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RESEARCH ARTICLE



Estimating tomato water consumption by sap flow measurement in response to water stress under greenhouse conditions

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ABSTRACT

This research was conducted to determine the water consumption of tomato plants, the effects of water stress on stem sap flow (SF) and its response to climatic factors. SFs in 100% irrigation (T_1), 75% (T_2) and 50% (T_3) of irrigation amount of T_1 were monitored using Dynagage sensors. Compared to T_1 , the difference in SF was observed under deficit irrigation in the same climatic conditions on sunny days although there was no apparent difference between T_1 and T_2 on cloudy days. Under T_1 , the correlation and regression relationships between SF and climatic factors were analyzed at daytime (6:00–22:00), morning (6:00–14:00) and afternoon (14:00–22:00). Considering daytime, the order of sensitive indicators to SF was $VPD > LI > T_a$ and $LI > VPD > T_a$ for the Fall-Winter sunny days and Spring-Summer season, respectively. The water uptake over SFs measured for Fall-Winter and Spring-Summer periods were calculated as 168.65 and 229.18 mm, respectively.

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KEYWORDS

Water uptake; transpiration; deficit irrigation; diurnal environment effects; greenhouse

Introduction

The process of crop transpiration is essential for the overall development of crops. It tends to promote the absorption of water and nutrients although it is often a complex physiological process, often influenced by a variety of environmental conditions, morphological structure and physiological status of the crop. It is quite challenging for it to be estimated precisely and existing methods for measuring crop water consumption such as the water balance method (Yuan et al. 2001), Bowen ratio energy balance method (Hanson and May 2006) and the use of weighing lysimeters (Orgaz et al. 2005; Miranda et al. 2006) are generally invasive and may damage the plant. Subsequent research efforts attempted to measure plant transpiration by the covering method, the bleeding flow method and the chamber method, but these methods did not improve on the efficiency of the existing methods. Generally, these methods are time-consuming and laborious, making it impractical and timely for research work.

Consequently, an attempt was made by Aiwang (1995) to determine the transpiration-based sap flow (SF) measurement using the stem gauge based on heat balance of the stem. In the course of this study on the stem SF rate, the theoretical basis of the stem heat balance theory was used to calculate the stem flow. These methods are preferred because they provide direct measurements of SF in situ with a high degree of accuracy and precision while being only mildly invasive. The SF can characterize plant transpiration directly, which can be used to calculate the crop transpiration easily (Zhang et al. 2011). SF measurement is considered as a good tool to illustrate water relations and also for irrigation scheduling (Juhász et al. 2011). Moreover, they are relatively inexpensive, easily automated for continuous high-resolution monitoring of water use by many replicate plants (Madurapperuma et al. 2009). The study of SF

can be helpful to evaluate the impact of environmental factors on transpiration and take necessary measures to improve plant water use efficiency (Ffolliott et al. 2003).

A recent study by Juhasz et al. (2013) focused on using SF measurements to estimate the water consumption of sweet cherry trees but their investigation was done under field conditions and they did not control the amount of water supplied to plants for growth and development. An earlier study by Ma et al. (2007), however, evaluated the effect of deficit irrigation on the stem SF of the pear-jujube tree under greenhouse conditions. Under deficit irrigation, plants undergo stress due to exceeding transpiration losses than absorptive capacity. From the aforementioned studies, with SF measurement it is possible to estimate the transpiration rate of plants. In fact, several studies have considered the study of the effect of water stress on plant development on one hand and the determination of crop water consumption, but little attention has been given to the estimation of total crop water consumption by using SF measurement in the greenhouse especially in the South-Eastern arid region of China. Additionally, there is little report on such studies covering Fall-Winter and Spring-Summer growth periods.

As a result of this, our study focused on achieving the following objectives: (1) to estimate diurnal and seasonal water consumption of tomato (*Solanum lycopersicum* L.) plants by measuring the stem SF; (2) to investigate the diurnal SF course on typical selected days along with diurnal course of climatic factors under different irrigation levels and (3) to investigate the response of daily SF course and the relationship between SF and climatic parameters. The results of this investigation could be helpful to develop an appropriate irrigation strategy for irrigation planners and managers considering water-saving and maintaining the crop production.

Materials and methods

Plant material and experimental setup

In this experiment, tomato plants (*Solanum lycopersicum* L.) were cultivated at a plant density of 4 plants m⁻² inside a greenhouse at the research station of the School of agricultural equipment engineering, Jiangsu university, Jiangsu Province, China (32.20°N, 119.45°E). The tomato variety used in this work was the 'hezuo 903' which is commonly cultivated in the South-Eastern part of China. The tomato seedlings were transplanted in pots of 25 cm height × 19 cm diameter filled with perlite substrates up to a height of 22.5 cm on 23 August 2015 and 5 March 2016 for Fall-Winter and Spring-Summer cropping seasons, respectively. Sufficient amount of irrigation with standard Hoagland nutrients solution was applied for the first 20 days to ensure the proper plant establishment after transplanting the seedlings. The crop evapotranspiration was determined using an equation taking data from plants in the Controlled (CR) without dynagage sensors placed adjacent to the plants with Dynagage sensors. The water treatment was subsequently imposed on the plants for the three different treatments (T₁, 100% of water retained in CR after drainage ceased, T₂ is 75% of water applied in T₁, T₃ is 50% of water applied in T₁). The amount of applied irrigation water (*I*) for CR was calculated by the following equation formulated by Ünlükara et al. (2010):

$$I = \frac{W_{CC} - W/\rho_w}{1 - LF}, \quad (1)$$

where LF is the leaching fraction, which was set to 0.15 leaching fraction as suggested by Ayers and Westcot (1985), W_{CC} is the pot weight at container capacity, W is the pot weight just before each irrigation event and ρ_w is the water bulk density (1 kg dm⁻³ or 1 kg l⁻¹). The container capacity of each pot was determined by initially saturating the pots with tap water and covering them to prevent evaporation. The water content of the pots after the drainage stopped was assumed to be the container's capacity (W_{CC}). Each pot was weighed before each irrigation session.

The staking of the plants was done using nylon cords to prevent sagging. SF measurement started on the 20th and 21st days after transplanting (DAT) in both the Fall-Winter and Spring-Summer seasons, respectively, when treatments were introduced to the plants. Dynagage sensors of different sizes (Model SGA5-WS, SGA9-WS and SGA10-WS) were used according to the size of the stem diameter at different times during the crop development. Pruning was done to maintain the proper growth following the well-managed agronomic local growth practices.

SF measurements

The SF rate (FH₂O) was measured continuously at the base of the stem of selected plants from each treatment (20 cm above the substrate) with Dynagage SF sensors (Model SGA5-WS, SGA9-WS, SGA10-WS, Dynamax Inc., Houston, TX, USA), installed according to the operation manual (Steinberg et al. 1990). Each gauge was enclosed in a thermally insulated sheath and wrapped around the stem to prevent it from direct sunlight and negative environmental effects. Subsequently, daily observation of SF was done. At an interval of 30 min, a CR1000 data logger (Campbell, Co., USA) was used to measure the SF output during the tomato growth seasons.

SF was measured from 14 September to 16 December for the 2015 Fall-Winter period and from 26 March to 5 July for the 2016 Spring-Summer period. T₁ was used to calculate the total water uptake by SF. Meanwhile, the deficit treatments, T₂ and T₃, were used to determine the SF result for different levels of water stress and their relationship with environmental parameters for some selected sample days.

