Predicting transpiration of shaded and non-shaded tomato fruits under greenhouse environments

C. Leonardi\textsuperscript{a,*}, A. Baille\textsuperscript{b}, S. Guichard\textsuperscript{b}

\textsuperscript{a}Istituto di Orticoltura e Floricoltura, Catania University, Via Valdisavoia 5, I-95123 Catania, Italy
\textsuperscript{b}I.N.R.A., Unité de Bioclimatologie, Domaine St-Paul, Site Agroparc, F-84914 Avignon Cedex 9, France

Accepted 18 October 1999

Abstract

Fruit water balance is determined by entry of sap through xylem and phloem, and losses due to back-flow from fruits to other organs, and to transpiration. The latter, which may vary according to growing and climatic conditions, plays a significant role in fruit water balance. To better understand and predict tomato fruit transpiration, measurements of the transpiration rate of shaded and non-shaded fruits were carried out under a wide range of climatic conditions in two greenhouse compartments with different levels of air vapour pressure deficit (VPD\textsubscript{air}). Linear models relating transpiration and either air VPD (VPD\textsubscript{air}) or fruit-to-air VPD (VPD\textsubscript{fr-air}) were proposed and their parameters were identified. The best fit was always obtained when using the explicative variable VPD\textsubscript{fr-air}. The model using VPD\textsubscript{air} as variable fits moderately well in the case of shaded fruits, but is not adequate for non-shaded fruits. Values of cuticular conductance, $g_c$ deduced from our measurements appeared to depend (i) on the growth-VPD regime and (ii) on the prevailing values of VPD\textsubscript{fr-air}. Our results suggest that, as for leaf transpiration, VPD between the evaporating surface and the air is the variable that drives the fruit transpiration rate, and that more realistic models could be based on the hypothesis of a variation of $g_c$ vs. VPD. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Model; Tomato; Transpiration; Conductance; Greenhouse; Humidity
1. Introduction

Water accounts for more than 90% of the weight of ripe tomato fruits (Ho et al., 1987), therefore, water transfers into and out of the fruit are primary processes in determining fruit growth and quality. Sink activity of fruits in terms of water import can vary according to its stage of development and to the rate of transpiration both at leaf and at fruit level (Boyer, 1985; Lee, 1995). Fruit water balance is determined by supply of sap through xylem and phloem (Ho et al., 1987), by losses due to back-flow from fruits to other organs (Johnson et al., 1992) and by cuticular transpiration, considering that there are no stomata on fruit skin (Ehret and Ho, 1986; Ben-Yehoshua, 1987; Czarnowski and Starwecki, 1991).

The relative contributions of the components of the fruit water budget are experimentally difficult to access. In previous studies dealing with the water balance of tomato fruits, the xylem and phloem pathways were taken into consideration, whereas water efflux due to fruit transpiration ($E$) was often neglected or considered only a function of weight (Ho et al., 1987). However, some results indicated that $E$ may vary significantly according to growth stage and climatic conditions (Ehret and Ho, 1986; Lee, 1990). Even if tomato fruit transpiration appears quantitatively low when compared to the transpiration of leaves (Ho and Adams, 1994), it plays a significant role in fruit water balance and consequently on its quality. Recent research reported that, on a whole day, transpiration of fruits of ca. 60–80 g was about 10–25% of the water flow entering the fruit under air vapour pressure deficit varying from 1.5 to 2.4 kPa (Leonardi et al., 2000). These results advocate for a deeper insight into the fruit transpiration process and its modelling in order to predict more accurately the dynamics of tomato fruit water budget and the consequences of environmental manipulation on fruit quality.

Up to now, few studies are available concerning modelling of tomato fruit transpiration. Most of them were related to the post-harvest period, under controlled conditions, considering that moisture loss due to transpiration is a major factor affecting fruit quality and shelf life (Sastry and Buffington, 1983; Chau et al., 1985; Ben-Yehoshua, 1987). In this study, experimental data of fruit transpiration and surface temperature of detached tomato fruits, shaded and non-shaded, were used to build and evaluate a model for predicting transpiration rate of tomato fruits in greenhouse conditions.

