STORED WATER TRANSPORT MODEL CONSTRUCTION FOR PEACH TREES

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Abstract

Potted peach trees were used to study the movement of water in different tissues of peach trees by using the resistor and capacitor (RC) model. The simulation results demonstrated that during the day time, there was a continuous flow of the stored tissue water into the transpiration stream and reached the maxima by 9 a.m. By 5 p.m. in the evening, the tissues began to absorb water and continued this process until the next morning. The dynamics of water storage across all parts were closely related to their tissue water potentials. The stem accounted for 58% of the total amount of water stored on sunny days, followed by the branches, roots and leaves, and the fruits contained the least amount. The numerical simulation showed that the model presented in this study may be used to simulate the dynamics of tissue water storage in different parts of potted peach trees. The model related parameters are relatively simple and can be obtained by conventional physiological instruments.

Introduction

The transpiration of plants plays an important role in the movement of water and latent heat between atmosphere and soil. Therefore, investigations on the principle of water transport by plants have always been the focus by meteorologists and ecologists (Jackson *et al.* 2000, Tomo'omi 2001). Water serves as an essential solvent for biochemical reactions of various molecules in plant cells and also acts as a carrier for material transport from soil to plant and inside the plant cells. It is a vital factor for maintaining plant morphology and growth. Besides, for high yielding crops, water is considered as a key factor (Jones and Tardieu 1998). The soil-plant-atmosphere continuum theory (SPAC) proposed by Cowan (1965) provided a theoretical framework for plant water research (García-Tejera *et al.* 2017, Huang *et al.* 2017). By simulating the physiological growth of plants with mathematical modeling, the effects of various external factors on plants and the interrelationships of various states can be studied synthetically. This deepens further the understanding regarding the principles of the plant physiological growth. The construction of a systematic model on tissue water storage in fruit trees, describes not only the dynamics of water movement of fruit trees comprehensively and precisely, but also can guide the quantitative irrigation, providing a theoretical basis for agricultural automation and information gathering (Moriana *et al.* 2012). Constructing systematic model could also be used to investigate the crop growth pattern.

Materials and Methods

The experiment was conducted at the experimental station in Beijing Vocational College of Agriculture in 2017. The test materials included 4-year-old potted peach trees *(Prunus persica* var. *nectarina* Maxim). The tree-plot experiment had 32 replicates, with favorable soil moisture and nutrient conditions, and the same cultivation management measures. The trees had approximately the same crown sizes and bottom stem thicknesses. During the early and middle stages of fruit

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ripening (from late May to early June), the different parts of each tree (including leaves, branches, fruits, stem, roots) were sampled three times separately. Then the pressure-volume (P-V) curves were drawn and the time parameters were recorded, and the water capacitance of each part was determined based on the P-V curve (Raymond *et al.* 1987). The stem and branch water capacitances were represented by the water capacitance of a 3-year-old branch. The water resistance of each part was determined based on the water capacitance and time parameters (Nobel and Jordan 1983).

The flow pattern of sap was studied in 16 selected trees using a heat pulse sphygmomanometer (Dauzat *et al.* 2001). Among them, eight trees with regular variations were selected to calculate the diurnal sap flow changes. The water potentials of the leaves (ψ_l) and the main root (ψ_{rs}) were measured with a Scholander water potential instrument from June 15 to 18. The water potential of the main root（ψ_{rs} was represented by the water potential of the root system connecting to the main root, and $\psi_{rs}/2$ was used to represent the water potential of the root system (Raymond *et al.* 1987, Nobel and Jordan 1983). To measure the stem water potential, the leaves from the sprout stem at their base were wrapped tightly with plastic bags, balanced for two hours before measuring the leaf water potential, and then it was used to represent the stem water potential (Abrisqueta *et al.* 2015, Simonin *et al.* 2015). The crown transpiration was determined by the modified Penman-Monteith equation from Caspari *et al.* (1993):

