J Plant Growth Regul (2005) 24:201–213
DOI: 10.1007/s00344-005-0040-z

J P G R
Journal of Plant Growth Regulation

Analysis of Growth and Water Relations of Tomato Fruits in Relation to Air Vapor Pressure Deficit and Plant Fruit Load

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Abstract

The influence of air vapor pressure deficit (VPD) and plant fruit load on the expansion and water relations of young tomato fruits grown in a glasshouse were evaluated under summer Mediterranean conditions. The contributions of phloem, xylem and transpiration fluxes to the fruit volume increase were estimated at an hourly scale from the growth curves of intact, heat-girdled and detached fruits, measured using displacement transducers. High VPD conditions reduced the xylem influx and increased the fruit transpiration, but hardly affected the phloem influx. Net water accumulation and growth rate were reduced, and a xylem efflux even occurred during the warmest and driest hours of the day. Changes in xylem flux could be explained by variations in the gradient of water potential between stem and fruit, due to changes in stem water potential. Misting reduced air VPD and alleviated the reduction in fruit volume increase through an increase in xylem influx and a decrease in fruit transpiration. Under low fruit load, the competition for assimilates being likely reduced, the phloem flux to fruits increased, similarly to the xylem and transpiration fluxes, without any changes in the fruit water potential. However, different diurnal dynamics among treatments assume variable contributions of turgor and osmotic pressure in F3 and F6 fruits, and hypothetical short-term variations in the water potential gradient between stem and fruit, preventing xylem efflux in F3 fruits.

Key words: Tomato; *Solanum lycopersicon L.*; Water flux; Water potential; Xylem; Phloem; Transpiration; Fruit growth; VPD; Plant fruit load; Fruit quality

Introduction

The supply of carbon and water to fruit via xylem and/or phloem tissues is crucial for growth and

Received: 8 April 2005; accepted: 5 July 2005; online publication: 31 October 2005
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accumulation of primary compounds, which determine the final fruit quality. In tomato, the number and size of fruits and the quality (dry matter content, taste, and blossom-end rot [BER]) have been improved by optimizing the water relations, assimilate supply, and nutrient status of the fruit (Ho and Adams 1995). Nevertheless under Mediterranean summer conditions, the high radiation and air temperature associated with elevated vapor pressure deficit (VPD) cause serious problems for climate control inside greenhouses, and the production of fresh tomato fruits is lowered in terms of yield and quality (Guichard and others 2001). In particular, problems of BER and cuticle cracking occur (Bertin and others 2000), leading to the production of unmarketable fruits. Cuticle cracking, which occurs when the extensibility of the skin exceeds its elastic limit (Ohta and others 1997), has been related to the frequency of irrigation (Abbott and others 1985). Blossom-end rot, a physiological disorder related to calcium deficiency in the distal part of the fruit (Ho and Adams 1994), results from complex interactions (reviewed by Saure 2001) between stress factors and factors causing rapid fruit growth (Ho and others 1993) and/or cell expansion (Ho and White 2005). Therefore further improvement of fruit quality relies on the optimization of fruit-water relations in response to environmental stress, in particular under summer Mediterranean conditions.

A mature tomato fruit is composed of 92%–95% water and only 5%–8% dry matter (Davies and Hobson 1981), depending on genotype and environment. The fruit-water balance is the result of sap influxes through the phloem and xylem tissue of the pedicel, and water efflux by transpiration. The respective contributions of phloem, xylem, and transpiration fluxes to fruit growth depend on fruit age (Ho and others 1987; Wolterbeek and others 1987), but phloem sap is the main source of water in tomato, and it accounts for most of the increase in fruit volume (Ehret and Ho 1986a; Ho and others 1987; Lee 1989; Grange and Andrews 1994). The low contribution of xylem tissue to the supply of water in tomato fruit would be due to the reduction in the number of conducting vessels in the pedicel abscission zone (Lee 1989) and to low fruit transpiration. Nevertheless, the contribution of xylem water flux to fruit growth is qualitatively important because calcium, involved in the occurrence of BER, is transported in the xylem sap (Ho and others 1987). Many authors have investigated the transpiration of tomato fruit (for example, Ehret and Ho 1986b; Lee 1990; Ho and Adams 1994). Tomato is considered a low-transpiring fruit, but the water efflux was shown not to be negligible in the fruit-water balance, especially under summer conditions (Leonardi and others 1999, 2000).

In the present study, we investigated the effects of VPD on the volume increase of tomato fruits grown at two plant fruit loads, in the range of conditions experienced in commercial glasshouses in the south of France. The volume growth of fruits was analyzed through the contribution of xylem, phloem, and transpiration fluxes at an hourly scale according to the method of Lang and Thorpe (1989), as done for grape (Ollat and others 2002), peach (Huguet and others 1998), apple (Lang 1990), and watermelon (Favé 1998) fruits. Leaf, stem, and fruit water potentials were measured as indicators of the plant water status. Vapor pressure deficit was expected to affect the plant water status through the evaporative demand, whereas plant fruit load directly affects the competition for carbon assimilates. Hypotheses were (1) that high VPD increases fruit transpiration and decreases water availability in the plant because of high leaf transpiration, with resulting effects on the xylem and phloem water influxes, and (2) that low plant fruit load increases the availability of carbon assimilates for fruit growth and thus increases the phloem influx.

Materials and Methods

Plant Material, Crop, and Treatments

The experiment was carried out in Avignon, France (43°55′N; 4°52′E), in two 200 m^2 adjacent glasshouse compartments. Tomato seeds (cv Raïssa) were sown in November in rock wool cubes and transferred to their final position on rock wool slabs in January at a plant density of 2.1 m^{-2}. In both compartments, inflorescences were pruned to three flowers on half of the plants (*F3*) and to six flowers on the other half (*F6*), at the time of 50% anthesis. Flowers were open pollinated by bumblebees, all side shoots were removed as they appeared, and old leaves were removed until below the truss at mature-orange stage. Plant nutrition and chemical pest and disease control followed commercial practices. The supply of nutrient solution to the plants was monitored according to the calculated potential evapotranspiration. The electrical conductivity of the nutrient solution ranged between 2.4 and 2.6 $mScm^{-1}$ at the early stages, and between 2.0 and 2.4 $mScm^{-1}$ after anthesis of the second truss.

