Path analysis of sap flow of tomato under rain shelters in response to drought stress

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Abstract: The physiological characters and growth of tomato (*Solanum lycopersicum* L.) were recorded to be largely affected by different levels of irrigation. The objectives of this research were to determine the effects of deficit irrigation and rain shelters on sap flow, relative water content and the relationship between sap flow and environmental parameters. Experiments under rain shelters conditions were conducted in southern China during the growing seasons in 2012. The threshold of irrigation was designed at 80% field capacity during the whole period (T1, the control), and 30%, 40% and 50% decreased water of T1 were applied as the treatments of T2, T3 and T4. The plants subjected to water stress exhibited a decrease in the values of sap flow rate and relative water content. Calculation of 95% confidence level revealed a significant difference of sap flow rate in T4 and T3 as well as the control on sunny and rainy days. The diurnal variation of the sap flow showed a single peak curve on sunny day, while it demonstrated irregular multi-peak variation on rainy days. The study also showed that the most sensitive environmental indicator affecting sap flow was solar radiation, followed by air temperature and vapour pressure deficit. Direct path coefficient was basically consistent with the coefficient of correlation, but there was slight difference between the total contribution R^2 and that of variable factors.

Keywords: drought stress, tomato, sap flow, rain shelters, deficit irrigation, path analysis

DOI: 10.3965/j.ijabe.20160902.1405

Citation: Shao G C, Huang D D, Cheng X, Cui J T, Zhang Z H. Path analysis of sap flow of tomato under rain shelters in response to drought stress. Int J Agric & Biol Eng, 2016; 9(2): 54－62.

1 Introduction

A major constraint of the tomato production in southern China is the abundance of rainfall besides heat, insect pests and diseases[1]. The yield and quality of fresh tomato are not only affected by genetic factors and also by growing conditions[2-4]. Rain-shelter measure could increase crop yields and improve fruit quality, thus it has been applied widely for the crops and fruit production in this region[5-7]. For tomatoes grown under rain shelters, the growth meteorological factors were significantly different from those under open-field conditions, leading to the change in the crop water consumption. Rohloff et al.[8] reported that the polyethylenethe decreased photosynthetic active radiation (PAR) as much as 47% in contrast to open field. Since the light underneath rain shelters is altered, the effects of such an alteration on the physiological processes related to crop growth should be investigated.

Tomatoes are characterized by their large canopies, which represent a large evaporative surface, while their stem and root hydraulic conductivities are low[9]. These factors, especially under deficit irrigation, may result in tomato transpirational losses exceeding its absorptive capacity, thereby giving rise to a plant water deficit. Transpiration is an important parameter for crop growth

Received date: 2014-08-26 **Accepted date:** 2015-11-25

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and water use[10-11]. The study of sap flow can be helpful to evaluate the impact of environmental factors on transpiration and take necessary measures to improve plant water use efficiency. The sap flow can characterize crop transpiration directly, which can be used to calculate the crop transpiration easily[12-13]. Usually, decrease in transpiration rate by reducing stomatal conductance will result in the loss of photosynthesis[14], leading to a reduction in biomass. Many authors have reported the influence of drought stress on photosynthesis under different conditions[15], Whereas very little work has been dealed with sap flow under the combination deficit irrigation with rain shelters[16-21]. Moreover, the mentioned studies on the relationship between plant sap flow and environmental factors were mostly concentrated on melon and corn[16,17]; The results were obtained only under open-field or greenhouse condition. It is necessary to investigate the influence of deficit irrigation on sap flow of tomato under rain shelters.

Path analysis between independent variables and dependent variable could reveal the effects and the associated extent to which various factors relate to the dependent variable[22-25]. In current study, path analysis has been widely adopted in crop breeding and cultivation, soil, medicine and other fields[26-28]. Plant sap flow is not only dependent on the gene type, but it is also influenced by the external environmental factors. It is often difficult to determine the relationship between multiple environmental factors and sap flow with traditional method. The aim of this study was to evaluate the responses of sap flow and relative water content to water stress in tomato plants under rain shelters and explore the relationship between environmental factors and sap flow. The underlying hypothesis is that transpiration in water-stressed tomato plants is limited by stomatal and non-stomatal factors, both contributing to the occurrence of metabolic alterations at the leaf level.