2. Experimental set-up

2.1. Plant material

The experiments were conducted at INRA, Avignon (South France, 44°N) during two years (1997 and 1998). Transplanting (cv. Raissa) on rockwool slabs
took place respectively in late January 1997 and in early February 1998. Plant density was 2.1 m\(^{-2}\).

To obtain a contrasted and wide range of air vapour pressure deficits (VPD\(_{\text{air}}\), kPa), plants were grown in two greenhouse compartments where VPD\(_{\text{air}}\) was controlled. In one compartment, “low” VPD conditions (L-VPD) were obtained by using a fog-system (relative humidity set point = 60% during 1997 and 70% during 1998). In the second compartment which had no humidity control, the VPD level was considered as a “high” VPD regime (H-VPD), as dry conditions were created during sunny days, mainly during the hottest hours of the day. In both compartments, the opening of vents was regulated to minimise air temperature differences (\(\leq 1 ^\circ\text{C}\)) between the two compartments.

2.2. Transpiration measurements

To evaluate the fruit transpiration rate, a weight-loss technique was adopted (Leonardi et al., 1999). The weight of detached fruits was determined by weighing to three decimal places on an electronic balance (mod. PB303, Mettler Toledo, Switzerland, precision \(\pm 1\) mg). The loss of weight due to respiration was considered negligible compared to that due to transpiration (Shirazi and Cameron, 1993). Equatorial and polar diameters were determined with a calliper, to calculate fruit area, considering the fruit as a sphere with the diameter represented by the mean value of polar and equatorial axis. Fruit transpiration rate, \(E\) (g cm\(^{-2}\) s\(^{-1}\)), was then calculated from the changes in fruit weight over time and expressed by dividing the weight loss (mg s\(^{-1}\)) with respect to its area.

In two greenhouse compartments, transpiration was measured under sunny conditions at different times of the day for a number of fruits weighing between 60 and 100 g.

To reduce the data variability, transpiration rate was measured on four fruits and the values were averaged. Measurements were performed on non-shaded fruits in summer 1997 and on shaded fruits in 1998. The fruits were shaded by means of a white plastic film in order to reduce the solar (direct and diffuse) light to reach the fruits. The light transmissivity of the shading film was estimated to about 10% (i.e. a radiation level that was of the same order of magnitude as in the lower part of the row canopy, where the bigger fruits are present).

At the beginning and end of each weighing, measurements of fruit temperature were carried out by means of an infrared thermometer (mod. Agri-Therm 112ALCS, Everest Interscience, California, precision = \(\pm 0.2 ^\circ\text{C}\)). IR temperature measurements were carried out in a way that the view angle of the apparatus included both shaded and sun lighted parts of the fruit in roughly the same proportion (i.e. parallel to the equatorial plan). A time-averaged surface temperature, \(T_{\text{sfr}}\) (°C), was deduced from these data, assuming that fruit emissivity was 0.98, and further used in the calculation of the average fruit-to-air vapour
pressure deficit \[\text{VPD}_{\text{fr-air}} = e_{\text{sat}}(T_{\text{fr}}) - e_{\text{air}}, \text{ } e_{\text{sat}}(T_{\text{fr}}) \text{ being the saturating vapour pressure at fruit temperature and } e_{\text{air}} \text{ the actual air vapour pressure}.\]

During weight measurements, climatic parameters were continuously recorded: air temperature \((T_a, ^\circ \text{C})\), global solar radiation at fruit level \((G, \text{ W m}^{-2})\) and air vapour pressure \((e_a, \text{ kPa})\). The air VPD was obtained from \(\text{VPD}_{\text{air}} = e_{\text{sat}}(T_a) - e_a\).

