

EFFECT OF TRANSPIRATION RATE ON WATER TRANSPORT RESISTANCE IN APPLE TREE ROOTS

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Abstract

Water relationships and microclimate in apple trees in the field were measured and analysed in order to determine the effect of transpiration rate on transport resistance of water in the roots and in order to evaluate different ways to estimate transpiration rate in the field. The young apple trees, cv. Jonagold, were growing in 25 l containers in soil kept near field capacity. The course of transpiration rate was measured by weighing; calculated from the microclimate, energy balance and stomatal diffusion conductance and measured by automated potometers containing cut branches. The course of twig water potential (Ψ_{twig}) was measured as well.

Throughout a range of soil to twig water potential gradients of -2 to -11 bar the apparent root transport resistance was constant at approx. $1.9 \times 10^5 \text{ bar kg}^{-1} \text{ m}^2 \text{ s}$. Transpiration rates were controlled by the stomates, effectively reducing water potential decreases at high evaporative conditions. No hysteresis was found in the course of Ψ_{twig} throughout increasing and decreasing transpiration rates.

Limitations are made clear of transpiration estimation of intact trees by calculation from the microclimate and by potometer measurements.

1. Introduction

The resistance to water transport through the roots is known to be the largest resistance in the pathway of the transpiration stream from soil to leaves in many plants including apple trees rooting in well-watered soils. Scarce and not uniform information exists on the magnitudes for root resistance and on the effects of pretreatment and transpiration rate on it. It is important to know its magnitude for modeling work and to have a better understanding on the extent to which apple trees are able to control water stress by root resistance.

For the calculation of root resistance in steady state conditions the relationship $\text{Flux} = (\Psi_{\text{soil}} - \Psi_{\text{twig}}) / r_{\text{soil-twig}}$ can be applied, in which Flux is the transpiration water flux; $\Psi_{\text{soil}} - \Psi_{\text{twig}}$ is the gradient in water potential from soil to twig and $r_{\text{soil-twig}}$ is the hydraulic transport resistance from soil to twig. In the chain of resistances between soil and twig the resistance in the soil and even in the soil-root interface can probably be neglected near Ψ_{soil} of -0.1 bar (-0.01 M Pa). Kramer (1983) recently gave a review on this subject. Several authors described the relation of decreasing Ψ_{leaf} to increasing transpiration rates and found a multitude of mostly not constant slopes (Kaufmann, 1976).

Camacho et al. (1974) compared citrus and pear with some herbaceous species and found constant resistances for trees in well-watered soil

and decreasing resistances in the herbaceous species. Apparent resistance (or impedance) in apple trees was found to change throughout the day by Powell (1974) and to be dependent on pretreatment by Powell (1974) and Davies and Lakso (1979). Landsberg et al. (1975) found a constant apparent resistance in apple trees. Hopmans and Schouwink (1982) reported a relation between Ψ_{twig} and transpiration rate for apple trees in which the slope, hence apparent resistance, decreased with increasing and high transpiration rates but expressed their doubts on the reliability of the transpiration rate measurements. In the present research the 2 methods to determine transpiration rate in the field used then plus weighing of apple trees growing in containers will be compared and evaluated and the apparent resistances to water transport in the roots will be calculated.

2. Materials and methods

Apple trees

Hundred 1 year old apple trees (*Malus pumila* cv Jonagold on M.9) had been planted 8 months earlier in white plastic 25 l containers filled with a peat, sand, clay soil mixture. Each container had a black plastic cover on top and 5 leakage holes in the bottom. With trickle irrigation soil water potential Ψ_{soil} had been kept between -0.09 and -0.24 bar during the month preceding the investigations. The trees were arranged in rows at distances of 0.90 m within and 1.0 m at one side and 1.50 m at the other side between the rows. At the start of the 3 days of investigations the soil was watered extra in order to realize uniform and high soil humidity.

Measurements

Microclimate. Air temperature and air humidity were measured with 5 screened and ventilated thermocouple psychrometers placed at 5 levels in the canopy. Using net-radiometers over, below and within the canopy the absorbed net total radiation was determined. Wind speed u was measured with a cup-anemometer on top of the canopy.

Plant water relations. Water loss from 14 trees in containers was measured weighing the containers with the trees every 30 min on a balance (Sauter SD-20T/1 with 1 g readability). Leaf area was measured for each tree and approximated 1 m^2 per tree. The average rate of water loss of the 14 trees was expressed as $E_{\text{tree(weighing)}}$ in $\text{mg cm}^{-2} \text{ s}^{-1}$. In the middle of a warm day rates of 40 $\text{mg m}^{-2} \text{ s}^{-1}$ or $40 \times 10^{-9} \text{ m}^3 \text{ s}^{-1}$ per tree were reached. Transpiration rates of 2 branches with 0.15 to 0.20 m^2 of leaf area cut from Jonagold trees (preventing air entry into the xylem) was monitored continuously by 2 automated potometers (E_{potom}). The branches were placed in the tree crowns at evaporative conditions identical to the intact tree branches.