$$\lambda E = \frac{sR_n + 0.93\rho c_p D_a / r_a}{s + 0.93\gamma(2 + r_s / r_a)} \tag{1}$$

where E is the transpiration rate per unit leaf area, R_n is the net radiation flux density absorbed by the leaf, ρ is air density, c_p is specific heat capacity of air, λ is the latent heat of evaporation of water, γ is the psychrometer constant, s is the slope of the curve relating saturation vapor pressure to temperature, D_a is the vapor pressure deficit of the air, r_a is the leaf boundary layer resistance, and r_s is stomatal resistance. Use of the factor 0.93 is based on the assumption that boundary layer resistance for vapor is 0.93 times that of sensible heat (Caspari *et al.* 1993).

The flow of water storage per unit volume (q) is as follows (Lhomme *et al.* 2001):

$$q^j = -C^j \frac{d\psi^j}{dt} \tag{2}$$

$$\psi^j = E^j(1 - e^{-t/R^jC^j}) \tag{3}$$

where, C^j is the water capacitance of part j; E^j is the difference between the tissue water potential and the soil water potential; R^j is the water storage resistance of part j; t is the time for water potential change.

Due to the limited sensitivity of the instrument, the water absorbed at night could not be determined accurately. Therefore, we assumed it to be the same as the stored water that moved to various parts of the plant. Subsequently, the percentage of the water storage change in each part to the total sap flow was calculated for different times of the day. The dry weight of each part of the eight plants was recorded. Moreover, the saturated water content of each part was estimated by the dry weight and the P-V curve (Nobel and Jordan 1983, Raymond *et al.* 1987).

Results and Discussion

Fig. 1 show the P-V curves from the tissues of root, branch, leaf and fruits of peach tree. The most stable curve was shown by branches, followed by the leaves and roots. The curve for fruits showed sharpest decline (Fig. 1). The P-V curve of roots crossed with that of the leaves. At a

normal range of water potential (0 to −2 MPa), the P-V curve of the roots was more stable than that of the leaves. The results demonstrated that when the water potential changed, the branches absorbed (or released) most of the stored water, therefore, their water regulation capacity was strongest, followed by the roots and leaves, and the weakest was in fruits. It can also be seen from Fig. 1 that the P-V curves of the leaves and fruits were stable at their terminal portion. Whereas, the curves changed sharply for the roots and branches. This was due to the fact that the water of the leaves and fruits was primarily stored in living cells. According to Van't Hoff's law, after turgor pressure dropped, the tissue water potential ψ_w equaled to its matrix potential ψ_s, proportional to the reciprocal of the tissue relative water content (RWC^{-1}). Nevertheless, the water of the roots and branches was mainly stored in the catheters. The changes in the P-V curves were related to the turgor pressure (which was usually a negative value), and the turgor pressure was determined by its structural characteristics. The exact underlying mechanism is still elusive.
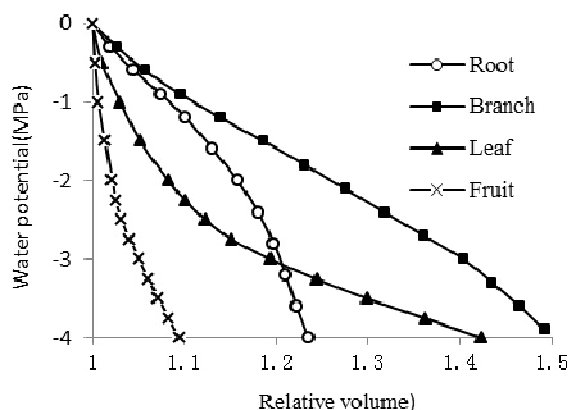

Fig. 1. P-V curves from the tissues of different parts of peach trees.

