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Research Paper

Use of transpiration water and leaf intracellular retained water in tomato (*Solanum lycopersicum* L.) plants subjected to different water supply strategies

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ABSTRACT

Leaf intracellular water is the retained part of transpiration water when it flows through leaf mesophyll cells, the intracellular water is directly and closely related to photosynthesis and growth of plant. However, little is known about the dynamic use traits of intracellular water and the influence on instantaneous water-use efficiency (WUE_i) of plants at different water conditions. In this study, tomato (*Solanum lycopersicum* L.) plants were subjected to three different water supply strategies by regulating the soil relative water content (SWC_R) (i.e., T1: 70 %–80 %–90 %, T2: 80 %–90 %–100 %, T3: 60 %–70 %–80 %) within three treatment phases (P1, P2 and P3). The electrophysiological and photosynthetic parameters, leaf water potential, nutrient contents, growth indices and yield were determined. Leaf intracellular water use traits including transport rate (LIWTR), water-holding capacity (LIWHC) and water-use efficiency (LIWUE) were calculated according to the Nernst equation using plant electrophysiological parameters. The results showed that photosynthesis, growth and yield of tomatoes could be promoted by increasing the water supply. Plants at T3 treatment initially experienced drought-hardening and then could adapt to the surroundings and maintain high WUE_i with increasing water supply at the following phases. Besides, the plants at T3 treatment only showed a small amount (9 %) of yield loss compared to control. High value of LIWTR and low value of LIWHC indicated that less water supply could facilitate the water transport within leaf cells, which improved the WUE_i rather than the LIWUE. Sufficient water supply promoted the transpiration but did not accelerate the water transport within leaf cells and caused low value of WUE_i. 70 %–80 % SWC_R was a turning point for the changing status of leaf intracellular water in plants. In this study, the water supply strategy at T3 treatment was more conducive to balance the WUE improvement and yield loss in tomato plants than the other two. The use traits of leaf intracellular water based on plant electrophysiological parameters could provide support for the quick evaluation of plant water status.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the major horticultural crops consumed and cultivated worldwide (Liu et al., 2021). Tomato fruits can be considered a source of various nutrients, such as minerals, fiber, phenolic compounds, and vitamins A (precursors: β-carotene) and E (α -tocopherol) (Lima et al., 2022), they have high level of acceptability by people in daily life activities in China (Chen et al., 2020). The largest harvested area of tomato concentrates in China, Nigeria, and India (Colimba-Limaico et al., 2022). This type of crop is characterized

Abbreviations: d, specific effective thickness of the leaf; DT_{log}, the duration of the logarithmic growth phase; E, transpiration rate; GR_{50}, the growth rate at half of the logarithmic growth phase; g_s, stomatal conductance; F, gripping force; IC, leaf physiological capacitance; LIWHC, leaf intracellular water-holding capacity; LIWTR, leaf intracellular water transport rate; LIWUE, leaf intracellular water-use efficiency; P_N, net photosynthetic rate; SWC_R, relative soil water content; WUE, water-use efficiency; WUE_i, instantaneous water-use efficiency; Ψ_L, leaf water potential.

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Table 1
Soil physicochemical properties of clay.

Field capacity	pH	Bulk density	Organic matter	Available nitrogen	Available phosphorus	Available potassium
35.40 %	7.39	1.24 g cm^{-3}	10.49 g kg^{-1}	56.40 mg kg^{-1}	26.38 mg kg^{-1}	90.40 mg kg^{-1}

by high growth rate and yield. However, it is also a highly water-demanding crop, thus requiring large amounts of irrigation water throughout growing season (Xing et al., 2022). Considering the socio-economic pressures on the country's water resources, the water management of tomato cultivation that leads to efficient use of water is of increasing importance.

Tomato producers always over-irrigate their crops to increase yield. However, an increase in water supply tends to cause an excessive accumulation of biomass in tomato plants, which reduces the yield as well as worsens the balance between supply and water demand (Ullah et al., 2021). On the contrary, the application of water to the crops in deficiency will cause water stress and reduce biomass production and marketable yield (Li et al., 2021). Many reports suggest the regulated deficit irrigation or alternate partial root-zone irrigation, which indeed improves the water-use efficiency (WUE) of plants (Abboud et al., 2021; Kang et al., 2023). Under deficit irrigation, crops are deliberately allowed to sustain some water deficit and yield reduction (Ali, 2010). However, different crop species have different drought tolerance (or sensitivity) capacity, hence adapting to different water deficit level and requiring different irrigation volume (Ali, 2010). Besides, plant drought tolerance varies along with growth period, and the drought tolerance can also be altered through drought-hardening (Khan et al., 2021). Therefore, compared with the conventional uniform irrigation management, variable irrigation based on the spatio-temporal change of plant adaptability is more conducive to maintain or promote plant growth and yield (King et al., 2006). However, the application of irrigation strategy requires accurately measuring the plant water status to prevent plant damage and yield losses. In this direction, plant-based indicators of water status have been widely used (Puig-Sirera et al., 2021).