Method of calculation

Healthy plants were samples which were selected as representatives of tomato crop for SF investigations. The amount of water uptake was estimated by integrating data from the SF and plant transpiration rate as shown in Tables 1 and 2.

This daily cumulated SF (l day⁻¹ plant⁻¹) was used to compute the plant transpiration in terms of the depth which we term calculated plant transpiration (CPT, mm day⁻¹ plant⁻¹) as shown in Tables 1 and 2, where the SF value (l day⁻¹ plant⁻¹) was related to the planting density (4 Plants m⁻²) in a specific area (1 m²) and expressed in mm day⁻¹ plant⁻¹.

In this study, the amount of pot evaporation was measured by the weighing method. For this, a perlite-filled pot was placed in the center surrounded by other plants and weighed before and after each irrigation. This perlite-filled pot was also irrigated with the same nutrient solution used for irrigating the tomato plants to keep its level between 60 and 80% of the container capacity weight consisting of perlite. The accumulated amount was estimated as monthly evaporation and added to transpiration for eventual estimation of evapotranspiration. However, since one of the key focuses of this study was to estimate the water uptake by considering transpiration of the crop plant, this parameter, together with the cumulated daily SF (calculated water uptake [CWU], l day⁻¹ plant⁻¹), was used for such computations. The daily average CWU and CPT values of the months were compared using the least significant difference test as shown in Table 3.

Microclimatic measurements

The greenhouse air temperature, relative humidity and light intensity (LI) were measured simultaneously along with SF of tomato plants by data logger (Hobo; Onset Computer, Pocasset, MA) at intervals of 30 seconds at 1.5 m above the ground level located in the center of the greenhouse. The vapor pressure deficit (VPD) could be calculated as:

$$VPD = 0.61 \times \frac{17.27 \times T_a}{T_a + 237.3} \times \left(1 - \frac{RH}{100}\right), \quad (2)$$

where T_a is the air temperature (°C), RH is the air relative humidity (%) and VPD is the vapor pressure deficit (kPa).

Crop physiological response to water stress

To observe the effect of water stress on crop physiological status during the growth period of the plants, the photosynthetic rate (P_n), transpiration rate (T_r) as well as the stomatal conductance (g_s) of young fully expanded leaves were measured on the 45th, 72nd and 105th days after transplanting with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, Nebraska, USA) at 9:00–11:00 h of local time on sunny days during Fall-Winter and Spring-Summer growth seasons.

Table 1. Calculated water uptake (CWU, l day⁻¹ plant⁻¹) of tomato plants estimated from SF measurement and calculated plant transpiration (CPT, mm day⁻¹ plant⁻¹) in Fall-Winter 2015.

September			October			November			December		
DOM	CWU	CPT	DOM	CWU	CPT	DOM	CWU	CPT	DOM	CWU	CPT
14	0.781	1.35	18	0.588	2.350	7	0.641	2.562	1	0.294	1.175
15	0.786	0.96	19	0.711	2.844	8	0.245	0.978	2	0.330	1.321
16	1.332	2.39	20	0.939	3.754	9	0.276	1.104	3	0.534	2.137
17	1.192	2.19	21	0.878	3.510	10	0.671	2.682	4	0.468	1.872
18	0.972	1.66	22	0.701	2.803	11	0.410	1.638	5	0.220	0.879
19	1.368	2.18	23	0.776	3.104	12	0.161	0.642	6	0.373	1.492
20	0.792	0.97	24	0.692	2.766	13	0.251	1.002	7	0.315	1.258
21	0.848	1.4	25	0.796	3.182	14	0.606	2.424	8	0.348	1.394
22	0.984	1.17	26	0.880	3.520	15	0.554	2.214	9	0.168	0.671
23	0.784	0.96	27	0.724	2.896	16	0.366	1.464	10	0.150	0.598
24	0.848	1.3	28	0.494	1.976	17	0.183	0.732	11	0.294	1.175
25	1.112	2.14	29	0.411	1.643	18	0.182	0.726	12	0.345	1.378
26	1.112	2.52	30	0.676	2.704	19	0.186	0.744	13	0.177	0.707
27	1.208	2.49				20	0.296	1.182	14	0.325	1.300
28	0.852	1.34				21	0.150	0.6	15	0.339	1.357
29	1.096	1.69				22	0.179	0.714	16	0.166	0.666
30	0.884	1.69				23	0.144	0.576			
						24	0.183	0.732			
						25	0.269	1.074			
						26	0.380	1.518			
						27	0.350	1.398			
						28	0.293	1.17			
						29	0.473	1.89			
						30	0.383	1.53			
Mean	0.249	0.997		0.713	2.85		0.326	1.304		0.303	1.211

Note: DOM means days of month.

Results

Water consumption of tomato plants based on SF measurements

Based on SF measurements, the average daily CWUs of tomato plants were 0.249, 0.713, 0.326 and 0.303 l day⁻¹ from September to December during the Fall-Winter season of 2015, respectively (Table 1). Meanwhile, during the 2016 Spring-Summer period, these values increased with increase in tomato growth stage and temperature, reaching the maximum of 0.763 l day⁻¹ in May and started to decline afterwards although the temperature continued to increase (Table 2).

The overall calculated transpiration per plant increased in Spring-Summer 2016 by 33.27% than the calculated transpiration in the Fall-Winter 2015 growing season. This difference possibly could be due to severity in climatic parameters during the Spring-Summer growing period. The calculated transpiration per plant during Fall-Winter 2015 was found to be a maximum of 3.75 mm day⁻¹ in October followed by a decrease in transpiration although the plant growth continued to increase. Similarly, daily transpiration values followed the same trend of decline after achieving the highest values in May. The smallest daily transpiration values during Fall-Winter of 2015 and Spring-Summer of 2016 were 0.58 and 0.47 mm day⁻¹ plant⁻¹, respectively, while the highest daily transpiration values were found to be 3.75 and 7.56 mm day⁻¹ plant⁻¹, respectively.

Also, from the cumulative transpiration data (calculated as average CPT multiplied by total number of days in each month used as growth period), the estimated water uptake by tomato plants in 2015 was found to be highest in October (88.36 mm) and decreased sharply in November (39.12 mm) and December 24.23 mm. The average data recorded for September during Fall-Winter 2015 also recorded a low average value of 16.951 mm. However, during the 2016 Spring-Summer period, the average values were 4.13, 54.00, 94.61 and 76.43 mm for March, April, May and June as shown in Figure

1. Using the total transpiration of tomato plants for the period under consideration to estimate SF, the average recording for the Fall-Winter 2015 period was found to be 168.65 mm. Meanwhile, the result for SF for Spring-Summer 2016 was 229.18 mm which in agreement with other works (Wang et al. 2011; Wang et al. 2015), although they used different methods in their estimations.

Consequently, by adding the surface evaporation from the perlite to transpiration estimated by SF, the total evapotranspiration values during the estimated period of Fall-Winter and Spring-Summer were found to be 223.41 and 292.07 mm, respectively. The distribution of water demand from September to December was 10.05%, 52.39%, 23.20% and 14.37% during the 2015 Fall-Winter season while that of the Spring-Summer growth period recorded were 1.80%, 25.63%, 42.71% and 33.35% for March, April, May and June, respectively.

