Influence of Water and Nitrogen Stress on Stem Sap Flow of Tomato Grown in a Solar Greenhouse

Rangjian Qiu

Jiangsu Provincial Key Laboratory of Agricultural Meteorology, College of Applied Meteorology, Nanjing University of Information Science and Technology, Nanjing, 210044, China; and the Center for Agricultural Water Research in China, China Agricultural University, Beijing, 100083, China

Taisheng Du¹, Shaozhong Kang, and Renqiang Chen

Center for Agricultural Water Research in China, China Agricultural University, 17 Qinghua East Road, Haidian District, Beijing, 100083, China

Laosheng Wu

Department of Environmental Sciences, University of California, Riverside, CA 92521

ADDITIONAL INDEX WORDS. meteorological factors, stomatal conductance, transpiration, nighttime sap flow

ABSTRACT. Accurate measurement of crop water use under different water and nitrogen (N) conditions is of great importance for irrigation scheduling and N management. This research investigated the effect of water and N status on stem sap flow of tomato (*Solanum lycopersicum*) grown in an unheated solar greenhouse in northwest China. A water experiment included sufficient water supply (T₁) based on in situ water content measurement, two-thirds T₁ (T₂) and half T₁ (T₃) under a typical N application rate (N₁); i.e., 57.4 g·m⁻² N. The N experiment included N₁, two-thirds N₁ (N₂), and half N₁ (N₃) under T₂ irrigation. Results showed that deficit water supply reduced the stem sap flow by 22.1% and 42.8% in T₂ and T₃, respectively, compared with T₁. The average daily stem sap flow between N₁ and N₂ was similar, and both were higher than that of N₃. Significant differences between N₁ or N₂ and N₃ were only observed on four dates (totally 34 days). Nighttime stem sap flow accounted for 6.0% to 6.9% of the daily value for the water treatments and 5.7% to 8.5% of the daily value for the N treatments. No significant differences for nighttime stem sap flow were found among water and N treatments. The daily stem sap flow was significantly and positively correlated with solar radiation, air temperature, vapor pressure deficit, and reference evapotranspiration under the water and N experiments. The slopes of the regression equations between the daily stem sap flow and these parameters were lower when soil water availability was limited, whereas the slopes of the regressions had no significant differences among N treatments. A parabolic relationship between the ratio of the daily stem sap flow of water deficit treatments to that of T₁ and soil relative extractable water content was observed.

The unheated solar greenhouse industry has been expanding rapidly and becoming increasingly important for local economies in the arid region of northwest China in recent years, because the region has abundant light resources but limited precipitation (rain and snow) in winter. However, shortage of water resources and N stress (too little or too much) often affects the sustainable production of greenhouse crops in the region. Water and N stresses not only affect water uptake and nutrient assimilation of plants, but also influence stomatal response and drought resistance ability (Chapin et al., 1988; Claussen, 2002; Davies and Zhang, 1991). Thus, accurate measurement of crop water use under different water and N conditions can provide information for precision irrigation and N management.

Water deficit has an adverse effect on transpiration, which has been confirmed in sap flow studies for many woody tree

species such as olive [*Olea europaea* (Fernández et al., 2001; Tognetti et al., 2004)], pear–jujube [*Ziziphus jujuba* (Ma et al., 2007)], lemon [*Citrus ×limon* (Ortuño et al., 2005, 2006)], and peach [*Prunus persica* (Gong et al., 2001)]. A limited number of studies have been conducted to test the effect of water deficit on sap flow of tomato plants. Yang et al. (2012) showed that sap flow of tomato was seriously reduced by a severe water deficit treatment at the flowering and fruit set stages, and the diurnal variation of tomato sap flow in sunny days followed a bimodal curve under normal irrigation and mild water deficit treatments. A reduction in sap flow that was observed for tomato 2 or 3 d after water stress was imposed became more significant over time (Grey, 2010; Vermeulen et al., 2007).

Contradictory results concerning the effect of N on sap flow have been observed for different plant species, and it is likely that soil water status may interactively influence the effect of N on sap flow. Zhang et al. (2009) found that stem sap flow of peach seedling was higher at the higher N application rate under higher water application treatment, but lower stem sap flow was observed at the higher N application rate if plants suffered water deficit. In a shrub (*Ligustrum ovalifolium*), the cumulative xylem sap flow with low N application rate was higher than those with high N application rate (Guérin et al., 2007). Guak et al. (2003) observed that there was no significant effect of N treatment on daily sap flow in apple (*Malus ×domestica*) trees when soil water content was sufficient.

Received for publication 29 Sept. 2014. Accepted for publication 1 Dec. 2014. We gratefully acknowledge the financial support by the China Scholarship Council for the senior author to carry out the research at the University of California, Riverside. We are grateful for the research grants from the National Natural Science Foundation of China (51222905, 51321001), the National High-Tech 863 Project of China (2011AA100502), the Discipline Innovative Engineering Plan (111 Program, B14002), the Program of New Century Excellent Talents in University, Ministry of Education (NCET-11-0479), and the Startup Foundation for Introducing Talent of NUIST (S8113113001).

¹Corresponding author. E-mail: dutaisheng@cau.edu.cn.

