High vapour pressure deficit influences growth, transpiration and quality of tomato fruits

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Abstract

Plants were grown in two glasshouse compartments under two vapour pressure deficit (vpd) levels: low vpd was obtained by increasing air humidity with a fogging system, and high vpd was obtained during sunny hours in a greenhouse where air humidity was not controlled. The mean value, of the six driest hours of the day concerning the growing period of the fruits considered, was 1.6 kPa under low vpd and 2.2 kPa under high vpd conditions. Over the whole experimental period, the difference in mean hourly temperature never exceeded 0.8°C. The oldest leaves were removed to different extents in different plots to analyse whether a different leaf/fruit ratio could modify the effect of high vpd.

Fruit growth and transpiration rates greatly varied during daylight hours; these variations were enhanced under high vpd condition. The increase in vpd produced a significant reduction in fruit fresh weight and in fruit water content, and an increase in soluble solids, while fruit dry weight was not affected. High vpd also enhanced the variability of fruit weight. When more leaves were removed the effect of vpd on soluble solids and water content was less important.

The study shows that during summer, as vpd increases from 1.6 to 2.2 kPa, effects can be observed both on tomato growth and quality characteristics. Therefore, an improvement of the control of vpd for the optimisation of greenhouse tomato production is discussed.

Keywords: \textit{Lycopersicon esculentum} Mill.; Tomato; High vpd; Growth; Transpiration; Quality

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1. Introduction

Among different factors, the effect of air humidity on plant growth is often neglected by growers. In a review, Grange and Hand (1987) quoted that variations of humidity between 1 and 0.2 kPa vapour pressure deficit (vpd) have small effects on the physiology and development of horticultural crops. Nevertheless, some authors observed that low vpd positively affects dry matter accumulation and can also promote the incidence of calcium related physiological disorders in leaves, but they did not record any calcium deficiency symptoms on fruits (Bakker, 1984; Bunce, 1984; Kreij, 1996; Holder and Cockshull, 1990). On the other hand, Janse and Welles (1984) observed that fruits grown at high humidity generally have a shorter shelf life because they become soft more quickly.

The effects of vpd have been often studied in the winter period when a very high air humidity inside the greenhouse often occurs. However in these conditions, reducing humidity to increase the vpd above 0.3 kPa does not seem convenient because the yield response to lower humidity is small (Holder and Cockshull, 1990).

In Mediterranean conditions, during the warmest months, high temperature in the greenhouse and low outside air humidity can determine an increase in air vpd in the greenhouse. The most obvious effect of very low humidity on open air crops is to induce leaf water stress when the uptake of water through the root system is inadequate to cope with high transpiration rate (Grange and Hand, 1987). According to Hoffman (1979), an increase in vpd from 1 to 1.8 kPa determines the major reduction in plant growth on several crops, and this could be probably due to the depression of photosynthesis (Xu et al., 1991), related to the reduction of stomatal conductance (Grange and Hand, 1987).

High vpd can play a role also at the fruit level by a variation in plant water status, and consequent supply of water to the fruit, and by an increased transpiration of the fruit. Fruit water balance is in fact determined by the 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 (Ben-Yehoshua, 1987; Ehret and Ho, 1986a). Fruit sink activity in terms of water import can vary according to the stage of development of the fruit and to the rate of transpiration both at the leaf and the fruit levels (Boyer, 1985). According to the above and considering that water accumulation in tomato accounts for more than 90% of the weight of ripe fruits (Ho et al., 1987) conditions that modify water transfer into and out of the fruit could also have some effects on fruit growth and final quality.

To our knowledge, there have been no experiments studying the effects of relatively high vpd in the greenhouse on fruit growth and qualitative characteristics. This work attempts to characterise the effects of low air humidity on tomato fruit. Considering that the transpiration demand under high vpd
increases and that this can reduce fruit growth (Pearce et al., 1993), the effects of vpd on fruit characteristics have been also studied in relation to different degrees of leaf removal in order to see if competition between fruits and leaves for water could occur under such conditions.

2. Material and methods

2.1. Crop and treatments

The experiment was conducted at INRA, Avignon (South France, 44°N). Tomato seeds (cv. Raissa) were sown in early December 1996 in rockwool cubes and transferred to their final position on rockwool slabs in early February, at a plant density of 2.1 m⁻².