2 Materials and methods

Experiments were conducted in the rain-shelter plot of Key Laboratory of Efficient Irrigation-Drainage and Agricultural Soil-Water Environment in South China, Ministry of Education (latitude 31°57'N, longitude 118°50'E 144 m above sea level) from March to August, 2012. The region is rich in solar radiation with mean temperature of 15.4°C, mean sunshine duration of 2115.8 h and frost-free days of 231 d. It is in a typical subtropical temperate climate zone with annual pan evaporation of 1522.4 mm and precipitation of 1106.5 mm. The experimental field is 18 m long and 7.8 m wide with planting area of 140 m^2. The soil type was clay loam with a pH of 6.1 and 0.72% of organic matter content. The mean dry bulk density and soil volumetric water content at field capacity was 1.35 g/cm^3 and 0.34 cm^3/cm^3 for the upper 0-30 cm soil layer. Seedlings (Xi Lan) were raised in a nursery and transplanted at the six-leaf stage (5 weeks after sowing). Tomatoes were cultivated on the experimental field at a spacing of 40 cm in each row and 50 cm apart from one row to the other. In all treatments, compound fertilizers (N-P_2O_5-K_2O, 15:15:15) at the rate of 1200 kg/hm^2 were applied and incorporated into soil. All the crops were irrigated and allowed to reach field capacity. Data on fruit yield were taken from the central row to decrease the influence of lateral soil water on yield. The plots were manually weeded three times in the season. The plants were sprayed against fruit worms and other pests with insect powder at the rate of 0.8 L/hm^2 at the 6th week.

Under rain shelters, four treatments, replicated three times in a completely randomized design, were applied to the experimental units (Table 1). Since seven days after transplanting (20 April 2012), tomato plants were irrigated to field capacity once average soil volumetric water content at the 0-60 cm layer in the control decreased to 80% of field capacity. Ten days before the end of harvest, irrigation was ceased for all treatments. Tomato plants were drip-irrigated and the irrigation amount was recorded using a water gauge. To avoid the influence of groundwater on crop, drainage pipe for all the treatments was arranged at the depth of 0.8 m.

The soil water content was measured and controlled with the time domain reflectometry (TDR) and by the microwave drying method. Soil water content was used to adjust irrigation schedule to ensure that the envisaged irrigation treatments could indeed be realized.

The tensiometers were placed at T1 treatment at uniform depths of 60 cm below the soil surface.

Table 1 Experimental design of tomato under rain shelters for different treatments in 2012 season

Treatments	Description
T1 (The control)	Irrigation lower limit is 80% of field capacity
T2	30% decreased water was applied at the irrigation time of T1
T3	40% decreased water was applied at the irrigation time of T1
T4	50% decreased water was applied at the irrigation time of T1

Note: Irrigation method is drip irrigation. The depth of drainage pipe for all the treatments is 0.8 m.

Plant water relations were measured 17, 57 and 97 d after transplanting. After cutting, the leaf was immediately enclosed in a bag filled with breathing air and the measurement started in less than 2 min. Six leaves per plant were detached in a similar position to determine relative water content (RWC). After cutting, the petiole was immediately immersed in deaerated distilled water inside a glass tube, which was immediately sealed. The tubes were then taken to the laboratory where the increased weight of the tubes was used to determine leaf fresh weight (FW, g). After 8 h in de-ionized water under dark and humid conditions, the leaves were weighed to obtain turgid weight (TW, g). Dry weight (DW, g) was then measured after oven-drying at 80°C for 48 h and RWC was determined using the Equation (1)[29]:

$$RWC = 100 \times \frac{FW - DW}{TW - DW} \tag{1}$$

Six leaves were used for each treatment. During each measurement, the plants on each plot were randomly selected for measurement. The sap flow was recorded at 30 min intervals using packaged sap flow gauge (Flow4-DL, Dynamax, USA) controlled by a data logger.

The air temperature, wind speed and direction, relative humidity, total solar radiation, photosynthetically active radiation (PAR) were measured at the experimental site, using the auto-instrument for meteorological measurements. Vapour pressure deficit (VPD) could be calculated by Equation (2):

$$VPD = 0.611 \times \frac{17.27 \times Ta}{Ta + 237.3} \times (1 - \frac{RH}{100}) \tag{2}$$

where, Ta is air temperature, °C; RH is air relative humidity, %.