Therefore, there has been a limited number of studies conducted to assess the effect of water and N deficit on plant sap flow. No study has been conducted to assess the effect of water and N treatments on stem sap flow of greenhouse-grown tomatoes in an arid region such as northwest China. In addition, nighttime transpiration, which accounted for a significant proportion of the total daily transpiration and lowered the crop water productivity, has been observed in many C_3 and C_4 species (Caird et al., 2007a, 2007b; Medrano et al., 2005; Snyder et al., 2003; Yoo et al., 2009). However, little information was available for tomato under different water and N treatments. The objectives of this study are to 1) evaluate the response of stem sap flow of tomato to water deficit in a solar greenhouse; 2) assess the effect of N stress (exceed or deficit) on stem sap flow; and 3) analyze the relationship between stem sap flow and meteorological parameters under different water and N treatments.

Materials and Methods

ENVIRONMENTAL CONDITIONS AND PLANT MATERIALS. The water and N treatment experiments were conducted at Shiyanghe Experimental Station for Water-Saving in Agriculture and Ecology of China Agricultural University, located in Wuwei City, Gansu Province of northwest China (lat. $37^{\circ}52'N$, long. $102^{\circ}51'E$, 1581 m altitude). It is in a typical continental, temperate climate zone. The annual mean temperature is $8.8^{\circ}C$ and the mean annual frost-free period is 150 d. Solar radiation is abundant in the region with annual mean sunshine of 3000 h. The mean annual precipitation in the region is only 164.4 mm, whereas the mean annual pan evaporation is 2000 mm. The groundwater table is below 25 m.

The solar greenhouse was made of a steel frame covered with a 0.2-mm-thick thermal polyethylene sheet. Because the greenhouse had no heat system, straw mats were spread over the roof of the thermal polyethylene sheet during the winter months to maintain the interior temperature at night. The interior temperature during daytime was controlled by a narrow ventilation system on the roof with the maximum opening of 0.5 m. More details of the solar greenhouse construction were described by Qiu et al. (2011). The soil is a desert sandy loam (Siltic-Orthic Anthrosols) with a mean bulk density of $1.46\text{ g}\cdot\text{cm}^{-3}$, field water capacity (θ_F) of $0.36\text{ (cm}^3\cdot\text{cm}^{-3}\text{)}$ and wilting point (θ_w) of $0.10\text{ (cm}^3\cdot\text{cm}^{-3}\text{)}$. Electrical conductivity of the irrigation water was $0.52\text{ dS}\cdot\text{m}^{-1}$.

Indeterminate tomato (cv. Zhongyan and Oyadi, respectively) plants were transplanted on 26 Dec. 2010 and 28 Feb. 2012, respectively, for the 2010–11 and 2012 seasons. Two rows of seedlings were evenly transplanted along the edge of each furrow with row spacing across the furrow of 0.40 m

Table 1. Amounts of irrigation and times in the 2010–11 season at different growth stages of tomato for different water treatments.^z

Treatment	Irrigation [mm (no.)]			
	Seedling stage	Flowering and fruit set stage	Fruit set and harvest stage	Entire season
T ₁	32.0 (2)	83.9 (3)	279.5 (10)	395.4 (15)
T ₂	32.0 (2)	83.9 (3)	186.3 (10)	302.2 (15)
T ₃	32.0 (2)	83.9 (3)	139.8 (10)	255.6 (15)

^zThe numbers in parentheses indicate the total times of irrigations for the respective growth stages. T₁, T₂, and T₃ are sufficient water supply, two-thirds T₁, and half T₁, respectively, under a typical nitrogen (N) application rate (i.e., $57.4\text{ g}\cdot\text{m}^{-2}\text{ N}$). Tomato growth stages in the 2010–11 season can be divided as follows: seedling stage (26 Dec. 2010 to 22 Jan. 2011, 27 d), flowering and fruit set stages (23 Jan. to 24 Mar., 61 d), and fruit set and harvest stage (25 Mar. to 26 June, 94 d).

Table 2. Nitrogen application rates in the 2012 season at different growth stages of tomato for different nitrogen (N) treatments.^z

Treatment	N application [$\text{g}\cdot\text{m}^{-2}$ (no.)]			
	Seedling stage	Flowering and fruit set stage	Fruit set and harvest stage	Entire season
N ₁	0.0	28.2 (3)	29.2 (3)	57.4 (6)
N ₂	0.0	18.8 (3)	19.5 (3)	38.3 (6)
N ₃	0.0	14.1 (3)	14.6 (3)	28.7 (6)

^zThe numbers in the brackets indicate the total times of N applications for the respective growth stages. N₁, N₂, and N₃ are typical N application rate (i.e., $57.4\text{ g}\cdot\text{m}^{-2}\text{ N}$), two-thirds N₁, and half N₁, respectively, under two-thirds sufficient water supply. Tomato growth stages in the 2012 season can be divided as follows: seedling stage (28 Feb. 2012 to 19 Mar., 20 d), flowering and fruit set stages (20 Mar. to 2 May, 44 d), and fruit set and harvest stage (3 May to 5 July, 64 d).