3. Modelling fruit transpiration

3.1. Review of the existing models

Most of the models for predicting fruit transpiration are based on Fick’s law. The diffusion of water vapour through the fruit cuticle and the boundary-layer is assumed to be driven by their respective conductances \(g_c\) (cuticle conductance, mm s\(^{-1}\)) and \(g_{bl}\) (boundary-layer conductance, mm s\(^{-1}\)). These two conductances are in series, so that the total conductance along the diffusion paths, \(g_t\), is equal to

\[
g_t = \frac{g_{bl}g_c}{g_{bl} + g_c}. \tag{1}
\]

Then, applying Fick’s law, the transpiration rate \(E\) can be expressed as the product of the total conductance and the vapour pressure deficit \(\text{VPD}_{\text{fr-air}}\) (kPa) between the internal sites of evaporation in the fruit \((e_i)\) and the ambient air \((e_a)\)

\[
E = \left( \rho C_p/\lambda \gamma \right) g_t \text{VPD}_{\text{fr-air}} \tag{2}
\]

with

\[
\text{VPD}_{\text{fr-air}} = e_i - e_a, \tag{3}
\]

where \(\lambda\) is the latent heat of vaporisation \((\text{J g}^{-1})\), \(\rho\) the density of air \((\text{g m}^{-3})\), \(C_p\) the calorific capacity \((\text{J g}^{-1} \text{ K}^{-1})\) and \(\gamma\) the psychrometric constant \((\text{kPa K}^{-1})\). It is generally assumed that the concentration of water vapour inside the cuticle pores is at saturation at the fruit temperature \((T_{fr})\). Then, \(e_i = e^*(T_{fr})\), where \(e^*(T_{fr})\) is the saturating vapour pressure at \(T_{fr}\).

The difficulty in measuring fruit temperature led some authors (Lentz and Rooke, 1964) to make the assumption that fruit temperature is equal to air temperature and to approximate fruit-to-air VPD by air VPD, thus leading to the following expression of the transpiration rate:

\[
E = \left( \rho C_p/\lambda \gamma \right) k_m \text{VPD}_{\text{air}}, \tag{4}
\]

where \(k_m\) is a “transpiration” (Sastry and Buffington, 1983) or “permeation” (Fishman and Génard, 1998) coefficient, which is similar in a physical sense to
the total conductance $g_t$ defined above. This assumption may be considered valid in post-harvest conditions and storage (refrigerated chambers), where the radiative load incoming on the fruit is very low and thus negligible, but is very questionable during growth conditions, when fruits are exposed to diffuse and/or direct solar light.

Sastry and Buffington (1983) proposed a model for storage conditions that allows the transpiration rate of fruits to be calculated knowing the rate of respiratory heat generation and some physical and anatomical properties of the fruit skin and content. In their model, fruit temperature was deduced from the equation of heat diffusion applied to a cylindrical pore, taking into account the source of heat (respiration) and the heat conductivity of the fruit. The transpiration rate was finally expressed as

$$E = \frac{\rho C_p VPD_{fr-air}}{\frac{\tau}{\delta \varphi} + \frac{1}{g_{bl}}},$$

where $\tau$ is the skin thickness (cm), $\delta$ the diffusion coefficient of water vapour in the air (cm$^2$ s$^{-1}$), considered as a function of fruit temperature, $\varphi$ the percentage of pores at the surface (dimensionless). Eq. (5) is equivalent to express $g_c$ as $\delta \varphi / \tau$. The conductance $g_{bl}$ was estimated by the following empirical formula giving the mass transfer for airflow over a sphere

$$Sh = 2 + 0.37 Re^{0.6} Sc^{0.33},$$

where $Sh = h_w D/\kappa$ (Sherwood number), $Re = VD/\nu$ (Reynolds number), $Sc = 0.63$ (Schmidt number for a mixture of air and water vapour). In these numbers, $D$ is the fruit diameter (cm), $\kappa$ the thermal conductivity of air (W m$^{-1}$ K$^{-1}$), $V$ the velocity of the ambient air (cm s$^{-1}$), and $\nu$ the cinematic air viscosity (cm$^2$ s$^{-1}$).