Traditionally, leaf water content, stomatal conductance (gs), transpiration rate (E), canopy temperature, water potential, leaf hydraulic conductance, and growth parameters are always determined to study plant water status (Zhang et al., 2018; Jafarikouhini et al., 2022; Gebauer et al., 2023). The reflectance spectra can be used for estimating the leaf water content, and the transpiration in plants can be analyzed according to the thermal imaging (Kior et al., 2021). In fact, most (~97 %) of the water absorbed by a plant's roots is carried through the plant and evaporates from leaf surfaces, water moves in the plant *via* the apoplast, symplast, and transmembrane pathways, only a small amount (1 %~3 %) of the absorbed water is retained in plant. The use traits including maintenance, transport, and utilization of the leaf intracellular retained water are directly and closely intertwined with the biochemical reactions, photosynthesis, and plant growth (Taiz et al., 2015). Leaf intracellular water becomes increasingly important to plant as water stress increased and can be regulated by some enzymes or proteins, i.e., carbonic anhydrase, aquaporins (Hu et al., 2011; Kapilan et al., 2018). As a result, the use traits of the intracellular water can be altered and the photosynthesis can be maintained or changed. It has been reported that some plants can maintain their photosynthetic capacities by alternatively using the leaf inter- and intracellular water with changing surroundings, which improve the WUE (Qin et al., 2022). Therefore, timely obtaining the use traits of leaf intracellular water helps to improve the accuracy of plant water status measurement. However, little is known about the dynamic use traits of leaf intracellular water and the influence on the use efficiency of transpiration water of plant at different water conditions.

Besides, traditional methods are hard to timely determine the dynamics of leaf intracellular water. As a newly emerging sensor technology, electrophysiology is sensitive to water changes and can be easily and timely measured, it has been increasingly used for monitoring plant responses to the environments (Jócsák et al., 2019; Sukhov et al., 2019; Steeneken et al., 2023). The intracellular water metabolisms have been successfully investigated by using this technique (Zhang et al., 2020; Xing et al., 2021). As we know, electrophysiological behavior of a plant is closely related to that of a single cell, which can be presumed as a spherical capacitor. Electrical characteristics vary between the organelles, the vacuole and the cytoplasm, which occupy most of the space in cells and can be regarded as resistors, while the plasma membrane has a capacitive characteristic (Zhang et al., 2020). Electric current can be affected by the resistors, capacitors and inductors in the alternating current circuit, and impedance is the sum of the resistance to current caused by the resistors, capacitors, and inductors (Schönleber and Ivers-Tiffée, 2015). Electric potential difference is produced when current passes the cell membrane, and it is retained by the efficient transport system and the alternative permeability of the cell membrane (Lindén et al., 2016). The water metabolism in cells alters the electrolyte concentration and changes the corresponding electrophysiological parameters (Qin et al., 2022). Therefore, the dynamics of the leaf intracellular water are correlated with cell electrical characteristics, which can be rapidly determined by using a nondestructive custom-made parallel-plate capacitor (Xing et al., 2021, 2022).

The present study determines the electrophysiological parameters, leaf water potential (Ψ_L), photosynthetic characteristics, WUE, growth, nutrient contents and yields of tomato subjected to different water supply strategies, calculates the leaf intracellular water transport rate (LIWTR), water-holding capacity (LIWHC) and water-use efficiency (LIWUE) according to the Nernst equation using plant electrophysiological parameters, investigates the water use traits within leaf cells of tomato plants. The objective of this study was to determine the dynamic use traits of intracellular water and investigate the influence of leaf intracellular retained water on the use of transpiration water at different water conditions. The determination of use traits of leaf intracellular water based on plant electrophysiological parameters helped to quickly evaluate the plant water status.

2. Materials and methods

2.1. Plant growth and treatments

The research was conducted in a greenhouse at the School of Agricultural Engineering, Jiangsu University, Jiangsu Province, China (N 32°11′ and E 119°27′). The seedlings of *S. lycopersicum* were grown from seed (Cooperation 906) in trays for 45 days and hand planted in pots (19.70 cm in depth, 29.60 cm in top diameter, and 17.80 cm in bottom diameter) filled with clay soil under a day/night temperature cycle of 25 °C/17 °C and 68 ± 4 % relative humidity. The cultivar Cooperation 906 is bred by the Institute of Northern Agricultural Science in Fushun city of China, and is a common tomato with a single fruit weight of about 250 g, it needs 40 days from flowering to fruit ripening, the fruits are good-tasting and have high product value. The soil physicochemical properties of clay were shown in Table 1. The water supply treatment started 35 days after transplanting and lasted for 30 days. The duration of the experiment from transplanting to termination was 75 days. 30 seedlings of uniform vigor were randomly assigned to each of the three treatments.

The three water supply treatments were conducted as follows:

The treatment period was divided into three phases and each phase lasted for 10 days, the first 10 days was defined as phase one (P1), the middle and last 10 days were defined as phase two (P2) and three (P3), respectively. The soil relative water content (SWC_R) of treatment one (T1, as control) at P1, P2 and P3 were controlled at 70 %±3 %, 80 %±3 % and 90 %±3 %, respectively; the SWC_R of treatment two (T2, excessive water supply) at P1, P2 and P3 were controlled at 80 %±3 %, 90 % ±3 % and 100 %±3 %, respectively; the SWC_R of treatment three (T3, relatively less water supply) at P1, P2 and P3 were controlled at 60 %±3 %, 70 %±3 % and 80 %±3 %, respectively. Wherein, the T1, T2 and T3 were regarded as normal, excessive and relatively less water supply for tomato plants. The 100 % SWC_R corresponded to the SWC at field capacity (that was 35.40 %). The excessive and relative less water supply treatments were intended to stimulate the changes of transport, retention and use of intracellular water in plant leaves, meanwhile the different use efficiency of transpiration water could be determined, which helped to investigate the relationship between the use of intracellular water and transpiration water in tomato plants. Firstly, the soil volume in each pot was calculated according to soil weight and bulk density. The soil water content was the product of SWC_R and field capacity, the water addition for each SWC_R level was the product of the soil volume in each pot and soil water content. Then the SWC_R at each phase of each treatment was maintained by weighing method, that meant the weight of each pot which contained a plant at each phase of each treatment level was maintained the same with that at the beginning of the corresponding phase of each treatment, respectively (The SWC_R at each treatment level would change as time increased compared with that at the beginning because of the growth of plant, but the stimulation effects of different water supply strategies on the use traits of intracellular water still exhibited difference).