Fig. 1. Variation of daily solar radiation (R_s), reference evapotranspiration (ET_0), air temperature (T_a), and vapor pressure deficit (VPD) during the sap flow measurement periods of tomato in the water and nitrogen (N) experiments.

and interplant spacing of 0.40 m. The widths of furrow and adjacent bed were 0.40 and 0.75 m, respectively. The plant rows were oriented in a north–south direction for better interception of sunlight. At 3 to 10 d after transplanting (DAT), the soil surface was covered with clear, 5- μ m-thick polyethylene film to reduce soil evaporation and to increase the soil temperature. On some sunny days during June 2012, the greenhouse was partially shaded around noon with straw mats to avoid high interior temperature.

EXPERIMENT DESIGN. The water treatment experiment was conducted from Dec. 2010 to June 2011. The water treatments included T₁, T₂, and T₃ under local farmers' N₁; i.e., 57.4 g·m⁻² N. The water deficit treatments were imposed after 89 DAT (at fruit set and harvest stages), when T₂ and T₃ received two-thirds and half of the full irrigation amount, respectively, at each irrigation event (Table 1). To keep the seedlings alive and enhance growth, two irrigations with the same amount of water (16.0 mm) were applied at transplanting and 15 DAT for all the water treatments. After 15 DAT, tomato plants were irrigated to 90% θ_F when average soil water content in the main root zone (Z_r = 50 cm) in T₁ was depleted to 75% $\pm$ 2% of θ_F . For each

irrigation event, the amount of water applied, D (mm), was calculated by:

$$D = 10 \times (0.9 \theta_F - \theta_i) \times Z_r \quad [1]$$

where θ_i is the actual average soil moisture content in the main root zone before irrigation (cm³·cm⁻³).

Irrigation was applied on the same day for all treatments. The irrigation water was applied to the dead-end furrow side and no tail flow was allowed. The irrigation amount was recorded for each plot by a water meter at the end of the irrigation pipe. To prevent lateral movement of soil water to neighboring plots, a plastic sheet was embedded in the soil to a depth of 0.6 m around each plot.

The N treatment experiment was conducted from Feb. to July 2012. Treatments included N₁, N₂, and N₃ under T₂ irrigation. Table 2 shows the N application rates for each treatment at different growth stages. For the 2012 season, the two irrigation events with the same water amount of 27.9 mm were applied at transplanting and 12 DAT. After 12 DAT, all N treatments received two-thirds of sufficient water amount.

Fig. 2. The diurnal variation of stem sap flow of tomato for selected dates under different (A) water and (B) nitrogen (N) treatments (n = two replications). T₁, T₂, and T₃ are sufficient water supply, two-thirds T₁, and half T₁, respectively, under a typical N application rate (N₁); i.e., 57.4 g·m⁻² N. N₂ and N₃ are two-thirds N₁ and half N₁, respectively, under T₂; R_s = solar radiation.

The fertilizer was dissolved in water before each irrigation event and supplied with irrigation water. To determine application timing, water treatment T₁ was also set up in the 2012 season.

The area of each plot was 19.32 m² (5.6 m long × 3.45 m wide), consisting of three furrows and three beds with 84 tomato plants. The water treatments in the 2010–11 season and N treatments in the 2012 season were replicated three times, respectively, and the plots were a randomized complete block design.

Throughout each crop season, other management practices such as pollination, pruning branch stem, and pest control were the same for all treatments. In the 2012 season, all the N treatments received phosphorus and potassium at rates of 17.9 and 12.8 g·m⁻², respectively, and they were supplied with irrigation water.

MEASUREMENTS AND METHODS. Soil water content was measured using a portable capacitance sensor system (Diviner 2000; Sentek, Stepney, Australia). Two polyvinyl chloride access tubes were installed with one in the center of the bed and the other in the middle furrow for each water treatment plot in the 2010–11 season and for T₁ in the 2012 season. Measurements were made at 0.1-m intervals with maximal soil depth of 1.0 m every 3 to 7 d as well as before and after irrigation. Soil relative extractable water content (REW) was defined as follows:

$$REW = \frac{\theta - \theta_w}{\theta_F - \theta_w} \quad [2]$$

where θ is the average soil moisture content in the 0- to 50-cm soil layer (cm³·cm⁻³).

Meteorological data were measured with an automatic weather station (Hobo; Onset Computer, Pocasset, MA) located in the center of the greenhouse. Solar radiation (R_s), air temperature (T_a), and relative humidity (RH) were measured every 5 s, and 15-min averages were calculated and stored in a data logger.

As a result of low air speed in the greenhouse, the FAO 56 Penman–Monteith method with a fixed aerodynamic resistance of 295 s·m⁻¹ (Fernández et al., 2010, 2011) was used to calculate the daily reference evapotranspiration. The calculated equation was described by Qiu et al. (2013).

Stem sap flow was measured by a Flow 32-1K system (Dynamax, Houston, TX). As a result of the limitation of the sensors (eight sensors in one Flow 32-1K system), only two tomato plants were randomly chosen at each treatment to monitor sap flow from 8 to 20 May and 27 May to 2 June 2011 for the water treatments and from 31 May to 5 July 2012 except for 20 June 2012 for the N treatments. Gauge output was monitored every 5 s and recorded as 15-min averages with a data logger (CR1000; Campbell Scientific, Logan, UT). Further details on the methods, theoretical background, and

installation procedure were described in Trambouze and Voltz (2001).

