BIOLOGIA PLANTARUM 46 (1): 41-47, 2003

Comparison between different methods for measuring transpiration in potted apple trees

G. FERRARA* and J.A. FLORE**

*Dipartimento di Biologia e Chimica Agroforestale ed Ambientale, University of Bari, Via Amendola 165/A, I-70126 Bari, Italy**
*Department of Horticulture, Michigan State University, East Lansing, MI 48824, USA***

Abstract

Five different methods for measuring transpiration, which include gravimetric analysis (control), heat pulse velocity (HPV), time domain reflectometry (TDR), single leaf and whole plant infrared gas-exchange measurements, have been tested on two cultivars (Redcort and Empire) of young apple trees (*Malus communis* L.). The objective was to compare these methods and establish the most affordable one to be used in greenhouse conditions in order to determine and/or estimate the amount of water for an efficient irrigation management. Results obtained with TDR were particularly accurate and not statistically different with respect to the control (-4.2 %) and this was supported by the correlation coefficient (r = 0.94) found. The HPV method was sufficiently accurate and reliable for small stems, however, in our conditions this method generally underestimated the transpiration (-32.4 %). Single leaf and particularly whole plant infrared gas-exchange measurements suffered an overestimation of the transpiration with respect to the control.

Additional key words: HPV, infrared gas-exchange units, *Malus communis*, TDR.

Introduction

The measurement of both transpiration rate and water use by plants is an important task for research in plant-water relationship as well as for irrigation management. There are many techniques available such as tensiometers, neutron scattering, gypsum blocks and gravimetric analysis for measuring soil water content or water balance of plants. However, many of these methods have limitations and drawbacks (Gee *et al.* 1976, Gardner 1986, Cassel and Klute 1986, Grantz *et al.* 1990) and in many cases they provide incorrect determinations.

In this study, five selected methods largely used to measure transpiration have been compared in greenhouse experimental conditions. The methods were the gravimetric analysis, time domain reflectometry (TDR), heat pulse technique (HPV), single leaf and whole plant infrared gas exchange measurements (Gucci and Corelli-Grappadelli 1989, Corelli-Grappadelli and Magnanini 1993, Long *et al.* 1993, 1996, Miller *et al.* 1996).

The TDR method is accurate and non destructive and allows portability, easy installation and rapid data collection (Topp *et al.* 1982, 1984, Topp and Davis 1985, Grantz *et al.* 1990, Richardson *et al.* 1992, Anisko *et al.* 1994). Most of the works conducted using TDR are field studies and only few informations are available on its applicability in containers (Richardson *et al.* 1992, Anisko *et al.* 1994). This method is based on the propagation velocity of an electromagnetic pulse at microwave frequencies. Electromagnetic pulses travel down a transmission line that terminates in a couple of parallel stainless steel rods inserted into the soil (Baker 1990). The propagation velocity is determined by probe length (the two rods) and pulse return time, which is induced by a high speed oscilloscope. This velocity is influenced by the dielectric constant of soil which depends mainly on soil water content. In fact, the dielectric constant of water is about 20 to 40 times larger than that of dry soil (80 *vs.* 2 - 4). The relationship between the apparent dielectric constant and the volumetric water content in soil is expressed by an empirically derived equation as described by Topp *et al.* (1980).

Received 5 June 2001, *accepted* 7 March 2002.
Abbreviations: E - transpiration rate; HPV - heat pulse velocity; LA - leaf area; TDR - time domain reflectometry; V_s - sap velocity.
*Corresponding author; fax: (+390) 80 5442850, e-mail: ferrara.g@agr.uniba.it

The HPV approach is a method for the direct measurement of transpiration using a continuous supply of heat as a tracer (Cohen *et al.* 1988, 1993, Green and Clothier 1988, Olbrich 1991, Smith 1992, Caspari *et al.* 1993, Hatton *et al.* 1995). Many studies have shown that there is a direct relationship between water uptake and heat velocity (Stone and Shirazi 1975, Swanson and Whitfield 1981, Olbrich 1991, Smith 1992, Cohen *et al.* 1993, Teskey and Sheriff 1996). This method is based on the temperature difference between two thermocouples inserted into the stem to estimate sap velocity, and the mass sap flow is calculated from heat balance (Cohen *et al.* 1988). The theoretical basis and the sampling strategies of the technique can be found in the recent literature (Cohen *et al.* 1988, 1993, Green and Clothier 1988, Hatton *et al.* 1995). The method is rapid and the instrumentation is sufficiently easy to carry and to implant.