The path analysis was conducted on sap flow (y) with PAR (x_1), solar radiation (x_2), VPD (x_3), air relative humidity (x_4), air temperature (x_5) and soil moisture content (x_6). Statistical indicators included the correlation coefficient between one another (r_{yi}), the coefficient of determination (d_{yi}), path coefficient (p_{iy}) and the total contribution on the regression equation (R_2).

All statistical analyses were performed using SAS software Version 9.2 (SAS Institute, Cary, NC, USA). Analysis of variance (ANOVA) was performed using the GLM procedure and multiple comparisons of mean values were performed using least significant difference (LSD) test at $p_{0.05}$ level. The matrix calculation was done with Matlab 7.0.4 (The Math works Inc.).

3 Results and analysis

3.1 Influence of deficit irrigation on sap flow and relative water content

Average changes in the sap flow rate of tomato at three stages were observed at 13 o'clock on sunny and cloudy days (Figure 1). For the well-watered treatment, the values of sap flow rate were 297.3 g/h for sunny day and 180.9 g/h for rainy day, respectively. Under rain shelters, the plants subjected to water stress exhibited a decrease in the values of sap flow rate. Calculation of 95% confidence level revealed a significant difference of sap flow rate in T1 as well as T2, T3 and T4 on sunny day.

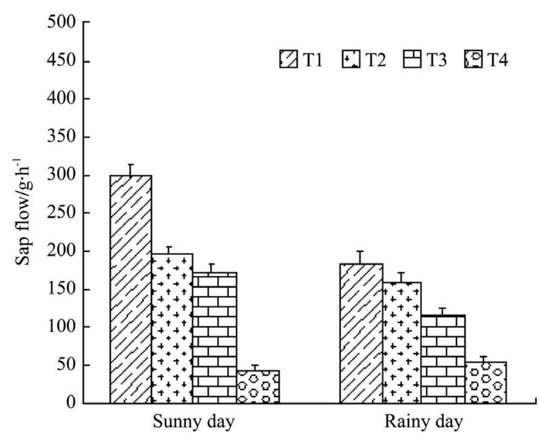


Figure 1 Sap flow of tomato leaves under different treatments on sunny day and rainy day (Columns with the same letter represent values are not significantly different at the 0.05 level of probability according to the LSD test. The standard error was calculated across three replicates for three measurements in 2012. The treatment symbols of T1, T2, T3 and T4 are the same as in Table 1)

Irrigation water levels significantly modified RWC of tomato leaf under rain shelters (Figure 2). Relative water content decreased as drought intenstiy increased. Tomato without water restriction (T1) had the maximum RWC. In addition, they also existed statistically significant differences (p<0.05) in RWC for T4 as compared to the leaves of T1. T2 also produced a decrease in the RWC, while no significant difference was observed compared to the control.

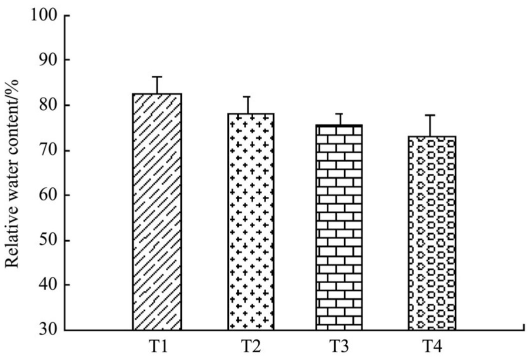


Figure 2 Relative water content of tomato leaves under different treatments

3.2 Diurnal variation of sap flow under different water supply

For water-stress treatments, the curve of diurnal sap flow changed relatively flat, and the rising rate was small, the maximum value appeared earlier and lasted longer (Figure 3).

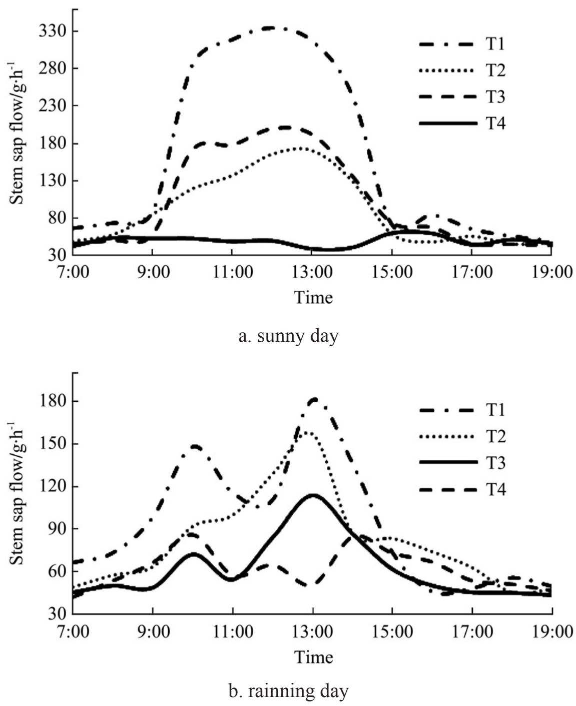


Figure 3 Diurnal variations of sap flow under different water supplies and weather conditions

