and equalling -0.1 MPa (Nadezhdina *et al.* 1988a) was also used. At this period $q = 0$ and transpiration coincides with root absorption, a. Points observed on the plot shift with the straight line from time t_1 to the sunset. Under these conditions, in Katerji and Hallaire's opinion, the abscissa of the extrapolation straight line correlating with the present ψ (for example, at 10.00 local time) always corresponds to the root absorption and the difference between the curve and the straight line is the contribution of the reservoir of the plant. From t_1 to t_2, q is positive which suggests that the reservoir returns water. After t_2, q is negative and the reservoir is replenished.

According to Katerji and Hallaire model (1984) the linear part of the studied curve on the plot $\psi = f(Q)$ is a graphic expression of the equation

$$\psi_S - \psi_F = R.a \qquad (1)$$

where ψ_S and ψ_F are water potentials of the soil and the foliage, respectively, a is root absorption, and R is resistance to water movement through capillaries of the soil surrounding roots and to radial penetration of water into roots. On the graph R corresponds to the slope of the straight line expressing equation 1. As we see, with increasing of stress of weather conditions (*cf.* Figs. 2a and 2b) or duration of effect of stressed meteorological parameters - accumulation factor (*cf.* Figs. 2b and 2c) - the

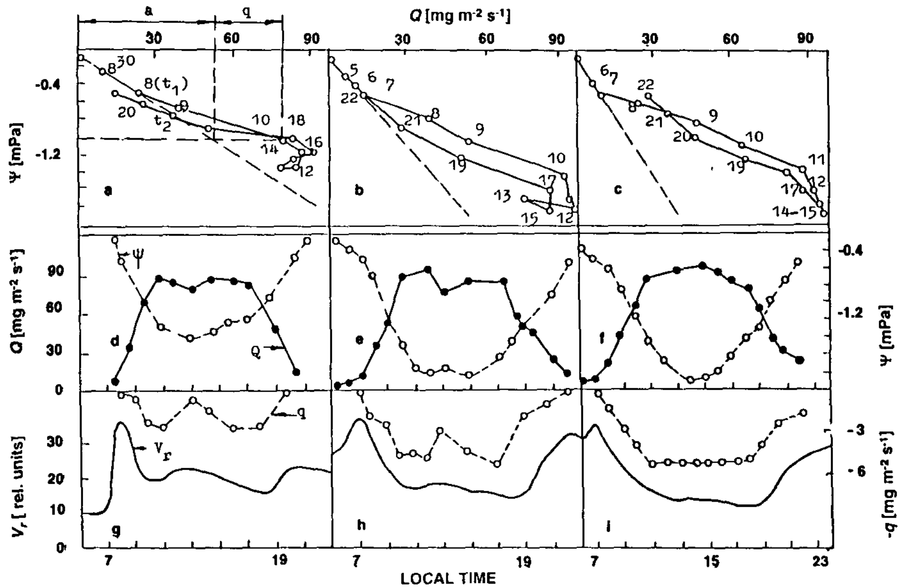

Fig.2. The daily rhythms of parameters of the apple tree water exchange at different degrees of stress of environmental conditions:
a,b,c - relationship between the leaf water potential and the transpiration rate in consideration of the internal flow (q) taken, as shown in Fig. 2a, at 10.00; a is root absorption;
d,e,f - changes in the leaf water potential, ψ, and the transpiration rate, Q; *g,h,i* - comparison of the daily moisture consumption from the trunk reservoir (q) with dynamics of the relative rate of water flow, V_r, in the trunk xylem.

slope of the curve increased because, despite the high soil moisture, the resistance to radial penetration of water into roots increased. At the moments of intensive suction

activity of roots in zones adjoining them, local desiccation of the soil occurs; the plant responds to this dessiccation in the same way as to the soil moisture deficit (Whitehead and Jarvis 1981). Acccording to the increase in the resistance *R*, the root absorption
decreased and the moisture consumption from the plant trunk increased ("the positive" part of the curve deflected from the straight line further and further). Noteworthy is the fact that in all the three considered cases the slope angle of the dependence $\psi = f(Q)$ practically remained the same. Thus, the total resistance to water flow remained constant. With changing of resistance constituents depending on ecological factors, the plant regulated the proportions of use of moisture reserves (the soil, the trunk reservoir).

We represented the consumption *q* from the trunk reservoir (calculated from q = Q -a) as daily variations over the curve of changing of the relative rate of water flow in the trunk xylem (see Figs. 2g, h, i). As we see, the beginning of involving the trunk reservoir in transpiration always coincided with the morning maximum of V_r. Time t_2 of the end of the reservoir use coincided with the evening maximum of V_r (see Figs. 2g,h). Under conditions of significant water stress because of the long effect of stressed weather conditions (see Fig. 2i), the trunk did not begin filling even at nightfall. It is obvious from both the dependence $\psi = f(Q)$ and the daily curve of V_r which has no evening maximum. The degree of depression of V_r corresponded to the level of transpiration consumption from the trunk moisture reserves. Thus, one can consider presented materials as evidence of the possibility to use the daily curve of V_r for determining the operation time of the trunk reservoir and the degree of its use. Technically, the carrying out of such investigations is significantly simpler, more exact and more operative.

Thus, the daily rhythm of the relative rate of water flow in the trunk xylem is an obvious index of the state of the plant water exchange. This enables to determine the period of its unbalance as well as the level of the forming water deficit owing to transpiration. On the grounds of analysis of presented materials one can draw a number of conclusions:

1. When there is no water deficit in the plant, the daily rhythm of the relative rate of xylem sap flow in the trunk with a single-peak maximum (autumn) or a plateau at the level of the maximum (summer) in the day-time and with zero or very low flows in the predawn time is recorded.
2. The double-peak daily rhythm of the relative rate of water flow in the trunk xylem with a maxima of V_r in the morning and in the evening, with depression in the day-time and with the level of night flow lower than that in the day-time, is characteristic of the moderate water deficit.
3. When the water deficit in the plant increases to the critical value or exceeds it, the period of the day-time depression of V_r increases and the nocturnal flow rises to the level of the morning maximum.
4. The deep water deficit in the plant is characterized by the smoothed curve of the daily rhythm of V_r recorded at the level of the usual depression in the day-time.
5. By the daily curve of V_r one can judge the role of contribution of the trunk reservoir to transpiration: the more stressed weather conditions, the greater is the consumption of moisture from the trunk reservoir (*i.e.* the degree of the depression of

V_r is higher) and the longer is the period of involving the plant reservoir in transpiration (*i.e.* the period between the morning maximum and the evening one of V_r is longer).

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