There were significant differences in the average daily transpiration for the 2015 Fall-Winter period except the period between November and December. Upon comparing the monthly average daily transpiration during the 2016 Spring-Summer, there were significant differences in plants' transpiration rate for each month from March to June as shown in Table 3.

Effect of water deficit treatments on seasonal variation of SF

The seasonal variation of SF under deficit irrigation treatments for the Fall-Winter and Spring-Summer growing seasons, respectively, is indicated in Figure 2. SF of tomato plants in deficit irrigated treatments T₂ and T₃ was reduced during their respective measured periods. The daily SF variation curve showed that T₂ and T₃ were apparently lower than T₁ except on cloudy or rainy days, when T₂ was not found to be apparently lower when compared with T₁. SF in T₂ showed a compensatory effect and remained almost equal to T₁ on cloudy days.

Table 2. Calculated water uptake (CWU, l day⁻¹ plant⁻¹) of tomato plants estimated from SF measurement and calculated plant transpiration (CPT, mm day⁻¹ plant⁻¹) in Spring-Summer 2016.

March			April			May			June		
DOM	CWU	CPT	DOM	CWU	CPT	DOM	CWU	CPT	DOM	CWU	CPT
26	0.058	0.23	20	0.225	0.90	1	0.944	3.78	1	0.286	1.14
27	0.218	0.87	21	0.759	3.04	2	0.336	1.34	2	0.463	1.85
28	0.224	0.89	22	0.642	2.57	3	0.951	3.80	3	0.340	1.36
29	0.195	0.78	23	0.208	0.83	4	0.931	3.72	4	0.416	1.66
30	0.197	0.79	24	0.512	2.05	5	0.593	2.37	5	0.794	3.18
31	0.142	0.57	25	0.629	2.52	6	0.801	3.20	18	1.165	4.66
26	0.058	0.23	26	0.118	0.47	7	0.566	2.26	19	1.037	4.15
27	0.218	0.87	27	0.463	1.85	8	0.395	1.58	20	1.103	4.41
28	0.224	0.89	28	0.758	3.03	9	0.297	1.19	21	0.272	1.09
29	0.195	0.78	29	0.806	3.22	10	0.892	3.57	22	0.693	2.77
			30	0.904	3.61	11	1.149	4.60	23	1.146	4.58
						12	1.200	4.80	24	0.272	1.09
						13	0.701	2.81	25	0.330	1.32
						14	1.069	4.28	26	0.823	3.29
						15	0.263	1.05	27	0.145	0.58
						16	1.174	4.70	28	0.221	0.88
						17	1.377	5.51	29	0.698	2.79
						18	1.890	7.56	30	1.265	5.06
						19	1.444	5.78			
						20	0.799	3.20			
						21	0.322	1.29			
						22	0.226	0.91			
						23	0.678	2.71			
						24	1.096	4.38			
						25	1.016	4.06			
						26	0.348	1.39			
						27	0.164	0.66			
						28	0.152	0.61			
						29	0.461	1.84			
						30	0.822	3.29			
						31	0.592	2.37			
							0.763	3.05			
	0.172	0.689	Mean	0.548	2.19					0.637	2.55

Note: DOM means days of month.

Variation of stomatal conductance in relation with SF under different irrigation levels

The data on the diurnal variation of leaf stomatal conductance (g_s) and the SF of tomato measured for T₁, T₂ and T₃ are presented in Figure 3(a). All the treatments showed a similar pattern of variation in leaf stomatal conductance and SF rate. In the morning, both leaf stomatal conductance and SF were lower. It was observed that sunlight stomatal conductance started to increase from 07:00 as a result of the likely opening of the stomata for photosynthesis. The maximum leaf stomatal was recorded around 11: 00 for both deficit treatments while in T₁ this happened around 12:00 at noon.

By taking the climatic parameters corresponding to SF and stomatal conductance on the same day as shown in Figure 3 (b), an increase in solar radiation (R_s) caused reduction in relative humidity from 6:00 to 15:00. Meanwhile, the tomato SF for T₁ and T₃ increased rapidly during this period. After 11:00, the solar radiation increased continuously, but SF showed a reduction. At 11:00, the solar radiation recorded a maximum value and then started to decrease with slight

fluctuations. However, T₁ did not show reductions until around 14:00. Also, it was observed that the air temperature had little influence on the SF due to minimum temperature variations in a day during these periods.

The effect of water stress on plant physiological characteristics, photosynthesis rate (P_n), transpiration rate (T_r) and leaf stomatal conductance (g_s) is shown in Figure 4(a–c). From Figure 4(a), it is shown that the photosynthesis rate decreased with increasing water stress compared to T₁ during both growth seasons. While taking the effect of water stress observed on 45, 72 and 105 DAT, photosynthesis showed an insignificant increase from 45 to 72 DAT in all the treatments. However, there was a rapid decrease in the photosynthesis rate on 105 DAT. A similar trend was found for transpiration rate and stomatal conductance under the effect of water stress as represented in Figure 4(b,c).

Diurnal SF course under different water conditions

The diurnal dynamics of SF rate for tomato plants under different levels of irrigation was observed on selected sunny and cloudy days during the Fall-Winter 2015 and Spring-Summer 2016 periods. The SF trends for irrigation levels are plotted in Figure 5. To elucidate the effect of irrigation levels on SF rate, the diurnal course of SF was observed on typical selected days under different soil water conditions. To observe the effect of different irrigation levels on SF, the typical sunny and cloudy days selected in 2015 Fall-winter were found to be 20 October and 18 November, respectively. Meanwhile, 18 May and 1 June were selected as typical sunny and cloudy days in 2016 Spring-Summer periods under irrigation treatments; T₁, 75% and 50% of T₁. This was done

Table 3. Monthly average of calculated water uptake of tomato plants based on SF measurement (CWU, l day⁻¹ plant⁻¹) and calculated plant transpiration (CPT, mm day⁻¹ plant⁻¹) on sample days from 2015 to 2016.

Fall-Winter 2015/2016			Spring-Summer 2016		
Months	CWU	CPT	Months	CWU	CPT
September	0.997	1.67 ^b	March	0.689	1.63 ^d
October	0.713	2.85 ^a	April	0.549	2.19 ^c
November	0.326	1.30 ^c	May	0.763	3.05 ^a
December	0.303	1.21 ^c	June	0.637	2.55 ^b

Note: Means followed by different letters indicate a significant difference (p < .05).