3.2. Adopted models

3.2.1. TR model

In this paper, we chose to test the following models for fruit transpiration:

(i) *Model M1*: $E$ is a linear function of $VPD_{fr-air}$ (Eq. (2)). The slope of the regression line gives a mean value for the total conductance, $g_{t, \text{mean}}$.

(ii) *Model M2*: $E$ is a linear function of $VPD_{air}$ (Eq. (4)). The slope of the regression line gives a mean value for the transpiration coefficient, $k_{\text{mean}}$.

3.2.2. Conductance model

For each measurement of $E$ and fruit temperature, the corresponding value of the total conductance $g_t$ was calculated (Eq. (2)), as well as $g_{bl}$ (Eq. (6)) and $g_c$ by
means of Eq. (1). The values of the cuticle conductance were afterwards analysed with respect to the prevailing climatic variables (mainly VPD_{fr-air}, VPD_{air}, and fruit temperature) in order to find some possible links between $g_c$ and these variables. Then, the possibility of predicting $g_c$ with a simple model from the knowledge of the greenhouse ambient conditions will be examined.

4. Results

4.1. Prediction of the transpiration rate

Under all climatic conditions, the best correlation was obtained when relating fruit transpiration to vapour pressure deficit. Fig. 1 presents the relations between $E$ (g cm$^{-2}$ h$^{-1}$) and both VPD_{air} and VPD_{fr-air} for two characteristic sunny days of August 1997 (non-shaded fruits) and August 1998 (shaded fruits). The values of $g_t$, $\text{mean}$ and $k$, $\text{mean}$ found by linear regression for shaded fruits and non-shaded fruits are presented, for both high and low VPD regimes,

![Graph showing fruit transpiration vs vapour pressure deficit](image)

Fig. 1. Fruit transpiration ($E$, mg cm$^{-2}$ h$^{-1}$) vs vapour pressure deficit (kPa).
In Tables 1 and 2, a better correlation was found between $E$ and $\text{VPD}_{\text{fr-air}}$ than between $E$ and $\text{VPD}_{\text{air}}$. In the case of non-shaded fruits, $E$ was highly correlated to $\text{VPD}_{\text{fr-air}}$ for the two VPD regimes ($R^2 = 0.94$ and 0.87, for low and high VPD, respectively), while there was no correlation with $\text{VPD}_{\text{air}}$ ($R^2 = 0.03$ and 0.15, respectively). These results can be logically explained by the differences between fruit and air temperature (Fig. 2). For unshaded fruit, for instance, the difference $T_{\text{fr}} - T_{\text{air}}$ reached highly negative values (until $-5^\circ \text{C}$) in the early morning and highly positive values in the late afternoon (until $+8^\circ \text{C}$) due to the difference of thermal inertia between the greenhouse atmosphere and the fruit.

The slopes, and therefore, $g_{\text{t, mean}}$ and $k_{\text{mean}}$, are higher for low VPD regime than for high VPD regime, for both shaded and non-shaded fruits.

The values of $g_c$ were also calculated by means of $g_c, SB = \delta \varphi / \tau$ with $\delta = f$ (fruit temperature), $\varphi = 0.000317$ and $\tau = 0.00598$ cm, which are the values given by Sastry and Buffington (1983) for the tomato cv. FTE-12. We found that varied only slightly (between 0.62 and 0.64), as the characteristics of the fruits were taken as constant, as well as the air velocity, $V$ (Tables 2 and 3). The variation of $g_{\text{t, SB}}$ (S.D. = 0.001) was due only to changes in fruit diameter and to variations of the air or water vapour properties with respect to $T'$. On the contrary, $g_{\text{t, meas}}$ showed a high S.D., which could be attributed to variability in the fruit characteristics (parameters $\tau$ and $\varphi$), and also, but probably to a lesser extent, to changes in convective conditions around the fruit (ventilation, fogging, radiation) which change $V$, and therefore, $g_{\text{bl}}$.