Moreover, sap flow decreased relatively slowly at later stage. For the control, sap flow rise and fell sharply on sunny day with solar radiation intensity increase. However, on rainy day, the diurnal variation of sap flow curve under different water supply showed obvious fluctuation, where sap flow showed no difference among the water supply treatments. Compared to the control, sap flow declined as drought stress intensity increased, however, no significant differences were observed for water-stress treatments except T4 on sunny day.

3.3 Daily variation of sap flow under different weather conditions

Sap flow presented obvious circadian rhythm (Figure 4a). A single peak curve for the daily changing process occured on sunny day, the sap flow rise with the increase of the radiation intensity. It began to increase from 8:00 am, and reached peak at about 13:00 pm, then began to decrease gradually to the lowest value at about 19:00 pm, and kept the minimum value during the evening. At noon, sap flow curves fluctuated markedly for T2 due to higher radiation intensity. The reason was that leaf stomatal conductance altered to maintain balance between root water uptake rate and transpiration rate[30].

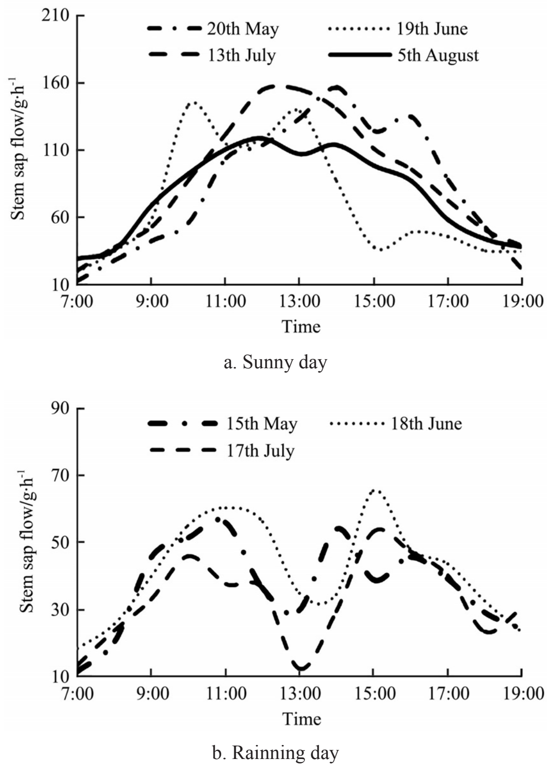


Figure 4 Diurnal variation of sap flow in T3 treatment on sunny day and rainy day in four or three months

On rainy day, because solar radiation was weak, sap flow showed obvious fluctuation and kept at a relatively low level, and presented irregular multi-peak variation (Figure 4b). Therefore, the changes of sap flow were not only related to the water supply, but also sensitive to the change of weather. The effect of meteorological factors on tomato sap flow was significant.

3.4 Relationship between sap flow and environmental factors

The regression relationship between sap flow and single environmental factor was shown in Figure 5. The sap flow increased lineally with increasing PAR. The sap flow was also significantly higher at high PAR levels (1850 w/m^2) than that at low PAR levels (1250 w/m^2). Similar to the relationship between sap flow and PAR, the sap flow increased linearly with increasing sun radiations. Sap flow was slightly influenced by RH and declined lineally with the increase of RH. VPD (r=0.467) and RH (r=0.557) did not correlate with the sap flow during the period of water stress, but a positive correlation (r=0.844, r=0.921) was found between sun radiation, PAR and sap flow during soil drought. Sap flow increased quadratically with increasing irrigation water volume.

