Sap flow in papaya plants: Laboratory calibrations and relationships with gas exchanges under field conditions

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Abstract

In papaya plants a study to quantify the water flow through the trunk is important for to promote a good water management in commercial orchard. The objective was to study the relationship between water flow through the trunk and temperature measurements determined by probes inserted in the papaya plant stem in laboratory. In addition, was possible to study the relationship between sap flow and instantaneous gas exchange in field conditions. We constructed an instrument that maintained a stable water flux through a 0.30 m stem section with a constant pressure, simulating the xylem sap flow through the stem. Water flux was adjusted by varying pressure of water in the stem section. The mathematical model used to fit the relation between $K$ (Granier heat coefficient) values and sap flow density was the exponential model: $u = 0.5511 \times K^{1.9104}$. Field studies was conducted in a commercial orchard located in North of the State of Rio de Janeiro, with 12 plants in October 2002, and eight plants in January 2003. We verified that instantaneous transpiration, measured by a portable system of gas exchange (porometry), presented a good ($R^2 = 0.75$) positive relationship with xylem sap flow. Estimates of papaya sap flow can be obtained by scaling portable photosynthesis system measurements with exposed leaves, however the relationship is non-linear in higher instantaneous transpiration rates. The causes of the non-linear relationship in higher transpiration are discussed. In addition, was possible to obtain a good ($R^2 = 0.76$) relationship between net photosynthesis rate and xylem sap flow in papaya field-grown.

Keywords: Papaya; Sap flow; Gas exchange

1. Introduction

The amount of water required for growth and development of higher plants is larger than those of all other constituents such as mineral ions or carbon dioxide (Steudle, 2002). Stomata are the primary conduit of water vapor to leaf to the atmosphere, and play an important role in water loss control in leaves.Stomata control is coordinated by light intensity and quality, CO₂ external concentration, leaf water condition, metabolites produced into foliar mesophyll and into roots, and air humidity (Farquhar and Sharkey, 1982). The leaf-to-air vapor pressure deficit influences stomatal closure, and high values of VPD_{leaf-to-air} cause stomatal closure (Yong et al., 1997).

Papaya, which presents stomata only in the leaf abaxial surface (El-Sharkawy et al., 1985), had a decrease of 47 and 48% in the stomatal conductance and photosynthesis net rate, when VPD_{leaf-to-air} changed from 1 to 1.5 kPa to 3.5–4.5 kPa (El-Sharkawy et al., 1985). According to the authors, in 19 species studied, including Carica papaya L., stomata closure caused by VPD_{leaf-to-air} was associated with the peristomatal evaporation (water loss directly from guard cells to environment).

In papaya, water limitations reduce stomatal conductance, net rate of photosynthesis and quantum yield, which significantly affect the crop yield (Marler et al., 1994; Marler and Mickelbart, 1998). These authors demonstrated that although the PS II, was tolerant in relation to the water stress in irrigated plants (ψw = −20 kPa), the maximum photosynthetic rate (measured in 1800 μmol m⁻² s⁻¹ of photosynthetic photon flux density-PPFD) was reduced 40% in plants on a soil with −60 kPa water potential and the quantum yield (A/PPFD) was reduced 50%.

Several techniques to estimate the transpiration rate have been developed to improve the irrigation control and elucidate...
plant–water relations. These techniques include xylem sap flow determination and transpiration rate measurements by porometry (Zhang et al., 1997). There are many techniques used to determine the xylem sap flow. All use heat as a tracer for sap movement, and each has advantages and limitations in terms of ease of use, cost and size of plant stem on which they can be used (Smith and Allen, 1996). The heat dissipation method was brought into use by Granier (1985) and it relates the xylem sap velocity to the temperature differences between heated and unheated probes inserted radially into the steam.