Table 1. Storage water capacitance and conductance in different parts of peach[a]

	Capacitance ($m^3 \cdot m^{-1} \cdot Mpa^{-1}$)	Conductance (($m^3 \cdot s^{-1} \cdot Mpa^{-1}$)
Leaf	0.0383c	$4.612 \cdot 10^{-4}$b
Fruit	0.0090d	$0.002 \cdot 10^{-4}$c
Branches	0.1050a	$0.086 \cdot 10^{-4}$c
Stem	-	$0.046 \cdot 10^{-4}$c
Main root	-	$0.090 \cdot 10^{-4}$c
Lateral root	0.0697b	$0.145 \cdot 10^{-4}$c
Fine root	-	$11.825 \cdot 10^{-4}$a

[a] Mean values and ± SE with different lower case letters in a row are sinificantly different at $p < 0.05$.

The range of water potential for different tissues of peach trees was as follows, 0 to −2.0 MPa for leaves, 0 to −1.5 MPa for branches and fruits, and 0 to −1.0 MPa for roots. Within their individual range, the branches had the largest average capacitance, with a value of 0.1050 $m^3 \cdot m^{-3} \cdot MPa^{-1}$, followed by the roots, leaves and fruits as 0.0697, 0.0383 and 0.0090 $m^3 \cdot m^{-3} \cdot MPa^{-1}$, respectively (Table 1).

The reciprocal of the water transport resistance R_s^j of each part was taken as the storage water conductance (Gw) to indicate the difficulty level for stored water entering and exiting the tissue. The larger the Gw, the easier the water gets in and out of the tissue. Because of the huge differences in the time parameters for each part, the differences of the water transport resistance and the transport indexes were high. Among them, the transport index of the fine roots was the highest, which was $11.825 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$ and was about 5000 times higher compared to that of fruits. The value for leaves was $4.612 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$, followed by lateral roots ($0.145 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$), main roots ($0.090 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$), stem ($0.046 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$), branches ($0.086 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$) and fruits ($0.002 \cdot 10^{-4}$ $m^3 \cdot s^{-1} \cdot MPa^{-1}$). The least water capacitance of the fruits indicated their weakest water regulation capacity (Table 1).

According to the transpiration model of canopy and the tree water transport model, the water transport rates of the canopy, stem and root system may be simulated (Fig. 2). It demonstrated that the dynamics of canopy transpiration, stem sap flow and root sap flow was highly consistent to each other. Each of the above-mentioned parameters exhibiting a curve with one single peak and slight fluctuations at noon (Fig. 2). The changes in stem and roots were relatively slight. Their peaks appeared later than that of the canopy transpiration, about 1 hour late for the stem sap flow and 2 - 3 hrs late for the root sap flow. The peak hysteresis was caused by the regulation of water storage in the tree body. As shown in Fig. 3, the stored water of potted peach trees gradually flew into the transpiration stream at 5 a.m. in the morning when the stomata began to evaporate water, and hit the peak at about 9 a.m. Throughout the day-time, the stored water continuously decreased. By 4 p.m. in the afternoon, as the decrease of the transpiration rate and the tissue water potential occur, the tissues began to intake water (Fig. 3). In the evening i.e., around 9 p.m., the water flowing into the tissues reached the maximum. The tissues were in a water uptake state throughout the night, and the tissue water potential kept increasing accordingly. The present simulations demonstrated that all parts of peach trees may store water at night for the transpiration during the
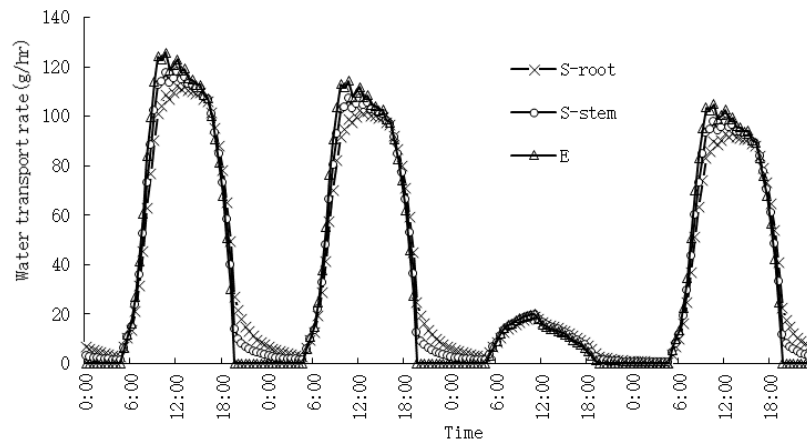