### Table 1
Coefficient of determination ($R^2$), slope, standard error ($\sigma$) and calculated value of $g_{\text{t, mean}}$ obtained with Model M1

<table>
<thead>
<tr>
<th></th>
<th>$R^2$</th>
<th>Slope</th>
<th>$\sigma$</th>
<th>$g_{\text{t, mean}}$ (mm s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shaded fruits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low VPD</td>
<td>0.70</td>
<td>0.24</td>
<td>0.015</td>
<td>0.091</td>
</tr>
<tr>
<td>High VPD</td>
<td>0.85</td>
<td>0.14</td>
<td>0.008</td>
<td>0.054</td>
</tr>
<tr>
<td>Unshaded fruits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low VPD</td>
<td>0.94</td>
<td>0.15</td>
<td>0.005</td>
<td>0.059</td>
</tr>
<tr>
<td>High VPD</td>
<td>0.87</td>
<td>0.13</td>
<td>0.007</td>
<td>0.049</td>
</tr>
</tbody>
</table>

### Table 2
Coefficient of determination ($R^2$), slope, standard error ($\sigma$) and calculated value of $k_{\text{m, mean}}$ obtained with Model M2

<table>
<thead>
<tr>
<th></th>
<th>$R^2$</th>
<th>Slope</th>
<th>$\sigma$</th>
<th>$k_{\text{m, mean}}$ (mm s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shaded fruits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low VPD</td>
<td>0.26</td>
<td>0.21</td>
<td>0.023</td>
<td>0.086</td>
</tr>
<tr>
<td>High VPD</td>
<td>0.53</td>
<td>0.17</td>
<td>0.018</td>
<td>0.061</td>
</tr>
<tr>
<td>Unshaded fruits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low VPD</td>
<td>0.03</td>
<td>0.20</td>
<td>0.042</td>
<td>0.075</td>
</tr>
<tr>
<td>High VPD</td>
<td>0.15</td>
<td>0.16</td>
<td>0.026</td>
<td>0.062</td>
</tr>
</tbody>
</table>
4.2. Conductance vs VPD

Using Eq. (6) and assuming that the diameter of the fruit is equal to 10 cm and air velocity was about 10 cm s\(^{-1}\) near the fruit gave \(g_{bl} \approx 8\) mm s\(^{-1}\). This estimation of \(g_{bl}\) was one or two orders of magnitude greater than the measured values of \(g_t\), and therefore, it was assumed in the following \(g_t \approx g_c\).

Within each measurement, the calculated data of \(g_t\) were most of the time higher for L-VPD fruits than for H-VPD fruits. When plotting \(g_t\) vs. VPD\textsubscript{fr-air}, we observed that the total conductance was not constant and decreased with increasing VPD (Fig. 3), this decrease being more evident in the L-VPD treatment and in the lower range of VPD\textsubscript{fr-air}(0–2 kPa). Above 3 kPa, the conductance is rather constant, about 0.05 mm s\(^{-1}\).

A curve can be fitted to the whole set of data, including shaded and non-shaded fruits, and high and low VPD, and used to predict the variation of \(g_t\) with

Table 3

The average and standard deviation of \(g_t,\text{meas}\) (derived from measurements) and \(g_t,\text{SB}\) (derived from the model of Sastry and Buffington, 1983)

<table>
<thead>
<tr>
<th></th>
<th>(g_t,\text{meas})</th>
<th>(g_t,\text{SB})</th>
<th>Average</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>L-VPD, unshaded fruits</td>
<td>0.063</td>
<td>0.064</td>
<td>0.009</td>
<td>0.001</td>
</tr>
<tr>
<td>L-VPD, shaded fruits</td>
<td>0.098</td>
<td>0.062</td>
<td>0.017</td>
<td>0.001</td>
</tr>
<tr>
<td>H-VPD, unshaded fruits</td>
<td>0.049</td>
<td>0.063</td>
<td>0.010</td>
<td>0.002</td>
</tr>
<tr>
<td>H-VPD, shaded fruits</td>
<td>0.050</td>
<td>0.062</td>
<td>0.009</td>
<td>0.001</td>
</tr>
</tbody>
</table>
The corresponding equation is \( g_c = 0.081 - 0.021 \times \ln(VPD_{fr-air}) \). A similar trend was also observed plotting \( g_c \) value vs. the fruit-to-air temperature difference.

