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Moderate salt stress aids in the enhancement of nutritional and flavor quality in tomato (*Solanum lycopersicum* L.) fruits

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ABSTRACT

Salt stress has been found to enhance the quality of certain plants, yet its influence on fruit flavor remains largely unexplored. Our study probes the impact of salinity on the nutritional and flavor profile of tomatoes. Tomato plants were exposed to 0, 30, 50, 70, 90, and 110 mM of NaCl. Moderate salinity levels (50–70 mM) were found to boost the nutritional value of tomatoes, with increases in soluble solids, protein, and sugar levels. However, the concentration of key minerals such as K, Mg, and Mn declined with escalating salinity. Furthermore, the number of volatile compounds has increased, and the content of different types (alcohols, aldehydes, esters, etc.) has also significantly increased. Salinity stress also significantly influenced the levels of characteristic volatile compounds, especially hexanal, phenylethyl alcohol, and 6-methyl-5-hepten-2-one. Overall, these results will provide valuable strategies for producing high-quality tomatoes.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is an important and widely consumed vegetable crop across the world. Presently, China is the largest tomato producer in the world, followed by India, Turkey, the United States, Egypt, Iran, and Italy (Kashyap et al., 2021). Tomato fruit is rich in nutrients and contains several health-promoting compounds, and can easily be integrated into a balanced diet (Martí et al., 2016). The quality of tomato fruit mainly depends on its color, texture, aroma, and the contents of primary and secondary metabolites. Among them, the content of soluble sugars, organic acids, and soluble protein plays crucial roles in the sensory quality of tomato fruit. Tomato is rich in minerals (calcium, phosphorus, magnesium and other secondary minerals), water-soluble vitamins (B and C), fat soluble vitamins (A, E and K), bioactive substances (Wang et al., 2016).

For consumers, the flavor and sensory attributes of tomato fruits hold equal importance, as they not only dictate the likelihood of repeat purchases but also the longevity of the products presence in the market. In previous studies, the sugars: acids ratio i has been a key breeding target for taste evaluation in processing tomatoes, to the detriment of other plant nutrients and aromas which remain largely untapped (De Luca et al., 2012). According to reports, flavor involves various quality attributes such as astringency, bitterness, sourness (acidity), sweetness, and volatile compound content (Mahajan et al., 2017). These parameters are composed of various compounds, including non-volatile compounds and volatile compounds such as sugars, organic acids, tannins, capsaicin, glucosinolates, esters, alcohols, aldehydes, ketones, etc. However, the historical focus on yield and appearance quality of fruits may have inadvertently contributed to the dilution of their intrinsic flavors. Given that fruit flavor is a quantitative genetic trait, research in this area is inherently challenging. Nonetheless, previous studies have reported improvements in the nutritional and flavor profiles of tomato fruits through the application of exogenous compounds or by employing optimal cultivation practices. For example, the exogenous application of methyl jasmonate has been shown to boost the accumulation of lycopene and total carotenoids in cherry tomatoes, as well as to enhance the levels of volatile organic compounds such as 6-methyl-5-hepten-2-one (Liu et al., 2018). Additionally, fertilization with arbuscular mycorrhizal fungi(AMF) has proven effective in increasing mineral elements and volatile compounds within tomato fruit tissues (Pasković et al., 2021).

Tomato fruit quality and metabolite biosynthesis are strongly affected by plant growth conditions, including soil salinity, drought, temperature, and other abiotic stresses (Zhou et al., 2019), among which salt stress is increasingly becoming a serious challenge for agriculture. Presently, one-third of the world's irrigated land is affected by salinity, and tomato is sensitive to salt stress. Tomatoes are more susceptible to

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salt stress when grown in areas with high evapotranspiration, high temperatures, and limited rainfall. Additionally, continuous cultivation in greenhouses and poor soil management can also lead to soil salinization, thereby subjecting tomato plants to salt stress (de Azevedo Neto et al., 2006). Severe salt stress can cause several morphological, physiological, and molecular changes in tomato, including nutrient imbalance, oxidative stress, and photosynthesis inhibition (Yang et al., 2022). It has been reported that high salt stress levels (100 mM NaCl) can induce changes in the metabolome, and it was found that although fruit yield was significantly reduced, fruit quality was improved (Massaretto et al., 2018). Therefore, some researchers have proposed achieving the latter without sacrificing the former, which can be realized by applying moderate levels of salt stress. The controlled application of salt stress in greenhouses has been proposed as an innovative strategy to improve crop quality (Toscano et al., 2019). Some findings suggest that moderate salt stress can improve fruit quality, including fruit pigmentation, and sugar, organic acid, and amino acid contents(Li et al., 2019). Tang et al. (Tang et al., 2020) reported that salt stress can induce proteins to participate in flavonoids biosynthesis, and linoleic acid, carbohydrate, and amino acid metabolism, and that these proteins can affect fruit development and quality through interactions. There are also studies indicating that adding appropriate salinity can effectively increase the concentration of volatile compounds in Myrtle (*Myrtus communis* L.) (Vafadar Shoshtari et al., 2017). Adding low concentrations of NaCl to nutrient solution can significantly improve the fruit quality of cherry tomatoes, with only a slight decrease in yield (Li et al., 2024). In addition, to balance the conflict between yield and quality, suitable salt can be applied during periods when crops are not sensitive to salt stress, thereby producing high-quality vegetables (Giuffrida et al., 2017).

Presently, salt stress is one of the most important abiotic stresses affecting tomato production globally. Although previous studies have shown that salt stress can enhance the quality of tomato fruits, the investigated salt concentrations have been too narrow, failing to elucidate the trends in fruit quality under different salinity levels. Moreover, given the recent drive for the consumption of high-quality foods, it is necessary to examine the effect of salt stress on the volatile compounds content of tomato fruits. Therefore, the aim of this study was to examine the effect of salt stress on the nutritional quality and volatile compounds content of tomato fruit. Multivariate analyses (correlation, orthogonal partial least squares discriminant, and hierarchical cluster analyses) were used to elucidate the regulatory effect of salt stress on the nutritional quality and volatile compounds content of tomato fruit.

2. Materials and methods

2.1. Plant materials and growth conditions

Tomato (*Solanum lycopersicum* cv MicroTom) seeds were surface-sterilized with 4 % (w / v) sodium hypochlorite (AR, 500 mL) for 15 min, rinsed with distilled water, and grown in the dark on two layers of filter paper in 9 cm Petri dishes at 28 °C. After germination, the seedlings were transferred to a plate containing seedling culture medium (Gansu Luneng agricultural science and Technology Co., Ltd., Gansu, China), and placed in a growth chamber. The growth conditions were as follows: 12 h day at 28 °C/12 h night at 20 °C; humidity, 50–70 %; and light quantum flux density, 350 $\mu mol \cdot m^2 \cdot s^{-1}$. At four- leaf stage, transplant them into plastic pots (size: 7 × 7 × 8 cm) for nutrient solution cultivation, with one plant per pot. After transplanting, cultivate the plants with half-strength Hoagland's nutrient solution for two weeks, then switch to full-strength Hoagland's nutrient solution until the end of the growth period. Add 650 mL of nutrient solution to each pot and replace it every 7 days.