Water was supplied every day at dusk to maintain the relative soil water content (SWC_R) during each treatment phase. Plant height, stem diameter and leaf area were measured from onset of the water supply treatment, and they were recorded every fifth day. The Ψ_L, photosynthetic, and electrophysiological parameters were determined on every tenth day after the onset of the treatment. The fourth and fifth youngest fully expanded leaves from the top (five plants from each treatment group) were chosen for measurements.

2.2. Determination of leaf water potential and leaf electrophysiological parameters

The variation of electrophysiological parameters as increased gripping forces was measured using the LCR tester (*Model 3532–50, Hioki*, Nagano, Japan), the frequency and voltage used were 3 KHz and 1 V, respectively (Xing et al., 2021). Three sites on each leaf were selected for recording the electrophysiological parameters at each gripping force, and the average value of each parameter was calculated. The measurements on five leaves from five different randomly selected plants at each treatment were recorded. With a dew point microvoltmeter in a universal sample room (*C-52-SF, Psypro*, Wescor, Logan, Utah), Ψ_L was measured at the same position of the leaves with the above electrophysiological parameters testing.

The coupling models of gripping force and electrophysiological parameters according to the Nernst equation and the law of energy conservation were established, respectively. Then the LIWTR (Xing et al., 2021), LIWHC and LIWUE (Zhang et al., 2020) can be calculated. The specific calculation formulas were as follows which have been described by Qin et al., 2022.

$$\mathrm{LIWTR} = \mathrm{bke}^{-\mathrm{bF}} \tag{1}$$

$$\mathrm{LIWHC} = \sqrt{(\mathrm{IC})^3} \tag{2}$$

$$\mathrm{LIWUE} = \frac{\mathrm{d}}{\mathrm{LIWHC}} \tag{3}$$

where b and k are parameters of the physiological impedance fitting equation, IC (pF) is the leaf physiological capacitance, and d is the specific effective thickness of the leaf.

2.3. Measurement of photosynthetic and growth parameters

The net photosynthetic rate (P_N, μmol m^{-2} s^{-1}), stomatal conductance (g_s, mmol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) were measured at 9:00–11:00 a.m. with a portable LI-6400XT photosynthesis measurement system (*LI-COR Inc., Lincoln*, NE, USA). The photosynthetic active radiation (PAR), temperature, CO_2 concentration and humidity during the measurements were 800 μmol m^{-2} s^{-1}, 30 °C 400 μmol mol^{-1}, and 60 ± 5 %, respectively. The actinic light was applied using a 6400–02B red and blue LED light control system, the duration of illumination before the photosynthetic parameters measurement lasted for 30 min. The instantaneous water-use efficiency (WUE_i, μmol $mmol^{-1}$) was calculated according to the following equation:

$$\mathrm{WUE_i} = P_N/E \tag{4}$$

Plant height was determined by tapeline and the unit was cm, stem diameter was determined by using a vernier caliper and the unit was mm, leaf area was determined by using a leaf area meter (*handheld laser leaf area meter, CI*, 203), the unit was cm^2. Dry weights of plant were measured at the end of the treatment, the plants were dried in an oven at 80 °C, plant dry weights were determined using an electronic analytical balance (*BSA124S, Sartorius*, Gottingen, Germany). The single fruit weight and fruit weight per plant were determined using the electronic analytical balance after the fruit was ripe.

2.4. Fitting equations of the relationship between growth indices and time

There are number of mathematical models describing productivity of agricultural plants at different spatial scales (Sukhova et al., 2023), the four-parameter logistic equation was selected in this study to analyze the upper limit of the growth index (a), growth rate at half of the logarithmic growth phase (GR_{50}), and duration of the logarithmic growth phase (DT_{log}) of plants, which were used to compare the growth status between different water supply treatments. The four-parameter logistic equation is as follows:

$$Y = \mathrm{Y_0} + \frac{\mathrm{a}}{1 + \left(\frac{X}{\mathrm{X_0}}\right)^{\mathrm{b}}} \tag{5}$$

where Y is the growth index, Y_0 is the initial value during logarithmic growth phase, a is the upper limit of the growth index, X is the number of days, X_0 is the number of days when the growth index reaches half of the maximum value during the logarithmic growth phase, and b is a constant. GR_{50} is the growth rate at half of the logarithmic growth phase, $GR_{50} = \frac{-ab}{4X_0}$. DT_{log} is the duration of the logarithmic growth phase, $DT_{log} = \frac{-4X_0}{b}$.