Portable infrared gas exchange units are used for the determination of transpiration of single leaves. These units allow to estimate the gas exchanges of a unique leaf within 60 - 120 s. Therefore, it is possible in a few minutes to collect data of a randomized sample of leaves of the whole plant. Limitations and problems are possible if the goal is to extrapolate the measurements to the whole plant. Leaf gas exchanges are variable due to many factors, such as stress, fruit load (Flore and Sams 1986), leaf position (Sams and Flore 1982), angle of incident radiation (Flore and Lakso 1989), or stomatal conductance (Schulze 1986).

Another method adopted to evaluate the whole plant transpiration consists in placing the plant in a chamber to measure gas exchanges (Corelli-Grappadelli and Magnanini 1993, Katerji *et al.* 1994, Miller *et al.* 1996). These chambers can be easily assembled and disassembled; furthermore they are not expensive and do not trap high quantities of infrared radiation avoiding an excessive heating effect. It is possible to couple the portable infrared gas analyzer units with the chamber to obtain affordable measurements of the whole canopy transpiration.

Several studies have been made to test the performances of each of these methods, either individually or coupled, in numerous herbaceous and woody species. All of these methods vary considerably in many aspects, from the theory to the application. Each of them needs a unique set of particular assumptions, technical difficulties, measurement errors, sampling problems, cost of tools. The methods also differ in whether they measure the transpiration, through the analysis of the soil, the whole canopy or single leaf gas exchanges or the sap flux in the stem. This also introduces a spatial and temporal aspect typical of each method, as a consequence, specific advantages and drawbacks are introduced for each of the methods.

The objective of this study was to apply the five techniques cited above (gravimetric analysis, HPV, TDR, single leaf and whole plant infrared gas exchange measurements) on two cultivars of apple to verify the accuracy and repeatability of each technique, and to compare them in order to establish which one results easier, more accurate and cheaper to utilize. A comparison from this practical point of view of all these methods is of great importance to determine and/or estimate the amount of water that should be used for crop irrigation. A particular purpose of this study was to determine the precision of transpiration measurements by using the HPV technique on small plants.

Materials and methods

The experiment has been carried out in a greenhouse at the Michigan State University, Department of Horticulture, on twelve potted one-year-old apple trees (*Malus communis* L.) of two different cultivars: cv. Redcort grafted to M7 and cv. Empire grafted to Mark. The twelve plants had a diameter ranging from 10 to 15 mm and were potted in 19-dm^3 pots. The plants were watered and fertilized regularly until the beginning of the experiment when the irrigation was suspended. All the pots were covered with a plastic bag to avoid evaporation from soil, in order that water loss depended only on plant transpiration. The measurements were taken in six different and consecutive days starting on the third decade of May until the end of the month (22nd - 27th). The temperature in the greenhouse was kept at 27 ± 2 °C through the use of a cooling system.

For the gravimetric method, used as control, the instrumentation consisted of a balance to take daily pot masses at 18:00.

The probes used in the HPV method were 2.0 mm in diameter and consisted of 2 thermistors placed, respectively, 10 mm upstream and 5 mm downstream from a heater (*Greenspan Technology*, Warwick, Australia). The two probes were inserted about 10 cm above the graft at a depth of 8 mm in parallel holes drilled radially into the stem of the plant, about 2 mm into the sapwood. Heat pulses (30 °C) are released from the heater and these pulses reach first the upstream sensor and then the downstream sensor and, after a time (Te), the temperature of the 2 sensors is equal. The HPV measurements were made and recorded automatically every 10 min on a data logger. The theory of the method and the procedures used are described below.