Plants were grown in two adjacent identical compartments 128 m² each; of the same glasshouse. The atmospheric vapour pressure deficit was controlled from the end of March (9 trusses stage); low vpd was maintained using a fogging system (set point 60% relative humidity during the hottest hours of the day, i.e. from 09:00 a.m. till 15:00 solar time) (low VPD), whereas high vpd corresponded to the control (high VPD). In both compartments, the opening of vents was regulated by a computerised climate-control system so that air temperature differences were minimised (≤0.8°C) between the two vpd conditions.

For all the plants and within each truss, all extra flowers were removed after the setting of the first five fruits. Fruits were harvested at the “orange” ripening stage (just when the fruit appeared externally all orange, number 6–7 in the CBT Dutch colour code).

In both VPD treatments 24 plants were selected in each compartment on 16 July, and the oldest leaves were removed differently in order to obtain different leaf/fruit ratios. On half of the plants of each compartment, the oldest leaves, except four leaves under the oldest present fruit, were removed (leaf+); on the remaining plants, all the leaves under the oldest present fruit were removed (leaf−). Subsequently, leaves were removed twice a week to maintain the fixed conditions. The measured reduction of plant leaf area in leaf+ compared to leaf− was ~30%, so that the leaf area was ~1.6 and 1.1 m² per plant, respectively. On the remaining plants of the greenhouse leaves were removed in the same way as in leaf+ conditions.

In the whole the studied treatments were: low VPD leaf+; low VPD leaf−; high VPD leaf+; high VPD leaf−.

2.2. Measurements and analysis

Under the two vpd conditions the growth and transpiration rates of fruit weighing 60–80 g (fresh weight) were evaluated on the leaf+ plants throughout sunny days.
Fruit growth was measured by linear displacement transducers (mod. CD 4112-1, Enertec, France) and recorded on a data logger every 30 min. The relative fruit growth rate (mg g\(^{-1}\) fruit per hour) was therefore calculated on the basis of variations in fruit diameter. Fruit relative growth rate has been calculated on the basis of an experimental formula established on fruits grown in the same conditions:

\[
\text{fruit volume} = 0.63 \times \text{fruit diameter}^{2.88} \quad (r^2 = 0.99; \ P \leq 0.001).
\]  

The water thermal expansion was considered to correct fruit volume variations due to temperature (\(T^\circ\)), according to the following equation:

\[
\text{corrected volume} = \frac{\text{initial volume}}{[f(25^\circ C)/f(T^\circ)]},
\]  

where (Zemansky, 1963).

\[
f(T^\circ) = 1 + (-6.43 \times 10^{-5}T^\circ) + (8.5 \times 10^{-6}T^\circ^2) + (-6.78 \times 10^{-8}T^\circ^3). \quad (3)
\]

Fruit volume variations were then transformed to fruit weight variations considering:

\[
\text{fresh weight} = 0.95 \times \text{volume} - 0.76 \quad (r^2 = 0.99; \ P \leq 0.001).
\]  

To evaluate the fruit transpiration under greenhouse conditions, the weight-loss technique was adopted. The weight of detached fruits was determined with the help of an analytical balance (mod. PB303, Mettler Toledo, Switzerland) within 30 min after harvest. The method, similar to that described by Shirazi and Cameron (1993), was tested to check the linearity of weight loss at least in the considered interval after harvesting (i.e. \(\sim 30–40\) min). Transpiration has been referred to fruit area which has been calculated from fruit diameter, considering the fruit as a sphere.

For each of the four treatments, the 120 fruits (5 fruits per truss, 12 plants per treatment and two trusses per plant: 18th truss and 20th truss) were sampled at the “orange” ripening stage. These fruits, at the moment of first leaf removal were, in both vpd conditions, at \(3–4\) cm diameter stage in the 18th truss and at setting stage in the 20th truss.

The following fruit characteristics were determined: unitary fresh weight, presence of cracking (0 = absent, 3 = particularly evident), blossom-end rot (0 = absent, 3 = particularly evident); soluble solids by refractive index (Brix\(^\circ\)), water content (%) by drying in a thermo-ventilated oven at 80\(^\circ\)C until constant weight was reached, and chromatic co-ordinates using a Chroma meter (mod. CR-200, Minolta, Japan). The latter were determined in order to check any relevant effects on colour lightness (\(L\)) and intensity (\(\sqrt{a^2 + b^2}\)), where ‘\(a\)’ is the green–red axis and ‘\(b\)’ is the yellow–blue axis in the CIE (Commission International d’Eleclairage) space colour co-ordinates.
Climatic conditions were continuously recorded. Fig. 1(a) presents the daily mean vpd achieved in the two compartments between flowering of the first considered truss (18th truss) and harvesting of the last considered fruit of the 20th truss (from 1 July to 26 August); Fig. 1(b) presents the vpd during the six driest hours of the day in the considered period (i.e. from 8:30 to 14:30 solar time).