During the flowering peak, select 4–6 flowers of the same blooming period on each tomato plant for marking and remove other inflorescences. Salt stress treatment was initiated when the fruits reached the green-ripe stage (25 d after flowering). At the beginning of the salt treatment, we selected fruits with uniform flowering time and size, and measured the fruit peel color using a colorimeter (CR-10 Plus, Konica Minolta, Inc., Tokyo, Japan) to verify the uniformity of the plants. The plants were exposed to six concentrations of NaCl (AR, 500 g, NaCl content≥99.5 %): 0 (control, CK), 30 (T1), 50 (T2), 70 (T3), 90 (T4), and 110 mM (T5), with 5 plants in each treatment were repeated 3 times in each treatment. The NaCl solution was prepared with the full-strength Hoagland nutrient solution. 650 mL of the NaCl solution was added to each plant, and it was replaced every 7 days. The fruit was harvested at the red ripening stage (50 d after flowering) to determine the nutritional quality and the content of volatile component.

2.2. Determination of nutritional quality

The soluble solid content of the fruits was determined using PAL-1 refractometer (ATAGO Co., Ltd., Japan). Titratable acid and soluble sugar contents were determined using the acid-base titration and anthrone colorimetric methods, respectively (Wang et al., 2013). Nitrate, vitamin C, and soluble protein contents were determined using the salicylic acid (Cataldo et al., 1975), 2,6-dichloroindole phenol staining (Arya et al., 2000), and the Coomassie brilliant blue (Sedmak & Grossberg, 1977) methods, respectively.

2.3. Determination of mineral elements

The determination of mineral content in tomato fruits follows the method of Jin, Zhang, et al. (2023) Tomato fruits were fixed at 105 °C, dried at 80 °C to constant weight, ground into powder, sieved through a 0.25 mm sieve, and used for the determination of mineral elements. Total K, P, Ca, and Mg are extracted using H_2SO_4-H_2O_2 wet digestion method. Samples for Cu, Fe, Mn, and Zn determination were extracted using the dry ashing method. Total P was determined by molybdenum antimony colorimetry, while total K, Ca, Mg, Cu, Fe, Mn, and Zn were determined using ZEEnit 700P atomic absorption spectrometer (Analytik Jena, Germany).

2.4. Determination of volatile component content

The determination of volatile components in tomato fruits was carried out with reference to the method of Gupta et al. (2024). and slightly modified. Sample extraction: Weigh 5 g of fresh tomato fruit sample, grind it into a homogenate, place it in a headspace vial, add 1.5 g of anhydrous sodium sulfate, then add a magnetic stirring rotor and 10 μL of 2-octanol standard sample (chromatographically pure) with a concentration of 88.2 $mg \cdot L^{-1}$. Quickly tighten the cap of the headspace vial. Stir on a constant temperature magnetic stirrer at 52 °C and 1340 g for 10 min. Insert the extraction needle into the headspace vial and continue to extract and adsorb for 45 min. After the extraction is completed, insert the extraction needle into the gas chromatographic vaporization chamber. After 3 min of desorption, perform gas chromatography–mass spectrometry (GC–MS) analysis. Each treatment is repeated three times.

Chromatographic conditions: Select a DB-WAX elastic quartz capillary column (20 m × 0.18 mm, 0.18 μm). The injection port temperature is 230 °C. Flow rate: 1.0 $mL \cdot min^{-1}$. The split ratio is 30:1. The injection method is splitless injection, and the split valve is opened after 1 min. The temperature programming is as follows: the initial temperature is 40 °C, and it is raised to 190 °C at a rate of 3.5 $°C \cdot min^{-1}$ and maintained for 3 min. The ion source temperature is 200 °C and the transmission temperature is 190 °C.

2.5. Data analysis

Significant differences between mean values were determined using one-way ANOVA, followed by Tukey's post-hoc test for multiple comparisions, and means were considered statistically significant at $p < 0.05$. Statistical analysis was performed using SPSS software (version

21.0; SPSS Institute Inc., Chicago, IL, USA), and all data were presented as mean ± standard error (SE). Data maps and correlation charts were generated using Origin 2018 (Origin, Inc., San Francisco, CA, USA). Orthogonal partial least squares discriminant analysis (OPLS-DA) and hierarchical clustering analysis were performed using Metaboanalyst 5.0 server (accessed on August 13, 2024).

3. Result

3.1. Effects of NaCl concentrations on tomato fruit quality

3.1.1. Nutritional quality

There was a significant increase in the soluble solid content of the tomato fruits with increasing NaCl concentration, with a 36.20 % increase in soluble solid content in the T3 group compared with the CK group (Fig. 1A). The titratable acid content of the fruits exhibited a quadratic pattern, decreasing with increasing NaCl concentration and increasing afterwards. Specifically, the titratable acid content of the T3 group was 7.96 % lower than that of the CK group (Fig. 1B). There was a 54.07, 62.22, 67.41, 72.59, and 80.74 % increase in the soluble sugar content of fruits in the T1, T2, T3, T4, and T5 groups, respectively, compared with the CK group, indicating an increase in soluble sugar content with increasing NaCl concentration (Fig. 1C). In contrast, there was a significant decrease in the nitrate content of fruits in the T2 group (5.62 %) compared with the CK group (Fig. 1D). Similarly, there was a 1.02 and 1.76 % decrease in the vitamin C content of fruits in the T4 and T5 groups, respectively, compared with the CK group (Fig. 1E). The soluble protein content of the fruits exhibited a quadratic pattern with increasing NaCl concentration, peaking in the T1 group and decreasing at higher NaCl concentrations. Specifically, there was a 40.74, 29.20, 30.66, and 20.07 % increase in the soluble protein content of fruits in the T1, T2, T3, and T4 groups, respectively, compared with the CK group (Fig. 1F). However, there was no significant difference in soluble protein content between the CK and T5 groups.

3.1.2. Mineral content

Table 1 shows eight mineral elements detected in tomato fruit, including four macro-elements (K, P, Mg, and Ca) and four trace elements (Fe, Zn, Mn, and Cu). Salt stress significantly decreased the K, Mg, and Mn contents of the fruits compared with the CK group; however, there was no significant difference in Mg content between the CK and T1 groups. Additionally, there was a significant decrease in the P content of fruits in the T1, T2, and T5 groups compared with the CK group. The Ca and Cu contents of the fruits did not show a consistent trend with increasing salinity; however, there was a 5.89 and 21.05 % increase in Ca and Cu contents, respectively, in the T4 group compared with the CK group. There was a significant increase in Zn content with increasing salinity, with a 42.97 % increase in Zn content in the T4 group compared with CK group; however, there was no significant difference in Zn content between the T3 and CK groups. Generally, there was a significant decrease in Fe content in the T1, T2, T3, and T5 groups compared with the CK group; however, there was no significant difference in Fe