The velocity (V_h) of the heat pulse is given by the equation:

$$V_h = (X_d - X_u)/2T_e$$

where X_u and X_d are the distances between the heater and

the upstream and downstream sensors, respectively. The values of V_h were calculated according to the method of Dye *et al.* (1992) and corrected both for wound and heat transfer of materials effects using empirical functions (Green and Clothier 1988, Swanson and Whitfield 1981). Sap velocity (V_s) was calculated from V_h (Marshall 1958) based on the known volume fraction of wood and water as shown by the equation:

$$aV_s = [(\rho_{sm} \times C_{sm})/(\rho_s \times C_s)] \times V_h$$

where a is the fraction of the cross sectional area of conducting sapwood occupied by moving sap streams and ρ and C are the density and specific heat capacity, with the subscripts s and sm referring to sap and sap plus woody matrix (including gas), respectively. The volume fraction of wood and water was calculated according to Greenspan Technology from fresh samples by measuring fresh mass, mass of displaced water by immersion in a vessel of distilled water on a balance, and oven dry mass. To determine the radius of heartwood and sapwood, some representative plants were cut and measured at the beginning of the experiment. Sap velocity was then converted to sap flux (u_v) by multiplying the sapwood area at the position of the probes:

$$u_v = a \times V_s$$

The fluxes are then integrated over the whole cross-sectional area of the stem using the step integration method (Hatton *et al.* 1990) to determine the sap flow rate [g s^{-1}]. The sum of these rates, recorded every 10 min as above reported, gave the daily total amount [g d^{-1} $tree^{-1}$].

The heat-pulse data and the values measured (wound diameter, volume fraction of wood and water, *etc.*) were processed using *SAPCAL* program supplied by the manufacturer. For species with sapwood that can be considered thermally homogeneous, like in apple trees where the vessels are small and pratically with uniform diameter, the HPV technique can be used with good precision (Green and Clothier 1988).

In the case of the TDR method, a *Tektronix 1502B TDR* cable tester (*Tektronix*, Beaverton, USA) connected to stainless steel rods (3.2 mm diameter and 150 mm long) by a coaxial cable was used. In all pots, a pair of rods were inserted into the soil at a parallel distance of 50 mm. Readings of soil electromagnetic capacitance were made by pulsing a wave (74 % of the light speed) down the rods with the tester and reading the value on the screen. These cable tester readings were then converted to the dielectric constant of soil (k_a) calculated according to Topp *et al.* (1984):

$$k_a = [(c \times t)/L]^2$$

where c is the velocity of an electromagnetic signal in free space (300 mm ns^{-1}), L is the length of the rods [mm] and t is the travel time of the voltage pulse as measured by TDR [ns]. Once obtained k_a, the volumetric water content was finally calculated through an empirical equation (Topp *et al.* 1980):

$$\theta_v = -5.3 \times 10^{-2} + 2.92 \times 10^{-2} k_a - 5.5 \times 10^{-4} k_a^2 + 4.3 \times 10^{-6} k_a^3$$

where θ_v is the volumetric water content [cm^3 cm^{-3}], and k_a is the apparent dielectric constant of soil. The volumetric content was then converted to the mass content [g cm^{-3}] based on the density of the water in the soil.

A portable infrared gas analyzer (IRGA; *ADC LCA-2, Analytical Development Co.*, Hoddesdon, UK) equipped with a Parkinson broadleaf chamber and an air supply unit (*Analytical Development Co.*) was used for the single leaf transpiration rate measurements. Data were collected on a randomized sample of leaves in the middle and upper part of the plants. Water transpiration rates were recorded at regular intervals (09:00, 12:00, 15:00 and 18:00). Gas exchange parameters were calculated as molar fluxes using mole fractions of water vapor as suggested by Cowan (1977). Canopy transpiration was estimated by multiplying transpiration per square meter by leaf area on each day of measurement and canopy leaf area was calculated from individual leaf area at the end of the experiment. Since trees were in the first growing season, canopy shading was considered negligible and transpiration per leaf was extrapolated for the entire canopy.