Analysis of variance (ANOVA) was performed to determine any significant difference in the fruit qualitative characteristics due to leaf pruning and VPD treatment. Due to some variations in thermo-radiative conditions during growing and ripening of the two considered trusses, and considering possible effects of fruit position on the plant on its characteristics (Bertin et al., 1998), statistical analysis has been performed separately for each cluster.

3. Results

3.1. Growth and transpiration

Data sets of fruit growth and transpiration were collected between the end of July and the beginning of August 1997. Typical examples of fruit growth and transpiration rates throughout daylight hours are presented in Figs. 2 and 3, both
Fig. 2. Variation in fruit growth during daylight hours (mean of two linear displacement transducers ±SE; \(n = 2\)) and corresponding vpd conditions.

Fig. 3. Daily course of fruit transpiration and vpd conditions during daylight hours (mean ± SE; \(n = 4\)).
recorded in the first 10 days of August. During these measurements, differences of more than 1 kPa vpd were recorded in the two compartments for more than 5 h.

Fruit relative growth rate was very responsive to the vpd treatment. Under low vpd, fruit relative growth rate increased from 0.7 to 4 mg g\(^{-1}\) h\(^{-1}\) during the morning and decreased progressively from 12:00 to the evening. A different trend was observed under high vpd where a greater amplitude of variation during daily hours was recorded. Relative fruit growth rate decreased till 1 p.m., reached the maximum value (6 mg g\(^{-1}\) h\(^{-1}\)) at 5 p.m., and thereafter decreased again reaching values similar to those observed under low vpd.

As expected, fruit transpiration varied during the daylight hours (Fig. 3) and changed from 0.1 to 0.75 mg cm\(^{-2}\) of fruit surface per hour. In the early morning and in the afternoon, fruit transpiration was similar under the two vpd conditions, whereas differences were observed between 10 a.m. and 2 p.m. when the fogging system in the low vpd compartment was working. At 1 p.m. fruit transpiration under high vpd was twice that under low vpd. Maximum values occurred at 1 p.m. and at 4 p.m. under high and low vpd, respectively.

On the whole, fruit transpiration value versus air vpd showed a positive trend, both under high vpd (\(r = 0.92; P \leq 0.01\)) and low vpd (\(r = 0.74; P \leq 0.01\)) conditions. The relation between air humidity and fruit relative growth was positive under low vpd (\(r = 0.60; P \leq 0.05\)), whereas under high vpd the relation between air vpd and fruit relative growth was not clear (\(r = 0.012\) NS).

3.2. Qualitative characteristics

The qualitative characteristics varied significantly in relation to the studied factors in both considered trusses. Only blossom-end rot did not show any significant differences and its percentage was in all conditions negligible (<1%).

In the first sampled truss (18th truss), significant effects of humidity levels were observed on unitary weight per fruit, soluble solids and water content (Table 1). Under the higher vpd the content of soluble solids was higher, whereas the fresh weight per fruit and the water content were lower. The removal of leaves did not modify the effect of vpd; indeed no significant interaction was recorded between the two factors. When more leaves were removed, an increase of fruit weight and water content and a decrease in soluble solids were recorded.

These differences were amplified on fruit collected on the second sampled truss (20th truss) (Table 2); probably because vpd, during fruit growth and ripening, differed between the two compartments (mean of the six driest hours of the day concerning the two weeks before harvesting) more for the second considered truss (0.85 kPa) in comparison to the first one (0.57 kPa). The higher vpd brought out an increase in colour intensity (\(\sqrt{a^2 + b^2}\)), and determined a reduction in fruit cracking and in the fresh weight per fruit. A significant interaction was observed between vpd level and leaf removal. When more leaves were removed (leaf—),
Apart from differences due to truss position, vpd determined an important variation in fruit weight (Fig. 4). The percentage standard deviation (C.V.) of fruit fresh weight of all sampled fruits, higher in the first harvested truss in comparison to the second one, was higher under high vpd. These effects were more evident in the 20th than in the 18th truss.

