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The Impact of Fulvic Acid on the Growth Physiology, Yield, and Quality of Tomatoes Under Drought Conditions

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Abstract

Increased global drought severity threatens crop yield and quality. Fulvic acid (FA), a humic acid compound, enhances crop stress tolerance. This study investigated FA application on drought-stressed tomato 'Provence' during the seedling and fruiting stages. Seedling-stage drought severely inhibited growth, physiology, biochemistry, and photosynthesis, reducing seedling quality. Subsequent fruiting-stage drought further significantly decreased photosynthetic efficiency and assimilate synthesis, drastically lowering fruit yield and quality. FA application mitigated drought damage, with 400 mg·L^{-1} being optimal. At this concentration, under seedling drought, Seedling strength index (Si), Photosynthetic efficiency (Pn), and Instantaneous water use efficiency (IWUE) increased significantly by 76.54%, 67.46%, and 36.97%, respectively, with no adverse morphological effects by flowering. Post-drought FA spraying later significantly enhanced leaf photosynthetic enzyme activity and WUE (by 89.16%, 98.48%, 42.20%, and 40%), boosting Pn, promoting assimilate accumulation and transport to fruits. This resulted in significantly improved fruit yield and comprehensive quality. In conclusion, spraying 400 mg·L^{-1} FA significantly enhances tomato drought tolerance and water use efficiency in arid/semi-arid regions, offering an effective strategy for saving irrigation water and improving crop productivity in water-scarce areas.

Keywords: stress mitigation; fulvic acid; tomato; photosynthetic efficiency; fruit productivity

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1. Introduction

Rapid changes in the global climate and decreasing rainfall have led to increasing drought severity and frequency around the world. According to statistics, about 43% of the world's arable land is threatened by drought and semi-drought [1]. Previous studies have shown that drought stress causes more economic losses to plants than other environmental stresses [2].

Tomato (*Solanum lycopersicum* L.) belongs to the tomato family of the Solanaceae annual or perennial herb, occupies an important position in the world vegetable consumption, and has become a model plant for the study of crop genetics and stress resistance of Solanaceae [3,4]. Dryland tomatoes refer to a specialized cultivation method of tomatoes involving open-field planting that relies solely on natural rainfall without any irrigation infrastructure. In contrast to conventionally cultivated tomatoes, dryland tomatoes are characterized by superior palatability, a sandy yet fine pulp texture, enhanced quality

attributes, and elevated lycopene content [5]. At present, the area of tomato cultivation in dry land is increasing year by year in the world, and has gained more and more attention in arid and semi-arid areas, and is gradually becoming an important agricultural planting industry [6]. In China, dry land tomato planting has gradually expanded from a small number of experimental plantings to major arid and semi-arid areas, with a planting area of up to several hundred thousand hectares, providing strong support for the sustainable development of Chinese agriculture [3].

Tomatoes are highly sensitive to water availability during the seedling stage, particularly in early growth. Drought stress at this critical phase severely impacts seedling development, leading to stunted plant growth, reduced leaf chlorophyll content, and decreased photosynthetic rate. This results in overall growth inhibition, developmental retardation, premature aging, and specific symptoms including plant dwarfism, reduced leaf number and area, diminished flowering, impaired fruit set, and increased fruit deformity in later stages [7,8]. Soil water is also one of the key factors in the formation of fruit quality and is closely related to the formation of yield. In the production process, if the water supply is insufficient, the yield and fruit quality will be adversely affected, but moderate drought will improve the fruit quality and increase the fruit flavor [9]. Previous research indicates that fruit subjected to moderate drought stress exhibits increased concentrations of total sugars, ascorbic acid, organic acids, and soluble solids [10,11]. Therefore, improving tomato drought tolerance is one of the effective measures to maintain tomato production, increase yield, and improve quality under drought conditions.

FA is not only a class of soluble organic compounds widely present in nature but also an important component of soil organic matter [12,13]. These organic compounds are rich in various active functional groups, such as hydroxyl, carboxyl, carbonyl, phenolic hydroxyl, and quinone groups, which all have the ability to chelate and exchange anions or ions. Existing research has found that the mechanism by which FA promotes plant growth mainly involves increasing cell membrane permeability and intracellular signal transduction functions, thereby stimulating root growth, enhancing chlorophyll content and photosynthetic efficiency, and activating carbon and nitrogen metabolism [14,15]. Previous studies have shown that spraying an appropriate concentration of FA can significantly increase the chlorophyll content, photosynthetic-related enzyme activity, and gene expression of crop seedlings under drought stress, and increase the net photosynthetic rate [16–18]. Yu et al. [19] showed that FA could reduce the damage caused by drought on the maximum photochemical efficiency and actual photochemical efficiency of leaves, the quantum yield of electron transfer, and the activity of PSII, maintain the ultrastructure of chloroplasts, and thus reduce the damage caused by drought stress.

Thus, this experiment aims to explore how different FA concentrations alleviate drought-induced damage, improve seedling quality, and enhance drought tolerance to promote subsequent plant growth and fruit quality under drought stress. The purpose of this study is to provide theoretical and technical support for applying FA in drought-resistant tomato seedling cultivation, water-saving practices, yield and fruit quality enhancement in arid regions.

2. Materials and Methods

2.1. Test Material

The experiment was conducted in the solar greenhouse of the Horticulture Station of Shanxi Agricultural University from October 2023 to May 2024 (Temperature: 10~40 °C, Illumination: 15,000~50,000 Lx, Humidity: 40~60%). The test variety is the 'Provence' tomato, purchased from Guangdong Jinzuo Agricultural Technology Co., Ltd. (Guangzhou, China); the cultivation medium is turf, vermiculite, and perlite (pH: 5.5~7.0,

humic acid content ≥5.0%, organic matter content ≥25.0%), purchased from Shouguang Ward Agricultural Technology Co., Ltd. (Weifang, China); FA (Purity: 85%, molecular weight: 308.24) is a brown powder, purchased from Shanghai Yi En Chemical Technology Co., Ltd. (Shanghai, China), dissolved in distilled water.

2.2. Experimental Design

2.2.1. Seedling Treatment

The experiment adopted a completely randomized design with eight treatments: CK, F0, F100, F200, F400, F800, F1600 and F3200 (Table 1). Seedlings were raised in 15-cell trays and irrigated with Hoagland nutrient solution (pH 5.8~6.2). Treatments were applied when seedlings developed three leaves and one terminal bud. The seedlings were flooded 48 h before treatment, and then natural drought was applied. The water supplement was calculated by the weighing method at 8:00 AM every day to control the soil water content of the drought treatment to 30~35% of the field water capacity (Severe drought). FA use involved foliar spraying, front and back spraying until the leaf dripping, and continuous spraying for 3 days; after that, samples were taken every 5 days for 4 times (0 d, 5 d, 10 d, 15 d). The third fully expanded leaves were collected from five randomly selected plants per treatment, with three biological replicates. The fresh leaves collected were immediately frozen with liquid nitrogen and stored at −80 °C for the determination of other growth and physiological indicators, and, finally, the optimal concentration was selected.

Table 1. Test FA settings of different concentrations.

Number	Treatments
CK	Normal irrigation
F0	Drought + 0 mg·L^{-1} FA
F100	Drought + 100 mg·L^{-1} FA
F200	Drought + 200 mg·L^{-1} FA
F400	Drought + 400 mg·L^{-1} FA
F800	Drought + 800 mg·L^{-1} FA
F1600	Drought + 1600 mg·L^{-1} FA
F3200	Drought + 3200 mg·L^{-1} FA

2.2.2. Result Period Processing

The tomato seedlings of the two optimal concentrations (F400 and F800) and the control group (CK and F0) were planted on the greenhouse land and were rewatered once during the planting and the early bearing period, respectively, and dried during the rest of the time. The experiment was planted in single rows with 30 plants per row, a plant spacing of 35 cm, a row spacing of 75 cm, and five fruit clusters retained per plant. Disease and pest prevention measures were taken at the early stage of fruit setting, and foliar fertilizer was applied appropriately. In April 2024, fruits with uniform color, similar size, and similar maturity were randomly selected for fruit quality determination.