Fig. 2. Water transport rate of canopy transpiration (E), stem sap flow (S-stem), and root sap flow (S-root).

day-time, and the peach tree may store up to 20 - 30% of the total sap flow on sunny morning. This dynamics in stored water is crucial for the maintenance of stomatal opening and gas exchange in the daytime. However, it should be pointed out that the processes of water uptake for different tissues varied a lot due to the differences in the water storage resistance of different parts.
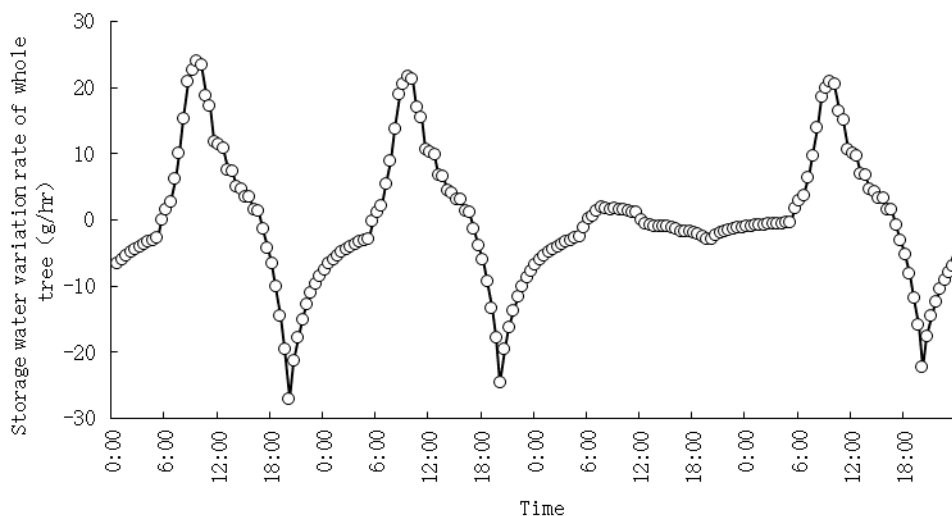
Fig. 3. Dynamic simulation of stored water in peach tree body.

Fig. 4 showed that the water storage dynamics were different for various tissues of potted peach trees on different days (June, 15 - 18), which was caused by the diurnal course of water potential. The stored water increased with the decrease of water potential, then flew into the transpiration stream from the tissues. On the other hand, when the tissue water potential increased, the stored water reduced, then the tissue absorbed water. The water potential varied significantly for different parts, with the biggest change in leaves, followed by branches, the stem, roots and the smallest in fruits. This difference was caused due to the various water storage resistance of each part of the experimental tree. The rule followed is, the greater the resistance, the smaller the change. In addition, due to the small changes in transpiration on cloudy days, the range of variation in tissue water potential and water storage also decreased. From Fig. 4, it can be seen that there was a remarkable difference in the regulation capacity of water storage in each part, with the largest in the stem (include taproot) which accounted for 58% of the total water storage regulation on sunny days (calculated by the ratio of the maximum amount of stored water released in sunny days to the sap flow rate in that period). This was followed by branches, roots and leaves and the least in fruits. The water regulation capacity of stem is high because of its bigger water capacitance and volume. Due to the small water capacitance and huge resistance present in the fruits, they only regulate the water storage slightly.