Diurnal variation of leaf stomatal conductance (g_s) was measured by a leaf porometer (SC-1; Decagon Devices, Pullman, WA) for the water treatments and a portable photosynthesis system (LI-6400; LI-COR, Lincoln, NE) for the N treatments. Three to five fully grown leaves of the plants that were used for measuring sap flow at each treatment were selected for the continuous measurement of leaf g_s. Measurements were taken every 2 h from 0900 to 1900 HR on 23 Apr. 2011 (at fruit set and harvest stages) for the water treatments and from 0800 to 2000 HR on 29 May 2012 (at fruit set and harvest stages) for the N treatments.

Leaf chlorophyll content was measured using a chlorophyll meter (SPAD 502; Minolta Camera, Osaka, Japan) every 3 to 13 d during sap flow measurement periods. The SPAD 502 has a 0.06-cm² measurement area and calculates an index in SPAD units (dimensionless) based on absorbance at 650 and 940 nm. The accuracy of the SPAD 502 is ± 1.0 SPAD units. In each N treatment, SPAD values of plants that were used for measuring sap flow on each leaflet of the leaf closest to each specific cluster were measured. Each SPAD value was the mean of the measurements in all leaflets of each plant.

Leaf area index (LAI) for each N plot was measured every 7 to 24 d for four numbers of measurements using a non-destructive canopy analysis system (SunScan; Delta-T Devices,

Fig. 3. Variation of daily stem sap flow of tomato under different (A) water and (B) nitrogen (N) treatments throughout the study period. Error bars indicate SE (n = two replications). Mean values at each time point followed by different letters (a–c) are significantly different at the $P_{0.05}$ level. For the N treatments, the dates with no significantly different were not marked. T₁, T₂, and T₃ are sufficient water supply, two-thirds T₁, and half T₁, respectively, under a typical N application rate (N₁); i.e., 57.4 g·m⁻² N. N₂ and N₃ are two-thirds N₁ and half N₁, respectively, under T₂.

Cambridge, U.K.). The system consists of 64 photosynthetically active radiation (*PAR*) sensors embedded in a 1-m-long probe, which uses field measurements of *PAR* in crop canopies to measure LAI.

DATA ANALYSIS AND STATISTICS. Mixed model analysis of variance was performed with SPSS (Version 21.0; IBM Corp., Armonk, NY) to determine the effects of water or N stress on stem sap flow, leaf g_s , soil water content, leaf SPAD, LAI, and slopes between daily sap flow and climate parameters.

Results

Microclimate conditions in solar greenhouse

Figure 1 shows the variation of daily microclimate conditions during the sap flow measurement periods. For the water experiment period, the daily values of R_s , T_a , vapor pressure deficit (VPD), and reference evapotranspiration (ET_0) ranged from 4.6 to 22.3 MJ·m⁻²·d⁻¹, 16.1 to 25.8 °C, 0.12 to 2.25 kPa, and 1.3 to 4.9 mm·d⁻¹, respectively. For the N experiment period, the daily values of R_s , T_a , VPD, and ET_0 were 7.2 to 21.5 MJ·m⁻²·d⁻¹, 18.3 to 25.1 °C, 0.35 to 1.68 kPa, and 1.9 to 4.9 mm·d⁻¹, respectively.

Dynamics of stem sap flow under different water and nitrogen treatments

HOURLY SCALE. Figure 2 shows the diurnal variation of mean stem sap flow of two replications for selected dates under different water and N treatments. For all water treatments, the diurnal patterns of stem sap flow on sunny days showed a steep increase with the increase in the morning in solar radiation, leading to a maximum rate near noon (when solar radiation was at its maximum) followed by a sustained gradual decrease until late in the afternoon (Fig. 2A). The peak stem sap flow in the daytime was highest in T_1 , followed by T_2 and T_3 ; and the trend was the same at night when there was stem sap flow although there was no solar radiation. Stem sap flow was lower on cloudy and rainy days when solar radiation was lower. Compared with a sunny day (12 May 2011), the maximum solar radiation was decreased by 59.1% on 13 May 2011, when the maximum sap flow decreased by 65.2%, 74.4%, and 63.2%, respectively, for the three different water treatments. The peak sap flow of T_2 was close to that of T_3 on cloudy days when solar radiation was low.

The diurnal pattern of stem sap flow for the N treatments was similar to that for the water treatments (Fig. 2B). The maximum stem sap flow of N_1 was close to that of N_2 , but both were higher than N_3 . Taking a sunny day (19 June 2012) as an example, the peak stem sap flow was 0.132 and 0.128 L·h⁻¹, respectively, for N_1 and N_2 , which was ≈30% higher than that of N_3 .

When the greenhouse was partially overshadowed around noon (e.g., 18 June 2012) with straw mats to avoid high interior temperature, the variation of stem sap flow with time did not correspond to that of solar radiation (Fig. 2B).