Heat dissipation increases and the temperature difference between the two probes declines asymptotically with increasing sap velocity (Clearwater et al., 1999). Granier adjusted the equation to: \( u = 119 \times 10^{-6}k^{1.0231} \), where \( u \) is the sap flow density and \( k \) is the Granier heat coefficient, calculated by the equation: \( k = (\Delta T_{\text{max}} - \Delta T)/\Delta T \), where \( \Delta T \) is temperature differences between the two probes. Heat dissipation probes have been used successfully in a number of studies of tree water use (Bréda et al., 1985; Loustau et al., 1996; Andrade et al., 1998). However, Smith and Allen (1996) advised that the technique should be calibrated for each species. Another advantage to this technique is the possibility of automating the irrigation system based on the plant transpiration (Van Bavel et al., 1996). An adjustment of this technique is the use of heat pulse method and not the use of constant heat (Fernández et al., 2001). In olive, the heat pulse method of sap flow measurement controlled an automated irrigation system, which formed this basis to calculate water movement in the root zone and predict plant water status (Nadezhdina, 1999; Fernández et al., 2001).

There are no reports of constant heat techniques in papaya. Therefore, it is necessary to evaluate the technology in this important tropical fruit crop.

The present study evaluated the relationship between water flow through the trunk and the temperature measurements determined by probes inserted in the papaya plant stem in laboratory and field studies and related the xylem sap flow values measured under field conditions with instantaneous gas exchange measurements.

2. Material and methods

2.1. Laboratory calibrations

The calibration experiment was performed at the State University of North Fluminense, Agricultural Engineering Laboratory, Campos dos Goytacazes, RJ. A device was construct that maintained a stable water flow through a stem (Fernández et al., 2001) (Fig. 1). Water flow, simulating the xylem sap flow through the papaya tree stem, was established with constant pressure in a papaya stem 30 cm in length and 5.5 cm in diameter. The water flow difference was measured by pressure changes in water injection into the stem.

Two thermocouples probes 2 mm in diameter and 30 mm in length were inserted radially into the node of the papaya trunk section. The node was selected cause this part of the trunk has the highest percentage of vascular bundles and minimal void space. The probes were vertically separated by 50 mm. The higher probe had an electric resistance heater. Three volts was applied to the resistance heater every 10 s, and the temperature difference (\( \Delta T \)) between the probes were recorded every 10 min.

The trunk and probes were covered with foam insulation to minimize trunk temperature variation. \( \Delta T \) was measured for 6 values of water flow and 5 replications of papaya stem sections. The xylem flow density values (\( u \ m^3 s^{-1} m^{-2} \) active xylem) were obtained from the relationship between water flux and the active xylem area. The active xylem area was estimated using the red-dye safranin staining from several cut stems of different diameters. The colored area was measured and considered the xylem area in cm². From these data, it was possible to make the relationship between \( K \) (Eq. (1)) and sap flow density (\( u \)).

\[
K = \frac{\Delta T_m}{\Delta T} - 1
\]
where $K$ is the Granier heat coefficient; $\Delta T_m$ the maximum temperature difference between sensors in active xylem, °C (zero flow); $\Delta T$ is the temperature difference between sensors in active xylem, °C; the sap flow system of Dynamax Co., Houston, TX, USA was used in laboratory and a field studies.

3. Field experiment

3.1. Plant material and field conditions

The study was carried out in a commercial ‘Formosa’ papaya orchard, located in the city of São Francisco do Itabapoana/RJ (21°27’S, 41°15’W, 12 m of altitude).

The study used 9 and 12-month papaya plants (Carica papaya L.) in October 2002 and January 2003, respectively. The orchard was center pivot irrigated. Tree spacing was 3.8 m between rows and 2.0 m between plants, totaling 1316 plants ha$^{-1}$. Trees were fertilized. The maximum value of photosynthetic photon flux density in October was 1877 μmol m$^{-2}$ s$^{-1}$ and in January was 2393 μmol m$^{-2}$ s$^{-1}$.

3.2. Xylem sap flow investigation in papaya field-grown

The study was carried out in two periods: October 2002 and January 2003 using eight plants for each period. In each sample period, the xylem sap flow was measured for 4 days; two plants each day. The probes were inserted into the stem to a height of 0.30 m from soil surface similar to the laboratory study.