2.5. Measurement of nutrient contents

Approximately 0.15–0.20 g of dried plant tissue was digested using the H_2SO_4-H_2O_2 digestion method. The N, P, and K contents were determined using the Kjeldahl, Mo-Sb Antispetrophotography and Flame Atomic Absorption Spectrophotometry methods, respectively (Xu, 2000).

2.6. Statistical analysis

Data were analyzed using exploratory data analysis by SPSS software (version 13.0, SPSS Inc.). Statistically significant differences between treatments were assessed by ANOVA followed by Duncan's multiple comparison at the 5 % significance level ($P \leq 0.05$). The data are shown as the means ± SE ($n = 5$).

Table 2
Leaf water potential (Ψ_L, MPa), leaf intracellular water transport rate (LIWTR), leaf intracellular water-holding capacity (LIWHC) and leaf intracellular water-use efficiency (LIWUE) under different water supplies.

Phases	Treatments	Ψ_L	LIWTR	LIWHC	LIWUE
P1	T1	−1.407 ±0.041d	0.060 ±0.009ab	0.050 ±0.001c	1461.864 ±96.911ab
	T2	−1.289 ±0.012c	0.029 ±0.001c	0.056 ±0.002b	1264.373 ±113.915ab
	T3	−1.666 ±0.030f	0.082 ±0.021a	0.042 ±0.001d	1265.102 ±58.159ab
P2	T1	−1.338 ±0.021cd	0.029 ±0.003c	0.050 ±0.002c	1456.420 ±144.867ab
	T2	−1.144 ±0.019ab	0.011 ±0.002c	0.063 ±0.001a	1534.373 ±288.588ab
	T3	−1.503 ±0.031e	0.073 ±0.007a	0.045 ±0.001d	1573.670 ±134.945ab
P3	T1	−1.197 ±0.009b	0.037 ±0.005bc	0.055 ±0.001b	1653.215 ±108.884ab
	T2	−1.082 ±0.010a	0.020 ±0.004c	0.063 ±0.002a	1738.185 ±177.315a
	T3	−1.378 ±0.019d	0.037 ±0.002bc	0.049 ±0.001c	1169.342 ±87.381b

Note: Means ± SE ($n = 5$) in the same column followed by different letters differ significantly at $P \leq 0.05$, according to one-way ANOVA.

3. Results

3.1. Leaf water potential and electrophysiological parameters

Low SWC_R was associated with a lower Ψ_L value at each phase (Table 2). The values of Ψ_L in T3 increased significantly as treatment time increased. The values in T2 increased at P2 and then kept stable from P2 to P3, and those in T1 showed a clear increase at P3. The LIWTR value in T2 was remarkably lower than those in T1 and T3 at P1. At P2, the value in T2 showed no clear difference with that in T1 but was clearly lower than that in T3. The LIWTR values at P3 exhibited no significant difference among all the three treatments. Low SWC_R was also associated with a lower LIWHC value at each phase. Clear increases of LIWHC values in T1 and T3 were both observed at P3, while the LIWHC values in T2 remarkably increased at P2 and then kept stable from P2 to P3. The LIWUE values at P1 and P2 showed no significant difference among all the three treatments, while the value in T2 was clearly higher than that in T3 at P3.

3.2. Effect of different water supplies on photosynthetic parameters

The P_N, gs and E values all decreased in the direction of: T2 > T1 > T3 at each phase and depended on the SWC_R (Fig. 1). The P_N values in T1 and T3 gradually increased as treatment time increased, while those in T2 kept stable during the whole treatment period. The highest gs values in T2 and T3 were all observed at P2 compared to the values at the other two phases, respectively. The gs value at P1 was significantly lower than those at P2 and P3 in T1. The E values at P2 had no clear difference with those at P1 but was remarkably lower than those at P3 in T1 and T2, respectively. The E values in T3 maintained stable during the whole treatment period. The WUE_i values in T3 showed no clear difference with those in T1 and T2 at P1, but became clearly higher than those in T2 at P2 and P3.

3.3. Effect of different water supplies on growth indices

The plant height, stem diameter and leaf area in T2 were all higher than those in T1 and T3 during the treatment period (Fig. 2). Those growth indices in T3 were the lowest.

The plant height, stem diameter and leaf area as time increased during the treatment period were estimated by using the four-parameter logistic equation (Table 3). With respect to plant height, the values of a, GR_{50} and DT_{log} in T2 were the highest and those in T3 were the lowest, while the GR_{50} value in T1 was close to that in T3. When referring to stem diameter, the values of a and DT_{log} in T2 were the highest, while

