Revised sap flow driven stem diameter model for tomatoes grown under assimilation lighting

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Abstract

A comprehensive plant model that was originally developed to predict short- and long-term variations in tomato stem diameter stopped working properly when used for tomato plants grown under assimilation lighting during winter. Under these prolonged day lengths in winter, an atypical diel pattern emerged showing an increase in stem diameter 1-2 h after the lights were turned on. In order to explain this specific plant behavior, sap flow sensors and linear variable displacement transducers were installed on tomato plants (*Solanum lycopersicum* L. 'Foundation'). Plants were lighted for 18 h day^{-1} with a combination of natural sunlight and HPS lamps (169 µmol m^{-2} s^{-1}). Two hypotheses to explain this atypical plant behavior were formulated, and subsequently examined: (i) transport of sugars from leaves to roots decreases phloem water potential, which imports water from the xylem and causes an increase in stem diameter; and (ii) the sudden increase in light intensity causes a drop in xylem water potential, resulting in changes in hydraulic conductance due to cavitation, which in turn affects the water exchange between xylem and storage and, hence, the variation in stem diameter.

Keywords: carbon relations, cavitation, heat balance, hydraulic functioning, linear variable displacement transducer, process-based plant modelling, stem diameter variations

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important crops in Belgium. It accounted for 20% of the total vegetable production in 2015 (VLAM, 2015). When narrowing it down to vegetables produced in greenhouses, tomato accounted for 71% of the total production. Worldwide, Belgium and the Netherlands are the top two most efficient tomato-producing countries with an average yield of 50 kg m^{-2} (FAO, 2014). In practice however, tomato growers can achieve a yield of 65 kg m^{-2} (S. Fabri and L. Wittemans, 2017 pers. commun.). Tomato growers implement all sorts of new technology to optimize yield even further in order to maintain their leading position. One of the possibilities is implementation of assimilation light in winter-time, when natural light intensities are low. This allows growers to harvest tomatoes year-round. Studies at the Research Center Hoogstraten have shown that yields >100 kg m^{-2} are possible when using high light intensity assimilation lamps (Moerkens et al., 2015; Vanlommel et al., 2017). The newest technologies include the use of plant sensors that allow growers to monitor plants in real-time. Examples of these sensors are sap flow sensors and linear variable displacement transducers, which measure water transport through the stem and stem diameter (D_{stem}) variations, respectively. A combination of these measurements gives an

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indication of the plant's water status (Van den Bilcke et al., 2013; Escalona et al., 2002; Steppe et al., 2008a, 2015; De Swaef et al., 2015) and can therefore assist the grower in adjusting irrigation and/or climate settings. These plant measurements can also be used to run a D_{stem} variation model that allows users to predict radial stem growth of their plants. This has already been implemented for tomato plants, and other crops and trees, and allows for a better understanding of the plant's physiological response to certain changes in the environment (Steppe et al., 2008a, b, De Swaef et al., 2013a, 2014). Specifically, for tomato, a model has been successfully used in the past (Hanssens et al., 2014, 2015; De Swaef and Steppe, 2011; De Swaef et al., 2013a, b). These previous experiments were conducted on tomato plants that had the sun as their only light source.

The above-mentioned assimilation light is different from the sunlight in two ways. First, there is a difference in light quality that is related to the wavelength distribution. Second, a distinction can be made in their light intensity and light pattern. The sun's light intensity on clear days has a sine-form pattern that increases in the morning, reaches a maximum in the afternoon and decreases during the evening. This is clearly different from the step-change pattern that results from the use of assimilation light. A typical diel pattern is observed when examining D_{stem} variations in plants grown under natural light (Steppe et al., 2015). At sunrise, plants lose water via leaf transpiration. Root water uptake prevents dehydration of the plant, but there exists a time lag between the onset of leaf transpiration and root water uptake during which water is used from the storage compartment, leading to shrinkage of cells and a decrease in D_{stem}. In the afternoon, when root water uptake exceeds transpiration, D_{stem} increases due to refilling of the storage compartment. D_{stem} variations in tomato plants grown under assimilation light deviate from this pattern. Assimilation light is not only used to increase light intensity, but also to increase day length. When the lights are switched on before sunrise, the same initial decrease in D_{stem} is observed for a period of 1-2 h, after which it suddenly starts increasing again. D_{stem} variations follow the normal pattern for the remainder of the day.