Whole plant transpiration was recorded using chambers made of *Mylar* film (*Dupont*, Wilmington, USA). Two chambers were used to measure simultaneously both cultivars and avoid different time influences. In order to homogenize the air within the chambers a small fan was used (model *IC982B, Dayton Inc.*, Dayton, USA). The fan was connected to a PVC pipe of T shape (10.2 cm diameter) which allowed the attachment to the two chambers through two pipes. At selected times, the airflow was recorded using a thermal anemometer (model *37000-00, Cole-Parmer Inc.*, Chicago, USA) and by taking three readings at a different depth in the pipe and then averaging them. The whole-plant chamber was placed around the tree and allowed to equilibrate for 10 min and then the gas-exchange measurements were obtained by the IRGA units, as previously described. Additional detailed information about chamber construction, calibration and measurement can be found in Miller *et al.* (1996). The calculations of transpiration when using the IRGA units were made using a computer program already described by Moon and Flore (1986). The transpiration E [mol m^{-2} s^{-1}] was obtained by the following equation:

$$E = \{[f_o \times (w_o - w_i)/(1 - w_o)]/LA\}$$

where f_o is the flow out of the sample chamber [mol s^{-1}], LA is the leaf area [m^2], w_i and w_o are the mole fractions of water vapor of the incoming and outgoing air streams. With the computer program then the transpiration was

expressed in mg cm^{-2} s^{-1} and finally converted in g d^{-1} $tree^{-1}$.

All data collected have been statistically analyzed by two-way analysis of variance (*ANOVA*) at both 95 % ($P \leq 0.05$) and 99 % ($P \leq 0.01$) confidence levels. The mean values were then separated by using the Duncan's test.

Results and discussion

Results of the two-way *ANOVA* test showed that statistically significant differences ($P \leq 0.01$) of transpiration existed among the data obtained by the various methods applied. The comparison of results from the five methods revealed that large differences occurred at different days, with maximum differences at the fourth day (Fig. 1). The marked and highly significant ($P \leq 0.01$) variability of transpiration data at different days was observed for results of all methods. The fluctuation of transpiration values should be related to the variable conditions of irradiance recorded at the various sampling days. In fact, the 3rd and 5th days were cloudy, whereas the other ones were characterized by sunshine which clearly caused an increase of irradiance in the greenhouse and a consequent enhancement of transpiration.

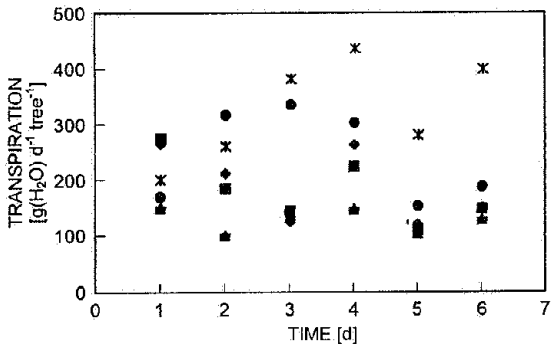

Fig. 1. Patterns of transpiration during the six days of measurement. Each point is based on averages of two cultivars. Five different methods were used: *rhombs* - gravimetric, *triangles* - HPV, *crosses* - single leaf, *squares* - TDR, *circles* - whole plant.

Also the interaction sampling time × methods was highly significant ($P \leq 0.01$). The mean value of transpiration recorded by the gravimetric method (control) was about 191 g(H_2O) d^{-1} $tree^{-1}$ (Fig. 2), with the highest transpiration values in the 1st and 4th day [264 and 265 g(H_2O) d^{-1} $tree^{-1}$, respectively]. The HPV method presented the lowest transpiration values with a mean value of 129 g(H_2O) d^{-1} $tree^{-1}$, whereas whole plant and single leaf methods apparently overestimated transpiration, with mean values of 246 and 328 g(H_2O) d^{-1} $tree^{-1}$, respectively (Fig. 2).

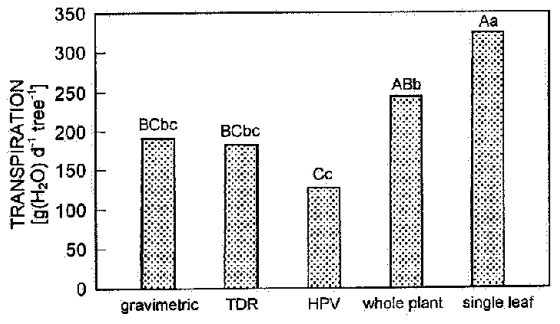

Fig. 2. Mean daily transpiration measured by the five methods as obtained by the Duncan's test. *Capital letters* and *lower case letters* refer to $P \leq 0.01$ and $P \leq 0.05$, respectively.

