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RESEARCH ARTICLE

Fruit growth, carbon allocation, and related enzymes in tomato under different irrigation and potassium application regimes

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Abstract

Background: The increasing concentration of atmospheric CO_2 not only affects the growing environment of crops but also aggravates the global greenhouse effect and further aggravates the problem of water shortage. The combined effect of water deficit and potassium (K) application has not been widely studied.

Aims: A pot experiment was conducted to investigate the effect of deficit irrigation (DI) and K application at different growth stages on carbon allocation and enzyme activities related to sugar metabolism.

Methods: Tomatoes were transplanted and planted on April 26, 2017 and harvested on August 15, 2017. Four irrigation regimes were implemented with two water levels (full irrigation-W and DI-W/2) in different growth stages, and each water treatment was equally divided into two subgroups: with K (K1) and without K (K0). Fruits from the first to fourth trusses of the tomato plants were sampled. Tomato growth, carbon allocation, and related enzyme activities were measured.

Results: The fresh weight (FW), dry weight, and relative growth rate of dry mass were sensitive to irrigation amount under K fertilization, enhancing the promotion effect of irrigation on fruit. Meanwhile, carbon allocation was sensitive to irrigation amount under K regime. Sucrose synthase (SuSy), acid invertase (AI), and sucrose phosphate synthase (SPS) were also highly sensitive to irrigation amount under K application condition. Starch phosphorylase displayed a quadratic parabola for irrigation amount, and adenosine diphosphate glucose pyrophosphorylase (AGPase) was highly sensitive to irrigation amount without K fertilization. Carbon in the form of other carbohydrates, carbon in the form of soluble sugar (C*sol*), and fruit water content were the factors that had the greatest influence on the principal components. Classification by K-means algorithm and canonical correlation analysis showed that FW, fructose, sucrose, and starch could be used as significant indicators of the dry matter components of the fruit for the treatment without K. In the case of K regime, SuSy, AGPase, AI, and C*sol* could be used as a significant indicator of the correlation analysis of carbon metabolism activity.

Conclusions: The factors related to the improvement of fruit quality and carbon allocation by deficient irrigation and K application were explored. Water stress changed the

distribution of photosynthetic carbon between starch and soluble sugar. K application further changed the balance between soluble sugars and other compounds. In particular, it significantly increased the carbon content of soluble sugars and decreased that of other compounds. AI and SuSy are key enzymes affecting carbon metabolism under water-deficient conditions.

KEYWORDS
carbon allocation, fruit quality, K-means algorithm, tomato, water and potassium regulation

1 | INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most popular vegetables cultivated worldwide, with good taste, many nutrients, and abundant antioxidant substances (Savić et al., 2008). Sugars (sucrose, fructose, and glucose), which are the primary metabolites in tomato fruit, account for about 50% of fruit dry weight (DW) (Balibrea et al., 2006; Davies et al., 1981). Tomato quality is determined by many factors, including genotype, for example, cultivar (Caretto et al., 2008; Shokat et al., 2013); environment, for example, CO_2 and drought; and management, for example, irrigation and fertilization (J. Liu et al., 2020; Wei et al., 2018). Tomato fruit quality must be improved by optimizing irrigation and fertilization under an open field and protected conditions (Hartz et al., 2005; K. Liu et al., 2011), particularly in arid and semi-arid regions (Fereres & Soriano, 2007; Geerts and Raes, 2009), where water is the most limiting factor for crop cultivation.

The effects of different irrigation intervals, amounts, and techniques on tomato have also been extensively tested in terms of its yield and fruit quality (Harmanto et al., 2005; Kirda et al., 2004; Zegbe-Domınguez et al., 2003). However, all the stages of development in tomato are not equally sensitive to soil moisture deficit; therefore, identification of its critical irrigation stage and scheduling of irrigation based on crop water status are deemed to be the most cost-efficient methods to improve water use efficiency (WUE) (Ngouajio et al., 2007), facilitate the accumulation of dry matter, and improve fruit quality (Elvanidi et al., 2018; Patanè and Saita, 2015). Deficit irrigation (DI) during fruit development period could enhance the accumulation of glucose and fructose in tomato fruit (Ripoll et al., 2014), and DI at fruit maturity period could obviously improve the total soluble solids (J. Chen et al., 2013; Patanè & Cosentino, 2010; Yang et al., 2017). Thus, an enhanced understanding of water management in the special growth stage of tomato should enable growers to efficiently improve yield and fruit quality.

Potassium (K) is one of the most in-demand cationic minerals for vegetative growth (Kanai et al., 2011), and it is closely related to fruit yield and quality (Caretto et al., 2008; Daoud et al., 2020). On the one hand, K promotes the transportation and transformation of sucrose in plants and improves the efficiency of sugar transportation in the phloem (Kaya et al., 2001; J. Liu et al., 2021). On the other hand, plants could be resistant against abiotic stresses under K application (Vickery & Bruinsma, 1973). Judicious application of K fertilization could improve crop yield (Çolpan et al., 2013), and K deficiency could directly disrupt these activities, decrease plant growth, accelerate leaf senescence, and even induce early maturity (Pujos and Morard, 1997). Meanwhile, the harvested fruit removes a large amount of K from soil, intensifying the depletion of available K in soil; therefore, supplying K fertilizer in tomato production is important (S. Chen et al., 2017; Zhu et al., 2017).

The individual effect of DI (Patanè & Cosentino, 2010) or K fertilization (Çolpan et al., 2013; Daoud et al., 2020; Hernández-Pérez et al., 2020; Sonntag et al., 2019) on tomato quality has been intensively studied, whereas few literature referred to the combined effect of these two factors (Yao et al., 2016), especially during different growth stages, as fruit development. In addition, the combined effect of DI and K fertilization at a specific growth stage of tomato and its influence on carbon allocation and enzyme activities related to sugar metabolism have not been documented coherently. The present study aimed to explore the effects of DI and K application at different growth stages on carbon allocation and enzyme activities related to sugar metabolism and combine principal component analysis (PCA) and canonical correlation analysis to screen out the main factors under water and K supply conditions.

2 | MATERIALS AND METHODS

2.1 | Plant materials and treatments

Experiments were conducted in a greenhouse at the Shiyanghe Experimental Station (37° 52′ N, 102°50′ E, 1581 m elevation), Gansu Province, Northwest China, from April 2017 to August 2017. The 76 m × 8 m greenhouse was a steel-frame construction covered with 0.2 mm-thick polyethylene. A ventilation system on the roof controlled the interior daytime temperature in summer. The research plant was an indeterminate pink tomato (*S. lycopersicon* L. cv. Jinpeng 11; Xi'an Jinpeng seed Co., Ltd., China), a cultivar that is commonly planted by local farmers. A small automatic weather station (HOBO; Onset Computer Corporation, Bourne, USA) was installed to monitor the temperature and relative humidity (RH) in the greenhouse during the whole growth period of plants. Data were collected every 5 s. The mean value was recorded every 15 min. The temperatures and humidity in the greenhouse from April 2017 till

August 2017 ranged from 14.38 to 30.98°C and from 25.98 to 91.42%, respectively.

