Macro- and Microscopic Aspects of Fruit Water Relations Influencing Growth and Quality in Tomato

W. van Ieperen, U. van Meeteren, J. Oosterkamp and G. Trouwborst
Department of Plant Sciences, Horticultural Production Chains Group
Wageningen University, 6709 PG Wageningen
The Netherlands

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Abstract

Quality of fresh tomato fruits is basically determined during growth of the fruits on the plant. Import of water, nutrients and assimilates from other parts of the plant largely determine fruit growth. Previous research has shown that during fruit development 90% of all water entering the fruit is transported via the phloem. Water import via the xylem seems to cease after maximal growth rate of the fruit has be reached. It seems therefore logical to assume that somewhere along the xylem transport path between shoot and fruits a large hydraulic resistance exists, which besides water also restricts Ca^{2+} import. Though, previous research has shown that the xylem hydraulic resistance between stem and tomato fruits is not high enough to significantly restrict water flow via the xylem. Other explanations for the restricted water exchange between stem and tomato fruit should be investigated. In present research we examined macro- and microscopic aspects of water relations of tomato fruits, including changes in apo- and symplastic osmotic pressures and cell pressure (turgor, measured by cell pressure probe) in pericarp tissue of tomato fruit during development and due to water stress aiming to investigate the driving force for water exchange between apo- and symplast at cell level. Turgor pressure in tomato fruit cells was extremely low (< 0.1 MPa), almost constant during fruit development and not influenced by water stress during growth that actually reduced fruit size by 30%. Symplastic osmotic pressures in pericarp tissue slightly increased during fruit development (15 to 50 Days After Anthesis) and increased due to low water availability in the root environment. Apoplastic osmotic pressures in pericarp tissue also increased with fruit development and due to low water availability during growth. A possible role for apoplastic solutes, regulating the water exchange of fruit pericarp cells during growth is proposed.

INTRODUCTION

Maintenance of an adequate water balance is crucial to obtain maximal productivity of greenhouse-grown tomato. Importantly, however, is the recognition by growers of the need for high quality produce to meet the modern market demands. Maximal productivity might lead to low quality tomato fruits with inferior taste and texture (Jones and Tardieu, 1998). Post-harvest quality aspects of tomato fruits are clearly influenced by pre-harvest growth conditions. On process level, effects of growth conditions, and integration of assimilate and water relationships are expected to play an important role in the establishment of both production and post-harvest quality (Van Ieperen et al., 2003). Models might provide an increasingly useful tool for predicting water and assimilate relationships. However, over the past decades little attempts have been made to develop models to be used as a predictive framework (Jones and Tardieu, 1998). These models should account for processes such as water and assimilate transport into fruits as well as cell and tissue expansion to be able to predict the effects of changing plant water status on fruit growth at different time-scales. In this paper we describe some macro- and microscopic aspects of plant and fruit water transport during fruit growth in tomato in relation to water availability in the root environment in an attempt to analyze key factors for future predictive models for fruit growth in tomato.

MATERIALS AND METHODS

Tomato plants (*Lycopersicon esculentum* Mill. 'Belliro') were grown in a greenhouse in perlite at two constant levels of water content in their root environment: a control (70 v/v%) and a 'water stress' treatment (20 v/v%) (Van Ieperen et al., 2003). Fruits of different development stages, 15, 25, 40 and 50 DAA (Days After Anthesis), were harvested early in the morning to ensure maximal turgidity and transported and stored under conditions that minimized water loss before measuring water potential components.

Changes in driving force for xylem water transport between stem and fruits were determined by measuring turgor and osmotic pressure in fruit pericarp cells as well as osmotic pressure of sap extracted from the apoplastic space of the pericarp. Measurements were done on pericarp disks (8-mm diameter). Apoplastic fluid was extracted by centrifugation (Balibrea et al., 1999) and the apoplastic extracts were screened and corrected for cytoplasmic contamination by measuring malate dehydrogenase-activity relative to bulk extracts (Husted and Schjoerring, 1995). Osmotic pressures (VAPRO®, Wescor, Inc, Logan, UT, USA) were measured immediately after extraction (apoplastic osmotic pressure) and after a subsequent freeze-thaw cycle on the disk materials that remained after apoplastic extraction (symplastic osmotic pressure).

Turgor of pericarp cells was measured in cells in pericarp disks of fruits neighboring the fruits used for osmotic pressure measurements using a cell pressure microprobe (Tomos, 2000). These fruits were also harvested early in the morning and kept under minimal evaporating circumstances between harvest early in the morning and the actual turgor measurements.