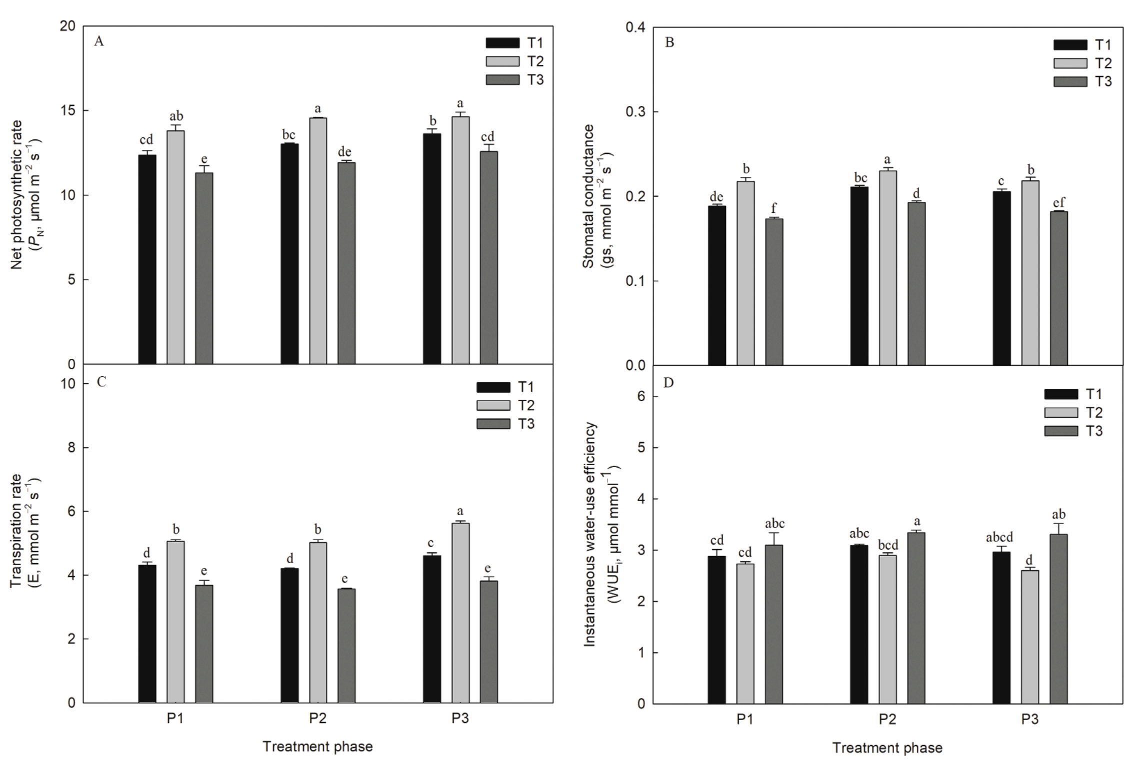

Fig. 1. Net photosynthetic rate (P_N, μmol m^{-2} s^{-1}) (A), stomatal conductance (gs, mmol m^{-2} s^{-1}) (B), transpiration rate (E, mmol m^{-2} s^{-1}) (C) and instantaneous water-use efficiency (WUE_i, μmol mmol^{-1}) (D) under different water supplies (Note: Different letters appear above the error bars of the same parameter when subsequent values differ significantly at $P \leq 0.05$, according to one-way ANOVA, $n = 5$).

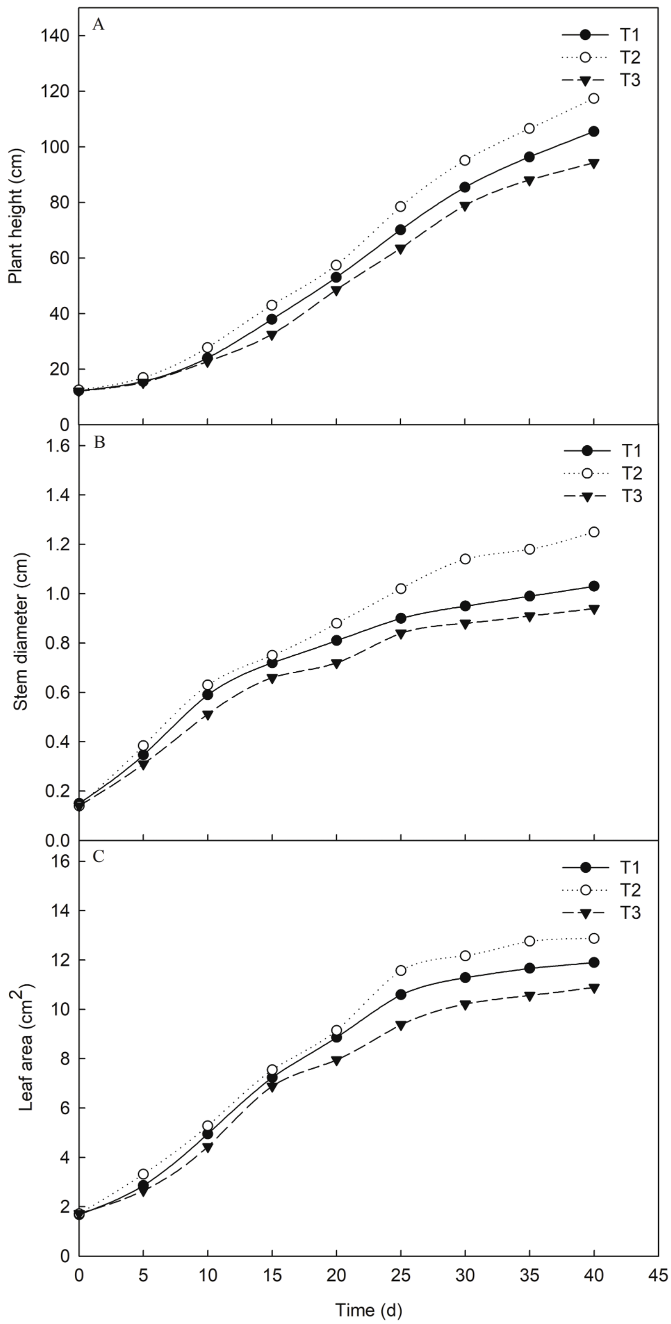

Fig. 2. Plant height (cm) (A), stem diameter (cm) (B) and leaf area (cm^2) (C) variations versus the treatment time (d) under different water supplies.

the GR_{50} value was the lowest among all treatments. The values of a, GR_{50} and DT_{log} in T1 were all very close to those in T3. The values of a and DT_{log} of leaf area in T2 were higher than those in the other two treatments, respectively. The GR_{50} value of leaf area in T2 was higher than that in T3 but was close to that in T1.