2.3. Parameter Measurement

2.3.1. Observation and Determination of Tomato Seedling Growth and Root Morphology

The plant height and stem diameter were measured by a straight ruler and vernier caliper, respectively; At 15 d, root systems were scanned using a root scanner (EPSON EU-235), and root morphological parameters were analyzed with the WinRhizo root analysis system; *Si*: [20].

$$Si = D \times \left(\frac{d}{h} + \frac{r}{a} \right) \quad (1)$$

where D is the whole-plant dry weight, d is the stem diameter, h is the plant height, r is the root dry weight, and a is the shoot dry weight.

2.3.2. Determination of Physiological Indexes of Tomato Seedlings

The content of hydrogen peroxide (H_2O_2) was determined using the potassium iodide (KI) colorimetric method, while superoxide anion (O_2^-) levels were quantified via the hydroxylamine oxidation method. Histochemical detection of H_2O_2 and O_2^- was performed separately using 3,3′-diaminobenzidine (DAB) and nitroblue tetrazolium chloride (NBT) staining, respectively [21].

2.3.3. Determination of Photosynthetic Indices in Tomato Seedlings

Chlorophyll content was determined by alcohol extraction; Pn, Transpiration rate (Tr), Intercellular CO_2 concentration (Ci), and Stomatal conductance (Gs) were measured by an LI-6800 portable photosynthesis system at 9:00 AM on sunny days; IWUE: IWUE = Pn/Tr × 1000; The Photochemical potential activity (FV/FO), Maximum photochemical efficiency (FV/FM), Actual photochemical efficiency (ΦPSII), and Non-photochemical quenching coefficient (QN) of PSII were determined by Imaging-PAM chlorophyll fluorescence IMAGING system [21].

2.3.4. Determination of the Growth Index of Tomato at the Flowering Stage

The calculating formula of the plant height growth rate is as follows:

$$RGR = \frac{W1 - W0}{T1 - T0} \tag{2}$$

The stem diameter growth rate calculation formula is as follows:

$$RGR = \frac{P1 - P0}{T1 - T0} \tag{3}$$

The leaf area growth rate is as follows:

$$LAG = \frac{S1 - S0}{T1 - T0} \tag{4}$$

where $W0$, $P0$ and $S0$ are plant height, stem diameter and leaf area at planting time; $W1$, $P1$ and $S1$ are plant height and stem diameter at the fruiting stage, and $T1 - T0$ is the time interval between planting time and fruiting stage.

Leaf number was recorded from ten randomly selected plants per treatment, with three biological replicates [22].

The specific leaf weight (leaf thickness) is as follows:

$$SLW = \frac{F}{L} \tag{5}$$

where F is the fresh leaf weight, and L is the leaf area.

The water use efficiency is as follows:

$$WUE = \frac{T1}{T2} \tag{6}$$

where $T1$ is the total yield, and $T2$ is the total irrigation amount.

2.3.5. Determination of Photosynthetic Enzymes in Tomato Leaves

The activities of ribulose-1,5-bisphosphate carboxylase (Rubisco), plant transketolase (TK), and plant chloroplast NADPH-glyceraldehyde-3-phosphate dehydrogenase (NADPH-GAPDH) were all determined according to the instructions of the Rubisco enzyme-linked immunosorbent assay (ELISA) kit (catalog number: KQ114011), TK ELISA kit (catalog number: KQ136530), and NADPH-GAPDH ELISA kit (catalog number: KQ142243) produced by Shanghai Kechuang Biotechnology Co., Ltd. (Shanghai, China).

2.3.6. Determination of Fruit Character, Yield, and Quality of Tomato

Fruit diameter was measured, and fruit type index was calculated; the number of fruit per plant was recorded, the weight of fruit per ear was measured, and the yield was converted.

Lycopene was determined by petroleum ether extraction: weigh 3 g fresh sample, grind into juice, wash four times with 20 mL anhydrous ethanol and six times with 30 mL methanol, then discard the filter residue; react filter residue with 98% petroleum ether and 2% dichloromethane, obtain extract, make up to 50 mL, measure absorbance at 502 nm.

Molybdenum blue colorimetry was used for vitamin C (Vc): grind 2 g fresh sample with 2 mL oxalic acid-EDTA into slurry, centrifuge at 3000 r, extract 1.5 mL supernatant, add 0.5 mL EDTA, 0.2 mL metaphosphoric acid-acetic acid, 0.4 mL sulfuric acid, 0.8 mL ammonium molybdate, react at 30 °C for 15 min, dilute to 10 mL and measure absorbance at 760 nm.

The soluble protein was obtained by the Coomassie brilliant Blue G-250 method: grind 2 g fresh sample, add water to make up to 6 mL, centrifuge at 6500 r for 15 min at low temperature. Take 1 mL supernatant, add 5 mL G-250, shake well, stand for 2~5 min, and measure absorbance at 595 nm.

The anthrone sulfuric acid method was used for soluble sugar: 0.5 g fresh sample was incubated with 5 mL 80% ethanol at 80 °C for 30 min, cooled, centrifuged at 3500 r for 10 min, and diluted. Take 2 mL of the diluted solution, add 5 mL anthrone-sulfuric acid reagent, incubate at 100 °C for 10 min, cool, and measure absorbance at 620 nm.

Titrable acids are titrated by acid-base titration: Weigh 2 g fresh sample, incubate in a water bath at 80 °C for 30 min, centrifuge at 4000 r for 5 min, and make up to 40 mL. Add appropriate phenolphthalein, titrate with Sodium hydroxide standard solution to pink, and calculate the dosage.

Soluble solids were measured with a hand-held refractometer, the relative content of flavonoids was extracted by Hcl and methanol, and fruit hardness was measured by a durometer.

2.4. Statistical Analysis

Using Excel 2016 for data wrangling. Analysis of variance (ANOVA) was performed using SPSS 20.0 (IBM Corp., Armonk, NY, USA). Normality and homogeneity of variances were assessed using Shapiro–Wilk and Levene tests, respectively. All treatment means (n = 3) were compared for any significant differences using Duncan's multiple range tests at $p < 0.05$. Graphical presentation was carried out in Graph Pad Prism 8.0.2 software for Windows (La Jolla, CA, USA).

3. Results

3.1. Analysis of Growth and Physiological Response of Tomato Seedlings Under Drought Stress with Different Concentrations of FA

3.1.1. Effects of Tomato Seedling Growth and Root Morphology

The normal growth and development of plants under drought stress are seriously affected. As shown in Figure 1, under drought stress, tomato seedlings were thin and their leaves curled and yellowed, showing a wilting state. With the prolonged duration of drought, the growth in plant height and stem diameter of tomato seedlings gradually decelerated and tended to plateau or even decline at 10~15 d. F0 treatment was the most significant, and the plant height and stem diameter were decreased by 45% and 42%, respectively, compared with CK treatment ($p < 0.05$). Spraying FA alleviated the inhibition of growth and showed a trend of first increasing and then decreasing with the increase in concentration, reaching a peak value under the F400 treatment. Compared with CK, plant height and stem diameter decreased by 20% and 10%, respectively, but increased by 45% and 36%, respectively, compared with F0. The seedling strength index of tomato seedlings under drought stress decreased significantly, and F0 decreased significantly by 71.23% compared with CK. The seedling strength index of tomato seedlings treated with exogenous FA increased significantly, and the seedling strength index of tomato seedlings treated with F400 was higher than that treated with CK and increased by 8.76% compared with CK ($p < 0.05$).