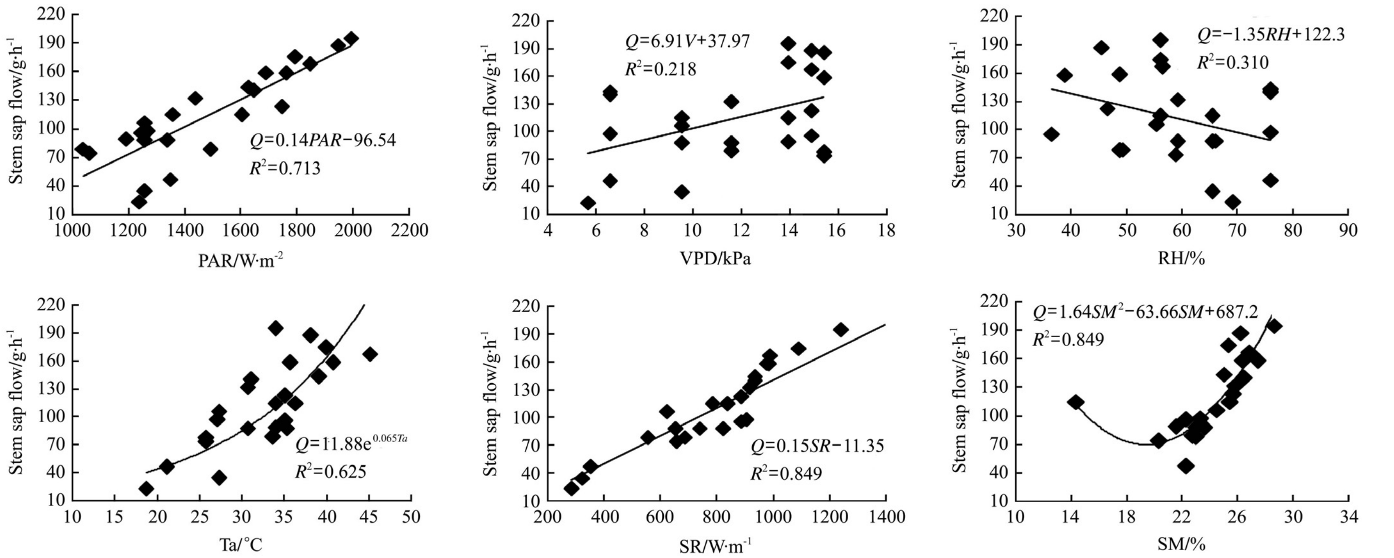


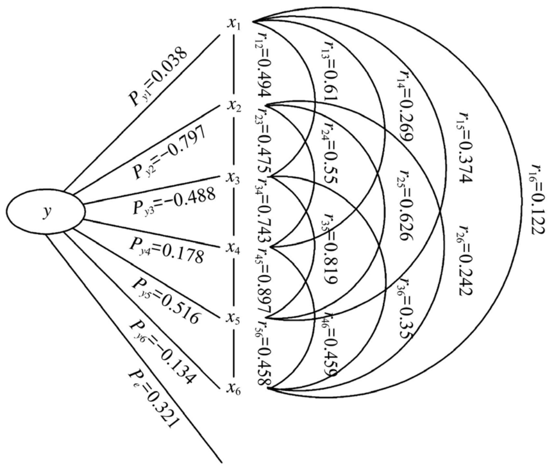
Figure 5 Relationship between daily sap flow and single parameter. Q, PAR, SR, RH, VPD, Ta and SM denote sap flow, photosynthetic active radiation, sun radiation, air relative humidity, vapour pressure deficit, air temperature and soil moisture

3.5 Path analysis of environmental factors on sap flow

With some mathematical algorithms related to path analysis[31], the correlation coefficient and path coefficient of six environmental factors on sap flow of tomato during the growth period were calculated (Figure 6). Based on path analysis principles, relevant equations were established to calculate the direct and indirect effect of various environmental factors on the results. The total contribution of each variable to the reliability of the regression equation R^2 was also analyzed (Table 2). Coefficient determination of each x_i, two joint indicators and error to sap flow were listed in Table 3.