3.4. Effect of different water supplies on N, P, k contents in plant tissues

The N and P contents in leaves, stems and roots all decreased with the decreasing SWC_R (Table 4). The N and K contents in each treatment showed no clear difference among leaves, stems and roots, respectively. The P contents in T2 had no remarkable difference among leaves, stems and roots. The P content of root was significantly lower than that of stem but showed no clear difference with that of leaf in T1. The P contents in T3 showed a remarkably higher value in stem than those in root and leaf.

3.5. Effect of different water supplies on yields of tomato

The plant dry weight, single fruit weight and fruit weight per plant all decreased with the decreasing SWC_R (Table 5). The plant dry weight, single fruit weight and fruit weight per plant were 87 %, 89 % and 91 % of those in T1, respectively. Excessive water supply in T2 improved the single fruit weight and fruit weight per plant compared to those in T1, however, the increase in single fruit weight was remarkably higher than that in fruit weight per plant. When the plants were supplied with relative less water, the loss of fruit weight per plant was the lowest.

4. Discussion

4.1. Photosynthesis, growth, yield production, Ψ_L and WUE_i under different water supply treatments

Tomatoes production is only effective when proper irrigation is provided, hence knowledge about plants' reaction to irrigation is very important (Takács et al., 2018). Ψ_L is recognized as an index for whole plant water status (Gebauer et al., 2023). Decreased water supply reduced the Ψ_L values of tomato plants at T3 treatment, which was accompanied by a clear reduction in P_N. Low level water supply at T3 treatment limited root water uptake and the accumulation of N, P and K in plant tissues, which inhibited the gs and P_N of tomato plants, since the macroelements N and K play significant roles in regulating stomatal function or photosynthesis (Warren et al., 2005; Rey-Caramés, et al., 2016). However, the decreased gs and leaf area reduced the transpiration consumption and saved water for plants at T3 treatment. Irrigation levels interfered in the photosynthetic process of the plants (Farias et al., 2019). In this study, the P_N, gs and E values were all higher for plants submitted to the higher water supply level, consequently these gas exchange traits have contributed to higher plant efficiency for growth, biomass accumulation and yield production. It can be clearly observed that when well-watered, the plants presented higher productivity, the fresh fruit weight per plant at T2 treatment (excessive water supply) was the highest, which was 118 % of that at control (T1 treatment). These results corroborate with those reported by Wang et al. (2019), where tomato plants improved photosynthetic assimilation when submitted to higher irrigation level. However, the excessive water supply at T2 treatment led to high transpiration water consumption in plants and was not conducive to the efficient use of irrigated water. Even if with significantly lower gs and E values, the plants at control still exhibited no clear increase in WUE_i compared to those at T2 treatment, which was attributed to the low photosynthetic carbon assimilation. WUE at leaf levels (e.g. WUE_i) is calculated from parameters of leaf gas exchange, representing the adaptability of plants to the changing surroundings (Hatfield and Dold, 2019). Stomatal control is a major physiological factor to optimize the use of water, and stomatal closure is the first events taking place during water deficit (Vaziriyeganeh et al., 2018). Our results indicated that the plants at T3 treatment (relatively less water supply) decreased the gs and increased the WUE_i for adapting to the water deficit environment once they were submitted to the 60 % SWC_R at P1, and then could keep a relatively higher WUE_i at the following phases among all the treatments.

4.2. Photosynthesis, growth, water status and WUE_i influenced by increasing water supply at each treatment

Crop's water demand varies with increasing growth time within a same environment (Al-Harbi et al., 2015). Variable irrigation is a potential way to enhance the high WUE and meanwhile maintain the crop yields. The changing water supply should be conducted based on the plant response as growth time increased. Xing et al. (2022) have reported that tomato plants submitted to continuous 60 % SWC_R clearly

Table 3
Plant height (cm), stem diameter (cm) and leaf area (cm^2) estimated using four-parameter logistic equation under different water supplies.

Indices	Treatments	a	GR_{50}	DT_{log}	Equations	R^2	P
Plant height	T1	179.87	1.13	159.20	$Y = 7.41 + \frac{179.87}{1+\left(\frac{X}{71.24}\right)^{-1.79}}$	0.99	<0.0001
	T2	221.02	1.17	189.07	$Y = 7.52 + \frac{221.02}{1+\left(\frac{X}{79.41}\right)^{-1.68}}$	0.99	<0.0001
	T3	143.22	1.12	128.00	$Y = 7.78 + \frac{143.22}{1+\left(\frac{X}{62.72}\right)^{-1.96}}$	0.99	<0.0001
Stem diameter	T1	1.06	0.014	76.23	$Y = 0.15 + \frac{1.06}{1+\left(\frac{X}{26.87}\right)^{-1.41}}$	0.99	<0.0001
	T2	1.98	0.008	237.91	$Y = 0.14 + \frac{1.98}{1+\left(\frac{X}{62.45}\right)^{-1.05}}$	0.99	<0.0001
	T3	0.98	0.013	76.54	$Y = 0.14 + \frac{0.98}{1+\left(\frac{X}{28.13}\right)^{-1.47}}$	0.99	<0.0001
Leaf area	T1	11.69	0.20	58.77	$Y = 1.79 + \frac{11.69}{1+\left(\frac{X}{31.59}\right)^{-2.15}}$	0.99	<0.0001
	T2	13.53	0.19	71.00	$Y = 1.91 + \frac{13.53}{1+\left(\frac{X}{34.79}\right)^{-1.96}}$	0.99	<0.0001
	T3	10.51	0.17	60.23	$Y = 1.76 + \frac{10.53}{1+\left(\frac{X}{32.07}\right)^{-2.13}}$	0.99	<0.0001