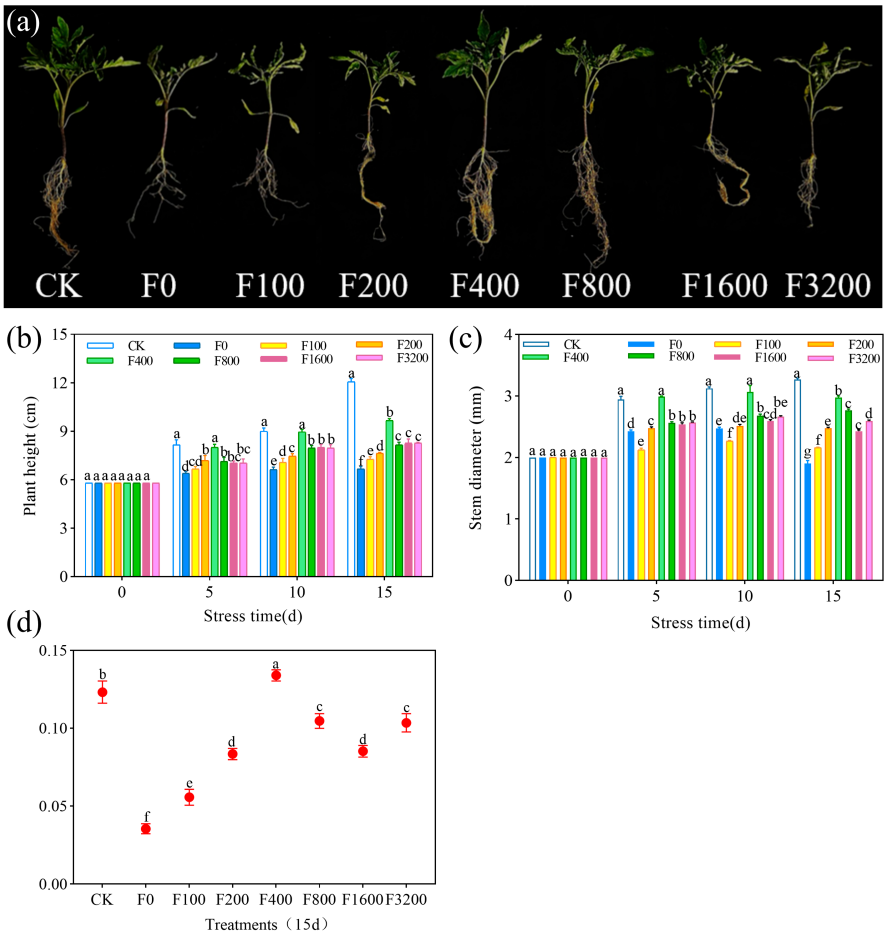


Figure 1. FA effects on 'Provence' tomato seedling morphology under drought stress. (**a**) Phenotype of tomato seedlings, (**b**) plant height, (**c**) stem diameter, (**d**) strong seedling index. Different lowercase letters (a–g) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

As can be seen from Figure 2, drought stress significantly reduced the mean root diameter, root surface area, total root length, and root branch points of tomato seedlings. Compared with the control, the mean root diameter, root surface area, total root length, and root branch points under F0 treatment were decreased by 32.25%, 68.09%, 64.04%, and 60.17%, respectively ($p < 0.05$). Compared with F0, the average root diameter, root surface area, total root length, and root branching points of F400 and F800 significantly increased by 35%, 153%, 151%, 143%, and 33%, 127%, 121% and 80%, respectively ($p < 0.05$). However, the mean root diameter, total root length, and root branch points in F400 did not decrease significantly compared with CK. In conclusion, FA can alleviate the damage to tomato seedling morphology and root system caused by drought stress.

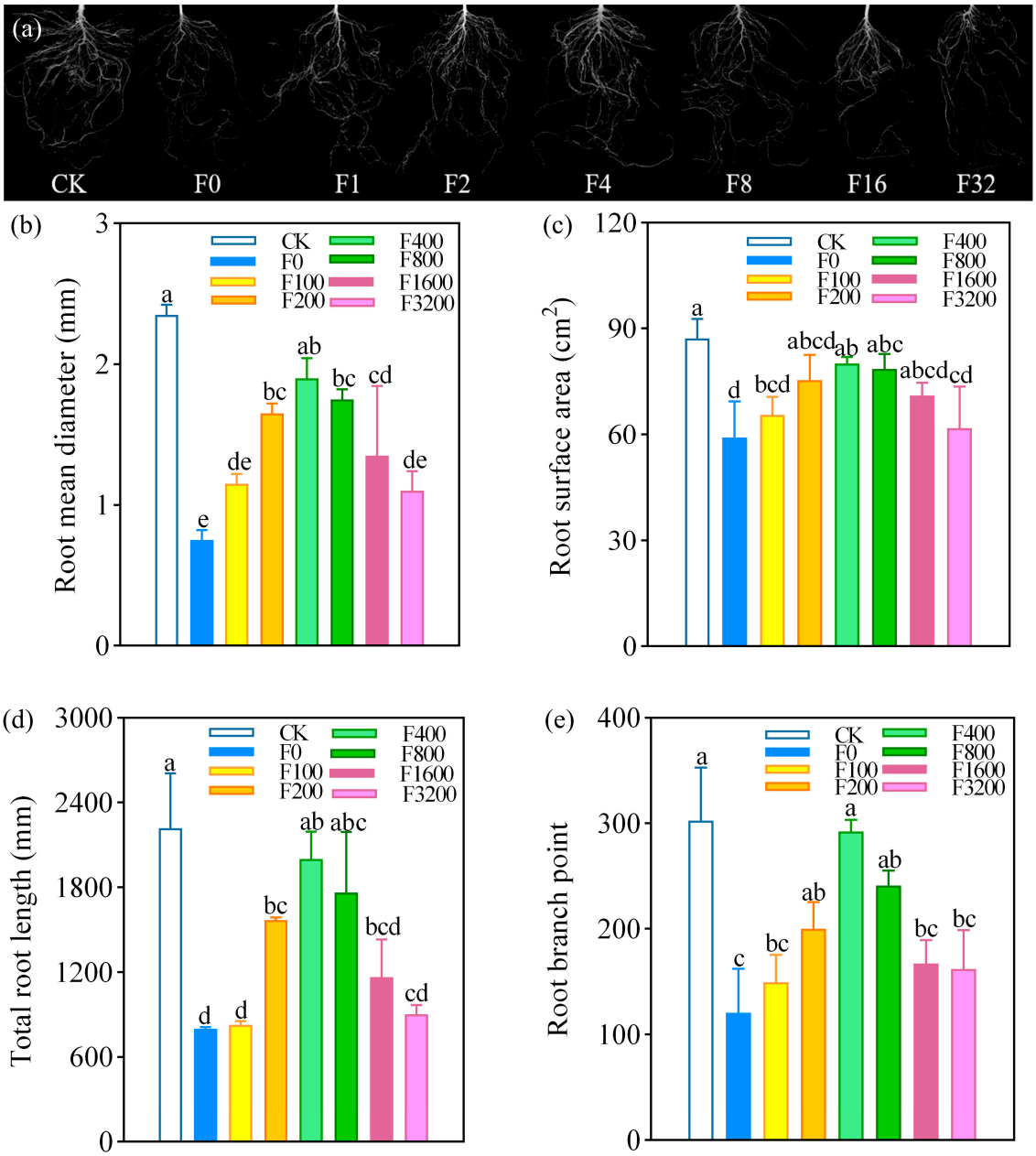
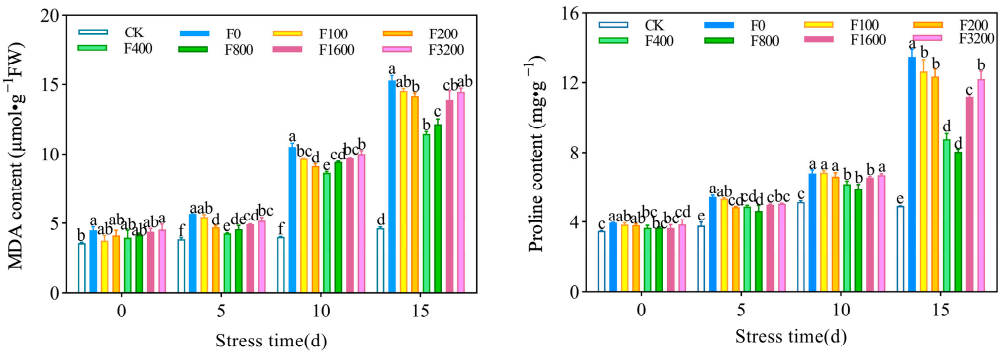