The single leaf method showed transpiration rate values that were very inconstant at the different days, and always higher than those obtained by the control method. The cumulative transpiration of the single leaf was the highest among all the methods applied (Fig. 3). Methods of scaling up from leaf stomatal conductance to canopy conductance have already been tested (Rochette *et al.* 1991), but results were often unsatisfactory and led to an overestimation of transpiration values. Limitations of the single leaf method, when the goal is to estimate the whole plant exchanges, are known (Gucci and Corelli-Grappadelli 1989, Miller *et al.* 1996).

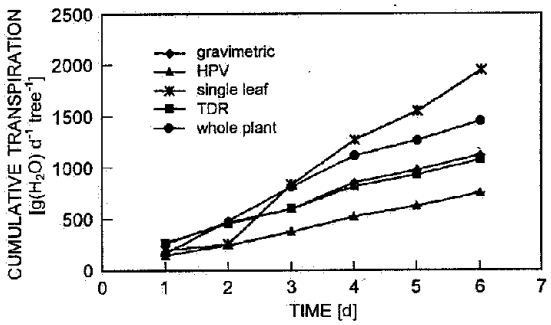

Fig. 3. Comparison of cumulative transpiration over six days measured by the five methods.

The whole plant method was more accurate than the single leaf method, although the fluxes were still overestimated with respect to the gravimetric method. At the first three days the trend and the daily values of transpiration measured by the whole plant method were very different from those of the control, whereas in the last three days both the trend and the daily values were close to the control. The cumulative transpiration (Fig. 3) resulted the 28.2 % higher value than the control, and the mean transpiration rate value was not statistically different from the value measured by the control method. Probably, in steady conditions and with lower water content this method could represent a more accurate measurement of transpiration because it monitors the gas exchanges of the whole plant and it is not based on a simplification of canopy structure as the previous

method. Whole plant chambers offer the possibility to measure both water vapor and CO_2 exchanges in trees, allowing a wide range of studies. Therefore, there is no need to determine leaf area, and since the leaves are under different light levels the transpiration rates can be better expressed per tree unit.

Among the five different methods used in this study, the TDR method gave results more similar to the control, whereas the other ones usually over or underestimated the transpiration. Results of the TDR method presented a mean value of 183 $g(H_2O)$ d^{-1} $tree^{-1}$ that was not statistically different with respect to the control (Fig. 2). The trends of transpiration of both methods were therefore very similar (Fig. 1). A good relationship ($P < 0.01$) exists between TDR and control with a correlation coefficient of 0.94 (Fig. 4). The cumulative transpiration indicated that TDR data are a little lower than the control method data (-4.2 %; Fig. 3). The TDR method offered a better accuracy and precision, and was practical, easy to install and fast to use. In particular, the data of transpiration obtained by the TDR method resulted significantly correlated to the control suggesting a good affordability of the method. From a practical point of view the TDR method presents itself as one of the most reliable, and is effective either in the greenhouse, or likely in the field. Although results of TDR analysis are good, problems may arise from the probe length influencing the accuracy of soil water measurements (Richardson *et al.* 1992, Topp *et al.* 1984), especially when deeper containers were used or open field analysis was required. The main limitation of TDR method was that it is extremely expensive and some problems can also arise from the high spatial variability in soil water content, but in a small environment like a pot this problem should be skipped. The response of TDR probes is sensitive to the region immediately surrounding the probe wire and is attenuated by a high soil electrical conductivity. Care should be also used when inserting the probes in the soil (Zegelin *et al.* 1990).

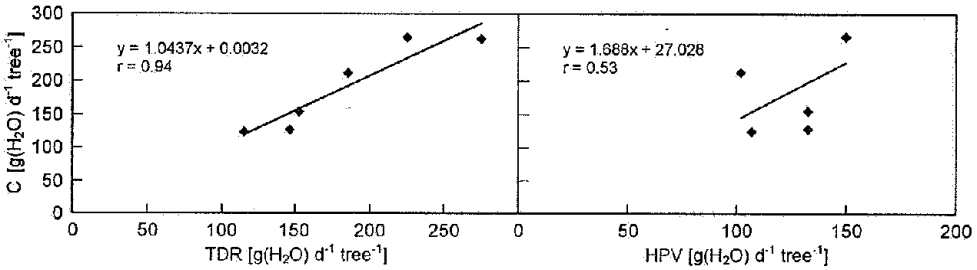

Fig. 4. Relationships between daily values of transpiration measured with time domain reflectometry (TDR) and gravimetry (C), and with heat pulse velocity (HPV) and gravimetry (C). The line shown is the linear regression, with r values of 0.94 and 0.53 in TDR and HPV, respectively.