RESULTS AND DISCUSSION

Xylem Hydraulic Resistance

The applied water stress treatments clearly influenced the growth rate of the tomato fruits (Fig. 1), mainly by reducing the fruit size. Previous research has shown that the applied water stress treatment influenced the overall xylem hydraulic resistance between the stem and fruits of a tomato plant. The majority of the hydraulic resistance was located in the pedicel of the fruit, and especially at the abscission zone (AZ) in the knuckle-like structure, midway the pedicel of the fruit. At this point almost all xylem vessels were ended, which enormously increased the hydraulic resistance (Van Ieperen et al., 2003). Preliminary measurements of hydraulic resistance in tomato fruits of comparable age (25 DAA) but without knuckles in the pedicel (cv. Apetito), showed a much lower hydraulic resistance in the pedicel, but in magnitude comparable with the hydraulic resistance of the stem segments of the pedicel of AZ containing pedicels tomato fruits (Van Ieperen, unpublished results). Water stress during growth of the fruits reduced the xylem hydraulic resistance in pedicels of the knuckle containing (Van Ieperen et al., 2003) as well as the knuckle-less tomato cultivar. However, after evaluating the possible impact of the measured hydraulic resistance of the xylem transport path on water transport between stem and fruit it could be concluded that these resistances were far not high enough to explain the low rates of xylem water flow between stem and fruit (Van Ieperen et al., 2003), when considering fruit water potentials at levels between -0.8 and -1.2 MPa (Johnson et al., 1992) and xylem water potentials in the stem between 0 and -1.5 MPa. It has been argued however, that net water import to tomato fruits via the xylem ceases after 10-15 DAA (Ho, 1996) and most of the water enters the fruit via the phloem. Consequently, there must be another reason for the restricted net water flow via the xylem than a high xylem hydraulic resistance between stem and fruit. A high hydraulic resistance of the xylem network within a fruit could be an explanation, but would possibly induce large apoplastic pressure differences between the proximal and distal side of the fruit.

Xylem water flow to transpiring organs such as leaves is driven by a pressure gradient which largely depends on transpiration. Fruits, however, hardly transpire (except

for possibly the calyx) and apoplastic pressure gradients will most likely tend to follow the fluctuations in the stem. Water import for cell expansion, however, involves transport over membranes and is therefore driven by a water potential gradient which includes osmotic components on both sides of the cell membrane. Differences in turgor pressure inside the cells, or changes in osmotic potential at one or both sides of the plasmalemma could therefore influence the water potential difference between cell and apoplastic environment and consequently water exchange.

If fluctuations in water potential in the stem are transmitted to fluctuations in apoplastic pressure in the apoplast of the fruit (due to the relatively small hydraulic resistance) fruit cells should be able to counterbalance those changes in pressure to protect themselves from excessive water loss during the day and extreme water import during the night.

Turgor

One of the possibilities mechanisms could be a fluctuating cell turgor, related to volume changes, counterbalancing the fluctuations in xylem pressure. However, tomato fruits seem hardly to change in volume due to water status fluctuations (Malone and Andrews, 2001). Measured turgor was low, relatively constant during fruit development and not influenced by the water stress treatment (Fig. 2A). Especially the continuous low value of cell pressure (0.04-0.05 MPa), which was measured on samples from fruits that were expected to be at maximal water content, indicates the impossibility to counteract expected daily changes in the water potential gradient between symplast of pericarp cells and surrounding apoplast. The herewith presented values for turgor pressure in tomato pericarp cells are in the same range as values previously reported (Mingo et al., 2003; Shackel et al., 1991) and much lower than values usually measured in other growing plant tissues. Pressure within the pericarp cells did not differ between the water stress treatment and the control. A rate determining role for turgor on cell expansion, such as assumed by Lockhart (1965) seems therefore unlikely.

Symplastic and Apolastic Osmotic Pressure

Another possibility to counterbalance differences and or fluctuations in apoplastic pressure potential in the fruit pericarp could be by adjusting the osmotic pressure gradient over the cell membrane. The symplastic osmotic pressure was clearly influenced by water stress compared to the control (Fig. 2B), probably due to osmoregulation. Significant osmotic pressures were also observed in the apoplast of the pericarp in all development stages. These apoplastic osmotic pressures were also influenced by the water stress treatment (Fig. 2C). Taking into account a correction for the cell turgor, the thus observed osmotic gradient still supports significant water import in the cells, which in reality did not take place. An explanation for this could be that in the pericarp disks matrix potentials add more to the water potential equilibrium between apo- and symplast than in whole fruits on the plant, because a relative small change in water content in the apoplastic space might result in a large change in capillary forces in the cell walls.