DAILY SCALE. Figure 3A shows the differences in daily stem sap flow relative to different water treatments. Water deficit decreased daily stem sap flow of tomato grown in the greenhouse. Compared with T_1 , the average daily stem sap flow was 22.1% and 42.8%, respectively, lower for T_2 and T_3 during the measurement period. The maximum daily stem sap flow was 2.16, 1.56, and 1.22 L·d⁻¹, respectively, for T_1 , T_2 , and T_3 on 17 May 2011 (sunny day), and the minimum was 0.23, 0.15, and 0.14 L·d⁻¹, respectively, on 20 May 2011 (cloudy

day). Climate conditions affected the difference of stem sap flow in different water treatments. On sunny days, there were big differences in stem sap flow among the water treatments. However, the stem sap flow on cloudy days (except for 29 May 2011) was similar between T_2 and T_3 . The cumulative nighttime stem sap flow during the measurement period (20 d) was 1.48, 1.33, and 0.90 L, respectively, for T_1 , T_2 , and T_3 , which accounted for 6.0% to 6.9% of the total stem sap flow. Significant ($P < 0.05$) linear relationships between nighttime sap flow and nighttime VPD were observed under different water treatments (Fig. 4A), but no significant differences were found for the slopes of the regression equations. The daily stem sap flow (SF) increased linearly with REW (SF = 2.56 REW - 0.13; $R^2 = 0.79$). During the water deficit period, the ratio of daily stem sap flow of water deficit treatments (T_2 and T_3) to that of non-deficit water treatment (T_1) was related to REW. The relative daily stem sap flow (SF_{*Ti*}/SF_{*T1*}) increased rapidly as REW increased. When REW reached a threshold of 0.57, the SF_{*Ti*}/SF_{*T1*} increased slowly (SF_{*Ti*}/SF_{*T1*} = -7.3 REW² + 8.3 REW - 1.6, $R^2 = 0.56$, where SF_{*i*} is daily sap flow for T_2 and T_3 and SF_{*T1*} is the daily stem sap flow for T_1).

The daily stem sap flow varied from 0.35 to 1.32, 0.33 to 1.32, and 0.18 to 0.80 L·d⁻¹, respectively, for N_1 , N_2 , and N_3 . The daily stem sap flow of N_1 was similar to that of N_2 , but both were higher than that of N_3 (Fig. 3B). Significant differences between N_1 or N_2 and N_3 were only observed on 3 June, 4 June, 7 June, and 28 June 2012. The cumulative nighttime stem sap flow during the measurement period (34 d) was 2.46, 2.03, and 1.15 L, respectively, for N_1 , N_2 , and N_3 , which accounted for 5.7% to 8.5% of the total daily stem sap flow. A significant

Fig. 4. Relationship between nighttime sap flow (SF_n) of tomato and vapor pressure deficit (VPD) under different (A) water and (B) nitrogen (N) treatments. T_1 , T_2 , and T_3 are sufficient water supply, two-thirds T_1 , and half T_1 , respectively, under a typical N application rate (N_1); i.e., 57.4 g·m⁻² N. N_2 and N_3 are two-thirds N_1 and half N_1 , respectively, under T_2 .

($P < 0.05$) linear relationship was also found between nighttime sap flow and nighttime VPD under different N treatments (Fig. 4B), but no significant differences were found for the slopes of the regression equations. During the period of N stress in this study, the relative daily stem sap flow rate [$SF_i/SF_{(N_1+N_2)/2}$] increased linearly as the relative leaf SPAD [$SPAD_i/SPAD_{(N_1+N_2)/2}$] increased from 0.90 to 0.96 [$SF_i/SF_{(N_1+N_2)/2} = 3.96 (SPAD_i/SPAD_{(N_1+N_2)/2}) - 2.91$, $R^2 = 0.86$, where SF_i is stem sap flow for N_3 , $SF_{(N_1+N_2)/2}$ is the mean value of stem sap flow for N_1 and N_2 , $SPAD_i$ is leaf SPAD for N_3 , $SPAD_{(N_1+N_2)/2}$ is the mean value of leaf SPAD for N_1 and N_2].

RELATIONSHIP BETWEEN DAILY STEM SAP FLOW AND METEOROLOGICAL FACTORS AND ET_0 . Figures 5 and 6 show linear relationships between daily stem sap flow and meteorological factors as well as ET_0 under different water and N treatments. The relationships between measured daily stem sap flow and daily R_s , T_a , VPD, and ET_0 were very significant ($P < 0.001$) for all water treatments (Fig. 5A–D), whereas the slopes of the linear regression were the highest in T_1 followed by T_2 and T_3 . All the differences of slopes between T_1 and T_3 were significant.

The measured daily stem sap flow was significantly ($P < 0.001$) and positively correlated with R_s , T_a , VPD, and ET_0 for all N treatments (Fig. 6A–D), but the slopes of the regressions were not significantly different among N treatments. The coefficients of determination for the N experiment in the 2012 season were lower than that for the water experiment in

the 2010–11 season, which to some extent was attributed to the partial shade around noon by the straw mats.

LEAF STOMATAL CONDUCTANCE UNDER DIFFERENT WATER AND N TREATMENTS. The diurnal variations of leaf g_s on 23 Apr. 2011 had a similar trend for all water treatments except for the 1500 HR reading in T_3 (Fig. 7A). The g_s values were lower in the morning and evening and higher around noon. They decreased with the decrease of soil available water (Fig. 8). At 1300 HR, the g_s values were 10% and 31%, respectively, lower in T_2 and T_3 than in T_1 .

In the N treatments, there was a slight midday depression in g_s because of irrigation (two-thirds of sufficient water supply) after 12 DAT (Fig. 7B). There were no significant differences for g_s among the N treatments at each time.