The linear regression equation between various environmental factors (X_1-X_6) and sap flow (Y) was:

$$y = 242.34 - 0.04x_1 + 8.81x_2 + 2.29x_3 - 2.73x_4 + 6.09x_5 - 1.57x_6 \qquad (R^2 = 0.69) \tag{3}$$



Note: y, x_1, x_2, x_3, x_4, x_5, x_6, r_{yi} (i=1,2…6), P_{yi} and P_e denote sap flow, photosynthetic active radiation, sun radiation, relative humidity, vapour pressure deficit, air temperature and soil moisture, the correlation coefficient between one and another, the path coefficient and the total contribution on the regression equation

Figure 6 Correlation analysis between each environmental indicator and sap flow of tomato under rain shelters

Table 2 Direct effect and indirect action of each environmental indicator on sap flow of tomato

Impact factor	Correlation coefficient r_{yi}	Direct effect p_{yi}	Indirect effect							Contribution of variables on R^2 $r_{yi}p_{yi}$
			x_1	x_2	x_3	x_4	x_5	x_6	Total	
x_1	0.065	0.038		−0.394	0.155	−0.048	0.193	−0.016	−0.11	−0.002
x_2	0.835	−0.797	0.019		0.232	−0.098	0.323	−0.032	0.444	0.665
x_3	−0.518	−0.488	−0.012	0.379		0.132	−0.423	0.047	0.123	−0.253
x_4	−0.154	0.178	−0.01	0.438	−0.363		−0.463	0.062	−0.336	0.027
x_5	0.310	0.516	0.014	−0.499	0.400	−0.160		−0.061	−0.306	0.160
x_6	−0.244	−0.134	0.005	−0.193	0.171	−0.082	0.236		0.137	0.033

Note: x_1, x_2, x_3, x_4, x_5, x_6 denotes photosynthetic active radiation, sun radiation, relative humidity, vapour pressure deficit, air temperature and soil moisture.

Table 3 Determinant coefficient of each environmental indicator on sap flow of tomato

Decision Factor	x_1	x_2	x_3	x_4	x_5	x_6
d_{y1}	0.001	−0.03	0.012	−0.004	0.015	−0.001
d_{y2}		0.635	−0.369	0.156	−0.415	0.052
d_{y3}			0.538	−0.229	0.472	−0.046
d_{y4}				0.032	−0.165	0.022
d_{y5}					0.266	−0.063
d_{y6}						0.018
d_e						0.103

Note: x_1, x_2, x_3, x_4, x_5, x_6 denotes photosynthetic active radiation, sun radiation, relative humidity, vapour pressure deficit, air temperature and soil moisture. d_{yi} and d_e denotes the coefficient of determination and the error of the coefficient of determination, i=1, 2, …6.

The regression equation was proved to be very significant (F=41.12, p<0.01), therefore, multiple regression relationship between sap flow and various environmental factors can be used in Equation (3).

Tables 2 and 3 showed that the three maximum factors to contribution of R^2 were x_2, x_3, x_5, and the three highest coefficient of determination were dy_2, dy_3, dy_{35}. In addition, calculation of 95% confidence level revealed a significant difference in p_{y2}, p_{y3} and p_{y5}. Among the path coefficients, the lowest value was for p_{y5}. This indicated that among the determination coefficient sorted order by the absolute value, the decision coefficient was significant if absolute value was greater than d_{y5} (0.266), otherwise it was insignificant

Path analysis of six variables on sap flow showed that the maximum coefficient of determination was x_2 to y, the relative determine degree was 0.635, and x_2 ranked the first in total contribution to the regression equation of R^2. It also showed that solar radiation had the most important effect on sap flow, the relative degree of x_3 to Y was 0.538, the direct path coefficient was −0.488, and the contribution of x_3 to the R^2 was −0.253 ranking the second, indicating that VPD was also an important indicator to sap flow; the coefficient determination of both x_3 and x_5 to Y was 0.472, and the contribution of x_5 to the R^2 was 0.160 ranking the third, indicating that in addition to VPD, the influence of air temperature on sap flow should also be paid attention to, if both were high, the sap flow might reach a higher value (r_{35}=0.819). The direct effect of x_6 on Y was −0.134, and the contribution to the R^2 was 0.033, so the soil moisture also had some influence on sap flow of tomato; the coefficient determination of relative error to Y was 0.103, the direct path coefficient was −0.488, therefore, the observation error of this test was large, so other influence factors on sap flow might not be considered.