The presence of a significant amount of solutes in the relatively low volume apoplast, 4% of total pericarp volume (Damon et al., 1988), points to the possibility that water exchange between cell and apoplast in tomato fruits is regulated by active regulation of the osmolality of apoplastic fluid in response to water stress. Active exchange of inorganic ions and/or sugars and or changes in apoplastic pH (Almeida and Huber, 1999; Husted and Schjoerring, 1995; Muhling and Lauchli, 2000) might play a role in establishing homeostasis upon fluctuating apoplastic pressure potentials in the tomato fruit. Understanding of these processes will be essential for modeling fruit water relationships in relation to growth and quality.

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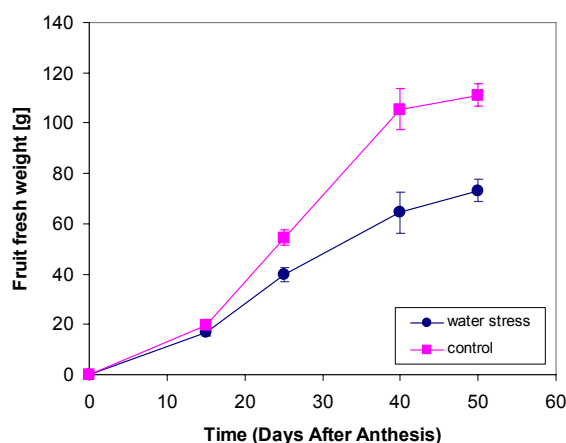
Figures

Fig. 1. Effect of water availability in the root environment on growth of tomato fruits during fruit development. First fruit of first truss ('water stress' 20 v/v% substrate water content and 'control' 70 v/v% substrate water content; averages and standard errors).
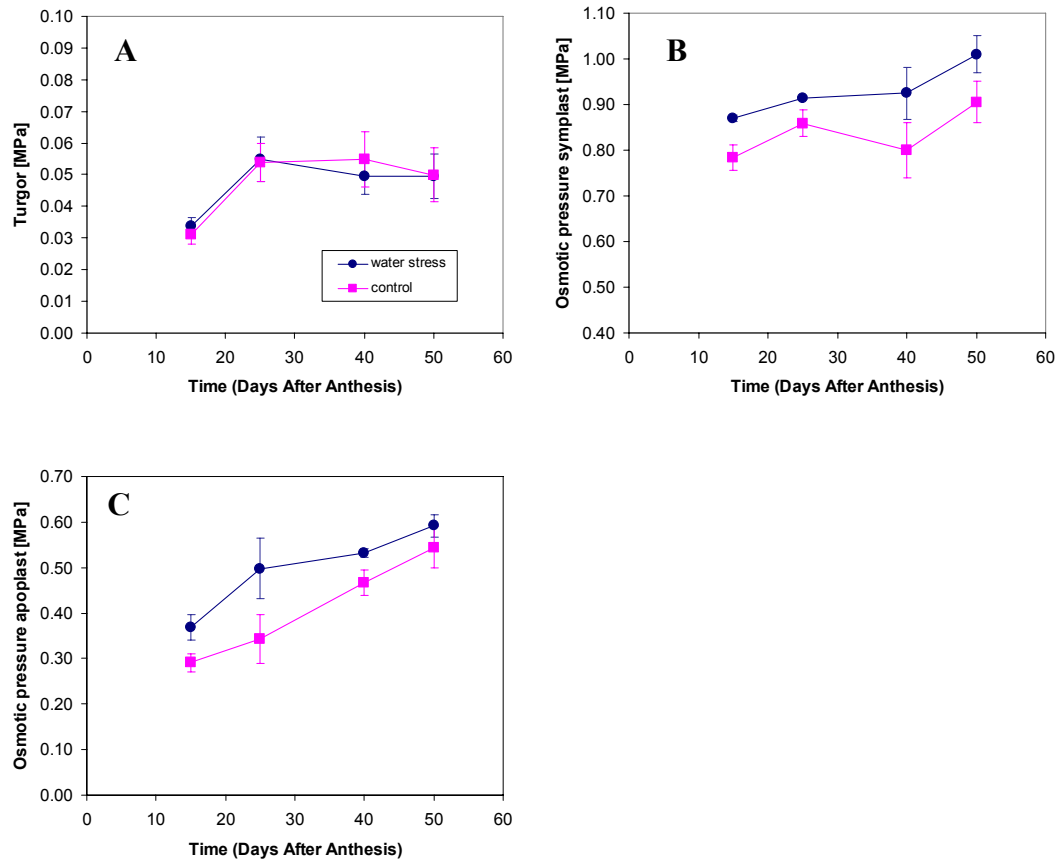
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Fig. 2. Effect of water availability in the root environment on (A) pericarp turgor of tomato fruits, (B) symplastic osmotic pressure and (C) apoplastic osmotic pressure in the pericarp during fruit development. Data from 1st and 2nd fruit of cluster 1-3 ('water stress' 20 v/v% substrate water content and 'control' 70 v/v% substrate water content; averages and standard errors; n=12).