Leaf diffusion conductance g_L was measured with a diffusion porometer (Delta-T, Mk 3) connected to a transportable micro-computer. Every 30 min g_L was measured on 6 leaves in the upper and 6 leaves in the lower half of the canopy of intact trees and on 3 leaves per potometer branch.

Twig water potential Ψ_{twig} . A pressure chamber with semi-automatic reading was used to follow the course of Ψ_{twig} of the intact trees. It was done on 10 leaves enveloped in aluminum foil picked every 30 min from the canopy of 100 trees. The leaf water potential of not transpiring leaves connected to the twigs is assumed to correspond to

Ψ_{twig}
 All microclimate sensors and the potometers were connected to a data-logger (Fluke 22 40A) and monitored and printed every 3 min.

Calculation of transpiration rate

For the calculation of transpiration rate E the Penman-Monteith equation (1) was used (Monteith, 1973).

$$E = \frac{(S R_{Nleaf} + \rho C_p \delta e g_b) \times 10^6}{\lambda (S + \gamma^*)} \quad (1)$$

E in $\text{mg m}^{-2} \text{s}^{-1}$ equals transpiration rate E_{leaf} for the hypostomatous apple leaves if

$$\gamma^* = \gamma (2 + g_b/g_l) \quad (2)$$

γ is the psychrometer constant in bar K^{-1} ; g_b is the boundary layer conductance in ms^{-1} ; g_l is the leaf epidermal water vapour diffusion conductance in ms^{-1} ; S is the slope of the saturation water vapour pressure curve in bar K^{-1} ; ρC_p is the heat content of the air in $\text{J m}^{-3} \text{K}^{-1}$; R_{Nleaf} is the net total radiation on the leaves in Wm^{-2} ; δe is the vapour pressure deficit of the air in bar; λ is the heat of water vaporization in J kg^{-1} . For the estimation of g_b the empirical relationship with windspeed on top of the trees u in ms^{-1} described by Powell (1976) was used.

$$g_b = 0.0303 u^{0.5} \quad (3)$$

Potential evaporation rate E_o in $\text{mg m}^{-2} \text{s}^{-1}$ for leaves with infinite g_l at both sides was calculated by taking

$$\gamma^* = 2 \gamma \quad (4)$$

Results and discussion

3.1. Measured and calculated transpiration rates

From the 3 days, from which results are presented, figures 1 and 2 show the course in time of in- and decreasing rates of evaporation and transpiration on two almost succeeding and nearly cloudless days. The first day (830819, fig. 1) was warmer and vapour pressure deficit δe mounted up to 22 mbar. For both days the course of twosided potential leaf transpiration rate E in figures 1 and 2 describes the course, and height of the evaporative condition, calculated with equations (1) and (4). As on both days shown in figures 1 and 2 leaf diffusion conductance g_l of the leaves on the cut branches on the potometers was much higher than of the leaves on the intact trees, both calculated and measured transpiration rates of the branches in the potometers $E_{potom. (calculated)}$ and $E_{potom.}$ were higher than the calculated and measured transpiration rates of the trees $E_{tree (calculated)}$ and $E_{tree (weighing)}$. The difference in g_l must be explained by decrease in stomatal opening due to higher Ψ_{twig} and Ψ_{leaf} in the cut branches having free water available at their bases placed in the potometer vessels. The potometers measured uptake of water by the branch $E_{potom.}$, whereas $E_{potom. (calculated)}$ indicates the calculated loss of water from the same branches. Real difference between loss and uptake may lead to differences in the course of both parameters as is the case in fig. 1 at 1200 h, where $E_{potom.}$ decreased and $E_{potom. (calculated)}$ kept increasing. During several hours on both days $E_{potom. (calculated)}$ was considerably higher than $E_{tree (weighing)}$.

Whether the overestimation of E_{tree} by the calculation estimation originates from overestimation of g_l or R_N or g_b has to be found out still.

On both days while δe was in the range of 10 to 15 mbar Ψ_{twig} seemed to reach a threshold near -9.5 bar at which g_l started to decrease. On 830822 (fig. 2) this happened at 1015 h leading to a turn in the course of both calculated and measured E_{tree} from a gradual increase, whereas E_o went on increasing. For the same reason the difference in level of E_o between both days in fig. 1 and fig. 2 is not found in E_{tree} of both days. The apple trees were protected from water stress at high evaporative conditions by stomatal regulation already in an early stage of stress development.