At the third to fourth leaf stage, single seedlings were transplanted into each plastic container (top diameter of 33 cm, bottom diameter of 25 cm, and depth of 28 cm). The container was buried in the ground up to its top edge to maintain a soil temperature similar to that in the surrounding field. Cheesecloth and 1 kg of small gravel were packed at the bottom of each container to prevent soil loss, and the containers were filled with 17 kg of air-dried sandy loam soil (particle size <5 mm) with bulk density of 1.3 ± 0.5 g cm^{-3}. The basic physical properties of the soil were volumetric field capacity of 0.258 cm^3 cm^{-3}, saturated paste extract electrical conductivity of 0.205 dS m^{-1}, available K of 88 mg kg^{-1}, available P of 5.14 mg kg^{-1}, available N of 20.57 mg kg^{-1}, organic matter of 6.49 g kg^{-1}, soil bulk density of 1.35 g cm^{-3} and pH 7.96. The fertilizer used was in the form of calcium magnesium phosphate (12% P_2O_5) and urea (46.4% N). Base fertilizer (0.2 g P_2O_5 kg^{-1} and 0.12 g N kg^{-1}) was mixed into the soil before the soil was filled into pots, and an equal amount of urea was supplied with irrigation.

Tomatoes were transplanted and planted on April 26 and harvested on August 15. The growth period was divided into vegetative growth period (2017/4/26–2017/5/13), flowering and fruit-bearing stage (2017/5/14–2017/6/15), fruit-swelling stage (2017/6/16–2017/7/13), and fruit maturation stage (2017/7/14–2017/8/15), with a whole growth period of 111 days. Four irrigation regimes were created with two water levels (full irrigation-W and DI-W/2) in different growth stages: (1) CK (all stages: W), (2) T1 (flowering and fruit-bearing stage: W/2), (3) T2 (fruit-swelling stage: W/2), and (4) T3 (fruit maturation stage: W/2). The plants in each water treatment were arranged in six north-south rows of 10 plants, with a total of 240 plants.

Each water treatment was equally divided into two subgroups: with K (K1) and without K (K0). The additional K treatment was the same for all treatments. Plants that were treated with K were identified as a subgroup by appending K to the group label. For example, in water treatment T1, K application was denoted as T1K, while no K application was still denoted as T1. The irrigation amount was completely the same, that is, 30 pots for T1 treatment and 30 pots for T1K treatment. The plants in the CK group, which was supplied with K, were identified as CKK, and the plants in the treatment group Ti, which was treated with K, were identified as TiK. Planting was carried out in a single hole and single plant, with a row spacing of 80 cm and a plant spacing of 60 cm at the experimental site and with one drip irrigation belt controlling one crop row. The K fertilizer used in the test was potassium sulfate (containing 50% K_2O; SDIC Xinjiang Luobupo Co., Ltd., Lop Nur, Xinjiang, China), and it was applied along with irrigation. K was applied in equal amounts twice at the flowering and fruiting stage (June 1–5) to ensure the adaptability of seedlings to the environment, and the optimal amount of K application (0.46 g K_2O kg^{-1} soil) was selected on the basis of previous literature (Feng et al., 2017; Han et al., 2012). A detailed description of the experimental design could be found in previous studies (Luo et al., 2020; Luo et al., 2021). The arrangement of plants and treatments is shown in Figure 1.

2.2 | Test items and methods

2.2.1 | Irrigation amount

The soil water content (SWC; cm^3 cm^{-3}) in the root zone of the plastic film-mulched tomato plants was measured by 5TE soil moisture sensors that were installed in the soil of the three central containers of each treatment. The sensors were connected to automated data loggers in groups of five (EM50; Decagon Devices Inc., USA). They were calibrated gravimetrically using sensor-measured data for volumetric water content. Data were recorded every 15 min. When the water content in the containers decreased to 70% of field capacity θ_f, which was determined using the cutting ring method, the irrigation was about 95% of field capacity. The amount of irrigation water was calculated using the following equation:

$$W = (\theta_{t1} - \theta_{t2}) \times V, \quad (1)$$

where W (cm^3) is the irrigation amount; θ_{t1} and θ_{t2} (cm^3 cm^{-3}) are the upper limits of SWC and the measured SWC before irrigation, respectively; and V (cm^3) is the pot soil volume. The irrigation amounts and K quantities applied during all the growth stages are given in Table 1.

2.2.2 | Index measurement

The fruits from the first to fourth trusses of the tomato plants were sampled in the experiments, and each treatment was replicated three times. The fruits were picked at 34 days after anthesis (DAA) from the first truss; 37, 48, and 57 DAA from the second truss; 58 and 65 DAA from the third truss; and 66 and 73 DAA from the fourth truss. The contents of glucose, fructose, and sucrose in tomato fruit were determined by high-performance liquid chromatography. The washed samples were ground and mixed evenly. Then, 0.5 g samples were weighed and placed into test tubes, extracted 2–3 times with 75% ethanol in a water bath at 80°C, and made up to volume with 1 mL of distilled water. Then, the supernatant was taken. The liquid was passed through a 0.45-μm filter into the liquid phase for determination. An amino column was used, the column temperature was 35°C, the mobile phase ratio was 80% acetonitrile +20% ultrapure water, the flow rate was controlled at 1.0 mL min^{-1}, and data were processed by HW–2000 GPC. The soluble sugar from the fruit was extracted using the procedure described by Gomez et al. (2002), and the starch content was determined by perchloric acid hydrolysis method (Gomez et al., 2003).

The enzyme solution was prepared in accordance with the method of Keller and Ludlow (1993). All operations were performed at 0–4°C. About 0.2 g of fresh plant samples were taken, 2 mL of extraction buffer were added, and the mixture was ground in ice bath and centrifuged at 11,000 × g for 10 min. The supernatant was taken as the enzyme solution. The enzymatic activity of sucrose synthase (SuSy) in the synthesis direction was determined in accordance with the method of Borisjuk et al. (2002), with slight modifications, that is, 50 μL enzyme

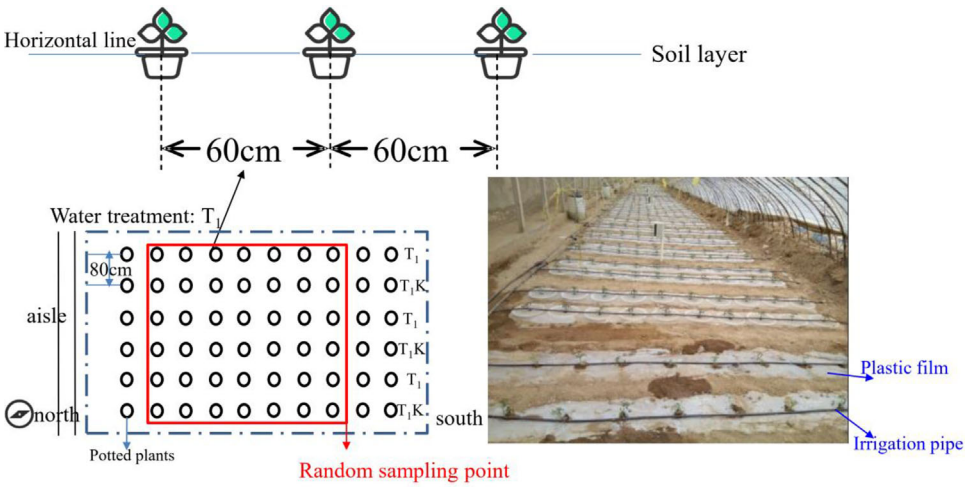

FIGURE 1 Details of the experiment site and plant layout in the greenhouse

TABLE 1 Irrigation amounts and potassium quantities applied in the experiment

	Irrigation amount (mm)				Potassium amount (g K_2O)	
Treatments	Stage I	Stage II	Stage III	Total	Date: 06/01	Date: 06/05
T1	30.33	114.92	91.64	254.97	0	0
T2	60.66	57.46	91.64	227.84	0	0
T3	60.66	114.92	45.82	239.48	0	0
CK	60.66	114.92	91.64	285.30	0	0
T1K	30.33	114.92	91.64	254.97	7.82	7.82
T2K	60.66	57.46	91.64	227.84	7.82	7.82
T3K	60.66	114.92	45.82	239.48	7.82	7.82
CKK	60.66	114.92	91.64	285.30	7.82	7.82