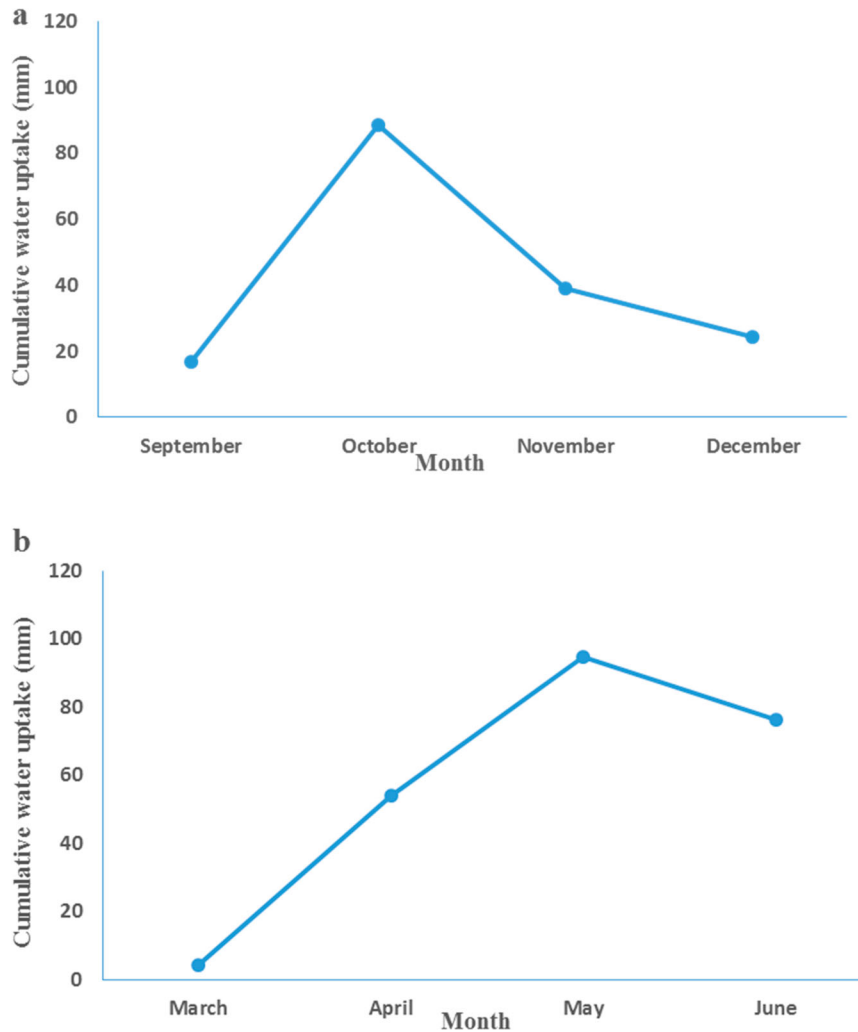


Figure 1. Comparison of monthly cumulative water uptake of tomato plants based on SF (a) Fall-Winter 2015, (b) Spring-Summer 2016.

without taking into consideration the leaching fraction and without reference to the control treatment.

With treatment under no water stress, the diurnal curve rose sharply with an increase in LI on the sunny days in both the Fall-Winter and Spring-Summer seasons. The peak values of the SF in water deficit treatments (T_2 , T_3) were reached earlier at noon 12:00 than in the control treatment which occurred at 13:00 on the Fall-Winter selected sunny day (20 October). However, on the Fall-Winter cloudy day (18 November), the SF reached its peak value at the same time (i.e. 13:00) of the day within all treatments. After sunrise accompanied with an increase in sunlight, the transpiration increased leading to an increase in the SF with sharp increment for T_1 and T_2 . It was also observed that the rate of increase in the SF under deficit irrigated treatment T_2 reduced after 10:00. The peak flow rates for T_1 in sunny Fall-Winter and sunny Spring-Summer were 197.73 g h^{-1} and 327.4 g h^{-1} observed at 13:00 and 12:30, respectively. On the other hand, the SF peak values in deficit irrigated treatments (T_2 and T_3) occurred earlier than in the control for the sunny days of Fall-Winter and Spring-Summer. The lower SF was observed on cloudy or rainy days when compared with bright sunny days. On cloudy days, the diurnal course of T_2 was close to T_1 while that of T_3 was far lower than T_1 and T_2 . However, there were no clear differences

observed between T_1 and T_2 on cloudy days during the Fall-Winter and Spring-Summer growing seasons.

SF characteristics of tomato plants during a day relative to climatic factors

This section presents the result of the SF characteristics in relation to daily climatic factors. Figure 6(a–d) shows the effect of greenhouse climatic factors on SF under diurnal climatic variations for typical sunny and cloudy days for the two growing seasons. Considering the response of SF behavior to climatic factors on 20 October, the SF rate started to increase rapidly following an increase in LI. The SF rate continued to increase alongside increasing LI and other climatic parameters including VPD and T_a . The SF curve showed fluctuations due to fluctuation in the LI curve but it reached its peak value at 13:00 with a lag period of 1 h (i.e. 12:00). Similarly, during Spring-Summer, the SF on 23 June (sunny hot day) started to increase with sunrise and achieved a steep slope from 07:00 with increase in solar radiation in the morning. Although there were fluctuations, the SF curve was found to have lagged behind the LI curve by 30 min. The peak values of three variables occurred between late morning and early afternoon except the VPD and T_a on 24 June. VPD and T_a had peak values before early morning on 24 June. The

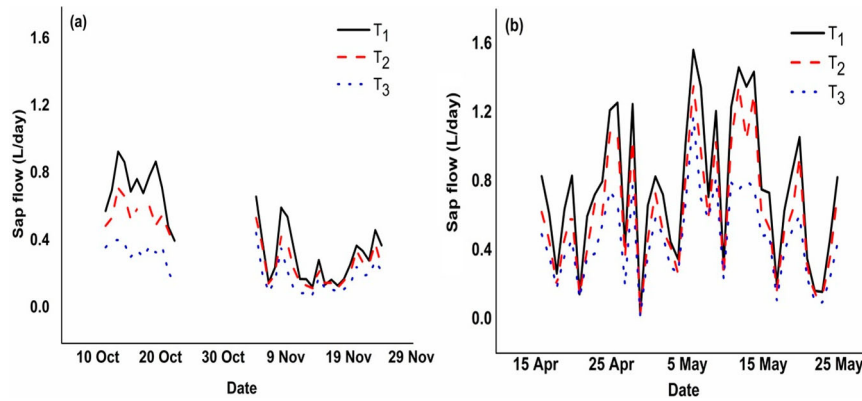


Figure 2. Effect of water deficit treatments on variation of SF in tomato plant in (a) Fall-Winter 2015 and (b) Spring-Summer 2016.

maximum values of SF, LI, VPD and T_a for a typical selected sunny day during the Spring-Summer crop were 153.83 g h^{-1} , 30469.43 lux , 0.80931 kPa and 41.99°C , respectively. Compared with the sunny day (23 June), the peak values of LI, VPD and T_a were found to have decreased by 65.52%, 73.27% and 35.88%, respectively, which also caused a decrease in the SF rate by 74.32% on a cloudy day (24 June). The T_a and VPD were high in the early morning of 24 June most likely as a result of the hot sunny day but it gradually decreased with relatively a flat curve. In the early morning, the sap flow followed the trend of VPD and air temperature even when there was no light and subsequently reached a minimum point before the appearance of light under decreased VPD and T_a values (Figure 6(d)). SF increased and was found to have lagged behind the sunlight and LI which reached its maximum value at 10:00, while the SF reached its maximum

value at 10:30. Hence, the SF gradually started to decrease under decreasing solar radiation (Figure 6).