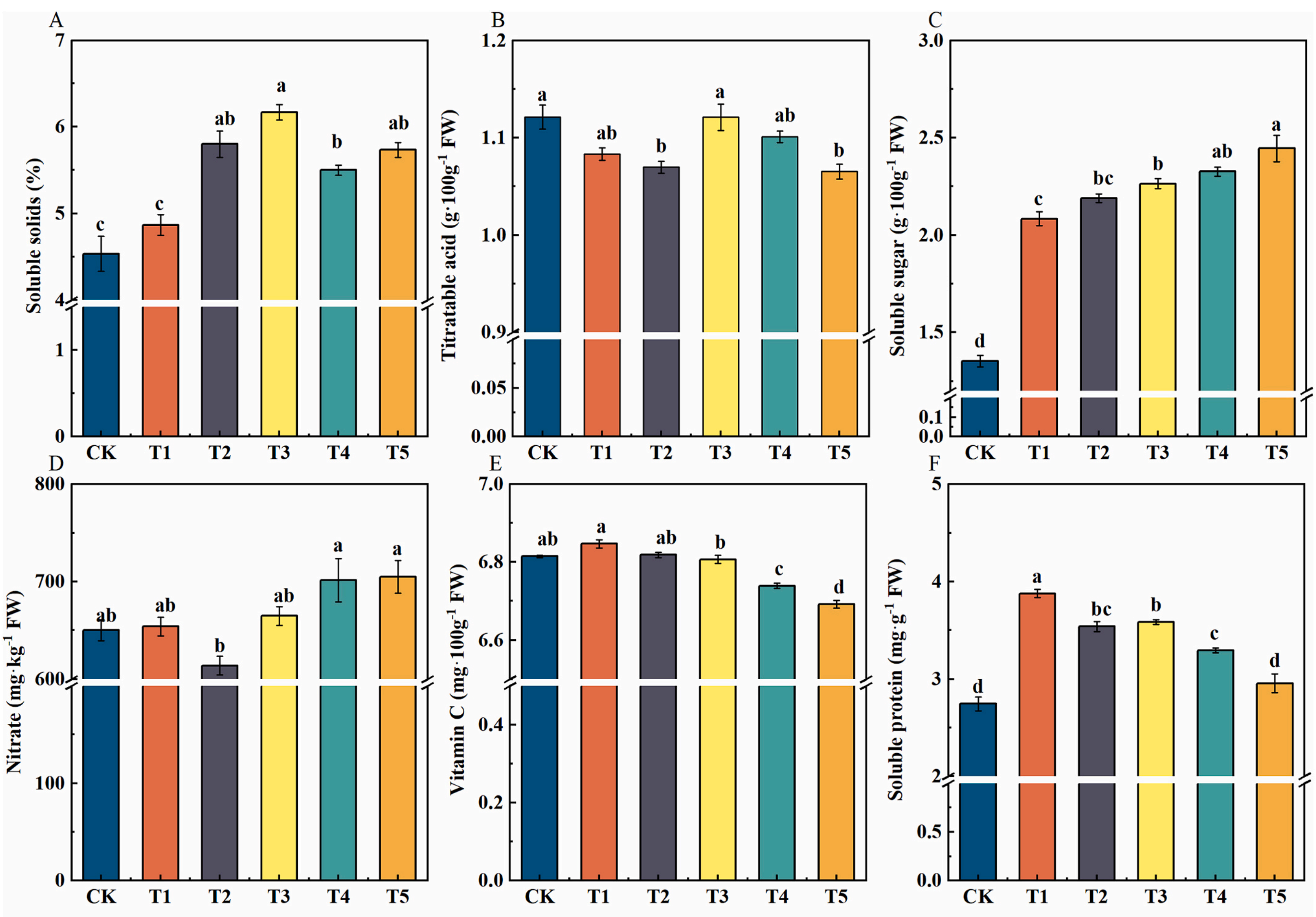

Fig. 1. Effects of different NaCl concentrations on the contents of soluble solids (A), titratable acid (B), soluble sugar (C), nitrate (D), vitamin C (E), and soluble protein (F) in tomato fruit. The data are expressed as average values ($n = 3$). Different lowercase letters showed significant difference between treatments ($p < 0.05$). The standard error is represented by a bar. Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

Table 1
Effect of different NaCl concentrations on the mineral content of tomato fruit.

Mineral elements	Contents (mg·kg^{-1} DW)					
	CK	T1	T2	T3	T4	T5
K	45,440.00 ± 280.00a	37,273.33 ± 648.76c	41,857.33 ± 954.91b	34,912.00 ± 486.97 cd	33,972.00 ± 319.03de	32,168.00 ± 212.80e
P	3994.00 ± 28.82a	3534.86 ± 19.95 cd	3341.37 ± 64.04d	3733.27 ± 83.82abc	3830.02 ± 65.65ab	3649.65 ± 82.37bc
Mg	1839.20 ± 6.06a	1734.90 ± 22.36ab	1517.70 ± 11.10d	1344.00 ± 16.25e	1691.80 ± 42.63c	1322.70 ± 15.90e
Ca	975.63 ± 6.64c	1005.13 ± 3.87b	870.53 ± 1.51e	896.63 ± 3.56d	1033.07 ± 6.09a	913.27 ± 2.58d
Fe	125.43 ± 0.47a	116.27 ± 1.99b	111.87 ± 2.61bc	105.47 ± 1.40c	127.63 ± 1.10a	115.53 ± 0.99b
Zn	35.40 ± 0.52d	44.79 ± 1.48bc	47.11 ± 2.02ab	40.09 ± 0.24 cd	50.61 ± 0.27a	50.23 ± 0.24a
Mn	43.96 ± 0.27a	36.99 ± 0.34b	35.41 ± 0.61b	30.69 ± 0.43c	31.03 ± 0.52c	28.51 ± 0.05d
Cu	16.67 ± 0.33d	19.95 ± 0.24ab	17.28 ± 0.44 cd	17.72 ± 0.24 cd	20.84 ± 0.05a	18.56 ± 0.46bc

Note: The data are expressed as average values ±SE (n = 3). Different lowercase letters showed significant difference between different treatments ($P < 0.05$). Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

content between the T4 and CK groups.

3.1.3. Correlation between the nutrients and minerals in tomato fruit

Soluble solid was negatively correlated ($p < 0.05$) with Mn and Mg contents, and titratable acidity was positively correlated ($p < 0.05$) with Fe and Ca contents under different salinity treatments. Additionally, soluble sugar content was positively correlated ($p < 0.05$) with Zn content but negatively correlated with K content (Fig. 2A), nitrate and vitamin C contents were negatively correlated ($p < 0.05$), and K and Mn contents were positively correlated ($p < 0.05$).

3.1.4. OPLS-DA and hierarchical cluster analysis of nutritional quality and mineral elements in tomato fruit

Changes in the nutritional quality and mineral contents of tomato fruit under different NaCl concentrations were evaluated using OPLS-DA (Fig. 2B). In the OPLS-DA score chart, the PC1 and PC2 axes accounted for 37.6 and 28.8 % of total variation, respectively. The different NaCl treatments were divided into three distinct clusters by PC1 and PC2: CK; T1, T2, and T3; and T4 and T5. Additionally, hierarchical cluster was performed to elucidate changes in nutritional quality and mineral contents of tomato fruits after salinity treatments (Fig. 2C). The results of the hierarchical cluster analysis were consistent with that of the OPLS-DA to some extent. Changes in the nutritional quality and mineral composition of tomato fruit under different NaCl concentrations are