Note: Stage I (the flowering and fruit-bearing stage): from 05/14 to 06/15, Stage II (the fruit-swelling stage): from 06/16 to 07/13, Stage III (the fruit maturation stage): from 07/14 to 08/15. The same potassium amount was applied to the flowering and fruit-bearing stage (June 1 and 5), a total of 15.64 g K_2O.

solution plus 50 μL of 100 mmol L^{-1} Hepes-NaOH buffer, 20 μL of 50 mmol L^{-1} $MgCl_2$, 20 μL of 100 mmol L^{-1} UDPG, 20 μL of 100 mmol L^{-1} fructose. After 30 min of reaction, 200 μL of 40% NaOH solution were added to stop the reaction, and then 1.5 mL of 30% HCl were added. In addition, 0.5 mL of 1% resorcinol were used to measure the amount of sucrose, and controlling was conducted without UDPG and fructose-6-phosphate. The 200 μL reaction medium for SuSy decomposition direction contained 50 mmol L^{-1} Hepes-NaOH buffer, 300 mmol L^{-1} sucrose, and 10 mmol L^{-1} UDPG. Twenty μL of enzyme solution were added, and the mixture was reacted at 30°C for 20 min, boil water. The reaction was terminated by bathing for 1 min. The fructose produced was determined by chromogenic assay with 3,5-dinitrosalicylic acid.

The method for measuring sucrose phosphate synthase (SPS) was consistent with that for determining the activity of SuSy, with slight modifications. First, 20 μL of 100 mmol L^{-1} fructose was substituted with 20 μL of 100 mmol L^{-1} 6-phosphate fructose (Albertson and Grof, 2007).

Acid invertase (AI) and SP activities were determined by the methods described by Merlo and Passera (1991). One gram of plant was taken as a sample, placed in a freezing mortar, and added with 4 mL of frozen 100 mmol L^{-1} Tris-buffer (pH 7.2). The buffer was composed of 5 mmol L^{-1} β-mercaptoethanol, 10 mmol L^{-1} erythorbic acid, and 1 mmol L^{-1} phenylmethylsulfonyl fluoride. It was frozen, ground into a homogenate, and centrifuged at 20,000 × *g* for 30 min. The supernatant was placed in 15 mmol L Tris-buffer (pH 7.2) containing 5 mmol L^{-1} β-mercaptoethanol and dialyzed overnight. The dialysate was used for AI and SP activity determination.

The activity of adenosine diphosphate glucose pyrophosphorylase (AGPase) was determined by measuring the pyrophosphate (PPi)-dependent glucose−1-phosphate (G1P) formed from adenosine diphosphate glucose (ADPG) (Fernie et al., 2001). Fresh sample (0.3 g) was peeled and placed in a mortar after ice bath. Then, 3 mL of extraction solution was added and ground into a homogenate. After the sample was centrifuged at 12,000 × *g* for 10 min, 2 mL of supernatant was taken into the 5-mL centrifuge tube for enzyme activity assay.

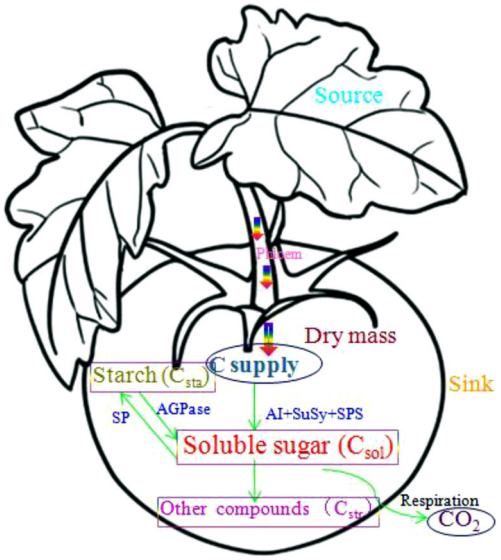

FIGURE 2 Schematic diagram of carbohydrate metabolism and related enzymes in tomato fruit. The carbon exists in the form of soluble sugar, starch, and other structural compounds in the fruit. Three rectangles identify the three major types of carbon compounds in the fruit, and the two ellipses show carbon supply and loss through respiration.

Afterwards, 50 μL of 50 mmol L^{-1} $MgCl_2$, 100 μL of buffer solution, and 50 μL of enzyme extract were added to 100 μL of 5 mmol L^{-1} ADPG, which was mixed with 100 μL of 20 mmol L^{-1} PPi to initiate the reaction for 15 min. The reaction was terminated in a boiling water bath for 1 min. After cooling, 100 μL of 6 mmol L^{-1} $NADP^+$, 1.5 U of phosphate glucose mutase, 50 μL of 5 U/L 6-P-G dehydrogenase, and 0.3 mL buffer were added. A total volume of 1.5 mL of the above mixture was taken, and 1-P-G was used as the standard curve after colorimetric reaction at 340 nm for 10 min at 30°C. Quantification by performed by measuring the pyrophosphate (PPi)-dependent G1P formed from ADPG.

K content was determined by atomic absorption spectrophotometry (Xue et al., 2006). In brief, 0.03 g sample was mixed with 10 mL H_2SO_4. After the sample was digested in a sand bath for 3–4 h, 1 mL of H_2O_2 was added to dilute the volume to a 100-mL volumetric flask, and then the sample was measured by an atomic absorption spectrophotometer.

2.2.3 | Fruit carbon metabolism

The main physiological processes of carbon metabolism in a tomato fruit are shown in Figure 2. C*sol*, C*sta*, and C*str* (g) represent the quantities of carbon as soluble sugars, starches, and other structural carbon compounds, respectively, and the process of solving the parameters has been explained in detail by Luo et al. (2020). In addition, the growth process of fruit DW is described by the following Gompertz function model:

$$DW(t) = ae^{-be^{-ct}}. \quad (2)$$

TABLE 2 Definition of all the abbreviations

Parameter	Definition	Unit
FW	Fruit fresh weight	g
DW	Dry weight	g
FWC	Fruit water content	%
RGR	Relative growth rate of the dry mass	dd^{-1}
Fc	Fructose concentration	g/100 g FW
Gc	Glucose concentration	g/100 g FW
Sc	Sucrose concentration	g/100 g FW
SP	Starch phosphorylase	μg pi/g FW min
AGPase	Adenosine diphosphate glucose pyrophosphorylase	nmol glucose/(g min) FW
SuSy	Sucrose synthase	μmol sucrose/(g h) FW
AI	Acid invertase	μmol glucose/(g h) FW
SPS	Sucrose phosphate synthase	μmol sucrose/(g h) FW
C*sol*	Carbon in the form of soluble sugar	g C
C*sta*	Carbon in the form of starch	g C
C*str*	Carbon in the form of other carbohydrates	g C

The fruit DW growth rate (dDW/d*t*) could be obtained as follows:

$$\frac{dDW}{dt} = c \times DW \times \log\left(\frac{a}{DW}\right), \quad (3)$$

where *a*, *b*, and *c* are Gompertz function model parameters. The relative growth rate (RGR) of the dry mass could be determined by Equations (2) and (3) as follows:

$$RGR = \frac{1}{DW}\frac{dDW}{dt}. \quad (4)$$

The fruit water content (FWC) could be obtained by the following formula:

$$FWC = \frac{FW_s - DW_s}{FW_s} \times 100. \quad (5)$$

All the abbreviations of the index are defined in Table 2.