Figure 2. FA of tomato seedlings under drought stress; the influence of root morphology (15 d). (**a**) Root scanning image, (**b**) average root diameter, (**c**) root surface area, (**d**) total root length, (**e**) root branching points. Different lowercase letters (a–e) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.1.2. Effects of Osmoregulatory Substances and MDA on Tomato Seedlings

The contents of MDA and proline can be used as one of the key indices of plant stress resistance, and their contents increase significantly under stress conditions. As shown in Figure 3, MDA and proline contents increased significantly under drought stress, and showed a trend of continuous increase with the extension of drought time. MDA and proline contents under the F0 treatment increased significantly at 5~15 d, reaching 15.29 μmol·g^{-1}FW and 13.48 mg·g^{-1} at 15 d. Compared with F0, MDA and proline contents decreased in different degrees during the whole drought stress period, and showed a trend of first decreasing and then increasing with the increase in concentration, and significantly decreased in the F400 and F800 treatments, respectively. At 5~15 d, the MDA content reached the minimum value with F400, which decreased by 24.38%, 17.73%, and 25.14% compared with the F0 treatment, respectively ($p < 0.05$). The proline reached the minimum value with F800, which decreased by 14.75%, 13.10%, and 40.27%, respectively, compared with the F0 treatment.



(**a**) (**b**)

Figure 3. Effect of FA on (**a**) MDA and (**b**) proline contents in tomato seedlings under drought stress. Different lowercase letters (a–f) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.1.3. Effect of Reactive Oxygen Species on Tomato Seedlings

Drought stress triggers excessive accumulation of reactive oxygen species in plants, inducing cellular oxidative damage that impairs growth and development, potentially culminating in plant mortality. As shown in Figure 4a,b, the contents of H_2O_2 and O_2^- increased significantly due to drought stress and showed a gradually increasing trend with the extension of time, reaching the maximum value at 15 d. Compared with the control group, the F0 treatment significantly increased the levels of H_2O_2 and O_2^- by 383.10% and 115.87%, respectively ($p < 0.05$). After spraying FA, all treatments inhibited the production of H_2O_2 and O_2^-, which significantly decreased by 20.25~45.57% and 10.88%~38.04% compared with F0 ($p < 0.05$). However, during the whole drought stress period, the H_2O_2 and O_2^- contents were the lowest in the F400 treatment, which decreased by 41.52% and 41.50% on average compared with F0. It can also be seen, from the hydrogen peroxide (DAB) and superoxide anion (NBT) staining diagrams (Figure 4c,d), that drought stress significantly increases the accumulation of reactive oxygen species, and reactive oxygen species gradually increase with the extension of time. For instance, as drought stress is prolonged, the stained area of the leaves increases, and the color becomes darker. In contrast, the stained area of the leaves treated with FA decreases, and the intensity of staining diminishes.

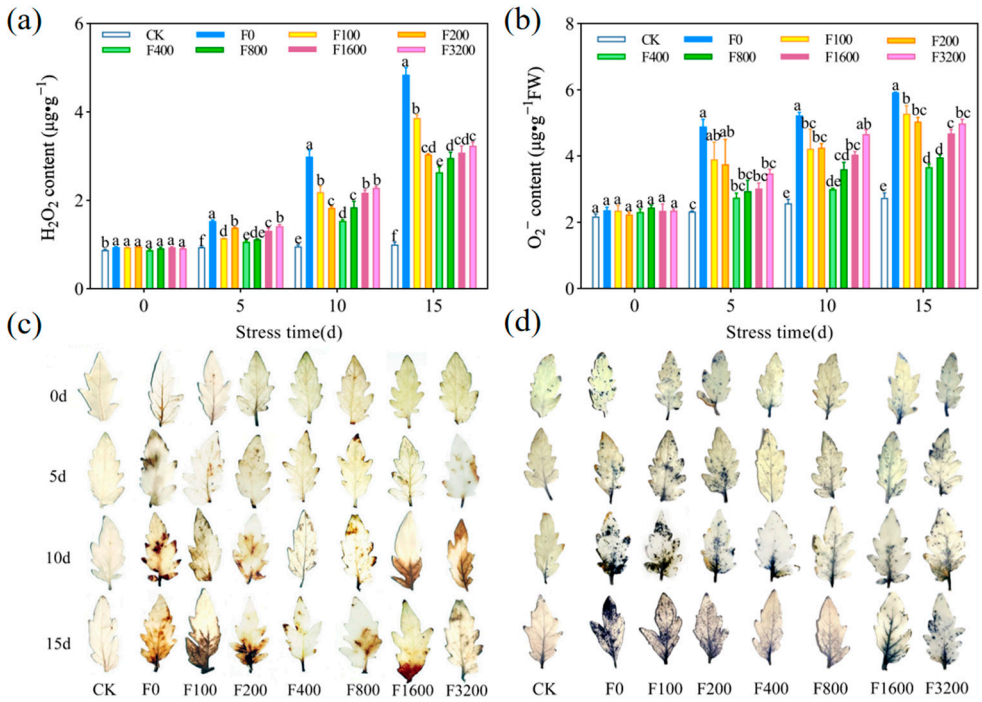


Figure 4. Effects of FA on the contents of H_2O_2 and O_2^- in tomato seedlings under drought stress. (**a**) H_2O_2 content, (**b**) O_2^-·content, (**c**) hydrogen peroxide staining in tomato leaves, (**d**) superoxide anion staining in tomato leaves. Different lowercase letters (a–f) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.2. Effects of Photosynthetic Characteristics on Tomato Seedlings

3.2.1. Effects on Chlorophyll

The chlorophyll content in tomato leaves decreased continuously with the extension of drought stress time. At 5~15 d, F0 decreased by 40.18%, 55.57%, and 63.44% compared with CK. After FA was applied, the chlorophyll content increased and showed a trend of first increasing and then decreasing with the increase in concentration. Compared with F0, the F400 treatment increased by 21.25% at 5 d, and the F400 and F800 treatments increased by 23.98%, 26.98%, 21.09%, and 25.42% at 10~15 d, respectively ($p < 0.05$).

3.2.2. Effects on Photosynthetic Parameters and IWUE

With the aggravation of drought time, the Pn, Tr, and Gs of tomato seedlings showed a gradual decline trend, and the most significant decline was at 15 d, in which F0 decreased 2.9 times, 2.4 times, and 2.5 times compared with CK ($p < 0.05$). At 5~15 d, FA treatment with different concentrations had a certain mitigation effect. With the increase in concentration, FA treatment first increased and then decreased, but the F400 and F800 treatments had the best effect, and Pn, Tr and Gs increased by 2 times, 1.1 times, 1.3 times and 2 times, and 1 time and 1.4 times, respectively, compared with F0 at 15 d. With the extension of drought stress time, Ci showed a trend of first increasing and then decreasing, and, at 5 days, compared with CK, each treatment significantly increased by 25.35%~33.79% ($p < 0.05$). However, at 10~15 d, the F400 and F800 treatments significantly decreased by 9.79%, 12.23%, 8.04%, and 13.74% compared with F0, and there was no significant difference compared with CK, while other FA treatments had no significant difference with F0 ($p < 0.05$).