3.2. Relation between water potential gradients and transpiration rates

In figures 3 and 4 for both days treated in the previous section and for 830818 the relation of Ψ_{twig} of the intact trees to measured transpiration rates of the same trees was best described by straight lines indicating that the slope over this range of Ψ_{twig} was constant. Ψ_{soil} on these days was between 0 and -0.2 bar, so the vertical axis practically represents the water potential gradient from soil to twig. According to several authors (see Kramer, 1983) it can be assumed that water transport in the soil and soil-root interface did not meet any significant resistance. Faiz and Weatherley (1982), however, described for sunflower root contractions and indications of considerable transport resistance in well watered soil. As discussed in the introduction the slope of the straight lines in figures 3 and 4 represents the apparent transport resistance to water from soil to twigs. This resistance is also called impedance, because in its appearance also capacitance (storage and release) of tissues connected to the transpiration pathway, plays a role. The average of the three slopes in figures 3 and 4 is near to 1.9×10^5 bar $\text{kg}^{-1} \text{m}^2 \text{s}$. With the leaf area per tree of 1 m^2 and $1 \text{ bar} = 10^5 \text{ Pa}$ this compares to $1.9 \times 10^{13} \text{ Pa s m}^{-3}$ a value similar to $1.78 \times 10^{13} \text{ Pa s m}^{-3}$ found by Davies and Lakso (1979) for root resistance in young apple trees grown in field conditions, in containers, removed from the soil and held in a container of water. On comparing the slope found in this investigation with others of the many described earlier it should be kept in mind that most other authors measured Ψ_{leaf} in combination with transpiration rate (Kaufmann, 1976) and so included in the relation the important resistance to water transport in the leaf.

The line for 830822 in fig. 4 intercepted the Ψ -axis at -1.8 bar. This value coming from measurements in the evening corroborates findings of Powell and Thorpe (1979) and Kaufmann and Hall (1974), while Kramer (1983) discussed the phenomenon. Explanations put forward are Ψ_{soil} remaining in the evening or uptake of water by growth. In our case Ψ_{soil} was -0.2 bar at most leaving a gradient of 1.6 bar, which would have to be caused by a water uptake by growth of 30 g h^{-1} per tree. We tend to explain the intercept found as an error met in the pressure chamber method. Ritchie and Hinckley (1975) reported that the pressure chamber generally gave too low water potential values.

In fig. 4 the line describing decreasing Ψ_{twig} with increasing E_{tree} during the first part of the day (830819) is at a lower level than the line describing increasing Ψ_{twig} with decreasing E_{tree} during the second half of the day (830822). Powell (1974, 1976), Powell and

Thorpe (1977) and Hopmans and Schouwink (1982) reported the opposite and the authors first mentioned explained the phenomenon with capacitances releasing water at decreasing and storing water at increasing Ψ^{twig} in apple tree. Landsberg et al. (1976) theoretically and experimentally analysed resistances and capacitances in apple trees. Measurements on the course of soil temperature in the pots used for this experiment in the following summer indicated that during the first day-half on 830822 soil temperature may have been 4-5 K lower than during the second half of the day on 830819. According to Kramer (1983) the rate of water movements through living roots increases by $4\% K^{-1}$ temperature increase throughout a wide range of temperatures. A temperature sensitivity of this magnitude might cause a difference in Ψ^{twig} between both days of 1.5 bar at Ψ^{twig} of -8 bar, which forms a large part of the difference observed here and moreover may have masked the action of capacitance in the tree.

In further research the soil temperature in containers must be kept constant.

3.3. Evaluation of methods to determine transpiration rates in the field

From the course and level of $E^{potom.}$ compared to $E^{tree(weighing)}$ in figures 1 and 2 it may be obvious that relating Ψ^{twig} of intact trees to $E^{potom.}$ can not yield useful information on the level and behaviour of root resistance in the tree, which removes the doubt expressed by Hopmans and Schouwink (1982) about its unreliability.

From the figures 5 and 2 it can be seen that also the estimation of E^{tree} by calculation from the microclimate and g_L did lead to over-estimation of E^{tree} especially at higher levels of E^{tree} . The line of 830822 is the reference here. Fig. 5 suggests a gradually decreasing root resistance with increasing transpiration rates. It must be clear that relating Ψ^{twig} to evaporative demand E_0 is also useless for the study of behaviour of root resistance.