In the past, scientists were puzzled by the research question - why water may travel from the roots to the top of the plant? In 1948, Honert proposed a steady state flow model of plant water transport based on the analogy to Ohm's law (Honert 1948). Later on, workers found that the water stored in plants had an important impact on the water transport (Nobel *et al*. 1983, García-Tejera *et al*. 2017), and further proposed a non-steady-state model of water transport, the RC model. All currently available water transfer models are based on the analogy to the electric circuit model, and the most common one is the RC model (Jones and Tardieu 1998). The water transport resistance comes primarily from the root-soil interface and the leaf-air interface and it is generally smaller in plant body, especially for the small plants (Jones 1994). The water storage that affects the water transport of trees mainly resides into the xylem tissues of the stem, branches, root system and leaves of plants (Holbrook 1995). To study the water transport principle of a whole tree, the water transport parameters from each tissue may be considered. The numerical simulation

showed that the model presented in this study may be used to simulate the dynamics of tissue water storage in different parts of potted peach trees. The model related parameters are relatively simple and can be obtained by conventional physiological instruments. It could be used as a reference for carrying out studies on water storage of other tree species too.
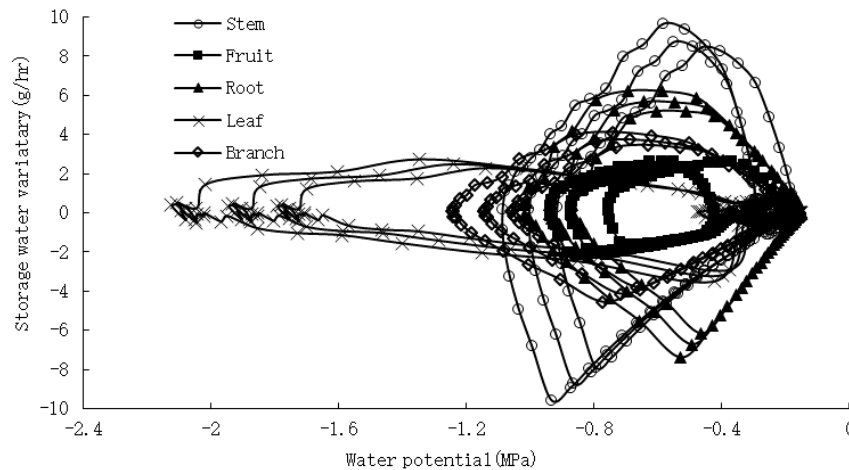

Fig. 4. Dynamic simulation of water potential and water storage in different tissues of potted peach trees.

The present analysis demonstrated that the water regulations of peach tissues were different at different times, and this difference was primarily caused by the variations of water potential and sap flow. The relative water regulation capacities of different parts were significantly different as well, with the strongest for the stem which regulated more than half of the water transport; followed by the branches and roots, and the weakest for the leaves and fruits. This difference was primarily determined by water capacitance, resistance and volume. Waring *et al.* (1979) concluded that 30 - 50% of the daily transpiration of Scots pine was from the stem water storage. Loustou *et al.* (1996) opined that when soil aridity increased, the contribution of the stem water storage to the transpiration stream could be increased from 12 - 25%. Other studies suggested that the water storage had different usages for different types of plants and did not work significantly for smaller plants (Carlson and Lynn 1991). In the past, the P-V curves of leaves were often used to compare the water regulation capacities under different conditions or for different plants. From the analysis of this study it can be seen that the water regulation capacity of leaves only accounted for 3.4% of the total water storage regulation. Therefore, the other method seems scientifically not much sound. However, the present study is only a trial on potted plants and has not been validated in the field study. So, there is an ample scope of carrying out further studies at field level for its improvement.