In this research, it was investigated whether the originally developed D_{stem} model can be used for tomato plants grown under assimilation lighting. Two hypotheses to explain the atypical increase in stem diameter were formulated and examined. The first hypothesis assumes that switching on assimilation light causes a sudden increase in photosynthesis, resulting in transport of sugars from leaves to stem and roots, a decrease in storage water potential, an import of water from xylem to storage, and an increase in D_{stem}. The second hypothesis states that a sudden increase in light intensity causes a drop in xylem water potential, resulting in a decreased hydraulic conductance due to cavitation. A subsequent increase in hydraulic conductance due to potential cavitation repair favors radial water transport into the storage compartment, leading to an increase in D_{stem}.

MATERIALS AND METHODS

Experimental setup

Tomato seeds (*Solanum lycopersicum* L. 'Foundation', Nunhems, Haelen, The Netherlands) were sown in rockwool blocks (Grodan, Roermond, The Netherlands) on September 4, 2015 and grafted on a 'Maxifort' rootstock (De Ruiter Seeds, Bergschenhoek, The Netherlands). On October 21, 2015, the grafted plants were transferred to rockwool slabs (Grodan, Roermond, The Netherlands) in a greenhouse (24×30×6 m) located at the Research Station for Vegetable Production (Sint-Katelijne-Waver, Belgium, 51°4'42"N; 4°31'41"E). An initial stem density of 2.5 stems m^{-2} was used. Both in week 49 and 52, an auxiliary stem was maintained for 1 in 4 plants. This resulted in a final stem density of 3.75 stems m^{-2}. During winter, high-pressure sodium (HPS) lamps (169 µmol m^{-2} s^{-1}) were used in addition to natural sunlight to increase light intensity and day length. From November 12, 2015 onwards, the lamps were switched on, and were used to gradually increase the day length. On December 18, 2015 the final day length of 18

h was reached by switching on the lamps from midnight until 6 PM. 50% of assimilation lights were switched off when the outside irradiation level reached 250 W, the remaining 50% were switched off at 350 W. Because lamps were switched on before sunrise, a typical winter day could be divided into two parts: (i) an artificial day when plants were lighted with assimilation light, and (ii) the natural day when sunlight possibly together with assimilation light was illuminating the plants. Plants were provided with a nutrient solution (3.5 mS cm^{-1}) using a drip irrigation system. The first three irrigation set points were at 3, 5 and 8 AM, followed by irrigation if the radiation sum exceeded 90 J cm^{-2} or if one hour had passed since the last irrigation event, but no later than 1:30 PM.

Microclimate and plant measurements

Microclimate was continuously monitored above the canopy. Photosynthetic active radiation (PAR) was measured using a PAR sensor (LI-190R, LI-COR Biosciences, Lincoln, Nebraska, USA). Relative humidity (EE08 series, E+E Elektronik, Engerwitzdorf, Austria) and temperature (Pt 1000, E+E Elektronik, Engerwitzdorf, Austria) were measured with an integrated sensor installed inside a ventilated radiation heat shield to minimize effects of direct light.

Sap flow rates were measured with Dynagage sap flow sensors (SGA13-WS, Dynamax Inc., Houston, Texas, USA). Stem diameter (D_{stem}) variations were measured with linear variable displacement transducers (Solartron Metrology, Bognor Regis, UK). Measurements of stem water potential were carried out on leaflets enclosed in aluminium foil using a pressure bomb (Model 1000, PMS Instrument Company, Albany, Oregon, USA).

All data (microclimate and plant) were recorded using a datalogger (CR1000, Campbell Scientific, Logan, Utah, USA) and 5-min averages were sent to the PhytoSense cloud service (Phyto-IT, Mariakerke, Belgium), which allowed for data storage, real-time data processing and visualization.

The atypical D_{stem} pattern during the artificial day has been observed over the course of two years on all measured plants (19 in total) at two different research stations and in five different greenhouse compartments. Measurements of one tomato plant from January 30 to February 1, 2016 are used in this paper to illustrate the phenomenon.

Model, calibration and simulation

The model developed by De Swaef et al. (2013a) was used. Sap flow serves as the main input for this model. Discrete measurements of stem water potential were used to calibrate the hydraulic conductance of the stem and D_{stem} measurements were used to calibrate the bulk elastic modulus, the maximum cell wall extensibility of the storage compartment, and the cell wall extensibility's time coefficient.