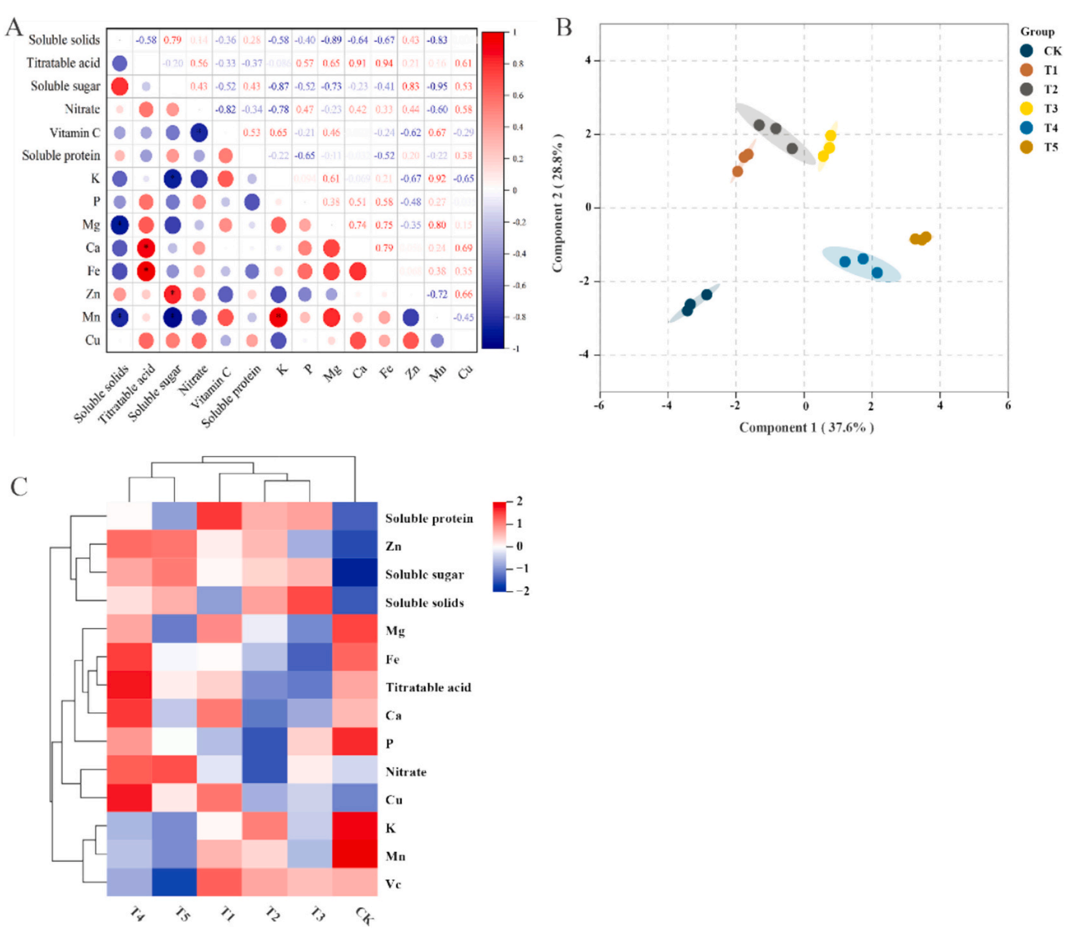

Fig. 2. Correlation analysis (A), orthogonal partial least squares discriminant analysis (OPLS-DA) (B) and hierarchical cluster analysis (C) of nutritional quality and mineral elements in tomato fruit. The data are expressed as average values (n = 3).* represents the significant difference at $p < 0.05$. Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

illustrated using a heatmap. Fruits in the T2, and T3 groups had higher soluble protein, soluble solid, and vitamin C contents; however, those in the CK and T4 group had the highest accumulation of most mineral elements.

3.2. Effect of different NaCl concentrations on the content of volatile compounds tomato fruit

3.2.1. Volatile substance composition and content

A total of 58 volatile compounds were detected in tomato fruits at different salinity level treatments (S Table 1). These include 11 alcohols, 20 aldehydes, 6 esters, 6 ketones, 6 hydrocarbons, 5 phenols, and 4 other compounds. The effects of different salinity levels on the types of volatile compounds are significantly different. The number of volatile compounds in T3 treatment is the largest, with a total of 50 kinds. Followed by T2 treatment, there are 45 kinds in total. T1 treatment has the least (29 kinds). There are a total of 20 compounds in each treatment, accounting for 34.48 % of all volatile compounds. There is 1 unique substance in T3, 3 unique compounds in T2, and a total of 8 compounds in T2, T3, T4, and T5 treatments (Fig. 3). The compounds with relatively high content in all treatments are hexanal, 2-hexenal, benzyl alcohol, phenylethyl alcohol, 1-octen-3-ol, etc., while the content of cis-4-decenal, (E, E) -2,4-decadienal, 3,5-dihydroxytoluene, and 2-ethylphenol is relatively low.

3.2.2. Classification and content of volatile compounds

From Fig. 4, it can be seen that alcohols are the category with the highest content of volatile compounds, detected in the range of 312.25–34.22 μg/kg. Among them, T3 treatment had the highest alcohol content, followed by T2 treatment. Compared to CK, T2 and T3 significantly increased by 17.47 % and 39.18 %, respectively. The total amount of aldehydes in T1, T2, and T3 treatments was significantly higher than that in CK, increasing by 13.05 %, 13.59 %, and 25.40 % respectively. However, T4 and T5 treatments were significantly lower than CK, with reductions of 12.23 % and 25.75 % compared to CK. The total amount of esters was highest in T4 treatment, followed by T3 treatment. T2, T3, T4, and T5 treatments were also significantly higher than CK. The total amount of ketones, hydrocarbons, and phenols was highest in T3 treatment, with significant increases of 40.57 %, 164.08 %, and 56.30 % compared to CK, respectively. The total amount of hydrocarbons and phenolic compounds treated with T2 was significantly higher than that of CK. The total amount of other volatile compounds was highest in CK, followed by T3 treatment, which significantly decreased by 24.64 % compared to CK. Other salinity levels were also significantly lower than CK. The total content of all compounds was highest in T3 treatment, followed by T2 treatment. T3 treatment significantly increased by 34.84 % compared to CK treatment.

