Diurnal Changes in Stem Diameter Depend Upon Variations in Water Content: Direct Evidence in Peach Trees

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Received 29 July 1992; Accepted 26 November 1992

ABSTRACT

Three to five-year-old peach trees (*Prunus persica* (L.) Batsch cv. 'Maycrest') grafted on *P.* 'Damas 1869' grown in a sand trench were removed in the spring and grown hydroponically for several months. The system comprised two balances continuously recording the mass of the nutrient solution and that of the tree, so as to estimate transpiration and water uptake rates separately. Diurnal variation in plant water content (transpiration minus water uptake) was observed, with rapidly decreasing values when the solar radiation increased, while the reverse occurred when radiation decreased. Changes in stem diameter were continuously recorded using linear variable differential transducers. Data collected over several days of contrasting climatic conditions revealed that rapid changes in the stem diameter occurred throughout the day and were closely related to plant water content. A lag-time not exceeding 10 min was found between changes in stem diameter and plant water content. These results are discussed in relation to the use of micromorphometric methods to control irrigation in fruit trees. Moreover, we give values for the water stored in the shoots which may contribute to the transpiration stream.

Key words: *Prunus persica*, stem shrinkage, plant water storage, water uptake, transpiration.

INTRODUCTION

Campbell and Turner (1991), like Li and Huguet (1990), stressed the advantages in scheduling irrigation by controlling plant water status rather than soil water content, or climate. Diurnal changes in plant water status have been described for a long time, with various plant indicators proposed. Among them, leaf water potential is a good candidate as it gives a measure of the energy developed for transpiration. However, methods of measuring water potential are not easy to use (Turner, 1986; Simonneau and Habib, 1991). Alternatively, relative water content is the most commonly-used measure of plant water status, despite difficulties in estimating small changes in stored water. Others indicators of the continuous response of the tree water status to environmental conditions have been proposed, such as attenuation of gamma radiation through stems (Edwards and Jarvis, 1983) or ultrasonic emissions (Jones, Higgs, and Bergamini, 1989). However, the micromorphometric technique based on stem shrinkage is simpler to use. Huguet (1985) developed it for use in irrigation systems and showed the benefits for manage-

ment of peach tree orchards (Li and Huguet, 1990). The method involves determining threshold values which are non-limiting for plant growth, but the corresponding water status (potential or water content) remains unknown. Moreover, relationships between stem shrinkage and plant water status are of particular interest in controlling limited water deficits, which may have advantageous effects on fruit crops (Jones, Lakso, and Syvertsen, 1985). Our aim was to define these relationships using experiments performed on peach trees where the micromorphometric method was used concomitantly with measurements of whole plant water content. Moreover, we determined the amount of water stored in the shoots which may contribute to the transpiration stream. To our knowledge, this has never been measured for such plants.

MATERIALS AND METHODS

Growing conditions

Experiments were conducted at the Montfavet INRA Centre in Southern France. Young peach trees (*Prunus persica* (L.) Batsch

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cv. 'Maycrest') grafted on *P. 'Damas 1869'* were first cultivated in a sand trench and then in sand containers as described by Simonneau and Habib (1991). In March 1989 and February 1991, some of these trees were removed from their containers and grown hydroponically in a greenhouse for several months.

Experimental device and data acquisition

At the start of the experiment, trees were transferred to a 35 dm³ pot of nutrient solution placed on a high precision load cell ('Uniweigh -50 Kgf -A3', 10 g accuracy) (Fig. 1). The solution (modified half-strength Hoagland solution) was maintained at a constant level by frequent additions, and was changed at least once a week. Each tree was suspended over the pot with its roots in the solution. The support holding the tree was placed on a balance ('Sauter Multirange EB 60', 5 g accuracy). Changes in stem diameter were continuously recorded using linear variable differential transducers (LVDT, 'Enertec CD41'). The sensor and its holder (5 μ m accuracy) have been described by Huguet (1985) and Li, Huguet, and Bussi (1989). Short-wave solar radiation was measured with a thermopile pyranometer ('Cimel Electronique CE 180') mounted near the top of the tree. Measurements of air temperature in the glasshouse were made with a copper resistance thermometer ('Cupro-SEM') placed in a ventilated screen. All the sensors were connected to an automatic data acquisition system (computer and 'AOIP SAM80' data logger).