2.2.4 | Statistical analyses and draft

Mean values were used for different treatments (shown by different letters), and the least significant difference and multiple range tests were used to calculate the differences between treatments at confidence level of $p < 0.05$ by R studio version 3.6.1 (Kabacoff, 2015). Multiple linear regression and nonlinear regression were all carried out using R, and *ggplot 2*-based plots were drawn using R packages

ggpubr, *ggthemes*, *FactoMineR*, and *factoextra* (Kassambra, 2017; Lê et al., 2008).

3 | RESULTS

3.1 | Effects of water and K regulation on growth and fruit quality

Table 3 shows the fruit fresh weight (FW), fruit DW, FWC, RGR of dry mass, fructose concentration (Fc), glucose concentration (Gc), sucrose concentration (Sc), starch phosphorylase (SP), AGPase, SuSy, AI, SPS, and carbon content in the form of soluble sugar (C*sol*), starch (C*sta*), and other carbohydrates (C*str*). The order of irrigation amount was CK > T1 > T3 > T2 (Table 1). The FWC, RGR, Fc, Gc, Sc, SP, SuSy, AI, and SPS under water-deficient condition were significantly higher than those in CK. However, FW and AGPase were significantly lower than those in CK. The DW, Sc, SP, SuSy, AI, and SPS of K treatments (T1K, T2K, T3K, and CKK) were significantly higher than those without K treatments (T1, T2, T3, and CK) under the same irrigation amount. Meanwhile, FWC and AGPase were significantly lower than those in without K regime. C*sol* and C*sta* under K treatments were higher than those in CK, but C*str* under K treatments was lower (Table 2).

The relative single FW and the relative irrigation amount during the whole growth period showed a very significant positive linear correlation ($p < 0.01$; Figure 3A). Under the same irrigation amount, the FW of K1 was significantly higher than that of K0, indicating that K application could enhance the promotion effect of irrigation on FW. A significant positive linear correlation was found between the relative dry mass (DW_a/DW_{max}) and irrigation amount under K1 ($p < 0.01$; Figure 3B). This finding indicated that the dry mass increased more quickly when K was applied under irrigation. The linear relationship between FWC and irrigation was not significant ($p > 0.05$) under K1 (Figure 3C). However, a significant positive linear correlation was observed between FWC and irrigation amount under K0 ($p < 0.01$). FWC was highly sensitive to irrigation amount under K0. RGR showed a decreasing trend with the increase in irrigation amount ($p < 0.01$; Figure 3D).

3.2 | Effects of water and K regulation on carbon allocation

The relationship between the relative carbon content of different forms of carbohydrates and the relative irrigation in fruits is shown in Figure 4. Under K0, the C*sol* of T2 was the largest, but the irrigation amount was only 0.2–0.8, that is, the highest C*sol* was obtained with a small irrigation amount. Under the same irrigation amount, the C*sol* under the condition of K application was greater than the C*sol* without K application (Figure 4A). C*sta* exhibited a very significant negative linear correlation with Irrigationa/Irrigationmax during the whole growth period ($p < 0.01$). With the increase in irrigation volume, C*sta* gradually decreased and CK showed a significant downward trend. Under the same irrigation amount, the C*sta* under K0 was greater than that under K1 (Figure 4B). Whether under K0 or K1, $Csta/Csta_{max}$ had a very significant negative linear correlation with $Irrigation_a/Irrigation_{max}$ during the whole growth period ($p < 0.01$). Under the same irrigation volume, the C*str* under K0 was greater than that under K1, indicating that K application inhibited the accumulation of other carbon-containing compounds (Figure 4C).

3.3 | Effects of water and K regulation on enzymes related to sugar metabolism

In the early stage of irrigation, the activity of SuSy was the largest, and it decreased significantly with the increase in irrigation amount ($p < 0.01$). Whether under K0 or K1, T3 had the largest SuSy under the same irrigation volume, and T1 had the smallest. The SuSy activity under K1 was also greater than that under K0 (Figure 5A).The linear equation showed that AI had a very significant positive linear correlation with the relative irrigation amount during the whole growth period ($p < 0.01$), with the AI activity of T2 treatment being the largest (Figure 5B). However, although CK had the greatest irrigation amount, its AI activity was the lowest. The AI activity in K1 was higher than that in K0. The linear equation in Figure 5C showed that the relative SPS (SPS_a/SPS_{max}) of the fruit and $Irrigation_a/Irrigation_{max}$ had a very significant negative linear correlation, and the activity of SPS in T2 treatment was significantly higher than that in other treatments. The SPS in T3 treatment was at a low level during the entire irrigation period. In K1, T2K had the highest SP activity. Under the same irrigation volume, the SPS under K1 was greater than that under K0. As shown in Figure 5D, the linear regression relationship between the relative starch phosphorylase (SP_a/SP_{max}) and $Irrigation_a/Irrigation_{max}$ of the fruit was not significant ($p > 0.05$) regardless of treatment conditions. From the beginning to the end of irrigation, the SP activity in CK was significantly lower than that in water-deficit treatment. AGPase had a very significant negative linear correlation with irrigation amount ($p < 0.01$), and it gradually decreased with the increase in irrigation amount (Figure 5E). In K0, especially in the period of increasing irrigation volume, the AGPase activity in CK was higher than that in water-deficit treatment. K1 also showed a similar situation.

3.4 | Main index most affected by DI and K application

The PCA of fruit growth and quality indicators and related enzyme activities showed that the first two principal components explained 75.5% of the variance difference, and the two principal components were retained (Figure 6A). C*sol* had the largest contribution to PC1, followed by C*str* (Figure 6B). FWC contributed the most to PC2, followed by Sc (Figure 6C). The PCA of different K regimes is shown in Figure 6D. A great difference could be found between the confidence ellipses of K0 and K1. K0 had a larger confidence ellipse due to outliers, and more negatively correlated variables that resulted in inclined elliptical left had a strong correlation with Sc, SuSy, and FWC. An obvious positive

TABLE 3 Fruit growth and related fruit quality indicators under different water and potassium treatments (mean ± SD)