From March on (eight trusses on the plants), VPD was controlled thanks to a fogging system from 9:00 to 15:00 UT (set point 70% relative humidity) in one compartment (*VPD−*), and left uncontrolled in

the other one (*VPD+*). Opening of the vents was regulated independently in each compartment so that air temperature differences between the two compartments were minimized (maximum 2.0°C). During daytime, the VPD differed between the two compartments only from 9:00 to 15:00 UT, with a maximum difference around midday (about 1 kPa). The resulting daily sum of radiation, and means of VPD and air temperature from 9:00 to 15:00 in each compartment during the experimental period are displayed in Bertin and others (2000). In the following, treatments will be referred to as: VPD + F3 (high VPD and three fruits per truss), VPD + F6 (high VPD and six fruits per truss), VPD − F3 (low VPD and three fruits per truss), VPD − F6 (low VPD and six fruits per truss).

Monitoring of Fruit Growth

Volume growth was measured on young tomato fruits 21 days after anthesis when the fruit growth rate was at its maximum (fruit diameter about 45 mm). Measurements were made on the second proximal fruit of the truss whatever the treatment (F3 or F6) to avoid interaction between treatments and fruit position. The second position was chosen as the average position in the F3 treatment. Changes in fruit diameter were measured using linear displacement transducers (model CD4112-1, Schlumberger, Enertec, France) and were recorded on a data logger (model 21X, Campbell Scientific Ltd, UK). Measurements were scanned every 10 s, and averages were recorded every 30 min. Sensors were positioned on the equatorial diameter of fruits thanks to holders made of INVAR, an alloy with a roughly nil expansion coefficient. Springs exerted just enough force to maintain contact but did not cause visible damage to fruits. The whole system was hung at the truss level so that the fruit was free to move. The measuring system was able to resolve diameter changes as small as 1.0 μm, but the actual accuracy of sensors was about ± 3.0 μm because of noise due to unavoidable mechanical disturbances related to the environmental conditions of a production glasshouse. Fruit volume growth was calculated from an experimental correlation between fruit diameter and volume, previously established on fruits grown under the same conditions ($r^2 = 0.99$; $n = 120$; $p \leq 0.001$):

$$\text{fruit volume } (\text{cm}^3) = 0.55\ [\text{fruit diameter } (\text{cm})]^{2.93}. \quad (1)$$

Because direct irradiance increased fruit temperature (until 10°C above air temperature), the fruit, the sensor, and the sensor holder were sheltered by aluminium foil. Thus, fruit temperature was near air temperature, and growth conditions were homogeneous among the different fruits used for the experiments. In addition, fruit temperature was continuously measured with thermocouples inserted into the pericarp to correct volume variations from the effect of temperature on water expansion. Then, fruit volume was corrected for temperature (T_f) according to the following equations (Zemansky 1963):

$$\text{corrected volume} = \text{calculated volume} * f(25^\circ\text{C})/f(T_f), \quad (2)$$

with

$$f(T_f) = 1 + (-6.43\,10^{-5}\,T_f) + (8.5\,10^{-6}\,T_f^2) + (-6.78\,10^{-8}\,T_f^3). \quad (3)$$

Estimation of the Contributions of Xylem, Phloem, and Transpiration Fluxes to Fruit Growth

For the present study, the technique developed by Lang and Thorpe (1989) was applied to separate xylem (X), phloem (P), and transpiration (T) fluxes, based on the hypothesis that the assimilate mass flow can be neglected compared to the water flux. The growth (G) of a control fruit may be written as

$$G = P + X + T, \quad (4)$$

assuming that the volume growth integrates fruit fluid inflows and outflows. Thus, the growth of a girdled fruit (pedicel girdling permanently disables phloem) can be written as X + T and that of a detached fruit as T. Transpiration was measured on detached fruits from which the pedicel and the calyx were removed and the abscission zone was recovered by silicon grease to avoid water lost. After normalization by the fruit volume, the growth differences between the control, girdled, and detached fruits enables us to estimate P and X. To determine phloem, xylem, and transpiration contributions to fruit growth, three kinds of fruits are needed: control, girdled, and detached fruits. During our experiments, four fruits of each category were measured. Thus, four estimates of G and T, and 16 estimates of P (four control × four girdled fruits) and X (four girdled × four detached fruits) were made.

Because the phloem network of a tomato plant consists of internal (perimedullary) and external phloem, the girdling as it is applied on woody spe-

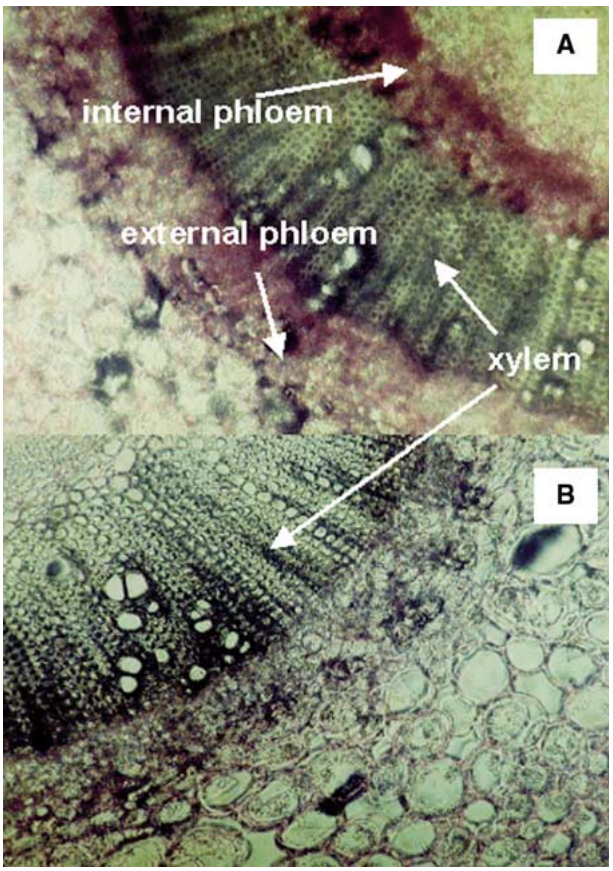

Figure 1. Cross sections of the pedicel of tomato (var. Raïssa) between the abscission zone and the fruit, for a control (**A**) and a girdled fruit (**B**). Mean pedicel diameter was 3 mm. The sieve tubes were colored with carmin and appeared pink. After girdling, the sieve tubes, pith and collenchyma were no longer visible, whereas the xylem vessels colored in green remained undamaged.