Calculations of water flow rates

The upper level of the solution was kept within a narrow range to cover main roots close to the collar. It has been shown on the basis of root diameter changes (see Fig. 6 as an example) that volume changes of the upper root fraction were not

significant, whatever water status they exhibited (Simonneau, 1992). Nevertheless, as the emerged fraction of the roots varied with the quantity of solution, mass changes recorded by the load cell were not exactly the same as the mass of solution withdrawn. Differences were only due to changes in Archimedes forces, resulting from changes in the emerged volume of roots, providing there were no roots floating over the solution or rubbing against the pot. Mass values delivered by the load cell (M) could have been experimentally related to the total volume of solution plus that of the roots bathing in it. A preliminary calibration for each tree set up, using known quantities (Q) of solution added to the system versus corresponding M values, was made. Thus, using a smoothed relationship: $Q=f(M)$, flow rate through the root collar (Ab) was calculated. It has been termed absorption for simplicity in the following, but may differ from water uptake since non-steady-state conditions have been observed for roots. Transpiration rate (Tr) was more easily assessed by summing masses from the load cell and the 'SAUTER' balance. Transpiration minus absorption rate gave St , the flow rate of water stored in or lost from the above-ground plant reservoirs.

Data were logged every 5 min and water flows were calculated by smoothing the values over 30 min intervals.

Plant material

Three-year-old trees were used only to compare transpiration versus absorption rates.

The main results presented were obtained on a five-year-old tree. The LVDT was placed 55 cm above the root collar on the trunk (65 cm tall) to monitor changes in diameter (initial value: 6.0 cm). At the end of the experiment total fresh and oven-dried weights were, respectively 8730 g and 4320 g for shoots, and 2970 g and 660 g for roots.

Additionally, a four-year-old tree about 2.5 m tall was used. The trunk, 58 cm tall, bore three main branches about 70 cm long. LVDTs were located (i) on a main root (25 mm diameter) a few centimetres from the collar, (ii) on the trunk (60 mm diameter) 40 cm above the collar, (iii) on a main branch (30 mm diameter) 12 cm from its base, and (iv) on a terminal shoot (5 mm diameter) 6 cm from its base.

RESULTS

Transpiration and solar radiation

The diurnal patterns of both water uptake and transpiration were very close to that of solar radiation. As the radiation sensor was affected by the shadows from the greenhouse structures, rapid changes in radiation did not translate into rapid changes in transpiration on a whole tree basis. On bright sunny days (29 April 1991, Fig. 2), flow rates reached their maxima only a few minutes after that of the radiation. When cloudy and sunny periods alternated (27 April 1991, Fig. 2), parallel responses of transpiration and absorption were still noted.

Transpiration versus water uptake

The relationship between transpiration and water uptake rates (Fig. 3) showed a slight lag under bright sunny conditions (Fig. 3a). As classically found, when transpiration increased in the morning, it was slightly higher than uptake (points over the 1:1 line in Fig. 3) and slightly lower when transpiration decreased in the

FIG. 1. Experimental device and sketch of the measured flows of water (arrows). a: Balance, b: load cell, c: container of nutrient solution. Flexible aluminium foil sealed the pot and the roots to prevent evaporation but the tubing (d) allowed aeration. Transpiration (Tr) minus water absorption (Ab) gives St , the flow of water stored in or lost from the shoot of the tree.

FIG. 2. Rates of transpiration (a) and water uptake (b) by a 5-year-old peach tree, with corresponding climatic data (c) solar radiation and air temperature for 5 d in April 1991.

afternoon (points below the 1:1 line in Fig. 3). Only steady rate periods of sufficient duration could have led to steady-state (1:1 line). This was essentially the case with nocturnal periods.