**Table 1**
Fruit characteristics in relation to vpd and leaf–fruit ratio: 18th truss

<table>
<thead>
<tr>
<th>VPD</th>
<th>Leaf</th>
<th>Cracking</th>
<th>Fresh weight per fruit (g)</th>
<th>Colour</th>
<th>Soluble solids (°Brix)</th>
<th>Water content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.2</td>
<td>162</td>
<td>52.8</td>
<td>37.9</td>
<td>3.28</td>
<td>95.26</td>
</tr>
<tr>
<td>High</td>
<td>0.1</td>
<td>148</td>
<td>52.8</td>
<td>38.2</td>
<td>3.79</td>
<td>94.92</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td></td>
<td></td>
<td>NS</td>
<td>NS</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td><strong>Leaf+</strong></td>
<td>0.1</td>
<td>147</td>
<td>53.1</td>
<td>38.7</td>
<td>3.61</td>
</tr>
<tr>
<td></td>
<td><strong>Leaf−</strong></td>
<td>0.2</td>
<td>164</td>
<td>52.5</td>
<td>37.4</td>
<td>3.46</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td></td>
<td></td>
<td>NS</td>
<td>NS</td>
<td>***</td>
</tr>
</tbody>
</table>

* Interaction effects were never significant ($P \leq 0.05$).
* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.001$.
*** Significant at $P \leq 0.01$.
NS: Not significant.

the effects of vpd levels were less evident both on soluble solids and on water content.

Apart from differences due to truss position, vpd determined an important variation in fruit weight (Fig. 4). The percentage standard deviation (C.V.) of fruit fresh weight of all sampled fruits, higher in the first harvested truss in comparison to the second one, was higher under high vpd. These effects were more evident in the 20th than in the 18th truss.

**Table 2**
Fruit characteristics in relation to vpd and leaf–fruit ratio: 20th truss

<table>
<thead>
<tr>
<th>VPD</th>
<th>Leaf</th>
<th>Cracking</th>
<th>Fresh weight per fruit (g)</th>
<th>Colour</th>
<th>Soluble solids (°Brix)</th>
<th>Water content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>Leaf+</td>
<td>0.6</td>
<td>175</td>
<td>52.2</td>
<td>39.9</td>
<td>3.21</td>
</tr>
<tr>
<td>Low</td>
<td>Leaf−</td>
<td>0.8</td>
<td>174</td>
<td>53.7</td>
<td>40.3</td>
<td>3.30</td>
</tr>
<tr>
<td>High</td>
<td>Leaf+</td>
<td>0.3</td>
<td>145</td>
<td>52.9</td>
<td>41.3</td>
<td>4.18</td>
</tr>
<tr>
<td>High</td>
<td>Leaf−</td>
<td>0.2</td>
<td>148</td>
<td>52.0</td>
<td>41.5</td>
<td>3.73</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td></td>
<td></td>
<td>NS</td>
<td>NS</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>0.7</td>
<td>175</td>
<td>53.0</td>
<td>40.1</td>
<td>3.26</td>
</tr>
<tr>
<td>High</td>
<td>0.2</td>
<td>147</td>
<td>52.4</td>
<td>41.4</td>
<td>3.95</td>
<td>4.44</td>
</tr>
<tr>
<td></td>
<td><strong>Leaf+</strong></td>
<td>0.5</td>
<td>160</td>
<td>52.5</td>
<td>40.6</td>
<td>3.70</td>
</tr>
<tr>
<td></td>
<td><strong>Leaf−</strong></td>
<td>0.5</td>
<td>161</td>
<td>52.9</td>
<td>40.9</td>
<td>3.51</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td></td>
<td></td>
<td>NS</td>
<td>NS</td>
<td>*</td>
</tr>
</tbody>
</table>

* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.
NS: Not significant.
4. Discussion and conclusion

In Mediterranean regions during hot and dry days, relative air humidity can decrease significantly inside the greenhouse (Boulard et al., 1991). Most of the studies carried out under greenhouse conditions deal mainly with relatively low levels of vpd. In this study we observed that as vpd reached values higher than 2 kPa during the hottest hours of the day, this had effects on growth and characteristics of tomato fruits.

During the daylight hours, relative fruit growth rate was significantly reduced on plants grown under higher vpd. A similar trend has previously been observed on tomato (Johnson et al., 1992) and on peach (McFadyen et al., 1996) and was explained by a reduction of the fruit–stem water-potential gradient (Johnson et al., 1992). The same trend was not observed at the lower vpd where fruit growth varied more regularly during the daylight hours.