cies was not possible. Therefore, we did not burn the fruit pedicel phloem with hot water steam, but with a constant yarn wound around the pedicel according to the technique of Ollat and others (2002). An electrical signal (0.4 A; 12 V) was delivered for 2.5 min so that the internal temperature of the pedicel reached 75°C within 10 s. Preliminary experiments were carried out to determine these values and to ensure that the heat-girdling method was accurate and repeatable. This was realized by two means. First, microscopic cross sections of the control and heat-girdled pedicels showed that internal and external sieve tubes were disorganized, whereas xylem vessels were left almost intact by the treatment (Figure 1). Second, we studied the effects of heat-girdling on the total water potential of fruits (Table 1). Because it was not affected until 12 h after girdling, it could be hypothesized that the xylem flux to the fruit was not disturbed during at least 12 h. The xylem, phloem, and transpiration contributions to fruit growth were studied from late June until early September 1998. In each series of measurements, 12 fruits of similar growth rate were initially selected in each treatment. Four fruits per treatment were girdled on the second day, and 4 fruits were detached on the third day. Fruit-water relations were studied on the third and fourth days. Initial and final diameters of all fruits were measured with an electronic caliper (± 0.01 mm). Results are presented for time sequences with constant climate conditions. The effects of VPD on volume growth and fruit-water relations are illustrated by the results obtained on 9–10 July for F6 fruits, whereas the effects of plant fruit load are illustrated by the results obtained on 7–8 August at high VPD (Figure 2).

Table 1. Total Water Potential (mean ± s.d.) of Control and Girdled Fruits.

Time	Ψcontrol fruit (MPa)	Ψgirdled fruit (MPa)
t_0	−0.36 ± 0.06	− 0.35 ± 0.03
t_0 + 5 h	−0.33 ± 0.03	−0.31 ± 0.01
t_0 + 12 h	−0.35 ± 0.02	−0.34 ± 0.01

Note: Fruits were chosen on the sixth truss of plants bearing nine trusses and grown on NFT in a controlled environment cabinet (temperature 22°C, relative humidity 65% and PAR 30 W m^{-2}). Fruit pedicels were girdled once at t_0 + 8 min. A Mann-Whitney test (n = 18) showed no statistical difference in fruit water potential after fruit girdling ($p > 0.05$).

Leaf, Stem, and Fruit Water Potentials

Leaf water potential was measured on the two last leaflets of fully exposed mature leaves with a pressure chamber. For each treatment, to avoid desiccation, leaflets were enclosed in a plastic bag just before the petiole was cut. Four measurements per treatment were made every 3 h from 5:00 to 20:00 UT. To obtain stem water potential, leaves were enclosed in a white plastic bag to prevent transpiration, and sheltered by aluminium foil; measurements were made 30 min later.

Fruit water potential was measured by using a multichannel psychrometer (model HR33-T, Wescor) calibrated with standard salt solutions. Pericarp discs were excised in the equatorial region of fruits and immediately sealed into the psychrometer chambers in the laboratory at constant temperature (22°C). Samples equilibrated during 5 h before measurements. Two young green fruits (21

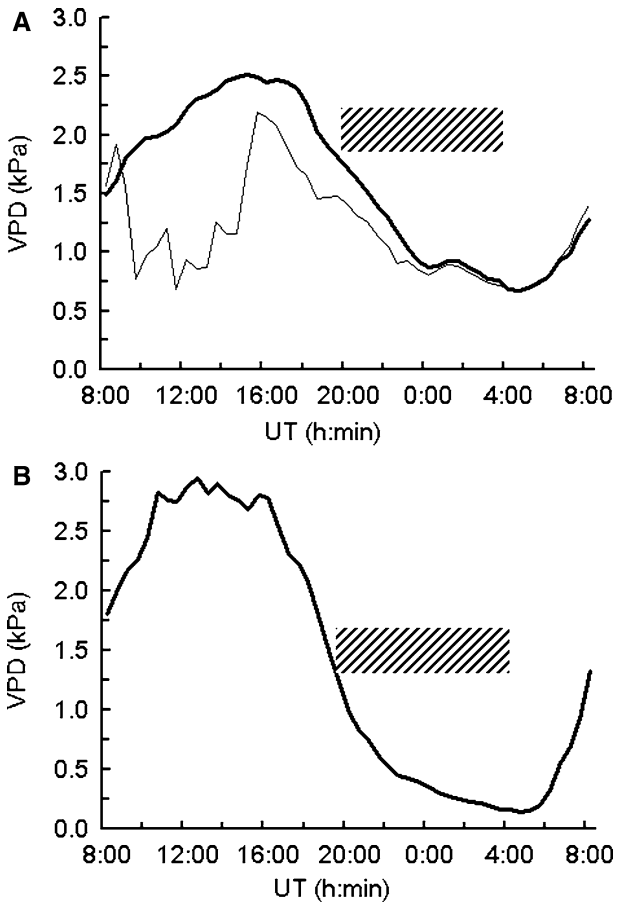

Figure 2. Air VPD in the VPD+ (bold line) and VPD– (solid line) greenhouse compartments on 9–10 Jul. (**A**) and in the VPD+ compartment on 7–8 Aug. (**B**). On 9–10 Jul., temperature in the two compartments varied between 20° (night) and 30°C (noon) and radiation between 0 and 400 W m^{-2}. On 7–8 Aug., temperature varied between 19° (night) and 35°C (noon) and radiation between 0 and 420 W m^{-2}. Shaded zones represent night periods.

days after anthesis) per treatment were measured three times on 10 September 1998.