To assess the atypical D_{stem} increase observed at the start of the artificial day, two model adjustments were implemented: (i) whereas sugar loading into the storage compartment is a fixed value in the original model, in the revised model a higher loading rate was used when D_{stem} increased, and (ii) whereas a constant hydraulic conductance value is assumed in the original model, this value was allowed to vary according to a Gaussian distribution in the revised model.

Implementation, calibration and simulation of the model versions were performed in the plant modelling software PhytoSim (Phyto-IT, Mariakerke, Belgium).

RESULTS AND DISCUSSION

Standard model

Measured variations in D_{stem} showed an atypical pattern when day length was extended with assimilation light (Figure 1a). A stronger than expected decrease in D_{stem} occurred 1-2 h after switching on the lights, followed by an unexpected increase in D_{stem}. The original model

could not capture this atypical behavior (Figure 1a). In general, D_{stem} increases when sap flow decreases (Figure 1b), but the measured decrease in sap flow was insufficient to explain the observed increase in D_{stem} (Figure 1a).

Revised model: sugar loading
To assess the atypical D_{stem} pattern, the original model was first adapted for its sugar loading. It was hypothesized that the increase in D_{stem} at the start of the day was linked to the abrupt increase in light intensity (a step change from 0 to 169 μmol m^{-2} s^{-1}), leading to a rise in photosynthesis, more sugar loading, a decrease in storage water potential, radial water transport towards the storage, resulting in an increase in D_{stem}. The increase in D_{stem} occurred at around 1 AM, 1 h after the lamps were switched on. It was hypothesized that this time lag between turning on the lamps and the increase in D_{stem} was related to the time necessary to transport assimilates from leaves to stem. Every 24-h period was therefore divided into three periods for which the sugar loading was re-calibrated: (i) 12 AM-1 AM, (ii) 1 AM-2 AM, and (iii) 2 AM-12 AM. The loading rates were 0.0455, 9.8367 and 4.0072. 10^{-5} g h^{-1}, respectively. This model adaptation led to better simulations (Figure 2a), but the overall reliability of the model was questionable. De Swaef et al. (2013a) calibrated sugar loading rates for 6 consecutive days on 3 different tomato plants and found values ranging between -0.0057 and 0.0055 g h^{-1}. The weighted average of sugar loading in this study was 0.4118 g h^{-1}, which is a factor of 100 higher. The high increase in sugar loading between 1 AM-2 AM also led to a daily decrease in simulated osmotic water potential in the storage compartment of 0.16 MPa without restore at the end of the day (Figure 2b). Simulated turgor, on the other hand, increased each day due to a large import of water, resulting in a balanced total water potential. It was concluded that the hypothesis of increased sugar loading to explain D_{stem} increase at the start of the day could be rejected.
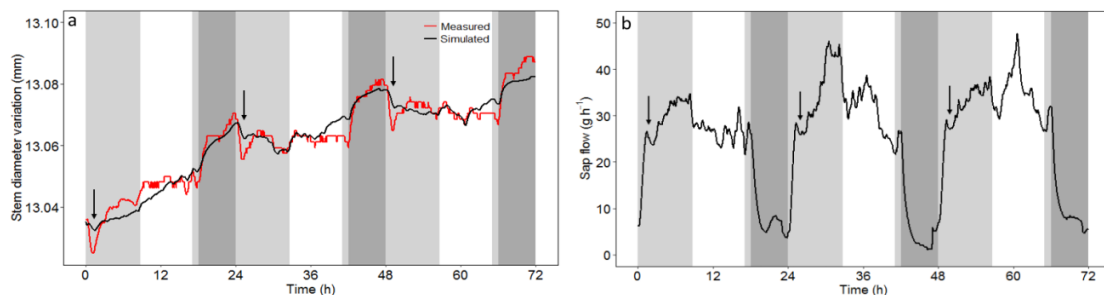