During cloudy days (Fig. 3b), the previous scheme was respected with the following periods alternating very quickly: either the transpiration rate was increasing and Tr was higher than Ab , or the transpiration rate was decreasing and Tr was lower than Ab .

Diurnal changes in the shoot mass balance

Transpiration rates differed from water uptake. Differences (St , Fig. 4a) were due to non-steady-state conditions in shoots, since water reserves of the plant were rarely constant: during diurnal periods, reserves were either

becoming depleted ($St < 0$) by contributing to the transpiration stream (mainly in the morning) or restored ($St > 0$) by using a part of the water absorbed (in the afternoon). Values calculated for St were never high, ranging from -0.03 g s^{-1} to 0.03 g s^{-1} , which are typically 10–20% of midday values of the transpiration or absorption rates.

Diurnal changes in trunk diameter

Trunk diameter showed a gradual increase over a 5 d period (Fig. 4c) as reported previously without a limited water availability (Chalmers and Wilson, 1978; Li and Huguet, 1990). An average daily increase in diameter of 0.014 mm was due to trunk secondary growth. More rapid changes occurred within each day due to changes

FIG. 3. Relationship between water absorption and transpiration rates by 3-year-old peach trees during (a) a bright sunny day (18 May 1989) and (b) a cloudy day (21 April 1989). The 1:1 line corresponds to steady-state (constant water content) in the emerged part (above the nutrient solution) of the peach trees.

in water status. As for flow rates, trunk diameter varied almost simultaneously with solar radiation.

Shoot mass changes in relation to diameter changes of the trunk

The fresh weight of the tree increased during the experiment with an average daily gain of about 60 g for the shoots (Fig. 4b). Regardless of this growth, a simple comparison of Figs 4b and c clearly demonstrated that the trunk diameter varied with internal water balance of the shoots. However, since integration of *St* to calculate mass evolution led to summation of errors, comparison of *St* versus rate of change in trunk diameter was preferred (Fig. 5).

Globally, the relation was linear (Fig. 5a, 26 April 1991). For the 5 d period (25–29 April 1991), the Y-axis intercept of the regression line was not different from zero, and its slope was $0.7 \mu\text{m g}^{-1}$ ($n=983$; $r=0.84$). This confirmed very significantly the similar relationship previously reported by Klepper, Browning, and Taylor (1971) and Jordan and Ritchie (1971) on cotton.

DISCUSSION

Diurnal shrinkage has been shown to depend on water availability in the growth medium (Li and Huguet, 1990). Despite constant water availability, our results exhibited wide differences between days (from 0.03 mm on 25 April 1991 to 0.12 mm on 29 April 1991), due only to variation in climate demand.

Numerous authors (Klepper *et al.*, 1971; Parlange, Turner, and Waggoner, 1975; Huck and Klepper, 1977; So, Reicosky, and Taylor, 1979) have suggested stem

diameter is related to water potential rather than water content. Both variables may be correlated to stem diameter providing they are themselves linearly correlated (that is a capacitance independent of water content).

Swelling and shrinking of the trunk may not be caused solely by hydration–dehydration since temperature fluctuations induce changes in trunk diameter due to thermal expansion of the tissues. This was clearly demonstrated on a pickled apple by Huguet (1985), whereas the sensor and its holder were shown to be temperature-insensitive. However, *in situ*, plant organs exhibit lower thermal fluctuations as a result of shading by the foliage and continuous ascent of sap. Hence, trunk diameter of the peach trees was less sensitive to air temperature fluctuations. For example, a slight increase in temperature on 28 April 1992 in the morning (Fig. 2c) did not induce any trunk expansion (Fig. 4c). On the contrary, with an accompanying increase in transpiration rate, trunk shrinkage was observed.

In addition, certain mechanisms of adaptation to water deficits, such as osmotic adjustment (as suggested by So *et al.*, 1979) or increase in tissue elasticity (Turner, 1986) may alter stem diameter. These latter mechanisms were not expressed in the experimental conditions reported here. Therefore, trunk diameter changes cannot be of long-term use to monitor continuously the amount of water stored in the tree.