Table 4
Effect of different water supplies on N, P and K contents in plant leaves, stems and roots.

	Treatments	$N/g\cdot kg^{-1}$	%[a]	$P/g\cdot kg^{-1}$	%[a]	$K/g\cdot kg^{-1}$	%[a]
Root	T1	6.10±0.14b	100	1.73±0.03b	100	5.12±0.05b	100
	T2	6.42±0.02a	105	1.91±0.03a	110	5.37±0.03a	105
	T3	5.89±0.08c	97	1.56±0.01c	90	4.83±0.05c	94
Stem	T1	6.41±0.11b	100	1.63±0.05a	100	6.88±0.12b	100
	T2	6.76±0.07a	105	1.78±0.02a	109	7.11±0.09a	103
	T3	6.15±0.01c	96	1.48±0.07b	91	6.71±0.01c	98
Leaf	T1	6.76±0.10b	100	1.84±0.07b	100	6.92±0.09b	100
	T2	7.20±0.04a	107	2.06±0.01a	112	7.17±0.01a	104
	T3	6.42±0.12c	95	1.66±0.01c	90	6.73±0.10c	97

Note: Means ± SE ($n = 5$) in the same column and the same tissue followed by different letters differ significantly at $P \leq 0.05$, according to one-way ANOVA. [a]This column indicates the percent value after different water supplies with reference to that of T1.

Table 5
Effect of different water supplies on yields of tomato.

Treatments	Dry weight per plant/g	%[a]	Fresh weight per fruit/g	%[a]	Fresh fruit weight per plant/g	%[a]
T1	52.27 ±1.44b	100	79.21 ±3.43b	100	413.47 ±4.49b	100
T2	64.68 ±0.94a	124	105.70 ±0.96a	133	488.42 ±3.36a	118
T3	45.54 ±0.79c	87	70.49 ±2.18c	89	374.50 ±7.36c	91

Note: Means ± SE ($n = 5$) in the same column followed by different letters differ significantly at $P \leq 0.05$, according to one-way ANOVA. [a]This column indicates the percent value after different water supplies with reference to that of T1.

decreased the photosynthesis, biomass accumulation and yield production but without improving the WUE_i when compared to those plants at the continuous 70 % SWC_R treatment. However, the results in the present study indicated that although submitted to a less water supply at each phase, those plants at T3 treatment maintained the growth status, the values of the fitted parameters a, GR_{50} and DT_{log} at T3 treatment were close to those at control, and those plants only showed a small amount of yield loss, which was indicated by the 9 % loss of fresh fruit weight per plant when compared to that at control. It demonstrated that drought tolerance of the tomato plants at T3 treatment were improved through drought-hardening at P1 (60 % SWC_R) (Khan et al., 2021), then the plant water status was improved and the P_N of the plants at T3 treatment could be promoted step by step as the SWC_R increased at the following phases. Growing plants at T3 treatment increased the water demand at P3 and avoided flooding stress when the SWC_R increased to 80 %. At T1 treatment, increasing water supply improved the P_N and gs at P3, but simultaneously increased the transpiration. As a result, it had no promotion effect on the WUE_i of the plants. At T2 treatment, when the SWC_R was higher than 90 %, the increasing water supply could not increase the Ψ_L and P_N any more at P2 and P3, which on the contrary led to a relatively low use efficiency of transpiration water.

4.3. Leaf intracellular water use and the influence on instantaneous water-use efficiency

Plant electrophysiological information provides insight into the water metabolism within cells and helps understand the role of intracellular water in maintaining the plant water balance (Zhang et al., 2020). Most of the water in a leaf resides in mesophyll cells, it is