	Treatments							
Index	**T1**	**T2**	**T3**	**CK**	**T1K**	**T2K**	**T3K**	**CKK**
FW (g)	76.65 ± 11.33bc	71.18 ± 11.20c	74.87 ± 11.52bc	97.88 ± 13.09a	88.55 ± 11.79ab	76.19 ± 12.03bc	82.74 ± 11.29abc	97.95 ± 13.27a
DW (g)	3.52 ± 0.71c	4.13 ± 0.75abc	3.83 ± 0.72bc	4.31 ± 0.78abc	4.45 ± 0.78ab	4.71 ± 0.78ab	4.49 ± 0.78ab	4.80 ± 0.80a
FWC (%)	0.95 ± 0.24ab	0.94 ± 0.24d	0.95 ± 0.24bc	0.96 ± 0.23a	0.95 ± 0.24cd	0.94 ± 0.24e	0.95 ± 0.24cd	0.95 ± 0.24bc
RGR (dd^{-1})	0.08 ± 0.02cd	0.10 ± 0.02ab	0.10 ± 0.02ab	0.07 ± 0.02d	0.10 ± 0.02ab	0.11 ± 0.02a	0.10 ± 0.02a	0.09 ± 0.02bc
Fc (g/100 g FW)	0.72 ± 0.20cd	0.89 ± 0.30ab	0.78 ± 0.29bcd	0.64 ± 0.15d	0.85 ± 0.14bc	1.02 ± 0.18a	0.88 ± 0.31ab	0.77 ± 0.25bcd
Gc (g/100 g FW)	0.74 ± 0.20cd	0.90 ± 0.30ab	0.80 ± 0.30bc	0.65 ± 0.16d	0.87 ± 0.34bc	1.04 ± 0.51a	0.89 ± 0.32ab	0.77 ± 0.30bcd
Sc (g/100 g FW)	0.09 ± 0.051d	0.12 ± 0.04abc	0.10 ± 0.04cd	0.08 ± 0.0d	0.12 ± 0.04ab	0.12 ± 0.03a	0.12 ± 0.04ab	0.10 ± 0.02bcd
SP (μg pi/g FW min)	290.84 ± 20.13abc	302.62 ± 26.91ab	285.08 ± 18.38bc	254.15 ± 15.03c	309.14 ± 27.32ab	328.01 ± 29.81a	302.49 ± 27.18ab	295.17 ± 21.34abc
AGPase (nmol glucose/(g min) FW)	309.11 ± 28.55b	293.55 ± 23.21bc	302.88 ± 28.13b	355.37 ± 26.71a	272.91 ± 21.34c	270.46 ± 21.53c	277.22 ± 22.45c	307.93 ± 22.33b
SuSy (μmol sucrose/(g h) FW)	21.14 ± 4.29d	30.07 ± 5.66abc	25.85 ± 5.13bcd	21.93 ± 4.67d	22.68 ± 5.19d	34.43 ± 6.72a	30.37 ± 5.68ab	23.46 ± 4.56cd
AI (μmol glucose/(g h) FW)	129.59 ± 7.19bc	155.69 ± 7.55ab	153.20 ± 7.51ab	112.62 ± 5.35c	148.54 ± 6.47ab	171.37 ± 8.21a	168.96 ± 8.32a	135.39 ± 5.87bc
SPS (μmol sucrose/(g h) FW)	14.82 ± 1.74c	18.69 ± 2.35b	10.76 ± 1.29e	12.46 ± 1.53d	18.70 ± 2.19b	21.24 ± 2.33a	14.99 ± 1.69c	17.30 ± 2.17b
C*sol* (g C)	29.10 ± 5.35c	30.25 ± 5.61ab	29.66 ± 5.35c	28.26 ± 5,19cd	31.40 ± 5.71ab	32.42 ± 5.74a	32.00 ± 5.73a	30.54 ± 4.68ab
C*sta* (g C)	5.37 ± 4.63a	4.92 ± 2.58a	3.98 ± 2.49a	4.31 ± 2.46a	4.58 ± 2.67a	4.44 ± 2.52a	4.11 ± 2.47a	3.88 ± 2.36a
C*str* (g C)	65.53 ± 4.85b	64.82 ± 5.02b	66.36 ± 5.99b	67.42 ± 5.42a	64.03 ± 5.54c	63.14 ± 5.32c	63.89 ± 5.62c	65.57 ± 5.79b

Note: Different letters after the values in the same row of quality indicators indicate that there is a significant difference under the LSD method at the $p < 0.05$ level.

Abbreviations: FW, fruit fresh weight; DW, dry weight; FWC, fruit water content; RGR, relative growth rate of the dry mass; Fc, fructose concentration; Gc, glucose concentration; Sc, sucrose concentration; SP, starch phosphorylase; AGPase, adenosine diphosphate glucose pyrophosphorylase; SuSy, sucrose synthase; AI, acid invertase; SPS, sucrose phosphate synthase; C*sol*, carbon in the form of soluble sugar; C*sta*, carbon in the form of starch; C*str*, carbon in the form of other carbohydrates. .

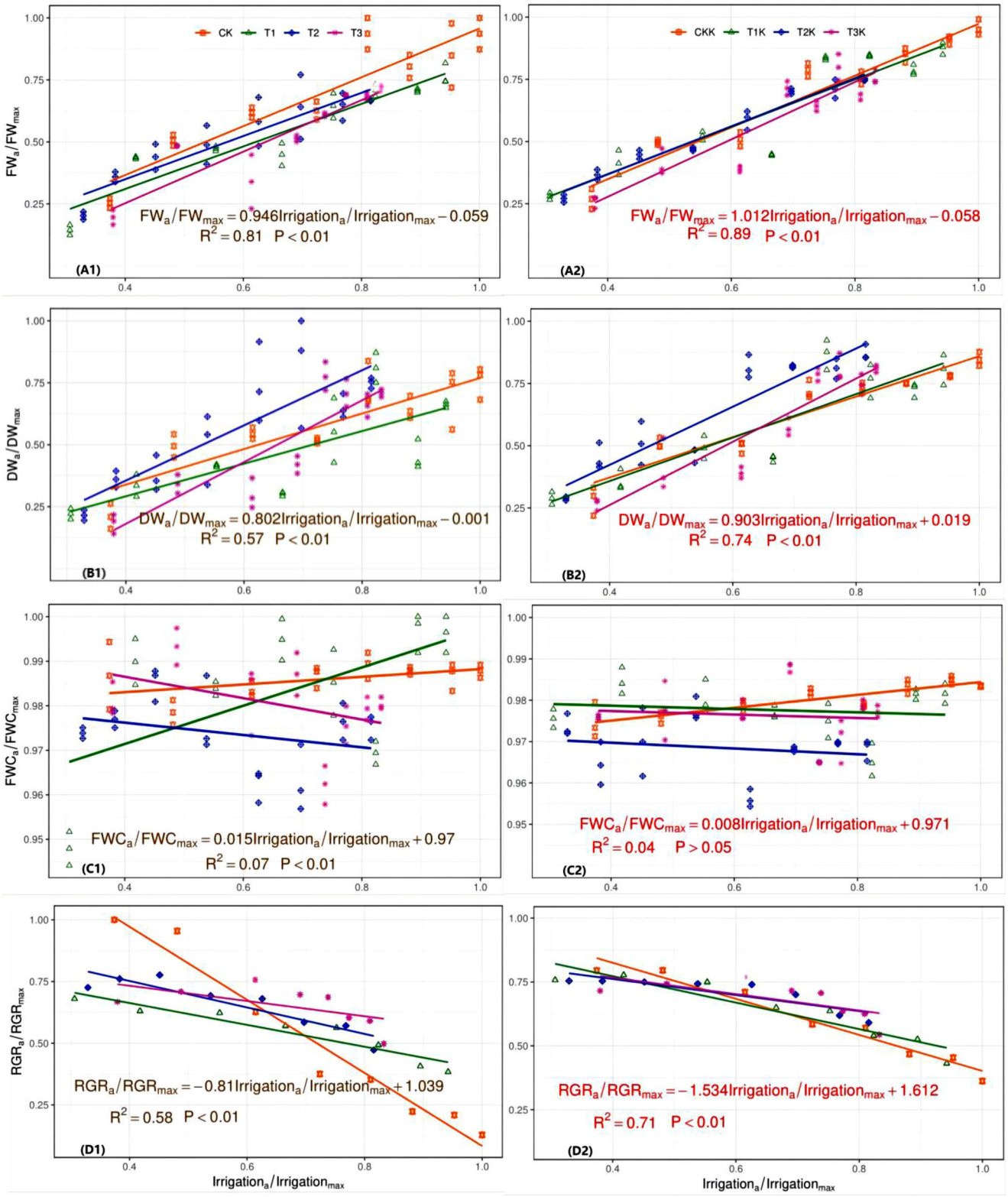

FIGURE 3 The relationship of relative fresh weight (FW) (A1, A2), dry weight (DW) (B1, B2), fruit water content (FWC) (C1, C2), and relative growth rate of the dry mass (RGR) (D1, D2) and the relative irrigation amount under different potassium application regimes K0 (A1, B1, C1, D1) and K1 (A2, B2, C2, D2).