LEAF SPAD AND LAI UNDER DIFFERENT N TREATMENTS. Figure 9A shows that, most of the time, leaf SPAD in N_1 was close to that in N_2 , but they were both significantly higher than that in N_3 . Leaf area index had a similar trend (Fig. 9B) as the SPAD reading among the N treatments. No significant differences were observed in LAI among the N treatments on 2 May 2012 and 5 July 2012.

Discussion

In this study, a pronounced reduction in stem sap flow was observed in response to water deficits (Figs. 2A and 3A), especially for T_3 (half of the sufficient water supply), which was

Fig. 5. Relationship between daily stem sap flow (SF) of tomato and (A) daily solar radiation (R_s), (B) vapor pressure deficit (VPD), (C) air temperature (T_a), and (D) reference evapotranspiration (ET_0) under different water treatments. T_1 , T_2 , and T_3 are sufficient water supply, two-thirds T_1 , and half T_1 , respectively, under a typical nitrogen (N) application rate; i.e., 57.4 g·m⁻² N.

Fig. 6. Relationship between daily stem sap flow (SF) of tomato and (A) daily solar radiation (R_s), (B) vapor pressure deficit (VPD), (C) air temperature (T_a), and (D) reference evapotranspiration (ET_0) under different nitrogen (N) treatments. N_1 , N_2 , and N_3 are typical N application rate; i.e., 57.4 g·m⁻² N, two-thirds N_1 , and half N_1 , respectively, under 2/3 sufficient water supply.

most evident when potential ET_0 was high (Fig. 5D). A reduction in sap flow that was observed for tomato 2 or 3 d after water stress was imposed became more significant over time (Grey, 2010; Vermeulen et al., 2007). Yang et al. (2012) also reported that on a sunny day, sap flow of tomato for severe water stress treatment (30% to 40% θ_F) was only 25.8% of that for normal water treatment (70% to 80% θ_F). Stomatal closure is generally the dominant mechanism for transpiration reduction as water stress develops (Hsiao, 1973), but transpiration decreases in response to water stress even when stomata are open if the water stress is a result of limited availability of water in the root zone as opposed to a large atmospheric demand for water (Grey, 2010).

When soil is subjected to drought, leaf stomata may reduce their opening to decrease water loss through transpiration (Davies and Zhang, 1991; Xiao and Wang, 2004). Many studies show that leaf g_s is reduced under water deficit treatment (Grey, 2010; Torrecillas et al., 1995; Vermeulen et al., 2007), which was also observed on a sunny day in this study (Fig. 7A). The relative daily stem sap flow increased rapidly with the increase of REW up to a threshold of 0.57 and increased slowly thereafter. This trend is different from the study of a pear-jujube tree grown under greenhouse conditions, which showed a linear relationship between relative daily stem sap flow and REW (Ma et al., 2007). The relationship from our study suggests that a signal from the roots may be transported to the shoots to lower the g_s and water loss from transpiration before a significant shoot water deficit takes place when roots experience drought stress (Davies and Zhang, 1991). This

mechanism of drought response can help plants prolong their lives with limited water supply.

On sunny days, as a result of high potential ET_0 , transpiration was high. However, water deficits restrict root water uptake, which in turn lower stem sap flow. Thus, big differences in stem sap flow among the water treatments were observed (Fig. 2B). On cloudy or rainy days, root water uptake meets the low potential ET_0 and soil water content did not significantly affect stem sap flow; thus, the differences in sap flow among the water treatments were small.

Leaf chlorophyll content is closely related to leaf N content in tomato (Sandoval Villa et al., 2000). When plants suffer N deficit, leaf SPAD is low. However, leaf SPAD can also be low when N content is excessively high (Li et al., 2010). Leaf SPAD and LAI were similar in N_1 to that in N_3 , but they were both significantly higher than that in N_2 (Fig. 9), which reflects that plants in N_3 may suffer N stress and suggest that plants in N_1 may receive excess.

The stem sap flow rates in N_1 and N_2 plants were similar, but a decline of stem sap flow was observed on 4 d in N_3 plants under two-thirds sufficient water supply (Fig. 3B). A linear ($P < 0.05$) relationship between the $SF_i/SF_{(N_1+N_2)/2}$ and $SPAD_i/SPAD_{(N_1+N_2)/2}$ suggests that N deficit may affect water loss from transpiration. Although a previous study showed that N deficit decreased g_s (Chapin et al., 1988), g_s among the N treatments under a water deficit condition was not significantly different in our study (Fig. 7B). The lower LAI (Fig. 9B) in N_3 may contribute to the difference because transpiration is usually directly related to LAI.

Fig. 7. Diurnal variation of leaf stomatal conductance (g_s) of tomato under (A) different water treatments on 23 Apr. 2011 and (B) different nitrogen (N) treatments on 29 May 2012. Error bars indicate SE. Mean values at each time point followed by different letters (a–c) are significantly different at the $P_{0.05}$ level. T₁, T₂, and T₃ are sufficient water supply, two-thirds T₁, and half T₁, respectively, under a typical N application rate (N₁); i.e., 57.4 g·m⁻² N. N₂ and N₃ are two-thirds N₁ and half N₁, respectively, under T₂.

Fig. 8. Dynamics of soil water content of tomato for different water treatment (n = three replications). Mean values at each time point followed by different letters (a–c) are significantly different at the $P_{0.05}$ level. T₁, T₂, and T₃ are sufficient water supply, two-thirds T₁, and half T₁, respectively, under a typical nitrogen (N) application rate (i.e., 57.4 g·m⁻² N).