The HPV method generally underestimated the daily and cumulative transpiration rates (Figs. 2, 3), but the trend was almost the same as for the control. The relationship between daily values measured with HPV and gravimetry was acceptable, but with a lower r (0.53 *vs.* 0.88) with respect to the value obtained by Yunusa *et al.* (2000) in irrigated grapevines. Probably, the lower values obtained with this method with respect to the control depended somehow on the installation and the setting of the data logger (*e.g.*, calculation of sapwood and heartwood areas, depth to insert probes, wound size), which requires particular attention and skillfulness. These operations represented the most time consuming and critical moment of the method, as already reported by other authors (Swanson and Whitfield 1981). The heater and the sensor need to be correctly positioned by using a guide jig when drilling the holes. The setting of the probes should be done carefully in order to avoid damaging the stem, because the diameter of the wound created could be one of the main sources of error (Hatton *et al.* 1995). In general, the probes should be moved regularly 14 - 21 d after the implant because of wound reactions that may cause cavitation or deposition of resin in the vessels or tracheids (Smith and Allen 1996). Because of the short period of measurement (6 d), this technical aspect was not a source of errors in our experiment. This technique can be used without calibration in apple trees, a species with a thermally homogeneous wood and with short, closely-spaced and interconnected xylem vessels, as reported by Green and Clothier (1988). The theory of the HPV technique is based on the assumption that the wood is thermally homogeneous and allows a rapid heat exchange between the water and the matrix of the xylem (Hall *et al.* 1998). However, precautions are always necessary otherwise errors could invalidate the technique and the results (Olbrich 1991). The application of the probes on such small stems did not seem to have damaged important portions of the sapwood, but their installation probably determined a reduction of the sap flows values obtained with respect to the control, nevertheless a narrow stem diameter can be a source of error (Cohen *et al.* 1993). Sapflow rates in this experiment followed a typical diurnal cycle increasing rapidly after sunrise to reach the highest values around 11:00 - 12:00 and then decreasing almost to zero in the late evening-night (data not shown).

Although results confirmed the affordability of the HPV method, further studies are required to verify the underestimation of transpiration rate recorded, in order to avoid technical errors and obtain more accurate results on small plants. In this experiment, the HPV method underestimated the transpiration rates of 32.4 %, with respect to the control. Errors associated with estimating individual tree water use can be as high 38 % when compared to a different method (Hatton *et al.* 1995).

Differences statistically not significant were observed between the two apple cultivars for any method adopted. The cumulative transpiration rate (data not shown) was almost identical for both cultivars, which suggests the absence of any particular influence of the rootstock on the scion in a short term period and under regular watering, although two different combinations of rootstock and scion have been used. Other researchers found that rootstock induced differences in transpiration (Hussein and McFarland 1994) on the same apple cultivar.

Conclusions: Of the five methods used to measure transpiration in young apple trees, the TDR method resulted the most similar to the gravimetric one used as the control method, giving the most reliable and accurate results. The TDR method, however, is particularly expensive and this could be a limit for a larger use. It was found to be sensitive to the probe surrounding and soil electrical conductivity. Nevertheless, this method is a less labor intensive way to obtain estimates of transpiration than measuring sap flux in many trees by the HPV method or assembling a whole plant chamber.

The reasonable agreement between HPV and gravimetric method suggested a potential application for measuring transpiration rates in small trees. But, the underestimation detected also suggested to use the appropriate cautions in determining all the parameters to avoid high errors. The single leaf transpiration rates showed limitations when values have been extrapolated to the whole canopy. The whole plant chamber seemed to partially overcome this problem, but errors of an overestimation can still occur. The major advantage of TDR, whole plant and HPV methods was that readings were easily and automatically recorded at frequent intervals. In experiments where there are large number of pots, and when trends in transpiration may be of interest, such methods may be superior to gravimetric measurements and the most appropriate to use.