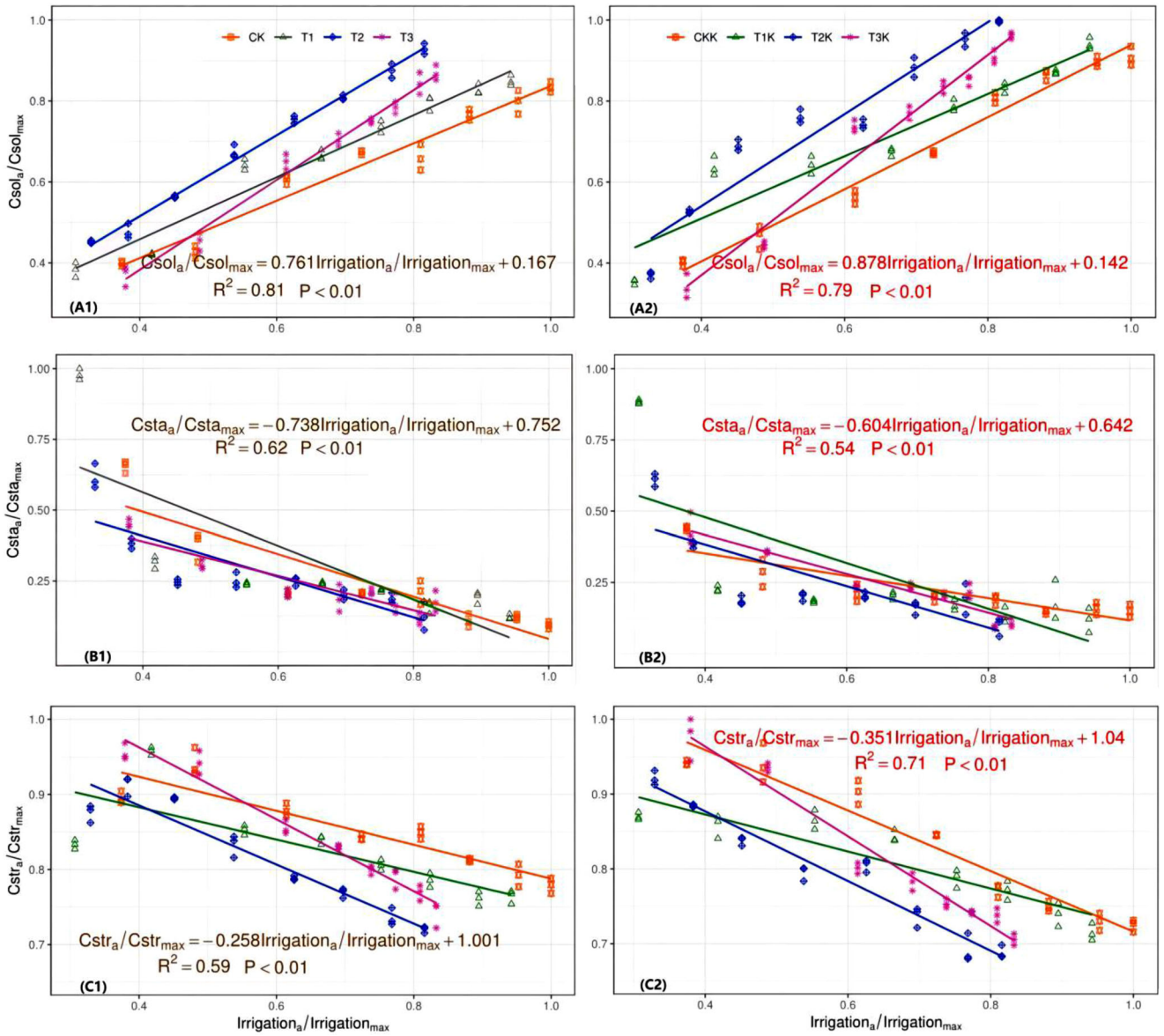

FIGURE 4 The relationship of relative carbon content of fruit soluble sugar (C*sol*) (A1, A2), starch (C*sta*) (B1, B2), other carbohydrates(C*str*) (C1, C2) and the relative irrigation amount under different potassium application regimes K0 (A1, B1, C1) and K1 (A2, B2, C2).

correlation could be observed between the variables of K1. The positive correlation with Fc, DW, and C*sol* was strong, whereas that with SP was weak.

The variable contribution rate of the grouping application of PCA are shown in Figure 6E. The contribution rate could be derived through the projection of the lines represented by multiple variables on PC1 and PC2. The longer the line is, the greater the projection, and the more significant the influence. The order of the contribution rate of PC1 was as follows: C*sol* > C*str* > DW > Gc > Fc > AI > SuSy > FW > AGP, where C*str* had a negative correlation with PC1. In addition, the angle between the two lines represents correlation. The angle of less than 90° indicated a positive correlation between two variables, and the angle of greater than 90° indicated a negative correlation. For example, the angle between C*str* and the first quadrant index was greater than 90°, thus displaying a negative correlation. On the contrary, the contribution to PC1 was the opposite. The order of the contribution rate of PC2 was as follows: FWC > Sc > SPS > Fc > Gc. FWC had the greatest contribution rate to PC2 and the most significant influence, but it was significantly negatively related to PC2.

The K-means clustering algorithm of PCA is shown in Figure 6F. The K-means algorithm divided all indicators into three disjoint clusters. The first cluster consisted of C*str*, AGPase, C*sta*, SuSy, SPS, and Sc, which were negatively correlated with PC1 and had a high contribution. The second cluster comprised Fc, Gc, DW, AI, C*sol*, and FW, which were highly correlated with one another and positively related to PC1. The third cluster included SP and FWC, which were positively and negatively correlated with PC2 but had less effect.