IWUE is a key factor in determining plant productivity, and F0 decreased by 7.57% compared with CK at day 15 of drought stress. After spraying FA, only F100 decreased significantly and was lower than F0, and other treatments were significantly higher than

CK, among which F400 and F800 increased 36.97% and 39.85% compared with CK ($p < 0.05$) (Figure 5).

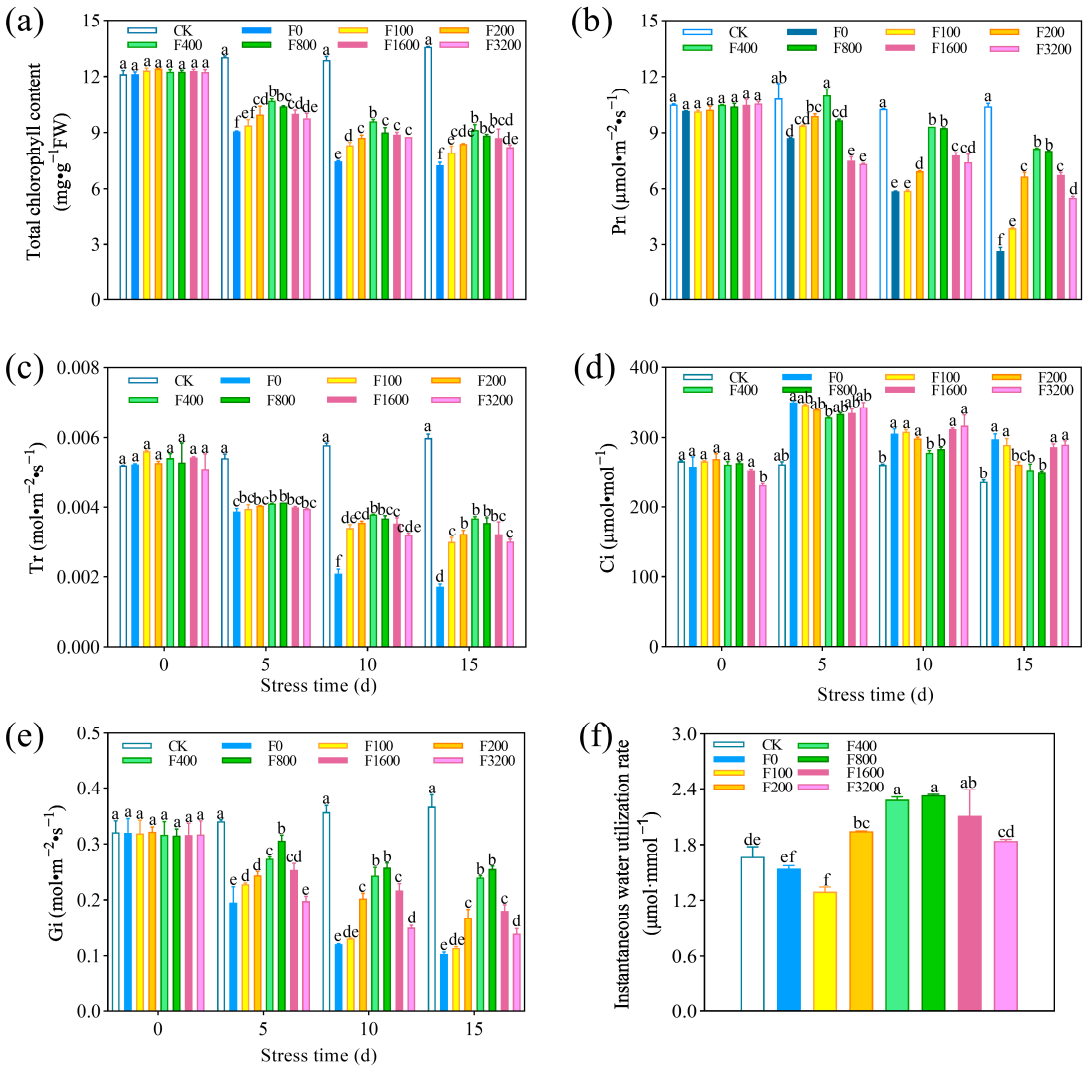


Figure 5. Effects of FA on chlorophyll, photosynthetic parameters, and water use efficiency (15 d) of tomato seedlings under drought stress. (**a**) Total chlorophyll content, (**b**) Photosynthetic rate, (**c**) Transpiration rate, (**d**) Intercellular CO_2 concentration, (**e**) Stomatal conductance, (**f**) IWUE. Different lowercase letters (a–f) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.2.3. Effect on Chlorophyll Fluorescence

Under drought stress, compared with CK, the FV/FO, FV/FM, ΦPSII, and QN of tomato seedling leaves decreased. On the fifth day, the FV/FO and FV/FM of each treatment had no significant change compared with F0, while ΦPSII and QN of the F400 treatment were increased by 20.96% and 14.42% compared with F0 ($p < 0.05$). At 10–15 d, the fluorescence parameters of spray FA treatment were significantly improved compared with F0 and showed a concentration dependence. The F400 treatment was the best, and, at 15 d, the fluorescence parameters of spray FA treatment were increased by 46.24%, 49.98%, 42.47%, and 39.94%, respectively, compared with F0 ($p < 0.05$). The F800 treatment was also significantly increased compared with F0. There was no significant difference between F400 and F800 (Figure 6).

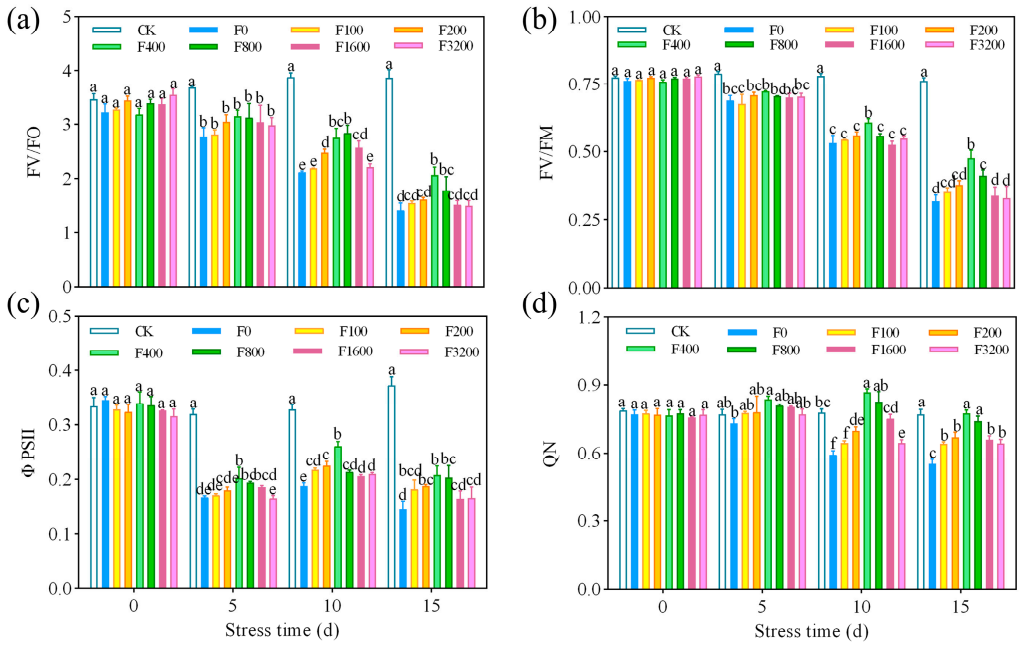


Figure 6. Effect of FA on chlorophyll fluorescence in tomato seedlings under drought stress. (**a**) FV/FO, (**b**) FV/FM, (**c**) actual photochemical efficiency of PSII, (**d**) QN. Different lowercase letters (a–f) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.2.4. Effect on the Activity of Photosynthetic Enzyme