References

Anisko, T., NeSmith, D.S., Lindstrom, O.M.: Time domain reflectometry for measuring water content of organic growing media in containers. - HortScience **29**: 1511-1513, 1994.

Baker, J.M.: Measurement of soil water content. - Remote Sens. Rev. **5**: 263-279, 1990.

Caspari, H.W., Behboudian, M.H., Chalmers, D.J., Renquist, A.R.: Pattern of seasonal water use of Asian pears determined by lysimeters and the heat-pulse technique. - J. amer. Soc. hort. Sci. **118**: 562-569, 1993.

Cassel, D.K., Klute, A.: Water potential: tensiometry. - In: Klute, A. (ed.): Methods of Soil Analysis. Part 1. 2nd Ed. Pp. 563-596. American Society of Agronomy, Madison 1986.

Cohen, Y., Fuchs, M., Falkenflug, V., Moreshet, S.: Calibrated heat pulse method for determining water uptake in cotton. - Agron. J. **80**: 398-402, 1988.

Cohen, Y., Takeuchi, S., Nozaka, J., Yano, T.: Accuracy of sap flow measurement using heat balance and heat pulse methods. - Agron. J. **85**: 1080-1086, 1993.

Corelli Grappadelli, L., Magnanini, E.: A whole-tree system for gas-exchange studies. - HortScience **28**: 41-45, 1993.

Cowan, I.R.: Stomatal behavior and environment. - Adv. bot. Res. **4**: 117-228, 1977.

Dye, P.J., Olbrich, B.W., Calder, I.R.: A comparison of the heat pulse method and deuterium tracing method for measuring transpiration from *Eucalyptus grandis* trees. - J. exp. Bot. **43**: 337-343, 1992.

Flore, J.A., Lakso, A.N.: Environmental and physiological regulation of photosynthesis in fruit crops. - Hort. Rev. **11**: 111-146, 1989.

Flore, J.A., Sams, C.E.: Does photosynthesis limit yield of sour cherry (*Prunus cerasus*) "Montmorency"? - In: Lakso, A.N., Lenz, F. (ed.): The Regulation of Photosynthesis in Fruit Trees. Pp. 105-110. New York State Agr. Exp. Sta., Geneva 1986.

Gardner, W.H.: Water content. - In: Klute, A. (ed.): Methods of Soil Analysis. Part 1. 2nd Ed. Pp. 493-544. American Society of Agronomy, Madison 1986.

Gee, G.W., Stiver, J.F., Borchert, H.R.: Radiation hazard from americium-beryllium neutron moisture probes. - Soil Sci. Soc. Amer. J. **40**: 492-494, 1976.

Grantz, D.A., Perry, M.H., Meinzer, F.C.: Using time domain reflectometry to measure soil water in Hawaiian sugarcane. - Agron. J. **82**: 144-146, 1990.

Green, S.R., Clothier, B.E.: Water use of kiwifruit and apple trees by the heat pulse technique. - J. exp. Bot. **39**: 115-123, 1988.

Gucci, R., Corelli Grappadelli, L.: [Measurement of photosynthesis. 2. Fields of applications and problems related to the plant material and environmental conditions.] - Frutticoltura **12**: 75-80, 1989. [In Ital.]

Hall, R.L., Allen, S.J., Rosier, P.T.W., Hopkins, R.: Transpiration from coppiced poplar and willow measured using sap-flow methods. - Agr. Forest. Meteorol. **90**: 275-290, 1998.

Hatton, T.J., Catchpole, E.A., Vertessy, R.A.: Integration of sap flow velocity to estimate plant water use. - Tree Physiol. **6**: 201-209, 1990.

Hatton, T.J., Moore, S.J., Reece, P.H.: Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. - Tree Physiol. **15**: 219-227, 1995.

Hussein, I.A., McFarland, M.J.: Rootstock-induced differences in sap flow of "Granny Smith" apple. - HortScience **29**:

1120-1123, 1994.

Katerji, N., Daudet, F.A., Carbonneau, A., Ollat, N.: Photosynthesis and transpiration studies with traditionally and lyre-trained vines. - Vitis **33**: 197-203, 1994.