Nighttime sap flow of tomato accounted for 5.7% to 8.5% of total daily sap flow, which could be attributed to rehydration and/or transpiration (Caird et al., 2007b). Nighttime transpiration has been found in many C₃ and C₄ species (Caird et al., 2007a, 2007b; Medrano et al., 2005; Seginer et al., 1990; Snyder et al., 2003; Yoo et al., 2009). Caird et al. (2007b) showed that the nighttime water loss in field-grown tomato measured by a lysimeter was 3.0% to 10.8% of the total daily water loss, and nighttime water loss for plants in the greenhouse could account for as much as 7.4% to 24.8% of the daily water loss. Joliet and Bailey (1992) also observed that nighttime water

Fig. 9. Evolution of (A) leaf chlorophyll content (SPAD) and (B) leaf area index of tomato under different nitrogen (N) treatments. Error bars indicate SE. Mean values at each time point followed by different letters (a–c) are significantly different at the $P_{0.05}$ level. N₁, N₂, and N₃ are typical N application rate (i.e., 57.4 g·m⁻² N), two-thirds N₁, and half N₁, respectively, under two-thirds sufficient water supply.

use was 9% to 22% of the total daily water use for greenhouse-grown tomato. Several studies suggested that nighttime water loss is primarily the result of incomplete stomatal closure at night (Caird et al., 2007b; Easlon and Richards, 2009; Snyder et al., 2003). In our study, significant correlations ($P < 0.05$) between nighttime sap flow and VPD were found for all treatments, especially for different water treatments (Fig. 4A and B), suggested that the stomata of tomato plants experienced incomplete closure and transpiration occurred at night.

Concluding Remarks

In this study, daily stem sap flow of tomato decreased when water deficit was imposed at fruit set and harvest stages (after 89 DAT). The average daily stem sap flow was 22.1% and 42.8% of that in sufficiently watered plants (T₁), for the two-thirds (T₂), and half (T₃) water treatments, respectively, during the measurement period. Stem sap flow, g_s , and LAI all decreased when the typical N application rate was reduced to half, but not when reduced to two-thirds.

Nighttime stem sap flow accounted for a significant proportion of the total daily stem sap flow under different water and N treatments, which might lower the crop water productivity. The magnitude of this effect is great enough to deserve further study, especially in regard to its physiological and ecological relevance. As a result of the limitation of the instruments, this research did not study the interaction between water and N under sufficient water supply and half of the sufficient water supply, but it also warrants further study.