Statistical Analyses

Statistical analyses were carried out on the measured diameter values and not on the calculated volume growth values. The influence of VPD or plant fruit load on the different fluxes was analyzed independently by unifactorial analysis of variance (ANOVA; Sigmastat 2.0 Jandel Scientific Software), considering cumulative fluxes over the day, the night, or the 24-h periods. Considering that the phloem and xylem fluxes were calculated, the ANOVA were performed on growth variations of the different types of fruit populations (control, heat-girdled, and detached fruits) according to the method of Montgomery (1984). Significant effects were reported when $p \leq 0.05$.

Results

Fruit Relative Growth Rate

High VPD conditions reduced the relative growth rate (RGR) of F6 fruits during the daylight period (Figure 3a). In these conditions, the fruit RGR could reach negative values as early as 10:00, revealing fruit shrinkage. In the VPD+ compartment, the fruit RGR was highest at the end of the day (0.0025 cm^3 cm^{-3} h^{-1}, that is 0.125 cm^3 h^{-1}, because fruit volume was about 50 cm^3), and it was higher on average at night than during the day. In contrast, in the VPD– compartment, the fruit RGR reached high values during the day when misting was applied, which led to a higher daily growth (2.15 cm^3 day^{-1} against 1.50 cm^3 day^{-1} for VPD+ fruits). However, when misting ceased in the VPD– compartment (from 15:00 UT on), the fruit RGR was comparable in the two compartments. The effects of VPD on fruit growth in the F3 treatment presented the same pattern (not shown).

Low fruit load increased the fruit RGR whatever the time of the day (Figure 3b), with maxima of 0.0040 cm^3 cm^{-3} h^{-1} and 0.0020 cm^3 cm^{-3} h^{-1} for F3 and F6 fruits, respectively, reached at the end of the day. The daily growth of F3 fruits was three times higher than that of F6 fruits (2.65 cm^3 day^{-1} and 0.90 cm^3 day^{-1}, respectively). The RGR of F3 fruits was positive during the day and almost nil around 14:00. In contrast, the RGR of F6 fruits was very low early in the morning, and fruit shrinkage occurred until 14:00. The effects of plant fruit load on fruit growth in the VPD– compartment (not shown) were similar, except that neither the sharp decrease in RGR nor the fruit shrinkage was observed around noon.

Phloem, Xylem, and Transpiration Contributions to the Fruit Volume Growth

Increasing VPD significantly affected all water fluxes, but in different ways (Figure 4a, b). At VPD+, the 24-h cumulative value of the xylem flux was significantly reduced (−29%) compared to the VPD– conditions. Similarly, fruit transpiration was increased by 36% at VPD+, whereas the phloem influx hardly changed (−5%). Transpiration and xylem fluxes were especially affected during the warmest and driest hours of the day, and a xylem efflux even occurred around noon at

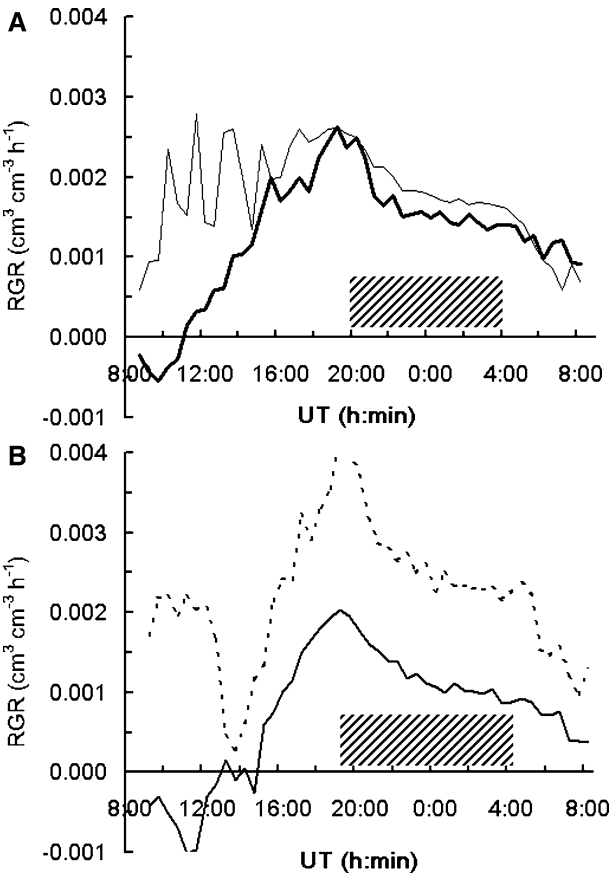

Figure 3. Effects of VPD (**A**; F6 fruits) and plant fruit load (**B**; at VPD+) on the RGR of young growing tomato fruits (regular: VPD–; bold: VPD+; dotted: F3; solid: F6). Data were recorded every 30 min and averaged from measurements scanned every 10 s; values on the graphs are means from 2 or 3 fruits per treatment. Shaded zones represent night periods.

VPD+ (until −0·001 cm^3 cm^{-3} h^{-1} for 4 h) (Figure 4b). Over the daylight period, high VPD reduced the accumulated xylem flux by 80% (0.05 cm^3 in VPD+ versus 0.25 cm^3 in VPD–), and increased the accumulated fruit transpiration by 47% (−1.10 cm^3 in VPD+ versus −0.75 cm^3 in VPD–).

Plant fruit load also significantly affected all water fluxes (Figure 5a, b). Low fruit load increased the xylem, phloem, and transpiration fluxes whatever the time of the day. The phloem flux of F3 fruits reached maximum values close to 0.004 cm^3 cm^{-3} h^{-1} versus 0.002 cm^3 cm^{-3} h^{-1} for F6 fruits. Similarly, the maximum transpiration rate of F3 fruits was about −0.0025 cm^{-3} cm^{-3} h^{-1} versus −0.0020 cm^3 cm^{-3} h^{-1} for F6 fruits. Under these conditions of high VPD, F6 fruits showed a xylem efflux in the afternoon, whereas the xylem flux of F3 fruits was low, but positive (Figure 5a and b). Over 24 h, the phloem, the xylem, and the transpiration fluxes of F3 fruits were increased by 52%, 58%, and 26%, respectively.