Potometers could be used to estimate transpiration rate of intact trees in the field in the following manner. By measuring on branches on potometers situated in the tree canopy g_L and leaf temperatures during steady state situations of $E^{potom.}$ the conductance to vapour transport in the air g_b can be solved by the relation

$$E = \frac{\rho C_p}{\lambda} \delta e_L (g_L + g_b) 10^6 \quad (5)$$

δe_L is vapour pressure gradient leaf - air in bar.

In the intact trees g_L and δe_L is determined in the same way as on the potometer branches situated in the trees. g_b estimation for whole branches in this way seems less complicated and more realistic than by the energy balance approach involving measurement of net-radiation and wind speed (equation 1) or by heat dissipation of non-transpiring leaves (Butler, 1976). g_b found for the potometer branch is applied to calculate E^{tree} with the same equation (5) using g_L and δe_L measured on intact trees.

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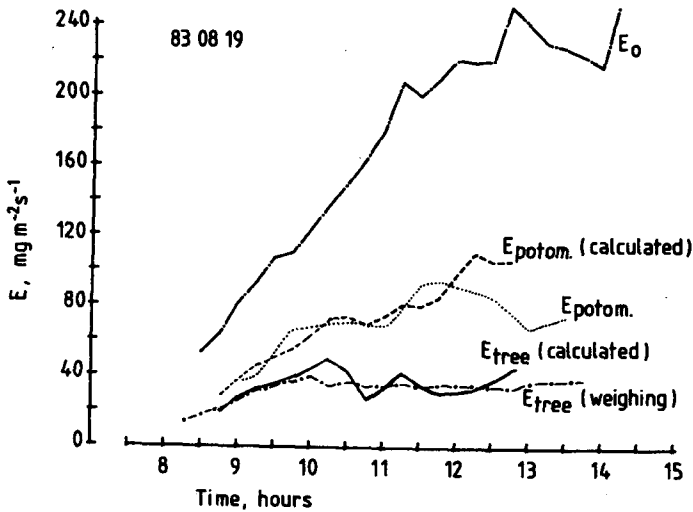


Figure 1. Course of potential bifacial transpiration rate E_0 , calculated with equations (1) and (4) and calculated mono-facial transpiration rates from leaves on the trees E_{tree} (*calculated*) on the branches on the potometers $E_{potom.}$ (*calculated*) using equations (1) and (2). Transpiration rate from intact trees in containers E_{tree} (*weighing*) measured by weighing 14 trees every 30 min and from cut branches on 2 potometers $E_{potom.}$. For the trees $40 \text{ mg m}^{-2} \text{ s}^{-1}$ equals $40 \times 10^{-9} \text{ m}^3 \text{ s}^{-1}$ per tree. Time in MET on 19 August 1983 (830819).

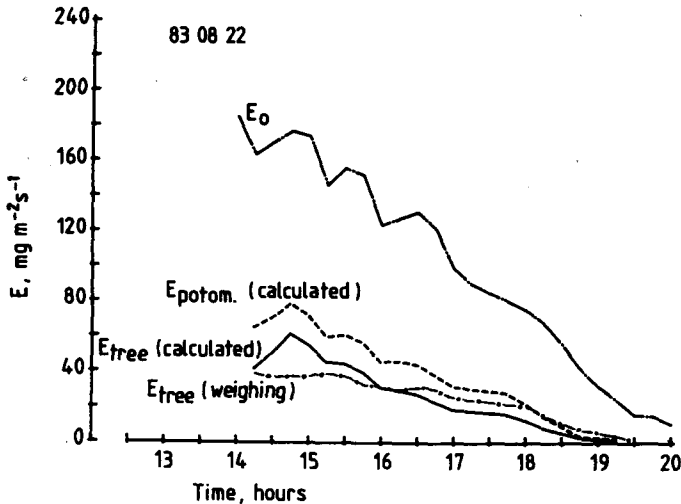


Figure 2. Course of potential bifacial transpiration rate E_0 calculated with equations (1) and (4) and calculated mono-facial transpiration rates from leaves on intact trees E_{tree} (*calculated*) and on the branches on the potometer $E_{potom.}$ (*calculated*) using equations (1) and (2). Course of transpiration rate from intact trees in containers E_{tree} (*weighing*) measured by weighing 14 trees every 30 min. Time in MET on 22 August 1983 (830822).