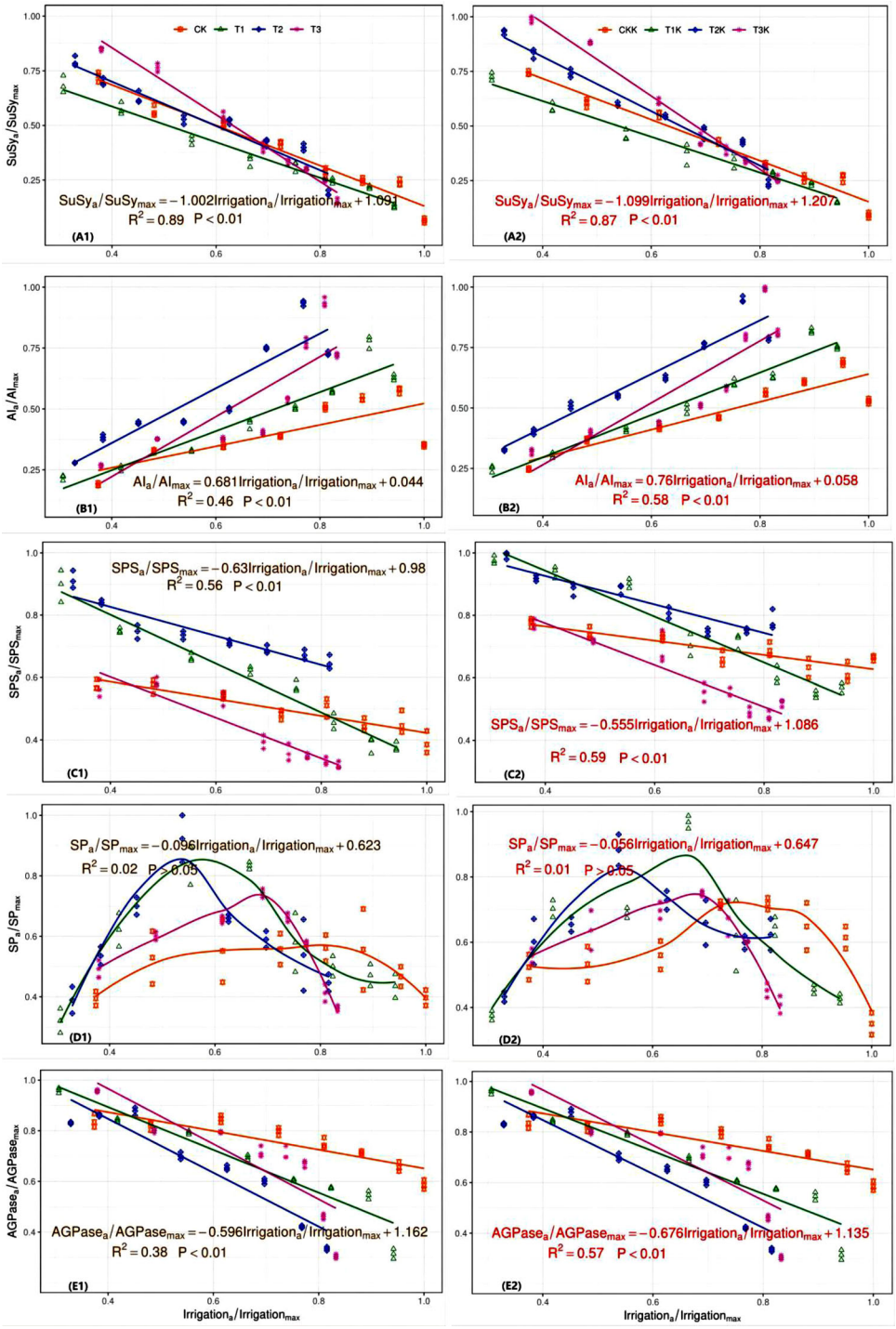

FIGURE 5 The relationship of relative sucrose and starch metabolism enzyme activities (Susy-A1, A2; AI-B1, B2; SPS-C1, C2; SP-D1, D2; AGPase-E1, E2), and relative irrigation amount under different potassium regimes K0 (A1, B1, C1, D1, E1) and K1 (A2, B2, C2, D2, E2).

4 | DISCUSSIONS

In this study, regardless of whether K was applied or not, a significant positive correlation was found between irrigation amount and fruit FW (Figure 3A). Under the same irrigation amount, K1 was significantly more than K0, indicating that K could enhance the promotion effect of irrigation on FW and significantly improve tomato yield (Çolpan et al., 2013). Kirda et al. (2004) attained a gain of 7%–10% additional yield and 10–27% higher marketable yield in partial root zone drying over conventional DI treatments. Patanè et al. (2011) also found that tomato (cv. Brigade) reflected 46.2% saving of water without losing any marketable yield when irrigation was given at 50% full crop evapotranspiration (ETc) level throughout the growing season in a typical semi-arid Mediterranean environment. However, Lahoz et al. (2016)

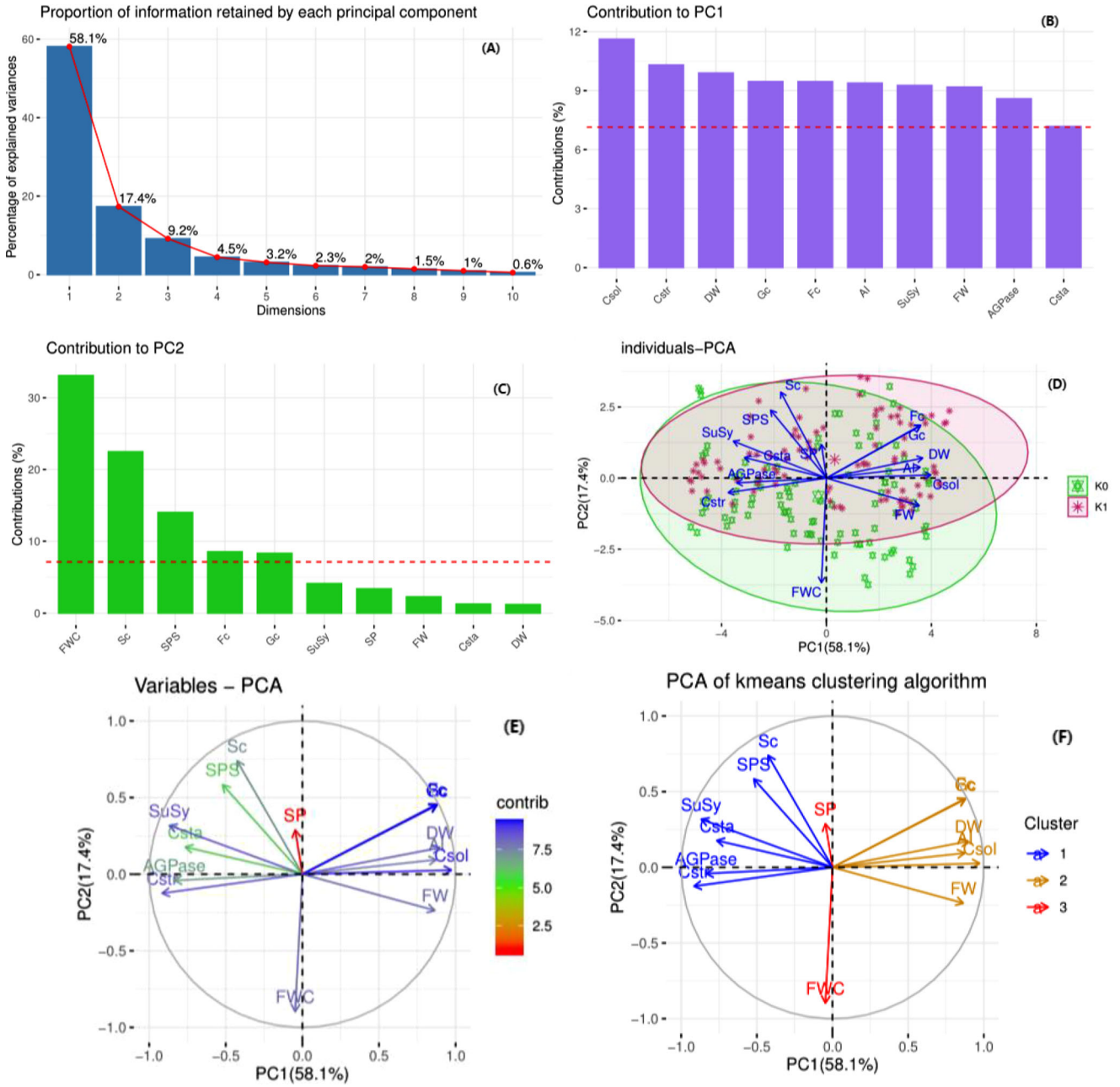

FIGURE 6 Correlation analysis diagram of fruit growth, carbon allocation, sugar concentration and related enzyme activities. (A) Proportion of information retained by each principal component (B). The order of variable contribution in PC1 (C). The rank of the variables contribution in PC2 (D). The PCA analysis of different potassium regimes (E). The variable contribution rate of the grouping application of PCA (F). The K-means clustering algorithm of PCA.

also registered considerable amount of water saving (28.2%) under DI (75% ETc), but the fruit yield was also reduced by 16.4% compared with that in the control (100% ETc). Therefore, careful implementation of DI is required as plants subjected beyond a certain level of water deficit may show adverse effect on marketable fruit yield (Kuscu et al., 2014; Nangare et al., 2016). The present study showed that the dry-matter increase rate of T2 treatment (fruit-swelling stage) was the fastest (Figure 3B), indicating that water deficit in different growth periods has a significant effect on dry-matter accumulation, consistent with previous studies. DI during fruit development period could enhance the accumulation of glucose and fructose in tomato fruit (Ripoll et al., 2014), and DI at fruit maturity period could obviously improve total soluble solids (J. Chen et al., 2013; Patanè & Cosentino, 2010; Yang et al., 2017), which presumably occurred as a consequence of reduced transport of water to the fruits concomitant to increased accumulation of photo-assimilates under water-deficient condition (Nangare et al., 2016; Plaut et al., 2004; Zegbe et al., 2006). In the present study, the FWC of T2 and T3 was low during the DI stage, and the irrigation amount showed a significantly positive linear correlation with FWC under K0 (Figure 3C), whereas it was not significant in

K1. This finding indicated that K supply had no significant effect on FWC, although K is the most abundant cation in plant tissues and it plays a major role in various physiological and biochemical processes, including photosynthesis.