Whatever the VPD and plant fruit load treatments, the diurnal dynamics of flux were similar. The phloem flux was always the most important, with highest values during the day and lowest values at night. The transpiration of fruits was also higher during the day than at night, in contrast to the xylem flux. During the day, the volume efflux by transpiration was always higher than the volume influx through the xylem, particularly in the VPD+ compartment. At night, the xylem influx was higher than the transpiration efflux. The relative contribution of phloem and xylem to the influx of water in fruit are summarized in Table 2. High VPD slightly increased the contribution of phloem in the fruit water supply, whereas low plant fruit load slightly reduced it.

Stems, Leaves, and Fruit Water Potentials

Whatever the VPD and plant fruit load, stem and leaf water potentials decreased during the day (Figure 6 a and b), whereas the fruit water potential remained constant around −0.42 MPa (Figures 6c) and was not affected by the VPD. In contrast, the leaf and stem water potentials significantly decreased at high VPD, down to −1.1 MPa and −0.62 MPa, respectively. The plant fruit load had no significant effect on water potentials.

Discussion

Phloem, Xylem, and Transpiration Fluxes in Relation to Diurnal Fruit Growth

Under the conditions in this study, xylem, phloem, and transpiration fluxes showed opposite diurnal patterns. The xylem flow increased at night and decreased during the daytime (Figures. 4 and 5) when the stem water potential was reduced by the high evaporative demand. In contrast, transpiration and phloem flows were at maximums during the day and minimums at night. Fruit growth essentially occurred at night unless misting occurred during the day (Figure 3); it was highest at the end of the day (0.12 g h^{-1} at 18:00) and decreased down to negative values during the warmest and driest hours of the day, when VPD and temperature reached 2.7 kPa and 30°C, respectively. These observations are in agreement with those published

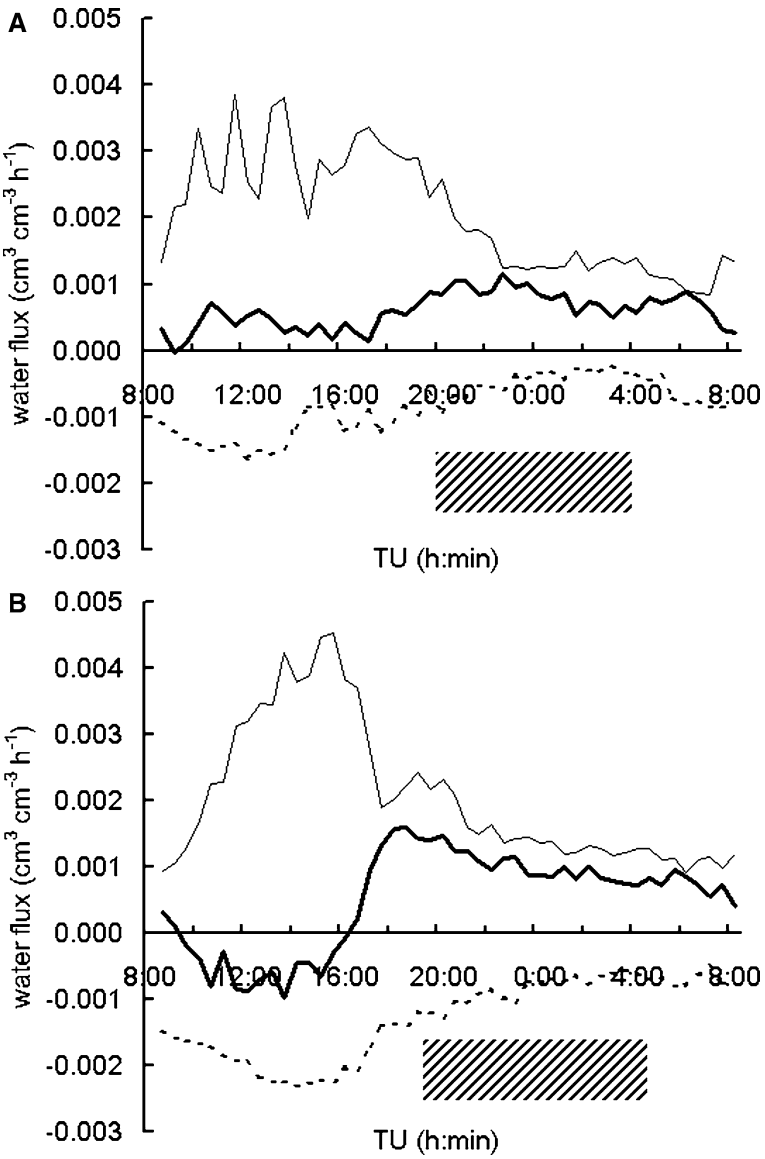

Figure 4. Effects of low VPD (**A**) and high VPD (**B**) on the phloem (regular), xylem (bold), and transpiration (dotted) fluxes (cm^3 of water per cm^3 of fruit volume per hour) of growing tomato fruits (9–10 July; F6 fruits). Transpiration means are based on changes of 2 to 4 fruits per treatment whereas phloem and xylem means are based on 4 to 16 estimates (compare *Materials and Methods*). Shaded zones represent night periods.

by Lee and others (1989), Grange and Andrews (1995), and van de Sanden and Uittien (1995), all of whom observed a decrease in fruit growth rate during daylight and an increase at night. Other authors (Ehret and Ho 1986b; Pearce and others 1993) reported a tomato growth rate higher during the day than at night, but as assumed by Pearce and others (1993) and demonstrated in the present experiment, this likely results from experimental conditions with a low diurnal stress environment. Indeed, misting prevented fruit shrinkage and maintained the diurnal RGR at the level of night values. The daily growth was about 2.2 g fluid $fruit^{-1}$ day^{-1} at VPD–, which is close to 2.7 g $fruit^{-1}$ day^{-1} measured by Ho and others (1987) and to 1.9 g $fruit^{-1}$ day^{-1} measured by Grange and Andrews (1993). In contrast, it was only 1.5 g $fruit^{-1}$ day^{-1} at VPD+. Similarly, Plaut and others (2004) reported a reduction of water transport from 2.7 to 2.0 g $fruit^{-1}$ day^{-1} in 20-day-old tomato fruits, resulting in salinity stress.