3.2.3. Characteristic volatile substance content

There are significant differences in the content of volatile compounds

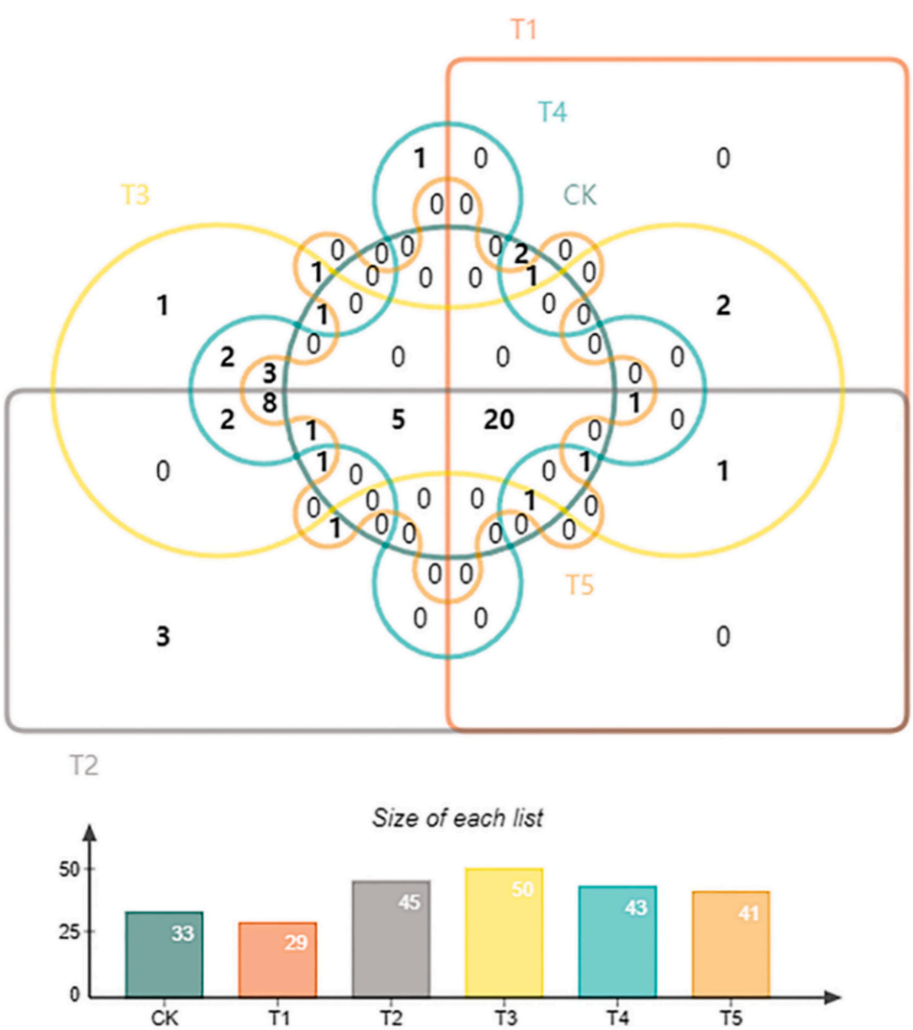

Fig. 3. Effect of different salinity levels on the number of various volatile compounds in tomato fruit. The data are expressed as average values ($n = 3$). Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

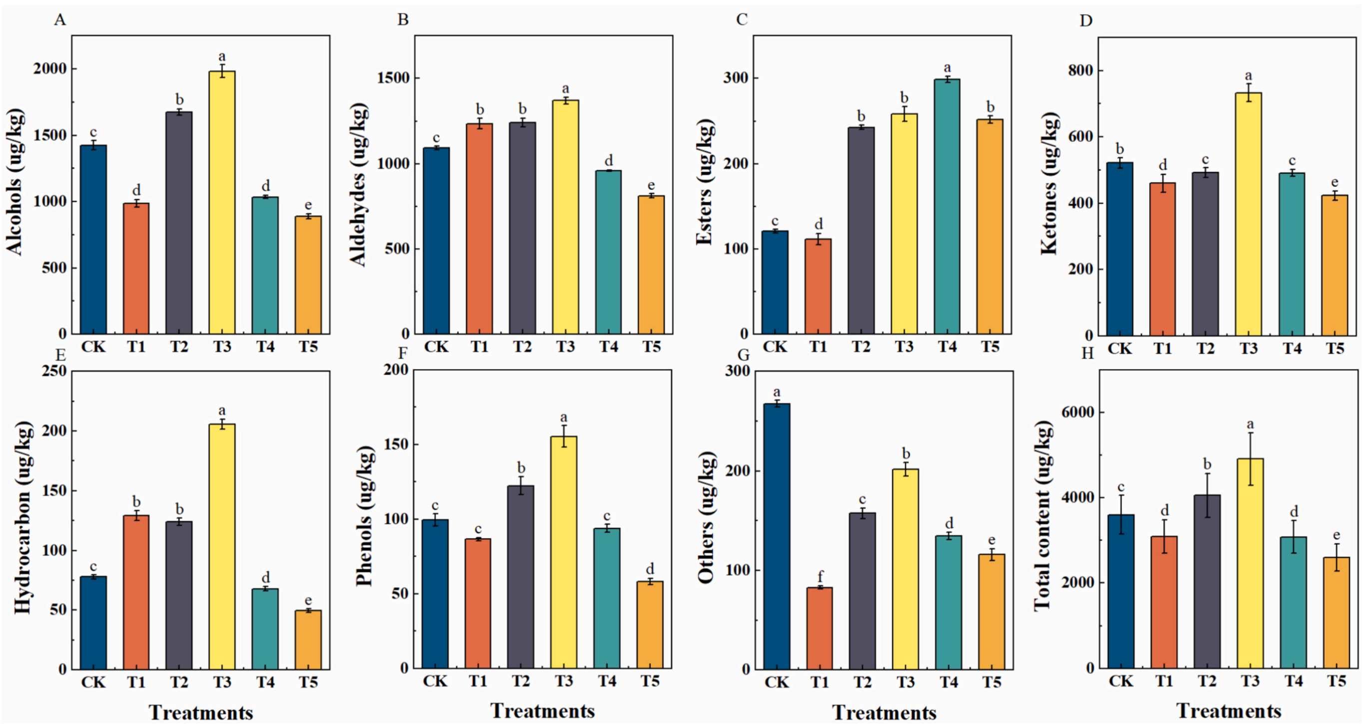

Fig. 4. Effect of different salinity levels on the classification and content of volatile compounds in tomato fruits, including alcohols (A), aldehydes (B), esters (C), ketones (D), hydrocarbons (E), phenols (F), other (G) and total content (H). The data are expressed as average values ($n = 3$). Different lowercase letters showed significant difference between treatments ($p < 0.05$). The standard error is represented by a bar. Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

in tomato fruits at different salinity levels (Table 2). A total of 10 characteristic volatile compounds were detected in this experiment, and 1-penten-3-one was not detected in the CK and T1 treatments. Hexanal, 3-hexenal, and 2-hexenal all have a grassy and green flavor, with hexanal being the most abundant characteristic volatile substance. The content of hexanal was highest in T2 treatment, and there was no significant difference between T3 treatment and T2 treatment, both of which were significantly higher than CK. (E) 2-Heptenaldehyde also has a grassy flavor, with the highest content in T3 treatment, significantly increasing by 32.67 % compared to CK. β - ionone, 1-penten-3-one, 2-isobutylthiazole, and 6-methyl-5-hepten-2-one all have fruity aroma. Among them, T3 treatment had the highest content of β - ionone, significantly increasing by 28.63 % compared to CK. The content of 1-penten-3-one was highest in T2 treatment, followed by T3 treatment. 2-isobutylthiazole and 6-methyl-5-hepten-2-one showed the highest levels in T1 treatment. Methyl salicylate has a mint flavor and its content is highest in T4 treatment, followed by T3 treatment, with significant increases of 143.68 % and 95.36 % compared to CK, respectively. Phenylethyl alcohol has a floral aroma, with the highest content in T2 treatment. There was no significant difference between T2 and T3 treatments, with significant increases of 27.69 % and 16.55 % compared to CK, respectively. The total content of characteristic volatile compounds was highest in T3 treatment, followed by T2 treatment, with significant increases of 17.74 % and 12.42 % compared to CK, respectively.

3.2.4. OPLS-DA and cluster heatmap analysis of volatile compounds

An OPLS-DA analysis was performed to investigate the content of characteristic volatile compounds in tomato fruits treated with different salinity levels (Fig. 5A). The Component 1 axis and Component 2 axis of

Table 2
Effects of different salinity levels on the content of characteristic volatile compounds in tomato fruit.