Under K0 and K1, the C*sol* in water-deficit treatments were higher than that in CK. Conversely, the C*str* was lower than that in CK, indicating that water stress caused the change in the carbon allocation in the fruit. Thus, more carbon accumulated to the C*sol* side. Majority of reports are in support of its positive effect on tomato fruit quality attributes, especially soluble solid contents, which presumably occurred as a consequence of reduced transport of water to the fruits concomitant to increased accumulation of photo assimilates under water-deficient condition (Garcia & Barrett, 2006; Helyes et al., 2012; Kuscu et al., 2014). K is an activator for many enzymes necessary for photosynthesis and respiration, as well as enzymes needed to form starch and protein (Jackson & Volk, 1997). When the K content is high in the soil or plants, the largest plant growth and the highest starch content could be observed. Therefore, the C*sta* levels were higher than those in K0 (Figure 4C). K also has a great influence on sugar content (Coetzee et al., 2019). In the present study, the C*sol* in K1 was greater than that in K0. K is beneficial to sugar accumulation, but K efficacy requires appropriate water level to play a role; too much water supply leads to K dilution, which affects its effectiveness, such as CKK.

A close relationship exists among water, K status, and fruit sugar metabolism, which affects the enzyme activity in plant. Therefore, studying the fruit sugar through the activity of sugar metabolizing enzymes and then analyzing the effects of water and K supply are of great importance (Almeselmani et al., 2009; Fontes et al., 2000; Lobit et al., 2006; Ruan et al., 2010). In the present study, the key enzymes affecting sugar metabolism in fruits are shown in Figure 1, including INV, SS, SPS, SP, and AGPase. The relationship between irrigation and enzyme activity was explored, and the results showed that SuSy gradually decreased with the increase in irrigation amount. Regardless of whether K was applied or not, the SuSy in T1 was lower than that in other treatments, and this finding may be related to the water stress during the flowering and fruit-bearing stage, which affected the normal growth and development, resulting in relatively slow physiological metabolism. For instance, DW, FW, and RGR were lower than those in other treatments at the early stage (Figures 3 and 5). Sensitivity to soil moisture deficit could vary with crop phenological stages; hence, the imposition of DI during noncritical stages may be more beneficial with respect to the enhancement of WUE (Nangare et al., 2016). Moreover, the flowering and fruit setting stages are reportedly most sensitive to water deficit in tomato (Kuscu et al., 2014). The AI of water-deficit treatments (T1, T2, and T3) was significantly higher than that of CK. Although AI had a significant positive linear correlation with irrigation amount, it did not increase indefinitely with the increase in irrigation. The AI in T2 was the greatest under K0, indicating that moderate water stress could enhance the AI activity, as reported in previous studies (Roitsch, 1999; Loka et al., 2000). K1 also showed a similar trend. The SPS activity was the largest at the early stage, with a significant negative linear correlation with irrigation. The SPS in T3 was the lowest, indicating that the water deficit during the maturation stage reduced the sucrose synthesis, accelerated the decomposition of sucrose, increased the sugar gradient between the fruits and leaves, and facilitated the transfer of photolytic sucrose to the fruit (Roitsch & González, 2004). Meanwhile, it could promote the acceleration of starch hydrolysis and further increase the soluble sugar content (Figure 4). In addition, fructose is 1.8 times sweeter than sucrose, and sucrose hydrolyzes into fructose and glucose, which is more conducive to the increase in the overall sweetness of tomato (Carli et al., 2011). The SP activity under water-deficit treatments were higher than that in CK. AGPase was also remarkably negatively correlated with irrigation. When the irrigation amount reached the maximum, the AGPase of CK was maintained at a high level, significantly higher than that under water-deficit treatments. SP and AGPase are the main enzymes involved in starch metabolism in tomato fruits. DI increases SP activity and reduces AGPase activity, resulting in the hindrance of starch synthesis direction and the enhancement of decomposition direction, which is conducive to the hydrolysis of starch, consistent with previous research results (Du, 2020; Wang et al., 2001).

The activities of AI, SuSy, and SPS were enhanced with the increase in K rate, promoting the synthesis and transportation of photo-assimilates, which is beneficial to the sucrose metabolism in ripening fruits (Cui et al., 2011). On the contrary, K inhibited AGPase, resulting in a reduction in starch accumulation in the fruit (Figure 5). Previous studies have shown that K inhibited the activity of AI in leaves (Büssis et al., 1997) and promoted the activity of SuSy, thus ensuring the Sc gradient at both ends of the source–sink, promoting sucrose transport in phloem, and facilitating the accumulation of sugar in fruits (Jákli et al., 2018). Meanwhile, the present study showed that water deficiency could improve SP activity and reduce AGPase activity, resulting in blocked starch synthesis direction and enhanced decomposition direction, which is conducive to starch hydrolysis, similar to the results of Du's study (Du, 2020).

Although multifactorial observation methods could obtain a large amount of data information, it could lead to data collection, and the analysis work becomes cumbersome. Therefore, to ensure the overall and objective study of tomato fruit quality, simplifying the analysis of the quality evaluation indicators of tomato fruit is necessary (Dong et al., 2011). In the present study, PCA was used to study the relationship among growth indicators, fruit quality indicators, and carbon content in tomato fruit to reveal the main factors that determine the quality index. The results showed that the cumulative contribution rate of the first two principal components was 75.5%, and the key factors that determine the first principal component were C*sol* and C*str*. All indicators were divided into three disjoint clusters by K-means algorithm. According to the load size, the first cluster was mainly affected by Sc and C*sta*, and the second cluster was mainly affected by DW and Fc in K0. The first cluster was mainly affected by SuSy and AGPase, and the second cluster was mainly affected by AI and C*sol* in K1. This finding indicated that K could regulate the activities of enzymes related to sucrose metabolism and starch metabolism and promote the accumulation of sugar. SuSy and AI are the key enzymes in fruit carbon metabolism, both of which are key enzymes in sucrose metabolism. Given that SuSy undergoes synthesis and decomposition during fruit

development, it is closely related to the composition of sugar (Nguyen-Quoc & Foyer, 2001). AI, as the most active sucrase, regulates the accumulation of sucrose and hexose in fruits (Roitsch & González, 2004), maintains the Sc gradient between source and sink and ensures the continuous flow of sucrose from leaves to fruits (Fisher & Wang, 1995).

5 | CONCLUSIONS

The factors related to the improvement of fruit flavor and quality by deficient irrigation and K application were explored. Water stress changed the distribution of photosynthetic carbon between starch and soluble sugar. K application further changed the balance between soluble sugars and other compounds; it significantly increased the carbon content of soluble sugars and decreased that of other compounds. AI and SuSy are key enzymes affecting carbon metabolism under water-deficient conditions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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