Rubisco is the most important enzyme in plant photosynthesis, and its activity directly affects the assimilation rate of CO_2 and the net photosynthetic rate. TK plays a central role in the Calvin cycle, controlling photosynthetic carbon fixation and RuBP regeneration to a large extent. NADPH-GAPDH is a key enzyme in the Calvin cycle, and its activity directly affects the transport efficiency of photosynthetic carbon assimilation and plays an important role in the process of glucose metabolism and energy metabolism [23,24]. In this study, in the early stage of drought stress, the enzyme activities of Rubisco and TK in leaves of tomato seedlings began to decrease, but the decrease was small, while the enzyme activities of NADPH-GAPDH increased significantly ($p < 0.05$). With the extension of drought stress time, the enzyme activities of Rubisco, TK, and NADPH-GAPDH decreased significantly, and F0 decreased by 54.58%, 50.65%, and 29.06% compared with CK at the end of drought stress on 15 d. Under drought stress, although the enzyme activities of Rubisco, TK, and NADPH-GAPDH treated with FA decreased compared with CK, the NADPH-GAPDH enzyme activities of F800 were lower than those of F0 treatment, and the rest were higher than those of F0 treatment. Compared with F0, F400 and F800 improved by 89.16%, 98.48%, 142.20%, 13.47%, and 58.75%, respectively ($p < 0.05$).

3.3. Effects of FA on the Growth, Yield, and Quality of Tomato Seedlings Under Drought Conditions

3.3.1. Effect of Tomato Growth After Colonization

The seedling quality and leaf growth status of crops will have serious negative effects on the growth and development of plants after transplantation, and fruit growth, yield, and quality at the fruiting stage. As shown in Table 2, when tomato experienced drought at the seedling stage, the growth rates of plant height, stem diameter, and leaf area at the flowering stage were severely inhibited, and the number of leaves and specific leaf weight were also significantly reduced, which were 14.52%, 29.36%, 35.76%, 14.42%, and 43.97% lower than CK, respectively ($p < 0.05$). The growth rates of plant height, stem diameter

and leaf area, leaf number, and specific leaf weight of F400 and F800 at the flowering stage were significantly increased compared with the F0 treatment. Among them, the F400 treatment increased by 14.05%, 35.06%, 47.33%, 19.10%, and 68.21% compared with F0, and there was no significant change compared with CK ($p < 0.05$). The F800 treatment increased significantly compared with F0, but its growth rate was lower than that of the F400 treatment.

Table 2. Effects of drought at the seedling stage on plant growth rate and leaf characteristics at the flowering stage.

Treatments	Growth Rate of Plant Height/%	Stem Growth Rate/%	Leaf Area Growth Rate/%	Number of Leaves	Specific Leaf Weight (Thickness) ($mg \cdot cm^{-2}$)
CK	135.7 ± 5.4 a	10.9 ± 1.6 a	9.90 ± 0.003 a	20.8 ± 1.4 b	34.8 ± 1.5 a
F0	116.0 ± 3.7 b	7.7 ± 0.4 c	6.36 ± 0.002 b	17.8 ± 1.1 c	19.5 ± 2.6 b
F400	132.3 ± 1.9 a	10.4 ± 0.8 a	9.37 ± 0.006 a	21.2 ± 1.3 a	32.8 ± 1.2 a
F800	131.5 ± 1.9 a	9.0 ± 0.4 b	7.63 ± 0.014 ab	19.6 ± 1.2 c	23.3 ± 5.1 b

Values are means and standard deviations of three replicates. Different letters indicate significant differences between means according to Fisher's protected LSD test ($p < 0.05$).

3.3.2. Effects of Photosynthetic Enzymes and Water Availability in the Fruiting Period

Drought in the tomato seedling stage and fruiting stage significantly decreased the enzyme activities of Rubisco, TK, and NADPH-GAPDH in leaves at the fruiting stage. As shown in Table 3, the F0 treatment significantly decreased by 54.58%, 50.65%, and 29.06% compared with CK ($p < 0.05$). The enzyme activities of Rubisco, TK, and NADPH-GAPDH in leaves increased significantly after FA treatment under drought stress in two periods ($p < 0.05$). In addition, the enzyme activities of Rubisco, TK, and NADPH-GAPDH in tomato leaves under the F400 treatment returned to normal levels, which had no significant difference compared with CK, but increased by 89.16%, 98.48%, and 42.20% compared with F0 ($p < 0.05$). F800 also improved, but not as significantly as F400, and NADPH-GAPDH was lower than the F0 treatment. Drought in both periods also resulted in a significant decrease in plant water use efficiency at the bearing stage, in which F0 decreased significantly by 40% compared with CK, while the water use efficiency of FA treatment increased, and there was no difference compared with CK ($p < 0.05$). However, compared with F0, the increase was 40% and 34.3%, respectively (Figure 7).

Table 3. Effects of drought at the seedling stage on photosynthetic enzyme activity and water utilization at the fruiting stage.

Treatments	Rubisco ($U \cdot L^{-1}$)	TK ($U \cdot mL^{-1}$)	NADPH-GAPDH ($U \cdot mL^{-1}$)	WUE/%
CK	369.8 ± 4.4 a	633.3 ± 21.3 a	258.6 ± 9.9 a	35 ± 0.06 a
F0	167.7 ± 9.0 d	312.6 ± 14.0 c	183.5 ± 6.9 b	21 ± 0.05 b
F400	317.7 ± 5.5 b	620.4 ± 15.9 a	260.9 ± 8.8 a	35 ± 0.03 a
F800	190.6 ± 2.8 c	496.2 ± 35.6 b	141.2 ± 5.0 c	32 ± 0.01 a

Values are means and standard deviations of three replicates. Different letters indicate significant differences between means according to Fisher's protected LSD test ($p < 0.05$).

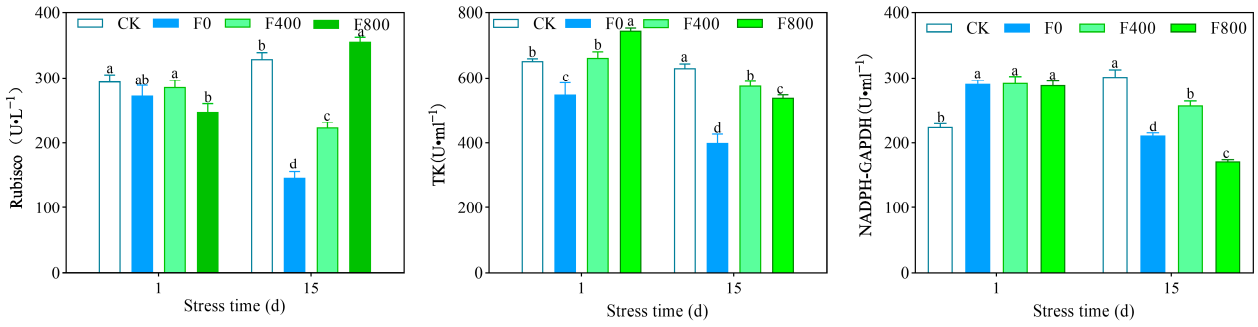


Figure 7. Effect of FA on photosynthase activity of tomato seedlings under drought stress. (**a**) Rubisco activity, (**b**) TK activity, (**c**) NADPH-GAPDH activity. Different lowercase letters (a–d) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

3.3.3. Effect on Yield and Quality of Tomato

The flower buds of fruits and vegetables are already formed at the seedling stage, so the quality of seedlings has a significant negative impact on crop productivity. As can be seen from Table 4, due to the poor quality of tomato seedlings caused by drought in the seedling stage and the drought in the fruiting stage, the fruit type index, single fruit weight, fruit setting rate, yield per plant, and yield per mu showed a significant decline trend. Among them, the F0 treatment significantly decreased by 8.43%, 30.06%, 22.73%, and 42.40% compared with CK, while F400 and F800 decreased but not significantly compared with CK ($p < 0.05$). Compared with F0, it significantly increased by 5.26%, 43.67%, 25.88%, 27.65%, and 27.69%, and 19.74%, 36.03%, 19.12%, 19.41%, and 24.97% ($p < 0.05$).