Figure 1. (a) Measured (red) and simulated (black) stem diameter variation for a 3-day period (January 30 to February 1, 2016). Simulated data are the output from the original model (De Swaef et al., 2013a). (b) Measured sap flow. Dark grey areas represent the dark period when there was no sunlight or assimilation light. Light grey areas represent periods when assimilation light was used to prolong the day length. White areas represent the day-time with sunlight and potential assimilation light. Arrows show unexpected D_{stem} increase.
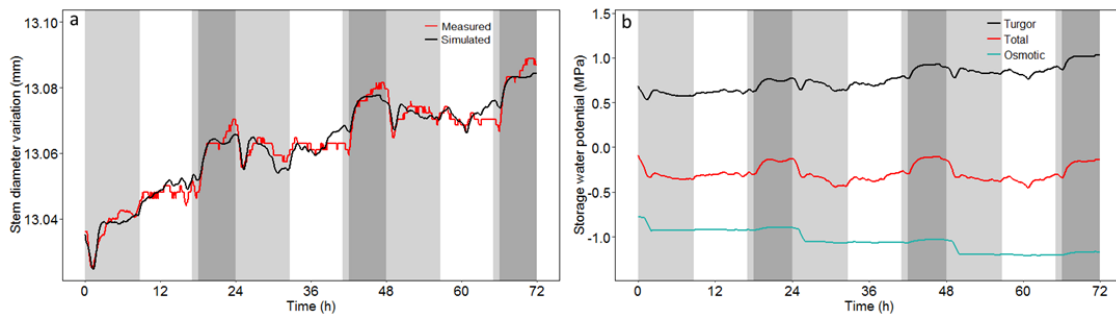
Figure 2. (a) Measured (red) and simulated (black) stem diameter variation for a 3-day period (January 30 to February 1, 2016). The original model by De Swaef et al. (2013a) was adapted to allow dynamic changes in sugar loading. (b) Simulated turgor (black), osmotic (blue), and total (red) storage water potential for the 3-day period. Light grey, dark grey and white areas have the same meaning as explained in Figure 1.

Revised model: hydraulic conductance

Turning on the lights at the start of the artificial day caused a steep increase in sap flow (Figure 1b). It is known that if root water uptake cannot keep up with a sudden increase in transpiration, the tension on the water column increases to such a level that xylem vessels cavitate. Since cavitated vessels are filled with air, they cannot longer transport water, leading to a decrease in hydraulic conductance (De Roo et al., 2016). To this end, the hydraulic conductance was allowed to decrease in the revised model (Figure 3a). After about an hour, stabilization occurred, and the hydraulic conductance was allowed to increase again to its initial value. This revised model simulated the measured data well, except for the overshoot at the end of the second and third day (Figure 3b). Previous research on tomato by Kageyama et al. (2009) showed an increase in acoustic emissions (as proxy for cavitation (De Roo et al., 2016)) when lights were switched on in growth chamber experiments, supporting our hypothesis. They also measured D_{stem} variations, which showed a similar increase in D_{stem}. Hydraulic resistance (inverse of conductance) increased about 2-fold in our model simulations (Figure 3a). This is in accordance with measurements by Zwieniecki and Holbrook (1998) on white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.).
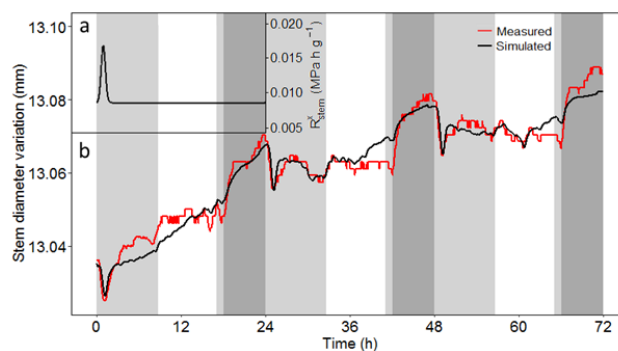

Figure 3. (a) Daily variation in simulated hydraulic resistance (Rx_{stem}) shown for a 1-day period. (b) Measured (red) and simulated (black) stem diameter variation for a 3-day period (January 30 to February 1, 2016). The original model by De Swaef et al. (2013a) was adapted to allow dynamic changes in hydraulic conductance. Light grey, dark grey and white areas have the same meaning as explained in Figure 1.

CONCLUSION

Tomato plants grown under a combination of assimilation light and sunlight show an atypical pattern in D_{stem}. The shrinkage that occurred at the start of the artificial day (before sunrise) was quickly followed by an increase in D_{stem}. A mechanistic tomato model (De Swaef et al., 2013a) was used to assess this unexpected behavior. When loading rate of sugars into the phloem was made variable, better simulations of D_{stem} were obtained, but the daily decrease in osmotic water potential without restore at the end of the day was considered unrealistic. When hydraulic conductance was allowed to vary, simulations of D_{stem} improved, and the magnitude by which the hydraulic conductance had to be changed was plausible when compared to literature values.

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