Papaya leaf area was estimated by $\log \text{AF} = 0.315 + 1.85 \log \text{NCF}$; $R^2 = 0.898$; where AF is the leaf area, and NCF is the central vein length (Campostrini and Yamanishi, 2001). The xylem sap flow was expressed by leaf area unit. A 9.83 cm$^2$ area of active xylem was used to estimate the xylem sap flow. In the calibration moment, 9.83 cm$^2$ was the active xylem area of the trunk used. When our equation is applied ($0.5511 \times K^{1.9104}$), the flow is expressed in l h$^{-1}$ cm$^{-2}$ (per cm$^2$ of active xylem area).

Then, to express it in leaf area, multiply the value by the active xylem area of the measured trunk (the flow is expressed in l h$^{-1}$ plant$^{-1}$), and divide the product by the leaf area. Now, the sap flow is expressed in $1$ h$^{-1}$ m$^{-2}$ (leaf area unit).

An equation was made to relate the circumference of the trunk with the active xylem area ($Y = 3.317X - 47.887$; $R^2 = 0.9356$); where Y is active xylem area (cm$^2$) and X is circumference of the trunk (cm) where the probes were inserted.

Transpiration ($E$, mmol m$^{-2}$ s$^{-1}$) and net photosynthetic rate ($A$, μmol m$^{-2}$ s$^{-1}$) were measured at the same time and at the same plant the xylem sap flow was measured (every hour, between 8 a.m. and 5 p.m.), using a portable system of gas exchange; model LI-6200 (LI-COR, Lincoln, NE, USA). Two illuminated mature leaves (9th and 10th leaf counted from the top) were used.

The main water potential of soil ($\psi_{soil}$), air temperature, relative humidity, air and vapor pressure deficit (VPD), of the October 2002 and January 2003 sampling periods were measured (Table 1).

4. Results and discussion

4.1. Laboratory calibration

Sap flow density ($u$; l h$^{-1}$ cm$^{-2}$ active xylem) was exponentially related to $u: 0.5511 \times K^{1.9104}$ (Granier, 1985). The derived laboratory calibration model estimated larger $u$ values than predicted by Granier (1985) for equal $K$ values (Fig. 2). Differences in xylem vessel distribution and diameter, and the higher water content of papaya stems may explain the differences in the results between our results and Granier (1985). As the xylem vessels are more concentrated at the trunk periphery (Fig. 3), this distribution could have provided the passage of a volume of water through the trunk corresponding to the temperature variation of the probes.

Table 1

<table>
<thead>
<tr>
<th>Month</th>
<th>Air temperature (°C)</th>
<th>Water potential of soil ($\psi_{soil}$, kPa)</th>
<th>Relative humidity (%)</th>
<th>VPD of the air (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>October 2002</td>
<td>29.4 ± 2.7</td>
<td>$-28.5 \pm 8.5$</td>
<td>48.3 ± 9.7</td>
<td>2.2 ± 0.7</td>
</tr>
<tr>
<td>January 2003</td>
<td>29.9 ± 2.7</td>
<td>$-12.1 \pm 8.7$</td>
<td>68.5 ± 11.15</td>
<td>1.4 ± 0.7</td>
</tr>
</tbody>
</table>

Daily medium values obtained from 8 a.m. to 5 p.m., $n = 40$. 

Fig. 2. Relationships between Granier heat coefficient and xylem sap flow ($u$; L h$^{-1}$ cm$^{-2}$ active xylem) estimated by laboratory calibration equation and Granier equation.
4.2. Relationships between xylem sap flow, photosynthesis and instantaneous transpiration