In the present study, the phloem influx accounted for the major supply of water to tomato fruit, representing 75%–80% of the daily water supply to the fruit (on average, 85% for the daylight period and 65% for the night period) and delivered 0.051 cm^3 cm^{-3} of fluid per day (that is, about 2.6 g of fluid per day). These values are close to those reported by Ho and others (1987), Wolterbeek and others (1987), and Plaut and others (2004), who analyzed water, carbon, and/or mineral accumulation in tomato fruits at different developmental stages; they found, respectively, a phloem contribution to fruit volume growth of

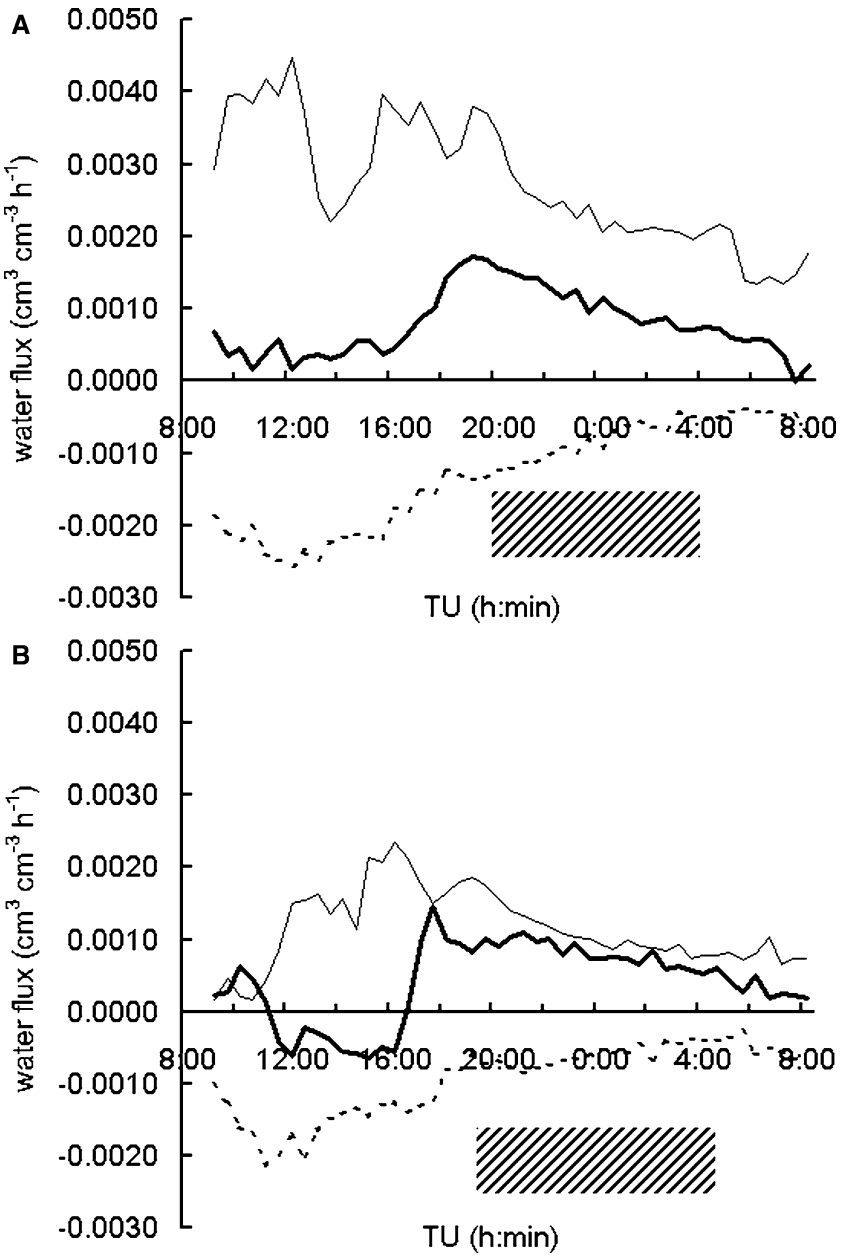

Figure 5. Effects of low (**A**) and high (**B**) plant fruit load on the phloem (regular), xylem (bold) and transpiration (dotted) fluxes (cm^3 of water per cm^3 of fruit volume per hour) of growing tomato fruits (7–8 August; VPD+). Transpiration means are based on changes of 2 to 4 fruits per treatment whereas phloem and xylem means are based on 4 to 12 estimates (compare *Materials and Methods*). Shaded zones represent night periods.

Table 2. Contribution of Phloem and Xylem Fluxes to the Influx of Water in Fruit Calculated for the Respective Days Illustrating the Effects of VPD (10 Jul) and Plant Fruit Load (7–8 Aug).

	F6 VPD–			F6 VPD+			F3 VPD+		
	24 hours	daytime	night	24 hours	daytime	night	24 hours	daytime	night
% Phloem	75	83	65	73	85	60	77	85	70
% Xylem	25	17	35	27	15	40	23	15	30

88%, 84%, and 80%, which corresponds to about 3 g of fluid day^{-1} in 3-week-old fruits. Consequently the xylem influx contributed only a minor part of the water supply to the fruit, and it could compensate for the transpiration efflux only at night. The transpiration values measured in this study were high, up to 1.4 mg cm^{-2} h^{-1} in the VPD+ compartment. In contrast, Ehret and Ho