Table 4. Effects of FA on tomato fruit traits and yield under drought stress.

Treatments	Fruit Shape Index	Weight of Single Fruit	Percentage of Fruit Setting/%	Average Yield per Plant	t·ha^{-1}
CK	0.8 ± 0.06 ab	245.2 ± 31.0 a	88.0 ± 4.0 a	22.3 ± 3.9 a	124.5 ± 20.76 a
F0	0.7 ± 0.04 b	171.5 ± 25.3 b	68.0 ± 4.0 b	17.0 ± 2.8 b	67.6 ± 12.39 b
F400	0.8 ± 0.06 ab	246.4 ± 20.8 a	85.6 ± 4.6 a	21.7 ± 4.3 a	93.5 ± 13.59 a
F800	0.9 ± 0.03 a	233.3 ± 6.8 a	81.0 ± 6.1 a	20.3 ± 2.1 a	90.1 ± 4.14 a

Values are means and standard deviations of three replicates. Different letters indicate significant differences between means according to Fisher's protected LSD test ($p < 0.05$).

A moderate water deficit during the fruit-bearing period can improve fruit quality and increase the contents of lycopene, VC, sugar, and acid in fruit. However, with the increase in drought stress time, the fruit quality decreased significantly. As shown in Figure 8, the contents of lycopene, VC, soluble solids, soluble sugars, organic acids, and flavonoids under F0 treatment were significantly reduced by 24.85%, 17.81%, 11.32%, 8.16%, 19.81%, and 6.01% compared with CK ($p < 0.05$). Soluble protein, sugar–acid ratio, and fruit hardness were significantly increased by 40.10%, 14.92%, and 42.80% ($p < 0.05$). After spraying FA, the effects of persistent drought on the fruit were alleviated, the quality of the fruit was improved, and the hardness of the fruit was reduced. Under the F400 treatment, lycopene, soluble protein, soluble sugar, sugar–acid ratio, flavonoid content, and fruit hardness of tomato fruits were significantly increased compared with CK, increasing by 40.51%, 67.83%, 13.98%, 162.28%, 14.83%, and 17.05%, respectively. Although VC and soluble solids were decreased, the organic acids decreased significantly by 53.77% ($p < 0.05$). Although the quality of F800 is improved compared with CK, the difference is not significant compared with the F400 treatment. Therefore, the comprehensive performance of each treatment is F400 > F800 > CK > F0. The results showed that spraying 400 mg·L^{-1} FA under drought

stress could improve the quality of tomato fruit, increase the content of flavor substances in tomato fruit, and enhance the taste of tomato fruit.

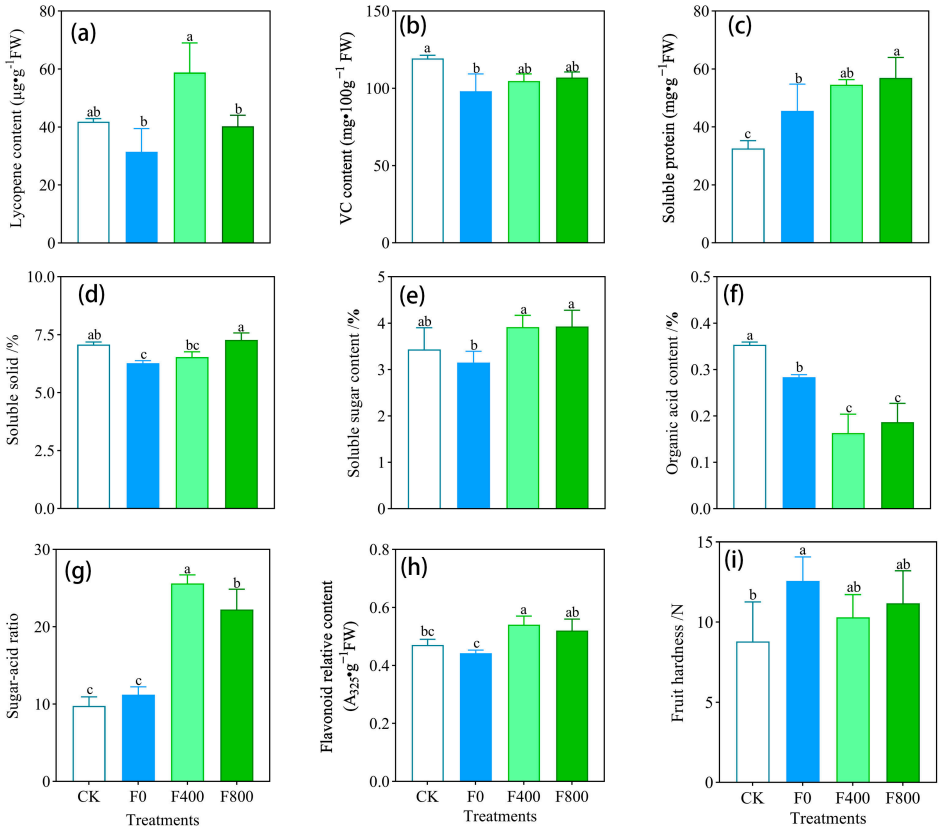


Figure 8. Effect of FA on tomato fruit quality under drought stress. (**a**) Lycopene content, (**b**) VC content, (**c**) soluble protein content, (**d**) soluble solids content, (**e**) soluble sugars content, (**f**) organic acid content, (**g**) sugar–acid ratio, (**h**) flavonoid content, (**i**) fruit firmness. Different lowercase letters (a–c) in the same column indicate significant differences between treatments for the same indicator ($p < 0.05$).

4. Discussion

Drought is one of the main factors that inhibit plant growth and development [25]. Studies have shown that the physiological metabolism of crops will be seriously disturbed when drought occurs at the seedling stage, causing a chain reaction that hinders growth and development [26,27]. In this study, drought stress exposure during the tomato seedling stage significantly inhibited shoot and foliar growth, resulting in weakened plants with reduced stem thickness and compromised nutritional status, so that the plant morphological development was poor at the flowering stage (Table 2) [5]. It was also found, in this study, that drought at the seedling stage did not enhance the drought tolerance of tomatoes at the fruiting stage, but deepened the damage caused by drought at the fruiting stage, which was contrary to the results of [28]. It is speculated that tomatoes in these two periods were both subjected to severe stress (soil water content of 30%~35%), or due to the limitations of the planting season and specific cultivation patterns in this experiment. Therefore, drought stress at the seedling stage did not enhance the drought tolerance of tomatoes during the fruiting stage, leading to a sharp decline in fruit traits (fruit shape index), yield, and quality. However, exogenous FA application alleviated the damage caused by drought in both periods, not only promoting plant growth and improving drought tolerance, but also increasing fruit yield and quality.

The reason may be that high levels of ROS and MDA accumulated in tomato seedlings under seedling-stage drought, which induced oxidative damage to the plants. Studies

have shown that FA may act as an antioxidant that clears excess ROS, or as a signaling molecule that induces the production of antioxidants, thereby reducing oxidative damage in plant cells [29]. In this study, the contents of H_2O_2, O_2^-, and MDA in tomato seedlings treated with exogenous FA were always lower than those treated with F0 during the whole drought cycle, thus reducing oxidative damage to tomato seedlings under drought stress and maintaining normal growth (Figure 4) [30].