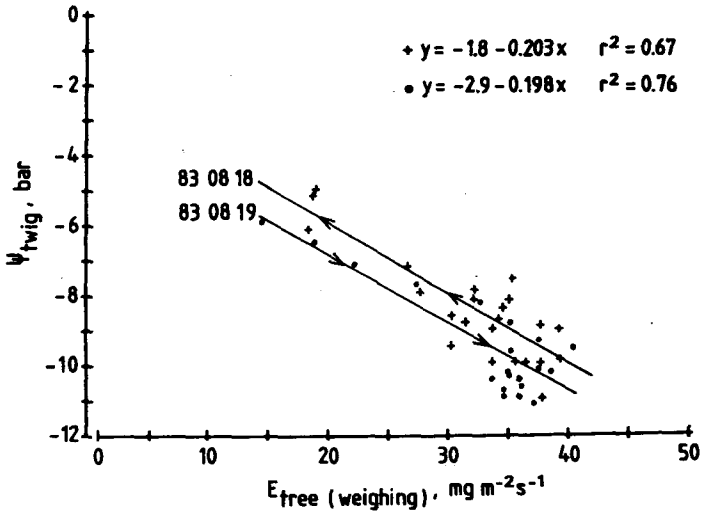


Figure 3. Decreasing 830819 and increasing 830818 twig water potentials Ψ_{twig} plotted against increasing 830819 and decreasing 830818 transpiration rates $E_{\text{tree(weighing)}}$ both measured on intact trees in containers in the field. The Ψ -value of each point is the average of 10 measurements. 1 bar = 10^5 Pa.

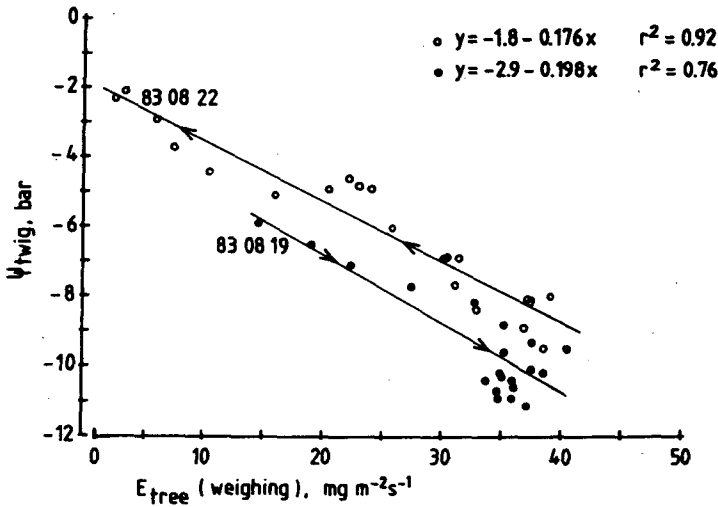


Figure 4. Decreasing (830819) and increasing (830822) twig water potentials Ψ_{twig} plotted against increasing (830819) and decreasing (830822) transpiration rates $E_{\text{tree(weighing)}}$ measured on intact trees growing in containers in the field. The Ψ -value of each point is the average of measurements on 10 leaves. 1 bar = 10^5 Pa.

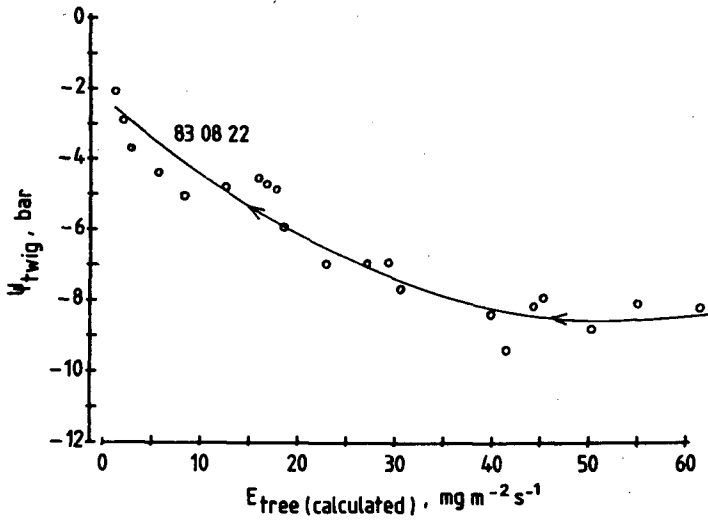


Figure 5. Increasing twig water potential ψ_{twig} in intact trees in containers plotted against decreasing transpiration rate from intact trees in containers $E_{\text{tree (calculated)}}$ calculated by equations (1) and (2) (on 830822 from 1415 h to 1915 h). 1 bar = 10^5 Pa. The regression equation of the curve is $y = -2.44 - 0.229 x + 0.0022 x^2$; $r^2 = 0.90$.