Characteristic volatile compounds	Odor description	Content(μg/kg)					
		CK	T1	T2	T3	T4	T5
Hexanal	Grassy, green	374.09 ± 5.84b	376.97 ± 10.51b	385.20 ± 9.32a	381.56 ± 8.81a	298.20 ± 1.90d	196.97 ± 5.83d
3-Hexenal	Grassy, green	145.33 ± 3.50b	179.58 ± 3.07a	144.19 ± 2.86b	185.80 ± 6.07a	115.13 ± 1.65c	81.02 ± 6.21d
2-Hexenal	Grassy, green	182.56 ± 6.65b	202.90 ± 4.65a	214.77 ± 8.71a	200.02 ± 2.72ab	185.31 ± 2.74b	140.47 ± 0.64c
(E)-2-Heptenal	Grassy	97.44 ± 3.05c	106.71 ± 3.45b	124.77 ± 1.01a	129.27 ± 2.34a	92.98 ± 2.79c	80.73 ± 2.10d
β-Ionone	Fruity, aromatic	42.72 ± 0.46b	32.36 ± 1.26d	33.22 ± 1.30d	54.95 ± 1.42a	42.39 ± 0.63b	38.31 ± 1.34c
1-Penten-3-one	Fruity	–	–	14.56 ± 0.69a	12.10 ± 0.64b	10.04 ± 0.45c	7.71 ± 0.28d
Phenylethyl Alcohol	Floral	233.05 ± 14.00b	241.16 ± 10.59b	297.60 ± 8.96a	271.62 ± 8.49a	187.58 ± 3.65c	133.98 ± 5.60d
Methyl salicylate	Mint	102.80 ± 2.04d	111.61 ± 6.77c	171.06 ± 2.02a	200.83 ± 6.90bc	250.27 ± 4.04a	224.53 ± 4.44b
2-Isobutylthiazole	Fruity, green	25.41 ± 0.12b	32.10 ± 1.07a	11.68 ± 0.38c	11.33 ± 0.44c	7.17 ± 0.81d	7.04 ± 0.69d
6-methyl-5-Hepten-2-one	Fruity	162.14 ± 15.22b	183.62 ± 31.76a	143.72 ± 12.39c	166.24 ± 13.72b	74.90 ± 2.15e	115.77 ± 5.18d
Total content/($\mu g \cdot kg^{-1}$)		1370.55 ± 60.39d	1467.01 ± 62.65c	1540.77 ± 70.49b	1613.72 ± 67.07a	1263.97 ± 57.99e	1026.51 ± 42.85e

Note: "–" indicates that the compounds were not detected. The data are expressed as average values ±SE (n = 3). Different lowercase letters showed significant difference between different treatments ($P < 0.05$).
Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

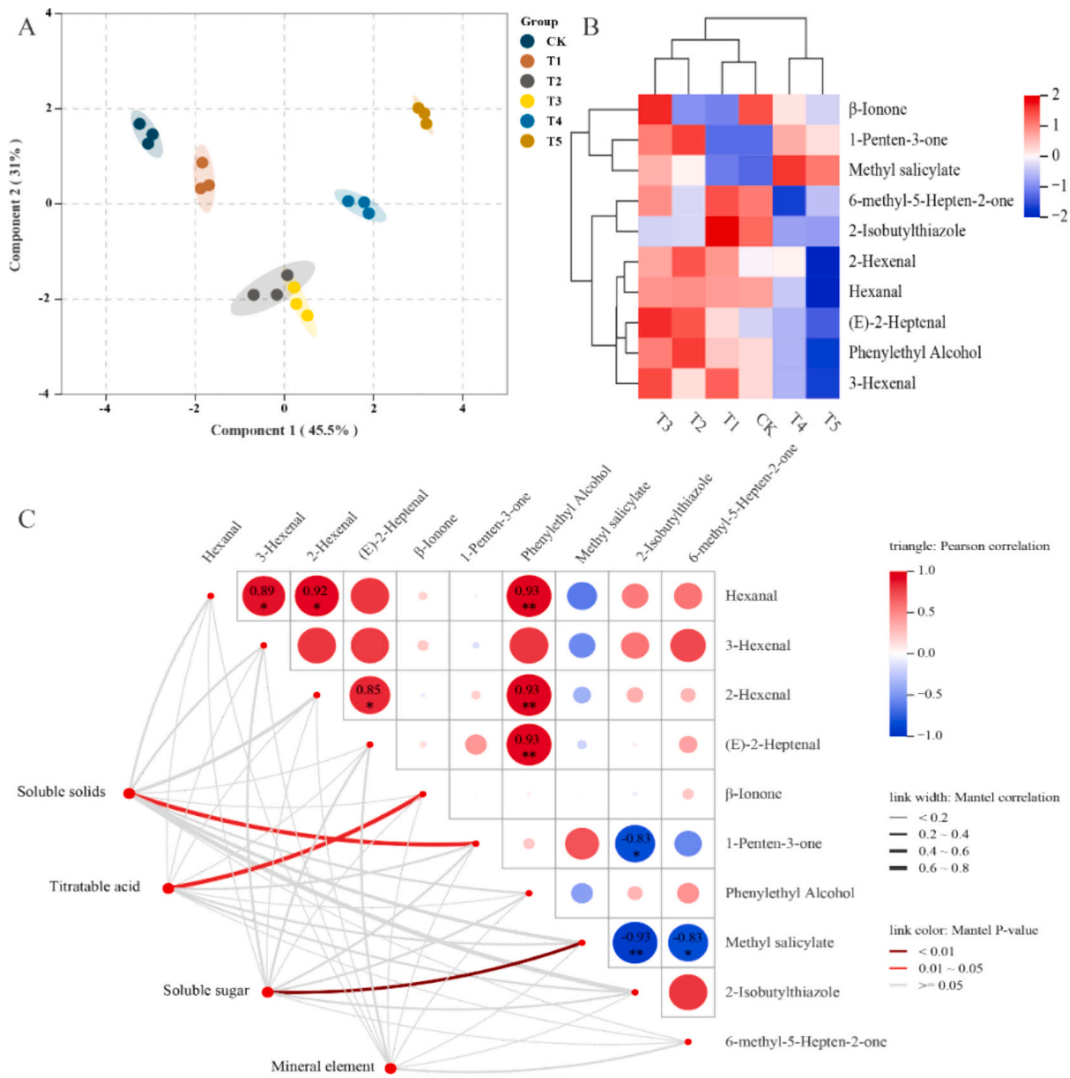

Fig. 5. OPLS-DA (A), cluster heatmap analysis (B) and correlation analysis (C) of tomato fruit flavor quality at different salinity levels. The data are expressed as average values ($n = 3$). The * and ** represent significant correlations at $P < 0.05$ and $P < 0.01$ levels, respectively. When analyzing the correlation between nutritional quality and characteristic volatile compounds, the Mantel test was used. The thickness of the lines connecting nutritional quality and characteristic volatile compounds represents the strength of the correlation between the two variables, with a correlation coefficient r greater than 0 indicating a positive correlation. The color intensity of the lines connecting nutritional quality and characteristic volatile compounds represents the significance of the correlation between the two variables, with $P < 0.01$ indicating an extremely significant correlation and $P < 0.05$ indicating a significant correlation. Abbreviations: CK: 0 mM NaCl, T1:30 mM NaCl, T2:50 mM NaCl, T3:70 mM NaCl, T4:90 mM NaCl, T5:110 Mm NaCl.

the OPLS-DA score plot explained 76.5 % of the total variance (31 % and 45.5 %, respectively). In the OPLS-DA score plot, it was evident that CK and T1, T2 and T3, T4 and T5 were relatively close to each other. The clustered heatmap (Fig. 5B) more intuitively showed that the content of characteristic volatile compounds in tomato fruits treated with T2 and T3 was higher and clustered into one group, while the content in T4 and T5 was lower and clustered into another group. The content of characteristic volatile compounds in CK and T1 was at a medium level and also clustered into one group.