Correlation and regression relationships between SF and greenhouse climatic factors

To explain the response mechanism of SF to climatic factors, relationships between environmental factors and tomato stem SF were analyzed. We studied the correlation and regression relationships among the climatic parameters and SF at certain phases of the whole day for three sunny days (20 and 21 October and 10 November) and four cloudy days (28 and 29 October and 17 and 18 November) during Fall-Winter. Also, the observation was done for selected five sunny (21 and 29 April, 12 and 19 May and 20 June) and six cloudy (23 and 26 April, 15 and 22 May and 21 and 28 June) days from the Spring-Summer growing season. The time span for the whole day was considered from 6:00 to 22:00 as a daytime and then it was split into two phases: morning phase from 6:00 to 14:00 and afternoon phase from 14:00 to 22:00 for a detailed study of the response of the tomato stem SF rate in relation to climatic factors. The morning water uptake was 43.51% to 46.91% more than the afternoon water uptake for sunny days during Fall-Winter and Spring-Summer, respectively. While during Fall-Winter and Spring-Summer cloudy days, the water uptake was 26.93–58.70%, it was observed that this occurred more in the morning than in the afternoon. The SF pattern was analyzed in relation to the T_a , VPD and LI inside the greenhouse to allow for better understanding of the relationship between tomato plants’ transpiration and greenhouse environmental conditions on selected sample days during the Fall-Winter and Spring-Summer periods. The classification was done as sunny and cloudy days of Fall-Winter and Spring-Summer. The correlation and results of regression analyses for typical selected days are shown in Tables 4–7. Under treatment T_1 , SF was taken as a dependent variable, while T_a , VPD and LI were taken as independent variables for the regression analyses.

During Fall-Winter growth, the SF showed variations in the relationship to different parts of the day. There was a quadratic relationship between SF and climatic factors except VPD in the morning, LI in afternoon as well as overall daytime on bright sunny days (Table 4). On cloudy days, all the climatic factors showed the same cubic relation with SF behavior in the afternoon but there was variation in relation to climatic factors and SF in the morning phase and the overall daytime. Considering VPD, it showed cubic correlation

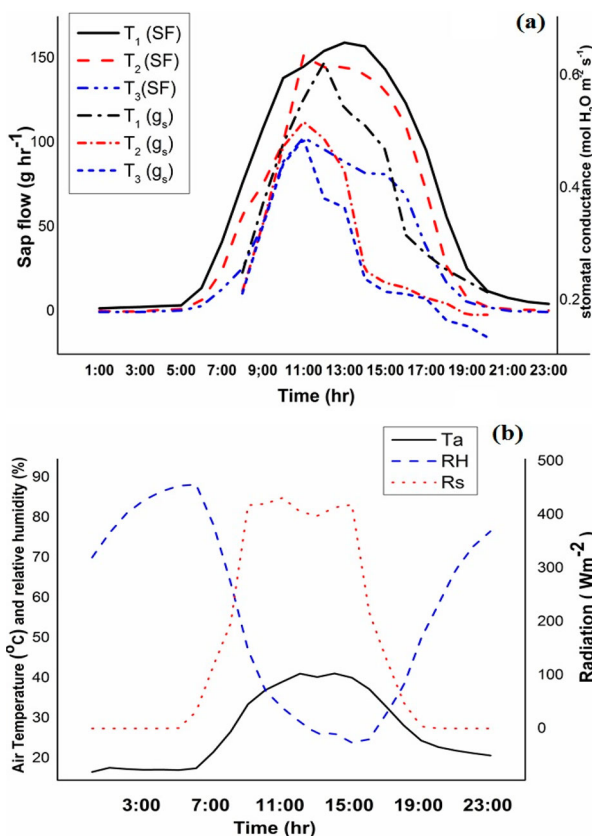


Figure 3. Diurnal variation of stem SF rate, leaf stomatal conductance (g_s) in tomato plant (a) and their corresponding climatic factors under different water conditions (b) (19 May 2016).

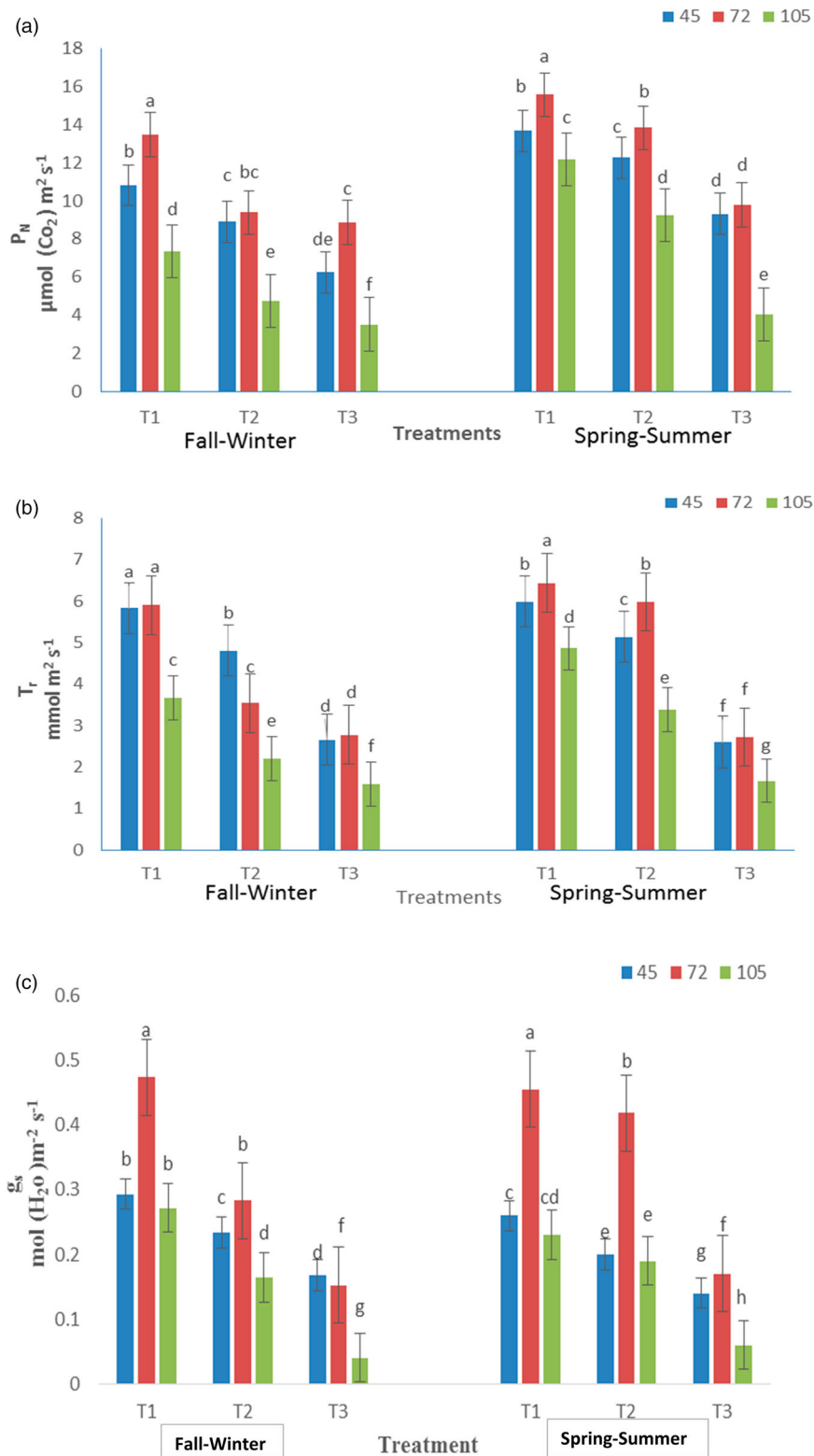


Figure 4. (a) Effect of water stress on photosynthesis rate of tomato at 45, 72 and 105 DAT. (b) Effect of water stress on transpiration rate of tomato at 45, 72 and 105 DAT. (c) Effect of water stress on stomatal conductance of tomato at 45, 72 and 105 DAT.

with SF throughout the daytime as well as its split phases (Table 5). Considering daytime span of 6:00–22:00, there was a linear relationship between the SF and LI on sunny Fall-Winter days during the daytime span of 6:00–22:00 which has been confirmed by similar other studies (Motzer et al. 2005; Liu et al. 2010).