In the literature it is found that canopy transpiration mainly depends on solar radiation, vapour pressure deficit and leaf area (Jolliet and Bailey, 1992). In our research, fruit transpiration showed important variations in relation to daylight hour and to vpd conditions. Even if tomato fruit transpiration appears low compared to other organs (such as leaves) or other fruits (Ho and Adams, 1994), fruit transpiration taken over the whole day, in our conditions, was \( \sim10\% \) and \( \sim25\% \) of the water entering the fruit, under low and high vpd respectively, assuming that:

\[
\text{water entering the fruit} = \text{cumulative growth} + \text{cumulative transpiration}. \tag{5}
\]

Johnson et al. (1992) showed that fruit shrinkage was related to water efflux from the fruit to the stem. This back flow could be due to an inversion of the fruit–stem water potential gradient, with a stem water potential lower than the fruit water potential. It is likely that plant transpiration was increased in our high vpd conditions so that the stem water potential was more negative during the daylight period and probably more negative than the fruit water potential. These
conditions added to a stronger fruit transpiration would explain the shrinkage of fruits submitted to high vpd.

Bakker (1991) reported that under high relative humidity, an increase in vpd determined only slight variations in qualitative fruit characteristics of different vegetables and he observed a reduction in mean fruit weight of cucumber and eggplant, and an increase in tomato weight. In the present study the increase of vpd from 1.6 to 2.2 kPa caused a relevant reduction in fruit fresh weight (\(-10\%\)). This response was associated with a significant reduction of fruit water content and to an increase in soluble solids. Nevertheless if fruit dry weight was considered (data not shown) the effects of vpd were negligible (\(<2\%\)). Therefore, if high vpd conditions have no effect on the fruit dry weight but have an effect on the fruit water content, the quality of these fruits will change in terms of dry matter content which is an important criterion of quality.

According to Slack (1986) the removal of leaves affects the total yield and not the fruit number and quality; our data showed that when leaf area was reduced from 1.6 to 1.1 m\(^2\) per plant, a decrease in soluble solids and an increase in fruit water content occurred. Indeed if the interaction between the two factors was analysed, we observed that with a lower leaf–fruit ratio the effect of higher vpd was lessened. Our hypothesis was that, in these conditions, when more leaves were removed, less competition for water occurred between fruits and leaves.

The increase in fruit cracking under a lower vpd agrees with the results obtained by Maroto et al. (1995) during a spring–summer cycle. Nevertheless, they did not observe any significant variation in mean fruit fresh weight. Moreover, within each truss, we recorded a more evident variability in fruit weight as a consequence of increased vpd; probably because of water competition among fruits within the same truss.

It is interesting that on the whole the effects of increased vpd (2.2 versus 1.6 kPa) were similar to those previously observed (Ho et al., 1987; Adams, 1991; Mitchell et al., 1991) in response to moderate water and salt stresses. It seems that a mechanism involved in the response to high vpd would be water shortage and not an assimilate shortage at the fruit level, since the vpd has an effect on fruit fresh weight, but not on the accumulation of dry matter. Ehret and Ho (1986b) found similar results studying the effects of salinity on dry matter partitioning in tomato fruit. Besides, considering our data, this reduction in fruit water amount could be explained by an increased fruit transpiration under high vpd and by a water shortage at the plant level because of increased leaf transpiration as a consequence of increasing vpd (Marcelis, 1989; Jolliet and Bailey, 1992).

From this study, we can conclude that the effects of high vpd on fruit growth and characteristics are more evident than those observed by other authors under low vpd. Therefore, if the goal is the optimisation of tomato greenhouse production and quality even during the hottest periods, it should be considered that high vpd can reduce the mean weight of fruits (yield) and their uniformity.
(visual quality) but can also increase their dry matter and soluble solid contents. Our results bring out the fact that an obstacle to improving the quality of tomato fruit is the inverse relationship between the yield and the dry matter content. The use of cultivation techniques such as high salinity or high vpd conditions to increase the dry matter content of tomato fruit also reduces the rate of water accumulation and thus cell enlargement, and drives inevitably to a loss in yield (Ho, 1990). Considering the above and to analyse the practical possibility to control vpd in greenhouse during summer season, further research is needed to understand better how high vpd affects fruit sink activity in terms not only of water, but also of assimilate import.

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