5. Discussion

The linear model of transpiration vs. \( VPD_{fr-air} \) (M1) seems to fit the data much better than the other two models, especially in the case of non-shaded fruits, for which the model M2 (with \( VPD_{air} \)) did not appear to predict adequately the transpiration rate. On the other hand, important temperature differences were observed between the fruit skin and the ambient air (Fig. 2). It is not surprising therefore, that the model M2 is not able to predict correctly the fruit transpiration using \( VPD_a \) as the driving variable. The current assumption that fruit temperature is equal to air temperature, if perhaps acceptable in post harvest conditions, is questionable under field or greenhouse conditions.

The slopes of the regression models, representing respectively the total fruit conductance \( g_t \) for M1 and the transpiration coefficient \( k_m \) for M2, varied significantly with respect to VPD growing conditions and fruit shading. The estimation of the cuticular conductance \( g_c \) (assuming \( g_t \approx g_c \)) gave values between 0.03 and 0.12 mm s\(^{-1}\), with an average of 0.065 mm s\(^{-1}\)). These values are in good agreement with the estimated value of 0.06 mm s\(^{-1}\) reported by Sastry and Buffington (1983) on cv. FTE-12, but little bit higher than 0.036 mm s\(^{-1}\) on cv. “Grosse Lisse” estimated by Nobel (1975).

Using the expression of Sastry and Buffington gave only slight variations of \( g_c \) (between 0.62 and 0.64), as the characteristics of the fruits and air velocity were
taken as constant. This model, like the models M1 and M2 when \( g_c \) or \( k \) were chosen as fixed values, does not take into account the natural variability of skin characteristics. The variability in individual skin fruit characteristics explains probably a major part of the scattering observed when plotting fruit skin conductance against VPD\(_{fr-air}\) or VPD\(_a\) (Fig. 3). The other sources of variability correspond to changes in skin properties due to environmental conditions prevailing in the greenhouse. The results seem to indicate that two types of environmentally induced changes coexist (Fig. 3):

Medium-term (week horizon) variations in skin properties due to the growing-VPD regime (Leonardi et al., 1999).

Short-term (hour horizon) modifications due to the instantaneous VPD and fruit temperature. It can be seen in Fig. 3 that it exists a decreasing trend of \( g_c \) when VPD\(_{fr-air}\) increases, this trend being more clearly evidenced in the low-VPD regime.

The consequences of these results for modelling purposes is that both medium and short-term environmental influences on skin properties must be taken into account when predicting tomato fruit transpiration rate, and thus fruit water budget.

6. Conclusion

In conclusion, simple models relating transpiration and VPD were proposed in this paper and their parameters were identified. The best agreement with the experimental data was obtained when VPD\(_{fr-air}\) was chosen as the driving variable. It appears that the variation of the skin cuticular conductance as a function of medium- and short-term climatic conditions has to be taken into account as appreciable variations in \( g_c \) seem to derive from (i) the average level of VPD experienced by the fruit during its growth and (ii) the prevailing skin temperature and related VPD.

The estimation of fruit transpiration by means of a relation with air VPD may lead to large errors in predicting fruit transpiration, implying that fruit temperature must be known in order to obtain realistic predictions of the transpiration rate. Therefore, coupling a transpiration model such as the model M1 with a fruit energy balance model that is able to predict fruit skin temperature seems to be the best way to get satisfactory prediction of fruit transpiration in field or greenhouse conditions.

Acknowledgements

The contribution of C. Leonardi, lecturer at Calabria and Catania Universities, was partially supported by CNR and MURST within the project “Tecnologie
innovative per il miglioramento qualitativo delle ortive in ambiente protetto nel Mezzogiorno d’Italia”. The contribution of S. Guichard was supported by a fellowship of the Conseil Regional ‘Provence Alpes Côte d’Azur’.

References