The maximum values of xylem sap flow were 0.55 L h\(^{-1}\) m\(^{-2}\) leaf area (Fig. 5). This value represented 15.6 L m\(^{-2}\) d\(^{-1}\). A 5-month-old papaya plant has a leaf area of approximately 5 m\(^2\) per plant, and therefore, transpires 78 L plant\(^{-1}\) d\(^{-1}\). In citrus, Steinberg et al. (1990) recorded values of 0.35 L h\(^{-1}\) m\(^{-2}\) leaf area or approximately 150 L of transpired water plant\(^{-1}\) d\(^{-1}\). In Prunus serrulata (Lindl., cv. Longipes), xylem sap flow values were 0.041 L h\(^{-1}\) m\(^{-2}\) (Dugas et al., 1993); young mangosteen (Garcinia mangostana L.), 0.043 L h\(^{-1}\) m\(^{-2}\) (Wiebel and Chako, 1992), mango (Mangifera indica L.), 0.84 L h\(^{-1}\) m\(^{-2}\) (Lu and Chacko, 1998) and grapevines 0.09 to 0.05 L h\(^{-1}\) m\(^{-2}\) (Schmid and Bettner, 1999).

The instantaneous transpiration rate (\(E\)) was correlated to xylem sap flow (Fig. 5) with the highest values of xylem sap flow between 10 a.m. and 2 p.m.

The non-linear relationship between transpiration and xylem sap flow may be explained by a lag phase in which transpiration increases without the same change in sap flow values. Zhang et al. (1997) observed a higher availability of stored water in Larix and Picea. In Pecan (Carya illinoensis ‘Wichita’), the small early morning lag may represent water immediately available in leaves, petioles and small branches (Steinberg et al., 1990). The stored water present in these structures could contribute to transpiration values without xylem water tension development. In addition, the decrease of the hydraulic conductivity (resistance to the movement of water through the xylem vessel and high resistance to water movement in the liquid phase between the epidermis and the mesophyll, El-Sharkawy (1990)) from probe to leaf can explain this non-linearity.

According to Ansley et al. (1994), the accuracy of scaling \(E\) values to \(u\) declined with increasing \(E\) values suggesting that \(E\) is greater than that measured by stem flow or gravimetric techniques during periods of high \(E\). Green et al. (1989) found good correlation between heat pulse and Penman-Monteith adjusted porometer data in kiwifruit vines (Actinidia deliciosa), although at peak transpiration, porometer values exceeded heat pulse values. Gucci et al. (1990) found that porometer measurements of apricot (Prunus armeniaca) leaves overestimated transpiration when compared to gravimetric measurements. Schulze et al. (1985) found that canopy transpiration in Larix and Picea trees scaled from porometer leaf measurements and total needle biomass was very close to that determined by a stem flow technique, although porometer transpiration (of needles) started about 3 h earlier each day than stem flow.

Scaling \(E\) values to \(u\) must recognize the confinement of the leaf into a chamber with differences in microclimate (Medermit, 1990). We think that porometers do provide an excellent complement to other measurements because conductance differences owing to the environment can be evaluated over time or between species. The large temporal and spatial variability may require a large number of measurements.
rate and Rubisco carboxylase sites are limited. For optimum values of water, light and nutrient, from a particular stomatal conductance value, photosynthetic rate remains dependent on the greater CO₂ uptake and from the Ribulose-1,5-biphosphate (RuBP) regeneration rate. This fact shows the non-linear response of the photosynthetic rate from sap flow values bigger than 0.28 L h⁻¹ m⁻². At this phase of stability, the net photosynthetic rate remains dependent on RuBP regeneration rate, the increasing of the number of actives sites to CO₂ fixation and the increasing of the CO₂ diffusion to the foliar mesophyll.

5. Conclusion

We have showed that mathematical model used to fit the relation between $K$ (Granier heat coefficient) values and sap flow density ($u$, L h⁻¹ cm⁻² active xylem) was the exponential model: $u = 0.5511 \cdot K^{1.9104}$ and instantaneous transpiration ($E$, mmol m⁻² s⁻¹), measured by a portable system of gas exchange, presented a good positive relationship with xylem sap flow. Estimates of papaya sap flow can be obtained by scaling portable photosynthesis system measurements with exposed leaves, however the relationship is non-linear in higher instantaneous transpiration rates. In addition, it was possible to obtain a good relationship between photosynthesis and sap flow measurements in papaya field-grown. This fact shows that handling strategies on the orchard, that provide high transpiration rates, can improve the carbon photosynthetic assimilation in papaya plants.

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