The root system is an important organ that absorbs water and nutrients [31]. In this study, the mean root diameter, root surface area, total root length, and root branch points of tomato seedlings were significantly reduced under drought stress, which hindered root activity and absorption capacity, thus affecting the growth of tomato seedlings. FA is endowed with abundant reactive functional groups and small molecular components, which can penetrate plant protoplasts. These constituents induce cell division and proliferation in tissues, thereby promoting root development and enhancing plant vitality [32]. In this study, after spraying FA, the damage to roots under drought stress was significantly reduced, and normal growth was maintained, thus improving the ability of roots to absorb water and nutrients under drought stress and promoting above-ground growth, which was also similar to the results of Hareem et al. [26]. Proline, as the most important osmotic regulator of plants, increases significantly in stress and improves crop stress resistance. In this study, the proline content of sprayed FA decreased significantly compared with that of untreated, indicating that FA could alleviate the damage caused by drought stress and improve the drought tolerance of tomato seedlings, resulting in no need to accumulate proline to resist drought stress, which was also consistent with the results of Ibrahim et al. [33].

Photosynthesis is the basis of plant growth and development, and assimilates are closely related to fruit growth and nutrient accumulation [34–36]. In this study, the Pn of tomato leaves decreased significantly under drought stress, which resulted in the growth of plants and leaves being hindered, and the photosynthetic mechanism of leaves was irreversibly damaged. Fan et al. [37] showed that spraying FA on leaves could improve chloroplast structure and increase light energy utilization in leaves. Fang et al. [16] showed that FA could alleviate the damage to photosynthesis caused by drought stress and improve the water utilization rate of plants. In this study, after spraying FA, the chlorophyll content, Gs, and WUE of tomato leaves increased significantly, while Tr decreased slowly. These results indicated that FA could not only alleviate the damage of chloroplast structure and promote chlorophyll synthesis under drought stress, but also maintain water balance in vivo and promote stomatal opening, thus improving photosynthetic efficiency and promoting the synthesis of assimilates, thereby promoting plant growth and yield [38]. The chlorophyll fluorescence parameter reflects the absorption, transfer, and reconversion of light energy in plant leaves and is an important parameter of the photosynthetic ability of crops under stress [39]. In this study, the FV/FO, FV/FM, ΦPSII, and QN of tomato leaves decreased significantly under drought stress, while the FA of sprayed tomato leaves increased, and F400 was the most significant. The results showed that FA could effectively alleviate the light damage caused by drought stress, improve the photochemical activity of PSII reaction center, and then improve the primary light energy capture efficiency of ΦPSII reaction system, reduce the damage degree of photosynthetic organs, and thus improve the photosynthetic efficiency of leaves, which was similar to the results of Huang et al. [40]. Huang et al. [41] showed that the photosynthesis of wheat is regulated by a series of photosynthetic enzymes, and the highly active photosynthetic enzymes can significantly increase the Pn of wheat, promote the accumulation of assimilates, and ultimately increase wheat yield. In this study, the enzyme activities of Rubisco, TK, and NADPH-GAPDH in tomato leaves were significantly decreased under drought stress, and the reduction in their activities was inhibited by exogenous application of 400 $mg \cdot L^{-1}$ FA. Moreover, according

to the enzyme activities of Rubisco, TK, and NADPH-GAPDH in tomato leaves during drought in the bearing period, under drought stress in the fruiting period, the photosynthetic enzyme activity of tomato leaves treated with 400 mg·L^{-1} FA was at a normal level. Therefore, it is speculated that FA can maintain a higher activity of key photosynthetic enzymes in tomato leaves under drought stress and promote the carbon metabolism pathway, which is conducive to maintaining normal photosynthesis and improving the efficiency of photosynthesis [42].

The results of this study showed that spraying FA under drought conditions could improve the photosynthetic characteristics of tomato seedlings leaves, effectively alleviate the inhibition of drought stress on photosynthesis of tomato seedlings leaves, increase dry matter accumulation in leaves, promote leaf growth, maintain the normal growth and development of tomato plants, and improve the drought tolerance of tomato seedlings. As shown in S1, under drought stress, tomato seedling morphological indices, physiological parameters, and photosynthetic characteristics exhibited highly significant correlations. Seedling vigor, root system architecture, and photosynthetic performance showed strongly positive correlations with subsequent vegetative growth post-transplantation. Furthermore, seedling quality and photosynthetic parameters were significantly positively correlated with photosynthetic enzyme activities, fruit yield, and quality parameters during reproductive-stage drought (S1). As a result, leaves can always maintain strong photosynthetic capacity during late drought, thus promoting the accumulation of assimilates, and significantly improving fruit yield and quality under drought stress [18,43,44].

5. Conclusions

The exogenous application of 400 mg·L^{-1} FA effectively alleviates drought-induced damage and enhances plant drought tolerance. Following post-fruiting drought recurrence, FA reapplication maintains enhanced stress resilience, thereby improving yield and quality under drought conditions. This provides a scientific reference for drought-resistant tomato cultivation and irrigation water conservation in arid regions (Figure 9). Future studies should adopt multi-level and comprehensive approaches to reveal the regulatory mechanisms, so as to promote the wide application of FA in agricultural production under drought conditions and effectively address the severe challenges of global climate change to agricultural production.

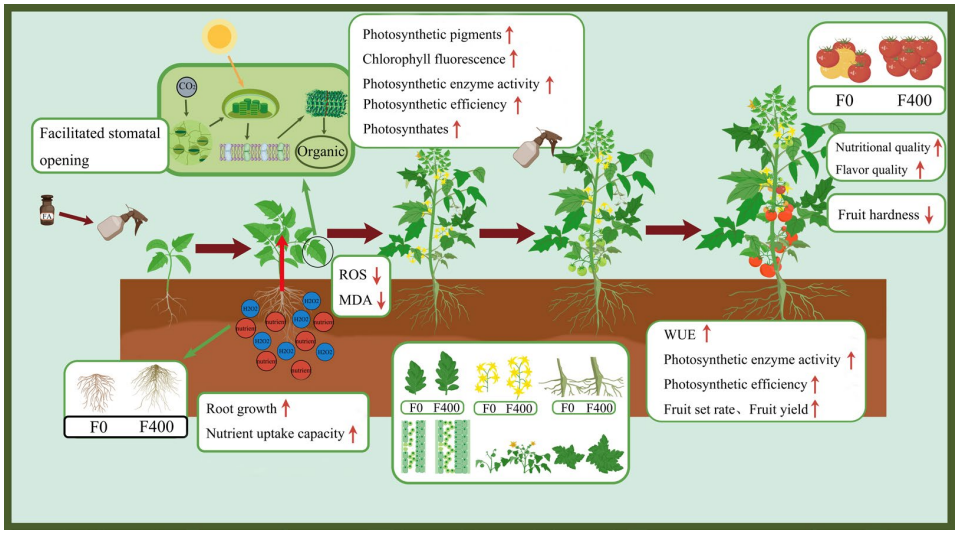


Figure 9. Schematic diagram of the physiological effects of FA in alleviating drought stress in tomatoes.

Author Contributions: H.S.: conceptualization, resources, supervision, writing—review & editing, funding acquisition. W.Z.: investigation, project administration, visualization, writing—original draft. Z.G.: formal analysis, data curation, writing—review & editing. T.S.: methodology, project administration, data curation. J.W.: formal analysis. C.G.: formal analysis. H.Z.: formal analysis. R.S.: formal analysis. All authors have read and agreed to the published version of the manuscript.

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