Literature Cited

- Caird, M.A., J.H. Richards, and L.A. Donovan. 2007a. Nighttime stomatal conductance and transpiration in C_3 and C_4 plants. *Plant Physiol.* 143:4–10.
- Caird, M.A., J.H. Richards, and T.C. Hsiao. 2007b. Significant transpirational water loss occurs throughout the night in field-grown tomato. *Funct. Plant Biol.* 34:172–177.
- Chapin, F.S., C.H. Walter, and D.T. Clarkson. 1988. Growth response of barley and tomato to nitrogen stress and its control by abscisic acid, water relations and photosynthesis. *Planta* 173:352–366.
- Claussen, W. 2002. Growth, water use efficiency, and proline content of hydroponically grown tomato plants as affected by nitrogen source and nutrient concentration. *Plant Soil* 247:199–209.
- Davies, W.J. and J. Zhang. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annu. Rev. Plant Biol.* 42:55–76.
- Easlon, H.M. and J.H. Richards. 2009. Drought response in self-compatible species of tomato (*Solanaceae*). *Amer. J. Bot.* 96:605–611.
- Fernández, J.E., M.J. Palomo, A. Diaz-Espejo, B.E. Clothier, S.R. Green, I.F. Girón, and F. Moreno. 2001. Heat-pulse measurements of sap flow in olives for automating irrigation: Tests, root flow and diagnostics of water stress. *Agr. Water Mgt.* 51:99–123.
- Fernández, M.D., S. Bonachela, F. Orgaz, R. Thompson, J.C. López, M.R. Granados, M. Gallardo, and E. Fereres. 2010. Measurement and estimation of plastic greenhouse reference evapotranspiration in a Mediterranean climate. *Irrig. Sci.* 28:497–509.
- Fernández, M.D., S. Bonachela, F. Orgaz, R.B. Thompson, J.C. López, M.R. Granados, M. Gallardo, and E. Fereres. 2011. Erratum to: Measurement and estimation of plastic greenhouse reference evapotranspiration in a Mediterranean climate. *Irrig. Sci.* 29:91–92.
- Gong, D.Z., J.P. Wang, S.Z. Kang, X.T. Xu, F.C. Zhang, and Z.J. Li. 2001. Variation of root and trunk sap flow rate under different soil water wetting patterns. *Trans. Chinese Soc. Agr. Eng.* 17:34–38.
- Grey, S.N. 2010. Monitoring the simultaneous response of various water status indicators for use in the irrigation scheduling and drought stress detection of a greenhouse tomato crop. Master's diss., Univ. Zimbabwe, Harare, Zimbabwe.
- Guak, S., D. Neilsen, P. Millard, R. Wendler, and G.H. Neilsen. 2003. Determining the role of N remobilization for growth of apple (*Malus domestica*) trees by measuring xylem-sap N flux. *J. Expt. Bot.* 54:2121–2131.
- Guérin, V., L. Huché-Thélier, and S. Charpentier. 2007. Mobilisation of nutrients and transport via the xylem sap in a shrub (*Ligustrum ovalifolium*) during spring growth: N and C compounds and interactions. *J. Plant Physiol.* 164:562–573.
- Hsiao, T.C. 1973. Plant responses to water stress. *Annu. Rev. Plant Physiol.* 24:519–570.
- Jolliet, O. and B.J. Bailey. 1992. The effect of climate on tomato transpiration in greenhouses: Measurements and models comparison. *Agr. For. Meteorol.* 58:43–62.
- Li, L.Z., R. Guo, H.P. Li, and Y. Cao. 2010. Effects of nitrogen concentration in hydroponics on growth and development of tomato and spectral characteristics of leaf in greenhouse. *Plant Nutr. Fert. Sci.* 16:965–969.
- Ma, F.S., S.Z. Kang, F.S. Li, J.H. Zhang, T.S. Du, X.T. Hu, and M.X. Wang. 2007. Effect of water deficit in different growth stages on stem sap flux of greenhouse grown pear-jujube tree. *Agr. Water Mgt.* 90:190–196.
- Medrano, E., P. Lorenzo, M.C. Sánchez-Guerrero, and J.I. Montero. 2005. Evaluation and modelling of greenhouse cucumber-crop transpiration under high and low radiation conditions. *Sci. Hort.* 105:163–175.
- Ortuño, M.F., J.J. Alarcón, E. Nicolás, and A. Torrecillas. 2005. Sap flow and trunk diameter fluctuations of young lemon trees under water stress and rewatering. *Environ. Expt. Bot.* 54:155–162.
- Ortuño, M.F., Y. García-Orellana, W. Conejero, M.C. Ruiz-Sánchez, J.J. Alarcón, and A. Torrecillas. 2006. Stem and leaf water potentials, gas exchange, sap flow, and trunk diameter fluctuations for detecting water stress in lemon trees. *Trees (Berl.)* 20:1–8.
- Qiu, R.J., S.Z. Kang, F.S. Li, T.S. Du, L. Tong, F. Wang, R.Q. Chen, J.Q. Liu, and S.E. Li. 2011. Energy partitioning and evapotranspiration of hot pepper grown in greenhouse with furrow and drip irrigation methods. *Sci. Hort.* 129:790–797.
- Qiu, R.J., J.J. Song, T.S. Du, S.Z. Kang, L. Tong, R.Q. Chen, and L.S. Wu. 2013. Response of evapotranspiration and yield to planting density of solar greenhouse grown tomato in northwest China. *Agr. Water Mgt.* 130:44–51.
- Sandoval Villa, M., E.A. Guertal, and C.W. Wood. 2000. Tomato leaf chlorophyll meter readings as affected by variety, nitrogen form, and nighttime nutrient solution strength. *J. Plant Nutr.* 23:649–661.
- Seginer, I., D. Kantz, N. Levav, and U.M. Peiper. 1990. Night-time transpiration in greenhouses. *Sci. Hort.* 41:265–276.
- Snyder, K.A., J.H. Richards, and L.A. Donovan. 2003. Night-time conductance in C_3 and C_4 species: Do plants lose water at night? *J. Expt. Bot.* 54:861–865.
- Tognetti, R., R. D'Andria, G. Morelli, D. Calandrelli, and F. Fragnito. 2004. Irrigation effects on daily and seasonal variations of trunk sap flow and leaf water relations in olive trees. *Plant Soil* 263:249–264.
- Torrecillas, A., C. Guillaume, J.J. Alarcón, and M.C. Ruiz-Sánchez. 1995. Water relations of two tomato species under water stress and recovery. *Plant Sci.* 105:169–176.
- Trambouze, W. and M. Voltz. 2001. Measurement and modelling of the transpiration of a Mediterranean vineyard. *Agr. For. Meteorol.* 107:153–166.
- Vermeulen, K., K. Steppe, N.S. Linh, R. Lemeur, L. De Backer, P. Bleyaert, J. Dekock, J.M. Aerts, and D. Berckmans. 2007. Simultaneous response of stem diameter, sap flow rate and leaf temperature of tomato plants to drought stress. *Intl. Symp. High Tech. Greenhouse System Mgt.* 801:1259–1266.
- Xiao, L. and S. Wang. 2004. Plant physiology. China Agr. Sci. Technol. Press, Beijing, China.
- Yang, Z.Q., H.T. Zhang, Y.X. Li, X.D. Peng, Z.L. Zhou, K. Zhu, and X. Zhao. 2012. Response of sap flow and leaf water potential for greenhouse tomato under moisture stress. *Chinese J. Agrometeorol.* 33:382–387.
- Yoo, C.Y., H.E. Pence, P.M. Hasegawa, and M.V. Mickelbart. 2009. Regulation of transpiration to improve crop water use. *Crit. Rev. Plant Sci.* 28:410–431.
- Zhang, Z.L., F.C. Zhang, C.X. Zheng, and F.Q. Ni. 2009. Study on variation law of sap flow of peach seedling under different water and nitrogen conditions. *Water Saving Irr.* 2:1–4.