As depicted from regression models shown in Tables 4–7, there was a positive correlation between SF and these climatic factors. While considering the correlation between SF and environmental factors on a typical selected bright sunny day

during the Spring-Summer period, a cubic correlation between SF and T_a , VPD, LI throughout all the daytime span was established. Meanwhile, the VPD in the morning and T_a in the afternoon had a quadratic relationship with SF. On a selected sample Summer sunny day, the strongest correlation was found between LI and SF in the afternoon phase as well as throughout the daytime except for mornings where VPD and T_a remain dominant than LI as shown in Table 6.

Overall the strongest correlation was found between VPD and SF during the sunny Fall-Winter growth (Juhász et al.

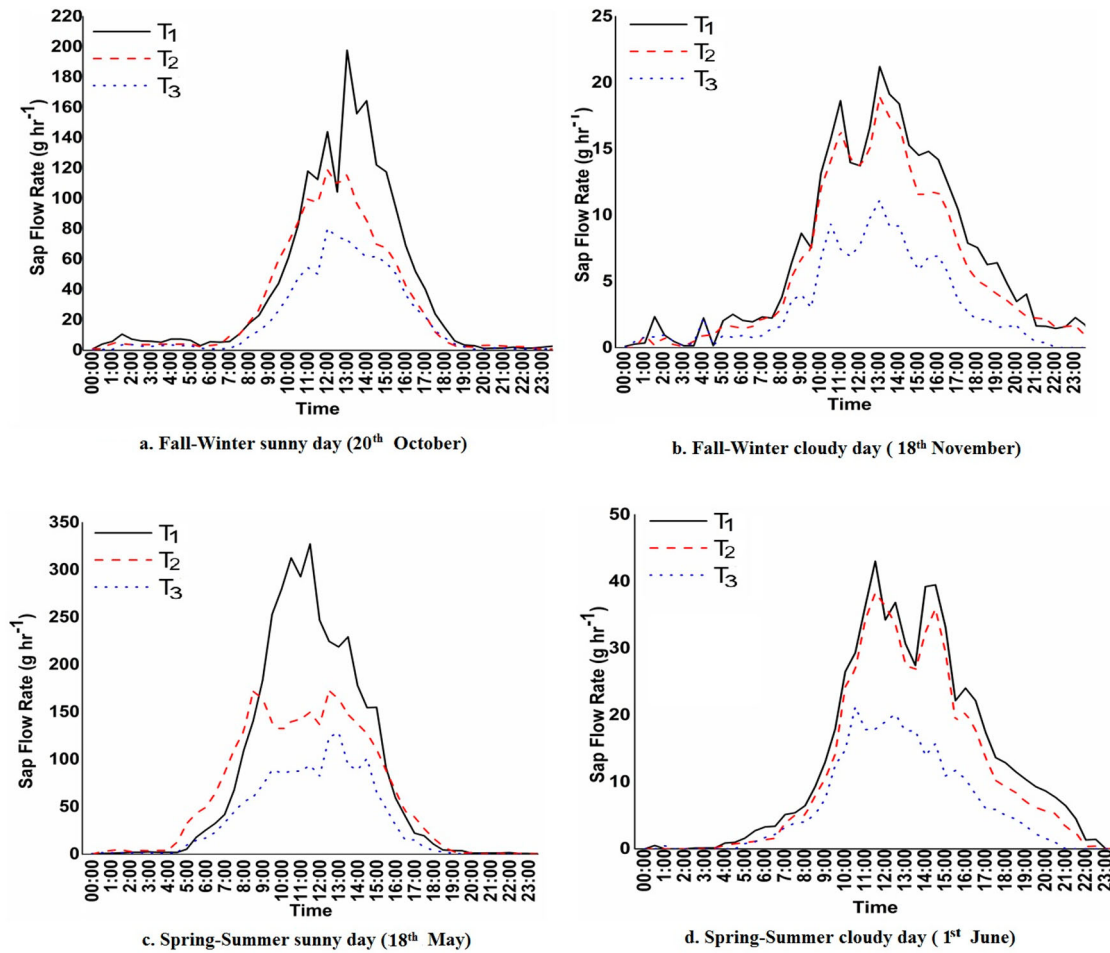


Figure 5. Diurnal variations of sap flow under different water supplies measured on typical sunny and cloudy days in Fall-Winter 2015 and Spring-Summer 2016.

2013), while the strongest correlation was between LI and SF for Spring-Summer sunny and cloudy days and Fall-Winter cloudy days (Table 7).

Discussion

Daily water uptake

Based on the SF measurements, the daily water uptake of Fall-Winter tomato growth was between 0.380 and 0.722 l day⁻¹

plant⁻¹ for full bright sunny days which is in agreement with the work of Harmanto et al. (2005) who reported values between 0.46 and 0.265 for cloudy days. Similarly, the water consumed during the Spring-Summer period for bright sunny days ranged between 0.758 and 1.890 l day⁻¹ plant⁻¹, while the values for cloudy days ranged between 0.118 and 0.348 l day⁻¹ plant⁻¹. This result is in agreement with other published work for tomatoes' daily water requirement by Snyder (1992), who found the maximum tomatoes' water requirement to be 1.8 l day⁻¹ plant⁻¹.

Table 4. Relationship between SF (g h⁻¹) and climatic factors of a typical Fall-Winter sunny day in the morning (6:00–14:00), afternoon (14:00–22:00) and day time (6:00–22:00).

Factor	Model <i>R</i>	<i>R</i> ²	Adjusted <i>R</i> ²	Standard error	ANOVA <i>F</i>	Sig.
Morning						
<i>T</i> _a	0.918	0.842	0.836	16.711	128.237	0.000
Function	SF = 0.170 <i>T</i> _a ² - 4.221 <i>T</i> _a + 30.021					
VPD	0.927	0.859	0.856	15.635	298.836	0.000
Function	SF = 106.020 VPD + 0.692					
LI	0.901	0.813	0.805	18.221	104.043	0.000
Function	SF = 3.240E-8 LI ² + 0.003 LI + 1.593					
Afternoon						
<i>T</i> _a	0.968	0.938	0.935	8.003	360.060	0.000
Function	SF = 0.264 <i>T</i> _a ² - 9.149 <i>T</i> _a + 78.365					
VPD	0.967	0.936	0.933	8.096	351.227	0.000
Function	SF = 78.578 VPD ² + 63.018 VPD - 9.4685					
LI	0.973	0.947	0.943	7.470	278.207	0.000
Function	SF = 9.449E-12 LI ³ - 3.513E-7 LI ² + 0.008 LI + 2.224					
Day time						
<i>T</i> _a	0.935	0.875	0.872	13.796	335.735	0.000
Function	SF = 0.221 <i>T</i> _a ² - 6.685 <i>T</i> _a + 50.767					
VPD	0.921	0.848	0.845	15.210	267.666	0.000
Function	SF = 81.444 VPD ² + 27.641 VPD + 0.820					
LI	0.927	0.858	0.857	14.599	588.277	0.000
Function	SF = 0.004 LI + 3.451					