3.2.5. *Correlation analysis with fruit flavor quality*

In the correlation analysis of tomato fruit flavor quality (Fig. 5C), Hexanal exhibited a significant positive correlation with 3-Hexenal, 2-Hexenal, and Phenylethyl Alcohol ($P < 0.05$). Phenylethyl Alcohol showed an extremely significant positive correlation with Hexanal, 2-Hexenal, and (E)-2-Heptenal ($P < 0.01$). However, Methyl salicylate demonstrated a significant negative correlation with 2-Isobutylthiazole and 6-methyl-5-Hepten-2-one. Additionally, soluble solids and titratable acid had significant positive correlations with 1-Penten-3-one and β-Ionone, respectively ($P < 0.05$), while soluble sugar exhibited an extremely significant positive correlation with Methyl salicylate ($P < 0.01$).

4. Discussion

The nutritional quality of tomatoes, including the flavor, is mainly dependent on the soluble sugar, acids, phenol, and mineral contents. Soluble solids include sugar and other minor components, and is highly correlated with the sugar content of tomato. In the present study, the soluble solid content of the fruits increased significantly with increasing salinity level, peaking in the T3 (70 mM NaCl) group (Fig. 1A). In mature tomato fruits, the primary function of high and stable invertase activity is to maintain the concentration of soluble sugars within the cells. Additionally, studies have shown that NaCl treatment increases the activity of acid invertase and sucrose synthase in the direction of hydrolysis, leading to an increase in the content of soluble sugars in tomato fruits. Furthermore, the decrease in fruit water content under salt stress further increases the content of soluble solids. (Naeem et al., 2020).

However, severe salt stress may interfere with tomato ripening, resulting in a decrease in the content of soluble solids (Zushi et al., 2024). In the present study, the titratable acid content of the fruits exhibited a quadratic trend with increasing salt salinity, decreasing initially and increasing in the T4 (90 mM NaCl) group (Fig. 1B). Additionally, there was a significant increase in the soluble sugar content of the fruits with increasing salinity level, peaking in the T5 (110 mM NaCl) group (Fig. 1C). High sugar content and optimal acid content have been shown to improve taste (Beckles, 2012). Moreover, Silvia et al. (Meza et al., 2020) showed that moderate salt stress significantly increased both soluble solid and soluble sugar contents in three tomato varieties without any reduction in yield. In the present study, salt stress did not significantly affect the nitrate content of the fruits (Fig. 1D). Excessive accumulation of nitrate has been shown to negatively affect food quality considerably (Rosas et al., 2015). Moreover, although excessive nitrate accumulation could lead to soil salinization, the salinity levels examined in this study had no effect on the nitrate content of the fruits. Vitamin C is a cofactor of various enzymes involved in plant and human metabolism, and an effective free radical scavenger (Paciolla et al., 2019). A previous study showed that salt stress increased the antioxidant capacity of amaranth leaves and the vitamin C content (Sarker & Oba, 2018). Similarly, the vitamin C content of tomato fruit was not affected by mild salt stress, but was significantly reduced by severe salt stress (Fig. 1E). Moreover, Lopez-Berenguer et al. (2009) reported that the vitamin C content of cauliflower was not affected by mild salt stress (40 mM NaCl). Under salt stress, plants produce soluble sugar, soluble protein,and proline to protect the cells (Chen et al., 2018). In the present study, exposure to 30–70 mM of NaCl significantly increased the soluble protein content of tomato fruit compared with the CK group (Fig. 1F). Protein plays an important role in fruit development and quality, including participating in sugar and energy metabolism pathways (Guo et al., 2017).

In the present study, the effect of salt stress on the mineral content of tomato fruit was examined (Table 1). The content of potassium (K) decreases gradually with increasing salt concentration. On one hand, this may be due to the antagonistic effect between K^+ and Na^+; under higher concentrations of Na^+, the concentration of K^+ tends to be lower. On the other hand, it may be related to the differential expression of K^+-related transport proteins in tissues under salt stress, which hinders the plant's absorption of K^+, thereby reducing the accumulation of this element in plant tissues. (Tanveer & Shabala, 2018). Additionally, it has been proven that calcium (Ca) and magnesium (Mg) elements also exhibit antagonistic effects with sodium ions (Na^+). A large number of studies have shown that when crops are under salt stress, the levels of calcium and magnesium significantly decrease, whether in the roots, leaves, or fruits (Smoleń et al., 2020). Our research also indicates that the content of Ca and Mg elements generally shows a gradual downward trend with the increase in salinity levels. Although there was no observable trend in the P content of tomato fruit in response to salt stress in the present study, exposure to 70–90 mM of NaCl did not significantly affect the P content of the fruits compared with the CK group. A possible explanation for the increase in phosphorus concentration under salt stress is that moderate levels of NaCl stimulate the plant's absorption of phosphorus, and moderate salt stress can increase the net uptake rate of phosphorus through low-affinity ion transport mechanisms (Gulmezoglu & Daghan, 2017). Similarly, Inal et al. (Inal et al., 2009) showed that the P content of the stem and root of carrot was not affected by salt stress. Additionally, the Mn content showed a decreasing trend with increasing salinity level, while Zn content showed an increasing trend, which was consistent with previous findings (Loudari et al., 2020). Due to the small proportion of trace minerals, it is difficult to propose a mechanistic explanation for their changes.

OPLS-DA and cluster analysis can be used to elucidate changes in biological components in response to different conditions, making them effective tools to examine changes in tomato quality under salt stress conditions (Toubiana et al., 2013). In the present study, correlation analysis showed that Fe, Ca, and titratable acidity; Zn and soluble sugar; and K and Mn contents were significantly correlated (Fig. 2). The OPLS-DA plot clearly showed separation of metabolite contents under T1, T2, and T3 treatments from other treatments on the X and Y axes (Fig. 3-A). This result was also supported by the hierarchical clustering diagram (Fig. 3-B). This further indicates that the changes in nutrient content in tomato fruits under moderate salt stress are consistent. In the study by Liu et al. (Liu et al., 2024), OPLS-DA was similarly employed to analyze metabolites in sorghum to discriminate differences among different varieties. Additionally, the heatmap showed that tomato fruits in the T2 and T3 groups had higher accumulation of soluble sugars, proteins, and solids.