Acknowledgements

References

Abrisqueta I, Conejero W, Valdés-Vela M, Vera J, Ortuño MF and Ruiz-Sánchez MC 2015. Stem water potential estimation of drip-irrigated early-maturing peach trees under Mediterranean conditions. Computers and Electronics in Agriculture **114**: 7-13.

Carlson TN and Lynn B 1991. The effect of plant water storage on transpiration and radiometric surface temperature. Agricultural and Forest Meteorology **57**: 171-186.

Caspari HW, Green SR and Edwards WRN 1993. Transpiration of well-watered and water stressed Asian Pear Trees as determined by lysimetry, heat-pulse, and estimated by a Penman-Monteith model. Agricultural and Forest Meteorology **67**: 13-27.

Cowan IR 1965. Transport of water in the soil-plant-atmosphere system. Journal of applied Ecology **2**: 221-239.

Dauzat J, Rapidel B and Berger A 2001. Simulation of leaf transpiration and sap flow in virtual plants model description and application to a coffee plantation in Costa Rica. Agricultural and Forest Meteorology **109**: 143-169.

García-Tejera O, López-Bennal Á, Testi L and Villalobos FJ 2017. A soil-plant-atmosphere continuum (SPAC) model for simulating tree transpiration with a soil multi-compartment solution. Plant Soil **6**: 1-19

Holbrook NM 1995. Stem water Storage. In Plant Stems: Physiology and Functional Morphology (ed. B.L. Gartner), Academic Press, San Diego. 151–174.

Honert TH 1948. Water transport in plants as a catenary process. Discussions of the Faraday Society 3: 146 -150.

Huang CW, Domec JC, Ward EJ, Duman T, Manoli G, Parolari AJ and Katul GG 2017. The effect of plant water storage on water fluxes within the coupled soil–plant system. New Phytol. **213**: 1093-1106.

Jackson RB, Sperry JS, Dawson TE 2000. Root water uptake and transport: using physiological Processes in global predictions. Trends in Plant Science **5**: 482-488.

Jones H and Tardieu G 1998. Modelling water relations of horticultural crops: a review. Scientia Horticulturae **74**: 21-46.

Jones H G 1994. Plant and Microclimate. Cambridge Univ. Press, Cambridge.

Lhomme JP, Rocheteau A, Ourcival JM and Rambal S 2001. Non-steady-state modelling of water transfer in a Mediterranean evergreen canopy. Agricultural and Forest Meteorology **108**: 67-83.

Loustou D, Berbigier P, Roumagnac P, Arruda-Pacheco JS, David MI, Ferreira JS, Pereira R and Tavares 1996.Transpiration of 64-year-old maritime pine stand in *Pordugal. L. Seasonal* course of water flux through maritime pine. Oecologia **107**: 33-43.

Moriana A, Pérez-López D, Prieto MH, Ramírez-Santa-Pau M and Pérez-Rodriguez JM 2012. Midday stem water potential as a useful tool for estimating irrigation requirements in olive trees. Agricultural Water Management **112**: 43-54

Nobel DS and Jordan PW 1983. Transpiration stream of desert species: resistances and capacitances for a C_3, a C_4, and a CAM plant. Journal of Experimental Botany **34**: 1379-1391.

Raymond HER and Nobel PS 1987. Non-steady-state water flow for three desert perennials with different capacitances. Australian Journal of Plant Physiology **14**: 363-375.

Simonin KA, Burns E, Choat B, Barbour MM, Dawson TE and Franks PJ 2015. Increasing leaf hydraulic conductance with transpiration rate minimizes the water potential drawdown from stem to leaf. Journal of Experimental Botany **66**(5): 1303-1315.

Tomo'omi K 2001. Modeling water transportation and storage in sapwood model development and validation. Agricultural and Forest Meteorology **109**: 105-115.

Waring RH, Whitechead D and Jarvis PG 1979. The contribution of stored water to transpiration in Scots pine. Plant Cell Environment **2**: 309-317.