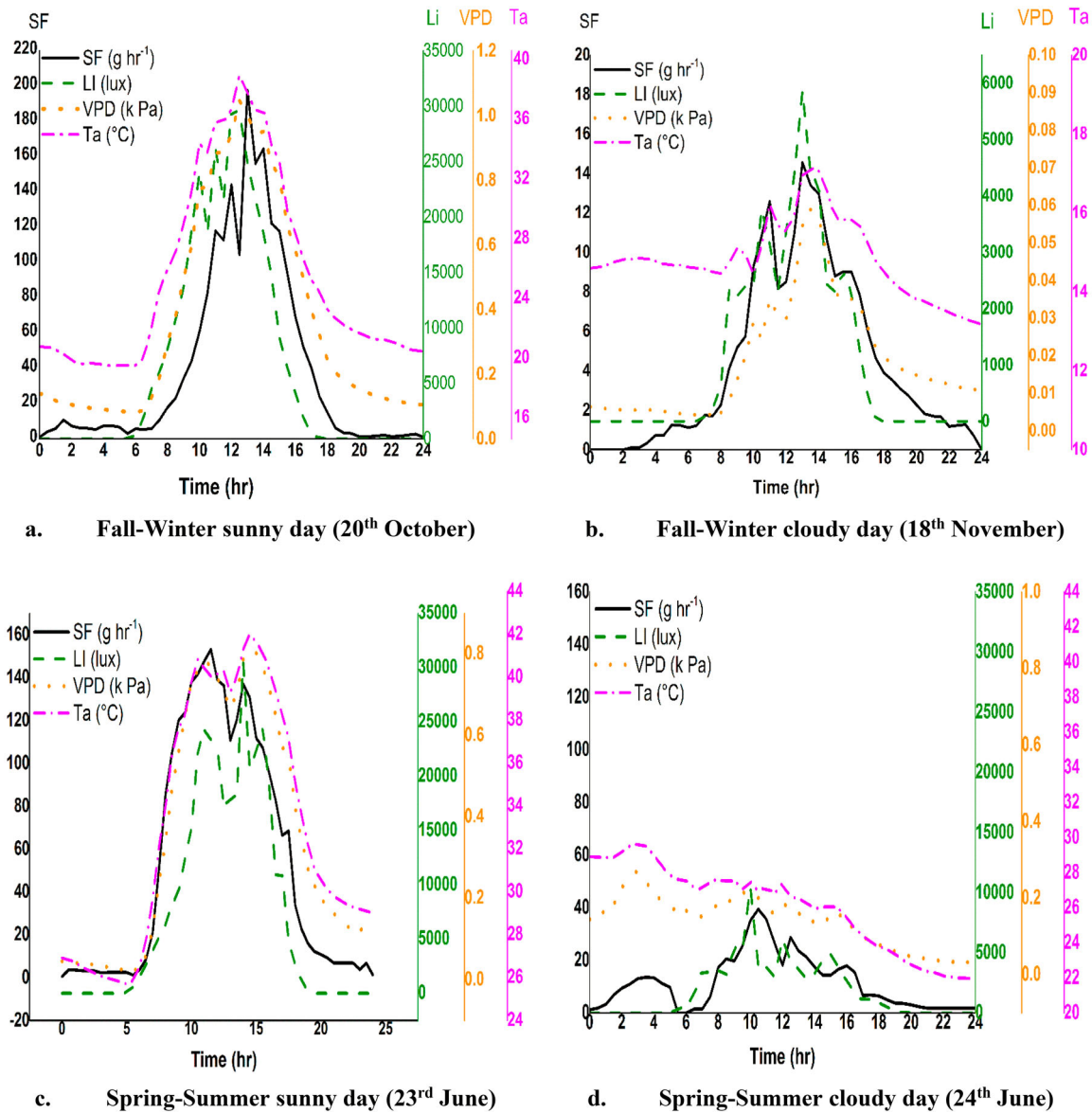


Figure 6. Dynamics of SF under well-watered condition (T_1), VPD, T_a and LI on typical sunny and cloudy days in two growing seasons.

Table 5. Relationship between SF ($g\ h^{-1}$) and climatic factors of a typical Fall-Winter cloudy day in the morning (6:00–14:00), afternoon (14:00–22:00) and day time (6:00–22:00).

Factor	Model R	R^2	Adjusted R^2	Standard error	ANOVA F	Sig.
Morning						
T_a	0.944	0.891	0.889	2.639	401.854	0.000
Function	$SF = 2.508 T_a - 31.081$					
VPD	0.858	0.726	0.720	4.196	43.767	0.000
Function	$SF = 469.157 VPD^3 - 421.175 VPD^2 + 132.982 VPD - 4.111$					
LI	0.946	0.894	0.890	2.633	202.421	0.000
Function	$SF = -7.422E-8 LI^2 + 0.003 LI + 1.756$					
Afternoon						
T_a	0.747	0.558	0.539	4.228	30.248	0.000
Function	$SF = 0.006 T_a^3 - 0.114 T_a^2 + 10.683$					
VPD	0.788	0.621	0.597	3.953	25.701	0.000
Function	$SF = 433.269 VPD^3 - 245.548 VPD^2 + 27.918 VPD - 4.175$					
LI	0.930	0.865	0.856	2.364	100.026	0.000
Function	$SF = 2.418E-11 LI^3 - 5.623E-07 LI^2 + 0.005 LI + 2.359$					
Day time						
T_a	0.802	0.644	0.636	4.572	86.732	0.000
Function	$SF = 0.062 T_a^2 - 0.130 T_a - 7.187$					
VPD	0.683	0.466	0.449	5.627	27.617	0.000
Function	$SF = 277.554 VPD^3 - 172.271 VPD^2 + 44.221 VPD + 5.044$					
LI	0.941	0.885	0.882	2.602	367.948	0.000
Function	$SF = -7.695E-8 LI^2 + 0.003 LI + 2.429$					

Table 6. Relationship between F and meteorological factors of a typical Spring-Summer sunny day in the morning (6:00–14:00), afternoon (14:00–22:00) and day time (6:00–22:00).

Factor	Model R	R ²	Adjusted R ²	Standard error	ANOVA F	Sig.
Morning						
T _a	0.881	0.777	0.769	24.594	94.018	0.000
Function	SF = -0.008 T _a ³ + 0.725 T _a ² - 17.042 T _a + 125.369					
VPD	0.881	0.777	0.771	24.446	142.736	0.000
Function	SF = -42.267 VPD ² + 161.800 VPD - 1.825					
LI	0.833	0.693	0.682	28.833	61.049	0.000
Function	SF = 1.259E-11 LI ³ - 7.312E-07 LI ² + 0.015 LI - 12.998					
Afternoon						
T _a	0.886	0.785	0.780	24.114	149.728	0.000
Function	SF = 0.099 T _a ² - 0.588 T _a - 39.218					
VPD	0.896	0.803	0.796	23.218	110.148	0.000
Function	SF = -215.351 VPD ³ + 540.223 VPD ² - 270.148 VPD + 36.397					
LI	0.944	0.892	0.888	17.212	222.573	0.000
Function	SF = 3.584E-12 LI ³ - 1.939E-7 LI ² + 0.007 LI + 2.335					
Day time						
T _a	0.874	0.764	0.760	26.279	173.920	0.000
Function	SF = -0.015 T _a ³ + 1.528 T _a ² - 43.403 T _a + 381.690					
VPD	0.829	0.687	0.682	30.258	117.999	0.000
Function	SF = -115.983 VPD ³ + 259.314 VPD ² - 49.337 VPD + 10.364					
LI	0.897	0.804	0.800	23.949	220.351	0.000
Function	SF = 7.106E-12 LI ³ - 4.153E-07 LI ² + 0.010 LI - 0.054					