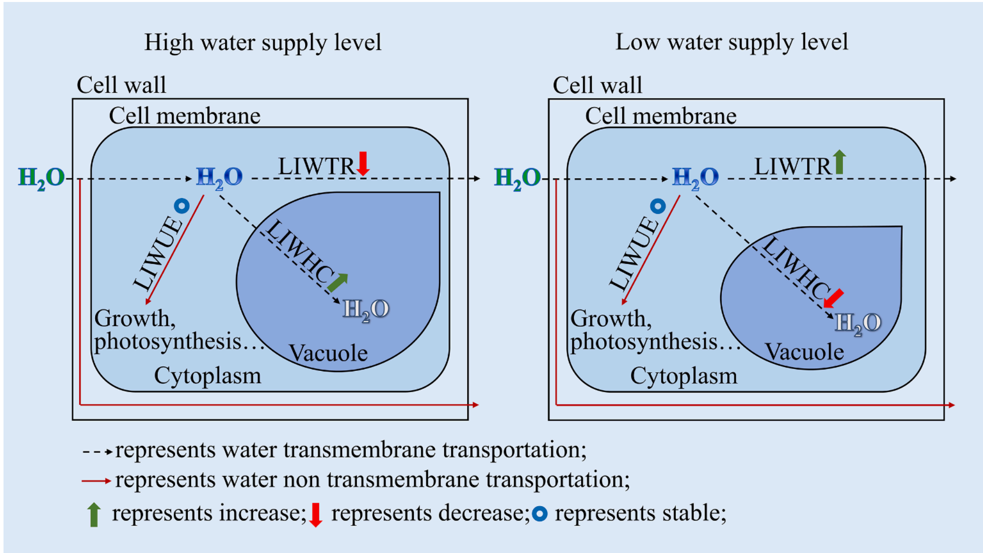

Fig. 3. Intracellular water use at different water supply level (Note: LIWHC represents leaf intracellular water-holding capacity, LIWTR represents leaf intracellular water transport rate, LIWUE represents leaf intracellular water-use efficiency).

unavoidable that these cells must change in size, swelling and shrinking as the balance shifts between the rate of evaporation and the rate of water supply (Canny and Huang, 2006). As a result, the water transmembrane transportation alters and the intracellular water status changes. At each treatment phase, a higher LIWHC value was associated with higher gs and E in plants which were submitted to higher water supply. The plants submitted to sufficient water supply (T1 and T2 treatments) increased their LIWHC once the SWC_R was higher than 80 %. The LIWHC was calculated according to the IC value, which was determined by the cell volume (Qin et al., 2022), the results in this study implied that tomato plants could swell the leaf cell volume and increase their water-holding capacity for adapting to the excessive water supply, the strong transpiration could promote the water uptake from soil and water transport through plant leaves, which provided leaf cells with sufficient water and therefore increase the Ψ_L. Leaf cells of plants with drought-hardening at T3 treatment became more sensitive to water change, they swelled once the SWC_R was higher than 70 %. During the whole treatment period, the LIWTR values at each treatment would decrease when the SWC_R was higher than 80 %. The LIWTR of plants at T3 treatment maintained higher values at P1 and P2 among all the treatments and phases. The plants at T1 treatment also had higher LIWTR value at P1 when the SWC_R was 70 %. In a word, the increased water supply swelled the leaf cells and improved the LIWHC values, but on the contrary decreased the LIWTR of plants (Fig. 3). Sufficient water supply promoted the transpiration but did not accelerate the water transport within leaf cells, and the transpiration water could not be utilized to the maximum, which led to low value of WUE_i. The drought-hardening at P1 and the efficient water transport within leaf cells of plants at the first two phases helped the plants maintain higher WUE_i at T3 treatment compared to those at T2 treatment during the whole period. Meanwhile, the tomato plants at T3 treatment only showed a small amount of yield loss compared to control. However, the excessive water supply at T2 treatment led to more remarkable increase in plant dry weight and fresh weight per fruit rather than fresh fruit weight per plant. This is consistent with the results reported by Day et al. (2022), which showed that the fruit volumetric growth was primarily driven by water accumulation. With regarding to the LIWUE, it was interesting that the values at each treatment kept stable almost all the time. No variation was observed in LIWUE even if the plants were supplied with only 60 % SWC_R at P1 of T3. However, our previous studies have shown that karst plants which suffer from serious drought stress can increase the LIWUE to adapt to the karst environment (Qin et al., 2022). We therefore inferred that tomato plants at P1 (60 % SWC_R) of T3 were just subjected to slight water stress. The LIWUE can also be selected as an indicator for determining the stress degree that plants are subjected to.

5. Conclusions

The photosynthesis, growth and yield of tomatoes could be promoted by increasing the water supply, but only the relative less water supply at T3 treatment kept high WUE_i in plants. Plants at T3 treatment initially experienced drought-hardening and then could adapt to the surroundings and maintain high WUE_i with increasing water supply at the following phases. Besides, the plants at T3 treatment only showed a small amount (9 %) of yield loss compared to control. High value of LIWTR and low value of LIWHC indicated that less water supply could facilitate the water transport within leaf cells, which improved the WUE_i rather than the LIWUE. Sufficient water supply promoted the transpiration but was not conducive to the water transport within leaf cells and caused low value of WUE_i. 70 % - 80 % SWC_R was a turning point for the changing status of leaf intracellular water in plants. In this study, the water supply strategy at T3 treatment was more conducive to balance the WUE improvement and yield loss in tomato plants than the other two, and could be recommended for enhancing the growth and physiological traits of these tomatoes. However, it needs further study to find the optimal water supply strategy for planting this tomato cultivar in the field conditions. The use traits of leaf intracellular water based on plant electrophysiological parameters could provide support for the quick evaluation of plant water status.

CRediT authorship contribution statement

Deke Xing: Writing – original draft, Data curation. **Qian Zhang:** Investigation, Formal analysis. **Yanyou Wu:** Writing – review & editing, Funding acquisition, Conceptualization. **Kuan Zhao:** Project administration, Funding acquisition. **Jing Wang:** Methodology, Investigation. **Shizheng Yan:** Methodology, Investigation. **Zhenyi Li:** Writing – review & editing, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2024.113520.

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