The *St*–diameter changes relation in Fig. 5 exhibited slight differences if separately drawn up for nocturnal and diurnal phases. During nocturnal phases and accompanying mass increases, very moderate changes in trunk diameter were seen compared with diurnal phenomena.

FIG. 4. (a) Flow rate of water stored in or lost from the emerged part of a 5-year-old peach tree; fluctuations of (b) the weight of the emerged part of the tree and (c) trunk diameter with time.

The presence of both primary and secondary growth in dicotyledons offers a possible explanation. Only secondary growth could lead to diameter increase. Thus, this fraction of the water, newly stored for primary growth, induced mass increase of the whole plant without a corresponding diameter change at the sensor site. Whether diurnal expansion and hydration–dehydration phenomena occur concomitantly is open to question since both processes may vary with turgor pressure (Lockhart, 1965; Tyree and Jarvis, 1982).

Lags between changes in diameter and in leaf water potential (Klepper *et al.*, 1971; Parlange *et al.*, 1975), or lags in diameter changes down tree stems have been reported (Wronski, Holmes, and Turner, 1985) and may affect the diameter–water status relation. Very scattered lag times were reported ranging from 0.25 h (down

20–25 m-tall *Pinus radiata* D. Don; Wronski *et al.*, 1985) up to 2.5 h between leaf water potential and stem diameter (on soybean submitted to a drought cycle; So *et al.*, 1979). Regarding our experiments on 2–3 m tall peach trees, changes in trunk or branch diameters were very close to changes in climate conditions, wherever the dendrometer was positioned on the plant (Fig. 6).

Theoretically, lags between changes in diameter and in xylem water potential depend on the rate of changes in the transpirational demand (Wronski *et al.*, 1985; Simonneau, 1992) and need the use of a diffusion model across the thickness of living tissues to be interpreted (Jarvis, 1975; Parlange *et al.*, 1975; Nobel and Jordan, 1983; Wronski *et al.*, 1985). Nevertheless, our results provided another way to maximize radial resistance to water diffusion between conducting and reservoir tissues, on the

FIG. 5. Relation between the rate of change in trunk diameter and St , the rate of water accumulation or loss from the emerged part of the peach tree (26 April data set of Fig. 2). (a) Rate of change in diameter related to St at the same time, (b) rate of change in diameter related to St 10 min earlier.

FIG. 6. Diurnal evolution of diameters for various locations of the dendrometers (LVDT) on a 4-year-old peach tree, and corresponding solar radiation for the same day (4 September 1990).

basis of the time lag (about 10 min) stressed in Fig. 5. Very low values for this hydraulic resistance were then suggested.

Moreover, St values were very low as compared with transpiration rates (Fig. 3a as compared with Fig. 4a), and must have excluded high values for the daily maximum dehydration of the shoots. Indeed, diurnal decreases in shoot mass never exceeded 150 g. It is possible to calculate the degree of daily plant transpiration that can

be obtained from the total water stored in the plant (Jarvis, 1975). But our results showed that a great part of the total water (4410 g) stored in the emerged parts of the peach tree did not contribute to the transpiration stream (or was simultaneously replaced). It is not known what anatomical compartment or tissue type was concerned with these fluctuations in water content. Changes in stem diameter have been demonstrated in the peripheral living cells in cotton (Molz and Klepper, 1973) and in trees (Jarvis, 1975) and have been related to changes in water content. However, the water content of the sapwood of trees has also been shown to vary (Waring and Running, 1978; Zimmermann, 1983; Kozłowski, Kramer, and Pallardy, 1991).

CONCLUSION

It is commonly agreed that changes in diameter and, more generally, shrinking and swelling of elastic tissues are related to changes in their water content. But since Klepper *et al.* (1971) and Jordan and Ritchie (1971) obtained a poor correlation between water content and stem diameter of cotton plants, no clear relation has been drawn up. Results obtained here on 3–5-year-old peach trees clearly demonstrated that stem diameter changed in close relation to the total water stored in the shoots, without any important lag. Corresponding changes in water content were very small. This stressed the high sensitivity of trunk diameter measured with LVDT.

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