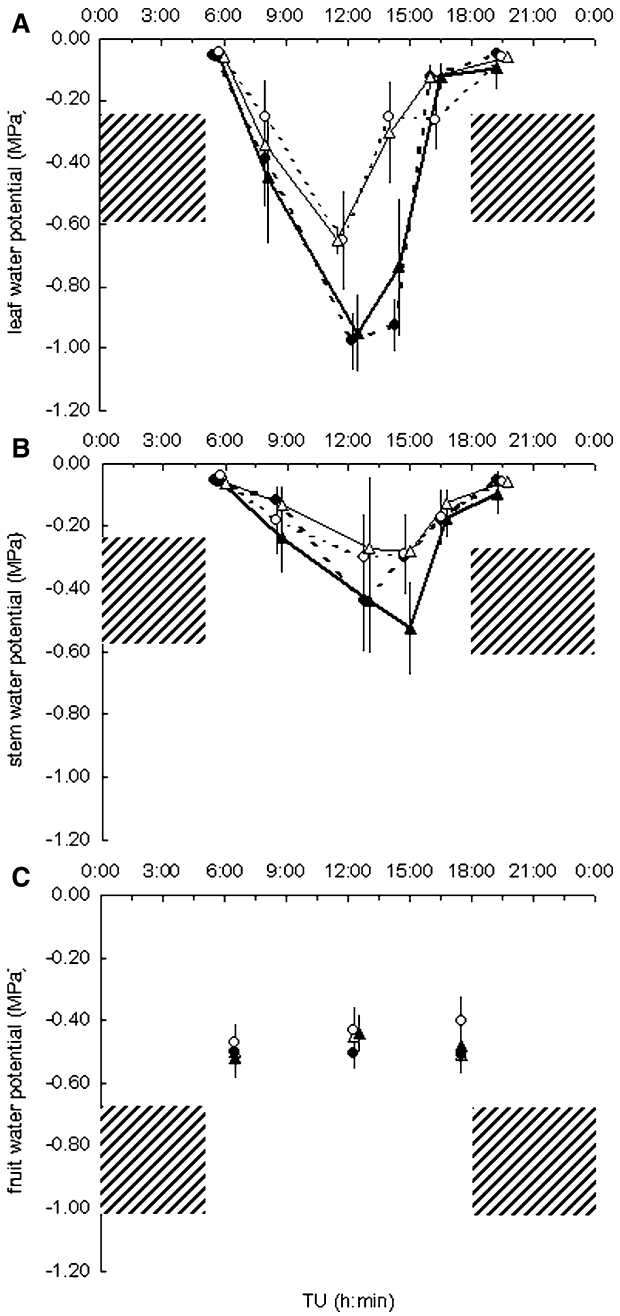

Figure 6. Effects of VPD and plant fruit load on the water potential of leaf (**A**), stem (**B**) and fruit (**C**) of tomato plants. Closed, VPD+; open, VPD–; circles, F3; triangles, F6. Means of 2 (fruits) or 4 (leaves and stems) replicates ± SE. Shaded zones represent night periods. Results were obtained on 10 September when the maximum temperature was 32°C, the maximum VPD was 2.5 and 1.5 kPa in the VPD+ and the VPD– compartments, respectively, and radiation about 600 W m^{-1} PAR.

(1986b) and Lee (1990) found values of tomato fruit transpiration below 0.3 mg cm^{-2} h^{-1}. However, these authors worked at VDP from 0.9 to 1.5 kPa, which is less than in the present experiment (up to 2.7 kPa). In a recent work, Kawabata and others (2005) reported rates of transpiration of 0.47 and 1.07 g $fruit^{-1}$ day^{-1} in moistened and dried air chambers, respectively. In the present study, transpiration was measured on detached fruits from which the pedicel and the calyx had been removed, and the contribution of the calyx to water fluxes from stem to inflorescence was not taken into account, as all calculations were based on fruit volume variations. However, the calyx has been reported to play an important role in the water potential at the fruit pedicel level (Bussières 2002), as its transpiration is of the same order of magnitude as that of the fruit (Ehret and Ho 1986b).

Effect of High VPD on Fruit Growth and Water Relations

The diurnal decrease in fruit RGR in the VPD+ compartment was due to decreased net water accumulation in the fruit, which received less water through xylem and lost more water through transpiration. Sometimes, fruits even experienced xylem efflux from the fruit to the plant. The gradient of water potential between stem and fruit drives the water import to fruit (Johnson and others 1992; YaLing and others 2004), because of variations in stem water potential and the relative stability of the fruit water potential during the day, as found in the present study. Thus, water outflow from the fruit under stressed conditions indicates that the stem water potential fell below the fruit water potential. This was not exactly observed, as low or negative values of xylem flux occurred from 10:00 to 15:00 (Figure 4), but the stem water potential remained higher than the measured fruit water potential until 12:00 (Figure 6). Two reasons for this may be put forward. The first may be an underestimation of fruit water potential, due in part to the fall in tissue water potential after excision. When measured on different days and under different conditions (greenhouse or climatic chamber), the diurnal dynamic of fruit water potential was always the same (no dynamic), but variations of ± 0.20 MPa were observed, with an average of about –0.40 MPa (data not shown). This value, close to the mean fruit water potential illustrated in Figure 6c, is in accordance with values reported in the literature (Ehret and Ho 1986b; Grange 1995; Ruan and others 1995). The second reason is the day-to-day variation in stem water potential, as data shown on Figures 4 and 6 were acquired on dif-

ferent days. Based on many days of measurements, the relationship between stem water potential and air VPD indicated a relatively stable stem water potential from 0.4 to 1.8 kPa and then a decrease when air VPD rose above 1.8 kPa (data not shown). Because the inversion of xylem flux indicates the fall of stem water potential under fruit water potential, then a fruit water potential of −0.35 to −0.40 Mpa would be realistic. Indeed, on 10 September (the day on which data shown in Figure 6 were collected) the air VPD rose above 1.8 kPa between 11:00 and 12:00, and that increase corresponded to a stem water potential of −0.35 to −0.40 MPa. Thus the xylem flux in tomato fruit would be directly correlated with the plant water status, which was affected by VPD through plant transpiration (Marcelis 1989) and, consequently modified the stem and leaf water potential (Bruggink and others 1988; Stirzaker and others 1997).

At high VPD, the fruit phloem influx was decreased in the morning, but the reduction of the phloem contribution to fruit volume growth was very low. Previous observations made by Peel (1965), Swanson and others (1976), Pickard and others (1979), Lang and Thorpe (1986), and Johnson and others (1992) showed that the plant water status may have a direct effect on phloem translocation through the effect of apoplasmic water potential on the turgor potential gradient in the phloem. Therefore it was expected that high VPD conditions would have greatly reduced the phloem influx, at least during the driest hours of the day, through the decrease of plant water potential or through a reduction of photosynthesis. High VPD may actually have reduced stomata opening (Boulard and Jemaa 1993) and concurrent photosynthesis (Romero-Aranda and Longuenesse 1995) without affecting the availability of carbohydrates for phloem transport possibly coming from carbohydrate reserves (Pearce and others 1993; Grange and Andrews 1994; Gary and others 2003). Similarly, Plaut and others (2004) observed that, unlike salinity stress, water stress only slightly reduces the rate of water transport to fruit and the contribution of phloem. However, in the VPD+ compartment, the slow rise of phloem flux from the lowest value in the morning to the highest level in the late afternoon (Figure 4b) may indicate a low fruit osmotic pressure in the morning, which was slowly attenuated as transpiration rose and xylem efflux occurred. Thus, despite apparently similar and stable fruit water potentials among treatments, some qualitative differences between turgor and osmotic pressure probably existed, and this would explain the different diurnal dynamics, as discussed below.