In the determinants of tomato fruit flavor, sugar and acid can activate the human taste receptors, while a variety of different volatile compounds can activate the olfactory receptors (Tieman et al., 2012). The impact of volatile compounds on fruit flavor is particularly important. The growth environment of tomatoes can strongly affect the volatile compounds characteristics of the fruit, such as light, moisture, and temperature (Wang et al., 2015). We detected a total of 58 volatile compounds in tomato fruits by GC–MS technology, mainly including alcohols, aldehydes, esters, ketones, hydrocarbons, phenols and other compounds. Different varieties of tomato fruits contain different kinds of volatile compounds. At present, more than 400 kinds of volatile compounds have been detected in different tomato fruits (Klee, 2010). The number of volatile compound types also varies among varieties and under growth environments. Under different salinity levels, aldehydes are the most abundant volatile compounds in tomato fruits, followed by alcohols. Under moderate salt stress (T3 treatment), the contents of alcohols and aldehydes in the fruits significantly increase. These compounds are the major products of the lipoxygenase pathway in tomatoes, and their content changes directly affect the flavor characteristics of tomato fruits. It has been reported that NaCl stress can promote the release of volatile organic compounds through the lipoxygenase pathway, thereby helping plants cope with the stress and maintain stomatal conductance and photosynthesis. However, under severe salt stress, the content of various volatile compounds in tomatoes significantly decreases. This may be because when plants are subjected to severe stress, they not only consume a large amount of volatile compounds but also reduce the expression of genes related to their synthesis. As a result, the plants are unable to synthesize these metabolic substances in a timely manner (Zhang et al., 2018). Most aldehydes and esters in tomato fruits have fruity aromas, most alcohols have grassy aromas, and ketones have strong floral aromas. This indicates that under moderate salt stress, the aroma of tomato fruits becomes more intense. This is also demonstrated in the study by Colla et al. (2013), which showed that salt stress can effectively influence the accumulation of aromatic volatiles in tomato fruits, thereby improving the aroma and flavor of the fruits.

Currently, among the more than 400 volatile compounds identified in ripe tomato fruits, only 29 have concentrations exceeding 1 $ng \cdot L^{-1}$. Among them, 16 have logarithmic thresholds (the logarithm of concentration in tomatoes divided by the odor threshold) greater than 0, indicating that these 16 compounds make significant contributions to the aroma of tomatoes (Distefano et al., 2022).BALDWIN et al. (Baldwin et al., 2000) also believed that these 16 compounds are the main characteristic effector compounds of tomato fruits. In this study,a total of 10 characteristic volatile compounds in tomato fruits were detected, among which hexanal, 3-hexenal, 2-hexenal, methyl salicylate, 6-methyl-5-hepten-2-one, and phenylethyl alcohol were present in high amounts. Hexanal, 3-hexenal, and 2-hexenal are generated through the lipoxygenase-catalyzed oxidation of linoleic and linolenic acids. Under moderate salt stress (T2 and T3 treatments), the levels of hexanal and 3-hexenal significantly increase, imparting a grassy, green aroma to the fruit. When plants perceive external stress, the fatty acid degradation pathway is triggered by stress factors, leading to the production of large amounts of volatile compounds such as 2-hexenal and 3-hexenol as response signals. Additionally, salt stress can promote the substantial synthesis of endogenous ethylene within the plant. However, the increased ethylene content in plants can significantly affect the release of certain aromatic compounds in fruits, such as hexanal, 3-hexenal, 2-hexenal, and 6-methyl-5-hepten-2-one. This may be because ethylene interferes with the substrate content or the activity of key enzymes in the synthesis pathway, thereby influencing the production of these aromatic compounds (Klee & Giovannoni, 2011). Moderate salt stress (T2 and T3 treatments) can significantly increase the levels of hexanal and 3-hexenal, which is beneficial for improving the flavor of tomato fruits. Phenylpropanoids also contribute significantly to the aroma of tomatoes. The phenylpropanoids detected in tomato fruits in this study were primarily phenylethyl alcohol, which is described as having a floral aromas and was found to increase significantly under T2 and T3 treatments. Phenylethyl alcohol is stored in the form of glycosides in tomato fruits. The content of phenylethyl alcohol increases significantly after exposure to stress. This is likely due to the disintegration of plant cells, causing the glycosides to be released into the cytoplasm and hydrolyzed, resulting in the release of volatiles. In addition, plants accumulate large amounts of volatile monoterpenes or sesquiterpenes to cope with external stress, such as β-Ionone and 6-methyl-5-hepten-2-one (Jin, Zhao, et al., 2023). Similarly, under moderate salt stress, we also observed a significant increase in these fruit-scented compounds, β-ionone and 6-methyl-5-hepten-2-one, which can make the flavor of tomato fruits more intense.

In the OPLS-DA and clustering heatmap analysis, the trends of characteristic volatile compounds among the six treatments are highlighted. Under moderate salt stress (T2 and T3 treatments), the changes in the content of characteristic volatile compounds in tomato fruits were significantly separated from other treatments. This may be attributed to the activity of volatiles within the concentration range of picomolar to nanomolar. Moderate salt stress may induce changes in compound concentrations within the fruit without disrupting cellular functions, thereby generating a concentration effect (Tieman et al., 2012). To clarify the impact of selenium-enriched treatment on the content of volatile compounds in tomato fruits, Shiriaev et al. (2023) established a PLS-DA model to investigate the effects of selenium. Correlation analysis indicates that volatile compounds influence each other. For instance, phenylethyl alcohol showed an extremely significant positive correlation with hexanal, 2-hexenal, and (E)-2-heptenal. However, methyl salicylate demonstrated a significant negative correlation with 2-Isobutylthiazole and 6-methyl-5-Hepten-2-one. Additionally, soluble solids, titratable acid, and soluble sugar can significantly affect 1-penten-3-one, β-Ionone, and methyl salicylate. This further confirms that sugars, acids, and volatile compounds have a synergistic effect (Tieman et al., 2012).

5. Conclusion

In the present study, we examined the effects of salinity stress on the flavor quality of tomato fruit. Moderate salt stress (30–70 mM of NaCl) generally improved or maintained the nutritional and flavor quality of tomato fruit, including soluble solids, titratable acids, soluble sugars, and characteristic volatile compounds contents. In particular, at a concentration of 70 mM NaCl, the quality of tomato fruits was significantly enhanced. In contrast, severe salt stress (90–110 mM of NaCl) reduced the nutritional and flavor quality of the fruits. Under moderate salt stress, the metabolites of tomato fruits clustered into one group in both OPLS-DA and clustering analysis, while those under severe salt stress formed another group. This further validates the changes in tomato fruit quality under different salt concentrations. Meanwhile, the correlation analysis also revealed a positive correlation between nutritional quality and volatile compounds. Overall, these results showed that moderate salt stress can ensure normal plant growth and significantly improve fruit flavor with minimal metabolic loss and lower yield drag, providing a valuable and cost-effective strategy for cultivating high-quality tomato.

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CRediT authorship contribution statement

Li Jin: Writing – review & editing, Writing – original draft, Visualization, Methodology. **Ning Jin:** Visualization, Methodology. **Shuya Wang:** Visualization, Supervision. **Shuchao Huang:** Validation, Formal analysis. **Xiting Yang:** Methodology, Investigation. **Zhiqi Xu:** Validation, Formal analysis. **Shuyan Jiang:** Investigation. **Jian Lyu:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Jihua Yu:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fochx.2025.102330.

Data availability

Data will be made available on request.

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