4 Discussion

Among the systems that counter certain adverse effects associated with local weather conditions and are increasingly altered to reduce pesticide reliance are arable habitats[32]. In southern China, rainfall varies dramatically from season to season and from place to place. Heavy rain has been linked to reductions in small fruit yield and shelf-life due to rain-driven epidemics of phytopathogens[33]. In addition, during the growth period of tomato, with an average midday temperatures of about 30°C, leaf transpiration may well exceed root water uptake even in well irrigated soils, leading to temporary water deficits. The previous studies have showed that crop productivity in different species may be reduced in environments with high radiation, high heat and high water vapour pressure deficits[34]. To avoid this situation in crops, cover cropping techniques such as polyethylene have been used to reduce heavy rain and the radiation load in southern China. It has been shown that such polyethylene distribute the radiation to the plants growing underneath with greater efficiency[35] and inhibit turbulence[36], creating a humidity blanket which contributes to a lower environmental evaporative demand[37]. To improve the quality of fruit, rain shelters cultivation is always associated with water deficit. Therefore, it is very difficult in tomato production to separate the effects induced by both environmental conditions. Most new agricultural management methods often focus solely on plants and overlook other environmental factors. However, the effects of new management methods on environmental factors can have implications for plant physiological and morphological characters.

The results of this study showed that shade leaves under different water supplies possessed differential sap flow. In accordance with the Penman–Monteith model, and taking into account rain shelters situations, the sap flow in the well-irrigated tomato would be 10% greater than that in the T4. The results indicated that water availability plays a primary role in modifying leaf water status. Leaves developed under T1 conditions have a higher RWC than leaves produced under water stress conditions (Figure 2). The transpiration proportionally decreased with the reduction of irrigation volume. The stomata are sensitive to leaf water stress and tend to close with decreasing leaf water potential[38-39], and so leaf stomatal conductance was lower under drought treatments than that under the control. Leaves subjected to drought usually have smaller and numerous stomata than those under well watered treatment[40]. Bosabalidis and Kofidis[41] showed that the increase in stomatal density unequivocally contributes to better transpirational control.

Tomato sap flow diurnal variation exhibited significant circadian rhythm changes whether on sunny day or cloudy day during the growth period, this was related to the change process of canopy meteorological factors, and was also affected by soil moisture and physiological condition. The sap flow rate under rainy days was significantly lower than that on sunny day at the same treatment. The diurnal variation of the sap flow showed a single peak curve in clear weather,which started in the morning, peaked at noon and kept low values during the evening. The trend was very similar to solar radiation and VPD. On rainy days, sap flow presented obvious fluctuation, kept at a relatively low level, and showed irregular multi-peak variation due to weak solar radiation. In this study, path analysis was used to analyze the influence of six kinds of environmental indicators on tomato sap flow under rain shelters. The regression equation between sap flow and the six environmental indicators was established. The maximiun coefficient of determination was for sun radiation, indicating that sun radiation has the most important influence on the sap flow. The result was similar to previous study on muskmelon and tomato[17, 21]. The rising temperature could increase VPD and lead to high differential pressure between cell gap and outside water vapour, accelerate the diffusion of water vapour in leaf, which has a direct influence on the sap flow. The decreased air relative humidity would increase differential pressure between cells in leaf and air water vapour, accelerate the rate of diffusion of water molecules and increase the sap flow. The smallest coefficient of determination was for the PAR. In addition, crop transpiration was affected and restricted by soil moisture, and the influences varied with growth period. In genreal, sap flow would decrease as water stress intensity increased.

5 Conclusions

In conclusion, the study showed that the water-stressed tomato had a lower RWC in relation to that of the control. The tomato plants under the control had a higher sap flow rate in contrast to those under deficit irrigation. The diurnal variation of the sap flow showed a single peak curve on sunny day, while it demonstrated irregular multi-peak variation on rainy day. With path analysis, relevant equations were established to calculate the direct and indirect effect of various environmental factors (photosynthetic active radiation, sun radiation, relative humidity, vapour pressure deficit, air temperature and soil moisture) on sap flow. It was showed that the most sensitive indicator affecting sap flow was solar radiation; followed by air temperature and vapour pressure deficit. Direct path coefficient was basically consistent with the coefficient of correlation, but there was slight difference between the total contribution R^2 and variable factors.

Acknowledgements

This work was funded by program granted by the National Natural Science Foundation of China (No. 51279059) and supported by the program of 'the Fundamental Research Funds for the Central Universities" (2015B14714) and the project of "the Priority Academic Program Development of Jiangsu Higher Education Institutions" and "Jiang Su Qing Lan". We extend our gratitude to editor and the anonymous reviewers for substantial comments on earlier versions of this article.

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