Additionally, the monthly water uptake showed significant variation corresponding to plant growth at respective growth stages (Figure 1). There was highest water consumption at the flowering/fruit set growth stages period in October during Fall-Winter, which decreased in November and December. This decrease in water consumption might be due to a drop in temperature during the months of November and December. Similarly, during the Spring-Summer growth, the water consumption began to increase from April to May and afterwards irrespective of the recorded high temperature in the greenhouse. The possible reason for this decline in water consumption might be the senescence of the leaves which tends to reduce the transpiration and ultimately affects water consumption. From our results, the most important irrigation period for the early ripening tomato is during the fruit growing period when the water uptake is the highest.

Diurnal SF in response to different water levels

Under different weather conditions, the SF course showed different characteristics on specific selected days. Considering

the effect of deficit irrigation, the SF course on cloudy days did not show a significant difference between T₁ and T₂, because T₂ was able to meet the water uptake requirement due to low potential evapotranspiration demand on cloudy days. Meanwhile, the difference in SF under T₃ was significant compared to T₁ and T₂ due to severe water stress (Figure 5(b,d)). The intensive water uptake began at 6:00 and reached peak value between 12:00 and 13:00 at noon. Under water deficit treatments, the increasing rate of SF became slow and showed fluctuation at midday on sunny hot days (Figure 5(a,c)). This fluctuation or decreased SF might be due to disturbed equilibrium and oscillated stomatal movement in water deficit-treated plants which cause equilibrium between transpiration and water absorption by roots due to insufficient availability of water (Yang et al. 2005). In the afternoon, the water uptake becomes reduced due to fall in LI and almost plateaued during 20:00–22:00. Our result is confirmed by Ferrara and Flore (2003) who had similar dynamics of daily SF using apple trees as test crops grown in greenhouse conditions. Their study observed the dynamics of daily SF which supports our work, in that under greenhouse conditions, the water uptake

Table 7. Relationship of SF and climatic factors of typical Spring-Summer cloudy day in morning (6:00–14:00), afternoon (14:00–22:00) and day time (6:00–22:00).

Factor	Model R	R ²	Adjusted R ²	Standard error	ANOVA F	Sig.
Morning						
T _a	0.617	0.381	0.369	7.204	30.504	0.000
Function	SF = 0.005 T _a ³ - 0.148 T _a ² + 31.360					
VPD	0.737	0.543	0.530	6.220	38.892	0.000
Function	SF = 3415.334 VPD ² - 1141.726 VPD ² + 173.477 VPD + 3.918					
LI	0.799	0.638	0.627	5.538	57.601	0.000
Function	SF = -2.368E-11 LI ³ + 2.363E-07 LI ² + 0.003 LI + 6.100					
Afternoon						
T _a	0.673	0.454	0.437	7.077	27.117	0.000
Function	SF = 0.022 T _a ³ - 1.411 T _a ² + 28.949 T _a - 186.821					
VPD	0.665	0.443	0.426	7.148	25.936	0.000
Function	SF = -2220.227 VPD ³ + 1310.539 VPD ² - 121.522 VPD + 7.491					
LI	0.840	0.705	0.702	5.146	239.230	0.000
Function	SF = 0.003 LI + 2.954					
Day time						
T _a	0.604	0.365	0.355	7.856	37.133	0.000
Function	SF = 0.022 T _a ³ - 1.431 T _a ² + 30.383 T _a - 202.510					
VPD	0.674	0.454	0.446	7.284	53.762	0.000
Function	SF = -1654.811 VPD ³ + 925.605 VPD ² - 51.573 VPD + 7.205					
LI	0.838	0.702	0.697	5.382	152.237	0.000
Function	SF = -1.938E-11 LI ³ - 1.319E-07 LI ² + 0.004 LI + 3.639					

increased dynamically after sunrise and reached the maximum between 11:00 and 13:00 showing the need for an irrigation event at early noon to avoid plants from experiencing adverse effect of water stress.

Daily SF and greenhouse climate interactions

Studying the correlation between the transpiration and the weather conditions (Tables 4–7), the strongest correlation was found between the SF and LI in Spring-Summer which is in agreement with literature (Pereira et al. 2007). Also, the established regression equation between SF and three environmental factors showed that the maximum coefficient of determination for VPD during Fall-Winter sunny days and LI during Spring-Summer shows that LI is the most influencing factor in the determination of SF during Spring-Summer sunny days, whereas VPD is the most important factor influencing SF during Fall-Winter sunny days. The result was found to be similar to previous studies found in literature on muskmelon and tomato (Liu H 2010; Bao et al. 2012).

Furthermore, by taking into consideration the whole daytime and its split phases as morning phase (6:00–14:00) and afternoon phase (14:00–22:00), there were varied correlations found between two phases according to the different conditions of the days (sunny or cloudy/rainy) and its crop growing seasons (Fall-Winter or Spring-Summer). Taking the most influential factor during Fall-Winter sunny days, the VPD showed quadratic correlation throughout the whole daytime as well except for the morning phase when it is in linear correlation with SF (Table 4).

According to the results, by taking LI as the most influential factor during Spring-Summer, LI showed cubic correlation throughout the daytime and its divided phases throughout the season. However, the LI did not show a very strong correlation in the morning phase of sunny days where T_a and VPD showed a strong correlation with SF rate (Tables 6 and 7). This variation might be due to the fact that the VPD and T_a increased quickly with LI in the morning phase. Consequently, the air temperature and vapor pressure were considered the most influential factors in relation to the effect of LI on SF.

Conclusions

The daily average water uptake of well-watered tomato plants calculated based on SF measurement ranged between 0.30 and 0.80 l day⁻¹ plant⁻¹ during Fall-Winter growth and 0.50 and 0.80 l day⁻¹ plant⁻¹ during Spring-Summer growth. The total consumption of water for the period under consideration through transpiration estimated based on SF measurement for two seasons were 168.65 and 229.18 mm, while the water requirement was 223.41 and 292.07 mm for Fall-Winter and Spring-Summer periods, respectively. SF was mainly driven by solar radiation and VPD. T_a was less sensitive to SF because of little variation during the whole day, while VPD and LI were highly sensitive under SF measurements. On sunny days, the water stress treatments showed a lower SF rate compared to control treatment and peak values of deficit irrigation (T_2 and T_3) reached earlier than sufficiently watered treatment (T_1) which gives an indication of the use of the irrigation event to match transpiration rate and water absorption by roots in order to have the curves coincide in the late afternoon. In sum, the order of the climatic factors affecting stem SF in

greenhouse grown tomato plants was: VPD > LI > T_a during Fall-Winter sunny days, while LI > VPD > T_a during Spring-Summer seasons and Fall-Winter cloudy days. The result of the study could be helpful for irrigation planners to determine irrigation needs of the plant in relation to climatic factors and the degree of water stress.

Disclosure statement

No potential conflict of interest was reported by the authors.

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