Long, S.P., Postl, W.F., Bolhàr-Nordenkampf, H.R.: Quantum yields for uptake of carbon dioxide in C_3 vascular plants of contrasting habitats and taxonomic groupings. - Planta **189**: 226-234, 1993.

Long, S.P., Farage, P.K., Garcia, R.L.: Measurement of leaf and canopy photosynthetic CO_2 exchange in the field. - J. exp. Bot. **47**: 1629-1642, 1996.

Marshall, D.C.: Measurement of sap flow in conifers by heat transport. - Plant Physiol. **33**: 385-396, 1958.

Miller, D.P., Howell, G.S., Flore, J.A.: A whole-plant, open, gas-exchange system for measuring net photosynthesis of potted woody plants. - HortScience **31**: 344-346, 1996.

Moon, J.W., Jr., Flore, J.A.: A BASIC computer program for calculation of photosynthesis, stomatal conductance, and related parameters in an open gas exchange system. - Photosynth. Res. **7**: 260-279, 1986.

Olbrich, B.W.: The verification of the heat pulse velocity technique for estimating sap flow in *Eucalyptus grandis*. - Can. J. Forest Res. **21**: 836-841, 1991.

Richardson, M.D., Meisner, C.A., Hoveland, C.S., Karnok, K.J.: Time domain reflectometry in closed container studies. - Agron. J. **84**: 1061-1063, 1992.

Rochette, P., Pattey, E., Desjardins, R.L., Dwyer, L.M., Stewart, D.W., Dubé, P.A.: Estimation of maize (*Zea mays* L.) canopy conductance by scaling up leaf stomatal conductance. - Agr. Forest Meteorol. **54**: 241-261, 1991.

Sams, C.E., Flore, J.A.: The influence of age, position, and environmental variables on net photosynthetic rate of sour cherry leaves. - J. amer. Soc. hort. Sci. **107**: 339-344, 1982.

Schulze, E.-D.: Whole-plant responses to drought. - Aust. J. Plant Physiol. **13**: 127-141, 1986.

Smith, R.E.: The heat pulse velocity technique for determining water uptake of *Populus deltoides*. - S. Afr. J. Bot. **58**: 100-104, 1992.

Smith, D.M., Allen, S.J.: Measurement of sap flow in plant stems. - J. exp. Bot. **47**: 1833-1844, 1996.

Stone, J.F., Shirazi, G.A.: On the heat-pulse method for measurement of apparent sap velocity in stems. - Planta **122**: 169-177, 1975.

Swanson, R.H., Whitfield, D.W.A.: A numerical analysis of heat pulse velocity theory and practice. - J. exp. Bot. **32**: 221-239, 1981.

Teskey, R.O., Sheriff, D.W.: Water use by *Pinus radiata* trees in a plantation. - Tree Physiol. **16**: 273-279, 1996.

Topp, G.C., Davis, J.L.: Measurement of soil water content using time-domain reflectometry (TDR): a field evaluation. - Soil Sci. Soc. Amer. J. **49**: 19-24, 1985.

Topp, G.C., Davis, J.L., Annan, A.P.: Electromagnetic determination of soil water content: Measurement in coaxial transmission lines. - Water Resour. Res. **16**: 574-582, 1980.

Topp, G.C., Davis, J.L., Annan, A.P.: Electromagnetic determination of soil water content using TDR: II. Evaluation of installation and configuration of parallel transmission lines. - Soil Sci. Soc. Amer. J. **46**: 678-684, 1982.

Topp, G.C., Davis, J.L., Bailey, W.G., Zebchuk, W.D.: The measurement of soil water content using a portable TDR hand probe. - Can. J. Soil Sci. **64**: 313-321, 1984.

Yunusa, I.A.M., Walker, R.R., Loveys, B.R., Blackmore, D.H.: Determination of transpiration in irrigated grapevines: comparison of heat-pulse technique with gravimetric and micrometeorological methods. - Irrigation Sci. **20**: 1-8, 2000.

Zegelin, S.J., White, I., Jenkins, D.R.: Improved field probes for soil-water content and electrical conductivity measurement using time domain reflectometry. - Water Resour. Res. **20**: 2367-2376, 1990.