Effect of Plant Fruit Load on Fruit Growth and Water Relations

In this study, reduction of plant fruit load increased the fruit volume growth through an increase of phloem, xylem, and transpiration fluxes. The increase in xylem flux was not expected because plant fruit load affected neither the stem nor the fruit water potentials (that is, the stem-fruit water potential gradient) at the time scale it was measured. Tomato fruits do not have stomata (Miller 1983; Johnson and others 1992), and therefore transpiration is only cuticular. F3 fruits lost more water by transpiration per unit area than F6 fruits in the same greenhouse compartment (VPD+). Jones (1992) and Leonardi and others (1999) reported an effect of growing conditions on the anatomy and water vapor conductance of the cuticle. Reducing the competition for assimilates presumably changed the fruit epicuticular wax in terms of composition, organization, and/or structure.

Interestingly, F3 and F6 fruits exhibited different diurnal dynamics of RGR (Figure 3), which could be related primarily to the higher phloem flux in the F3 fruits at the beginning of the day (Figure 5), likely due to the low number of competing sinks. Around 13:00, the fall of RGR indicated the stomata closure and arrest of photosynthesis, probably due to the peak of air VPD around 2.8 kPa (Figure 2). In contrast, F6 fruits did not grow in the morning due to a very low phloem influx. During the night the phloem flux was lower in F6 than in F3 fruits, probably because of a lower fruit osmotic pressure. In the morning the air VPD was already high and the low water availability in the plant coupled with a low fruit osmotic pressure may be responsible for the low RGR. It can be seen from Figure 5 that the phloem flux to F6 fruits increased precisely as the xylem efflux occurred. This efflux of water probably promoted a slight temporal increase of osmotic pressure in the fruit, which boosted the phloem flow. Thus differences in osmotic pressure may be responsible for the different dynamics of RGR between F6 and F3 fruits, as reported for peach (MacFadyen and others 1996). Fruit analysis at maturity showed that the dry matter content was similar in F3 and F6 treatments, but the sugar content was increased in F3 fruits (Bertin and others 2000), sustaining the hypothesis of a higher osmotic pressure. Moreover, cell wall relaxation was probably promoted by high

carbon import in F3 fruits. On the whole, the difference in water potential between stem and fruit was likely higher in F3 than in F6 fruits during a short time period in the morning, preventing xylem efflux in F3 fruits. Fruit and stem water potential should be measured at a shorter time scale to elucidate this point, which was not possible with the method used in the present study. In another experiment, continuous *in situ* measurements of water potential with micro-psychometric sensors inserted in the fruit pericarp showed rapid hourly fluctuations of ± 0.3 MPa (unpublished data). Moreover, the higher transpiration rate of F3 fruits at high VPD would enhance this hypothesis, although transpiration can not be considered as a driving force for phloem transport (Kawabata and others 2005).

Methodology

In the present study, the contributions of phloem, xylem, and transpiration fluxes were analyzed at an hourly scale according to the methodology developed and improved by Lang (1990). This method has been discussed especially with regard to the possible negative effects of pedicel steaming (or heat-girdling), which might induce xylem injuries or embolism and lead to underestimates of the xylem contribution to fruit growth. A theoretical analysis of the effect of peach pedicel girdling showed that the error induced for estimation of the xylem flux may be significant during intermediate periods between intensive growth and fruit shrinkage hours (Fishman and others 2001). Yet, there is no alternative method for estimating the phloem and xylem contributions to fruit growth on a short time scale. Neither the analyses of mineral accumulation in the fruit (Ho and others 1987) nor the application of ethylene diamine tetraacetic acid (EDTA) solution for collecting phloem exudates from the cut end of tomato pedicels (Araki and others 1997) would be adapted to such a time scale. Labeling methods with O^{18} or tritium would not be possible in greenhouse conditions because of radioactivity, and studies of symplasmic tracers such as carboxyfluorescein (Ruan and Patrick 1995; Patrick and Offler 1996) could only give qualitative information. Nuclear magnetic resonance (NMR) microimaging (Köckenberger and others 1998) seems to be more promising, but expensive. This is why we visually checked that the xylem was still intact after heat girdling (Figure 1), and it was still functional several hours later, as the fruit water potential did not vary. Plaut and others (2004) found a good fit between the transport of water to girdled fruits and the relative water transport by xylem calculated by a mechanistic model based on mineral accumulation.

Conclusions

Whereas phloem flux is the major contributor to daily variations in fruit volume, the effect of air VPD on fruit growth is rather controlled by changes in the xylem and transpiration fluxes in relation to plant water status. Plant fruit load affected all fluxes, indicating possible modifications of pedicel and cuticle traits. Interestingly, whereas fruit dry matter growth is irreversible and rather stable on a short time scale, fruit volume growth is reversible and variable. During a single day, we could observe changes in fruit volume growth essentially due to water movements (xylem flux, transpiration, and shrinkage) without any concurrent changes in fruit water potential. Tomato fruits may be considered as having a large hydraulic capacitance, which succeeds in attenuating the effects of environmental fluctuations through the importance of phloem flow in the water balance of the fruit. Investigating the short time scale variations of fruit water potential and the relative contribution of osmotic and turgor pressure under stress conditions may deepen our knowledge of fruit-water relations.

ACKNOWLEDGMENTS

This work was conducted in the framework of research programmes sponsored by INRA (AIP-AGRAF) and by the Provence Alpes Côte d'Azur Region. We acknowledge the helpful technical assistance of Béatrice Brunel, Jean-Claude L'Hôtel, Claudine Orlando, and Pierre Reich. Many thanks to Dr. P. Bussières for his valuable comments on the manuscript.

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