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Low Red to Far-Red Light Ratio Promoted Growth and Fruit Quality in Salt-Stressed Tomato Plants Based on Metabolomic Analysis

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Abstract: Salt stress poses a serious threat to tomato production. Red to far-red light ratio (R/FR) is actively involved in the regulation of tomato growth and development; however, it is still uncertain whether and how R/FR improves fruit quality under salt stress. Thus, we conducted metabolomic analysis of tomato fruits under four treatments, including R/FR = 7 (CK), R/FR = 0.7 (L), R/FR = 7 and 100 mmol·L^{-1} NaCl (Na), and R/FR = 0.7 and 100 mmol·L^{-1} NaCl (Na+L). Metabolomic analysis indicated that both low R/FR and salt stress enhanced organic acids and phenols accumulation; however, additional low R/FR mainly improved carbohydrates, organic acids, phenols and amino acids accumulation in salt-stressed tomato fruit. Physiological studies were consistent with the above results and further revealed that additional low R/FR drastically promoted plant growth, soluble sugar, total phenol and flavonoid contents, improved osmotic pressure balance and antioxidant capacity, and notably relieved the salt stress-induced suppressions. This study proved the importance of applying light quality regulation in salt-resistant tomato production.

Keywords: salt stress; R/FR; tomato; fruit quality; metabolomics

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1. Introduction

Tomato (*Solanum lycopersicum* L.) is an important horticultural plant worldwide. Its fruits are rich in a large number of metabolites, including vitamins, cellulose, sugars, carotenoids, lycopene, phenols and flavonoids compounds [1]. Numerous studies have demonstrated that in tomato production, fruit quality and metabolites were usually impacted by environmental changes, such as light and salt stress [2,3].

Salt stress plays a negative role in tomato production. Salt stress easily induces osmotic stress, ionic poisoning, nutrient deficiency and oxidative stress, thus affecting morphological, physiological and molecular characteristics in plants [4,5]. High salt concentration seriously inhibits plant growth and development and largely decreases tomato fruit number, weight and yield [6]. Meanwhile, salt stress influences tomato fruit quality, including total soluble solid (TSS), soluble sugar, amino acid, lycopene and organic acid accumulation [7,8].

Red to far-red light ratio (R/FR), a light environmental factor, takes an active part in plant photomorphogenesis, leaf photosynthesis, flowering, fruit quality and yield [9]. The R/FR is approximately 1.2 under sunlight, and it ranges from 0.1 to 0.7 under shade to 7 under LED irradiation [10]. Low R/FR always triggers shade avoidance responses, including reducing branches, elongating stem, petiole and leaf lengths, and enhancing apical dominance and shoot dry weight [11]. For tomato production, low R/FR decreases leaf chlorophyll content, shortens the time to flowering and reduces fruit yield [12]. Supplemental far-red radiation to red light dramatically increases tomato fruit quality, such as single-fruit weight, TSS and Na accumulation [13,14].

R/FR also regulates plant responses to abiotic stresses, including salt and cold stresses [15]. Wang et al. [16] suggested that low R/FR benefited the increase in salt tolerance in tomato plants mainly through increasing SOD, POD and CAT contents and decreasing H_2O_2 contents. Miao et al. [17] found that low R/FR improved cucumber photosynthetic efficiency through enhancing the photosynthetic electron transfer rate and Calvin cycle, effectively alleviating the negative regulations of salt stress. Hayes et al. [18] indicated that under low R/FR irradiation, PIFs up-regulated the expression of the *BSK5* gene and induced auxin signaling, finally accelerating hypocotyl elongation in salt-stressed *Arabidopsis*. Previous studies showed that under high salt concentration, R/FR regulated growth, antioxidant and photosynthetic capacities; however, its roles in fruit quality remain largely unknown.

Metabolomics analysis shows metabolites and metabolic pathways responses to salt, light, low temperature, drought and atmospheric gases stresses in horticultural plants [19,20]. Salt stress promoted the TCA cycle and generated more amino acid and most organic acids, including proline, glutamic acid, leucine and valine in soybean [20]. In tomato fruits, compared to darkness, white light enhanced the accumulation of most carotenoids and tocopherols, including alpha-carotene, lycopene and alpha-tocopherol; both red and blue monochromatic lights increased zeaxanthin content [1]. Previous studies indicated that both salt stress and light affected fruit metabolites; however, whether and how R/FR could affect metabolites and metabolomic pathways in salt-stressed tomato fruits is still unclear.

In the study, using metabolomic and physiological analyses, we determined the effects of R/FR on plant growth, fruit quality and metabolites, especially carbohydrates and organic acids, phenols and amino acids compounds in tomato fruits under salt stress. The findings reveal a metabolic mechanism of tomato fruit in response to R/FR and salt stress, and benefit management of salt-tolerant tomato production.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Tomato (*Solanum lycopersicum* L. cultivar 'Micro Tom') seeds were germinated and sowed into pots filled with substrate (peat: vermiculite: perlite = 2:1:1) and cultivated in an artificial climate chamber. All tomato fruits at the mature green stage were labeled, and plants were randomly exposed to four treatments. According to our previous results and the methods of Cao et al. [2], four treatments were set up: CK (normal LED irradiation: R/FR = 7), L (shade condition: R/FR = 0.7), Na (R/FR = 7 and 100 mmol·L^{-1} NaCl), Na+L (R/FR = 0.7 and 100 mmol·L^{-1} NaCl). Red (peaked at 660 nm) and far-red (peaked at 730 nm) light were provided by LED lamps. According to Kotilainen et al. [21], R/FR was calculated as follows: R/FR = photon irradiance between 655 nm and 656 nm/photon irradiance between 725 nm and 735 nm. The light intensity and spectral distribution were measured by Avaspec-2048 fiber optic spectrometer (AVANTES, Apeldoorn, The Netherlands, spectral range 300–900 nm, spectral resolution 1 nm) (Figure 1). The light intensity, photoperiod, day/night temperature and air humidity were 250 μmol·m^{-2}·s^{-1}, 12 h·d^{-1}, 26 °C/18 °C and 60%, respectively. The plants were supplied with full-strength Yamazaki tomato nutrient solution. Each treatment was replicated in 18 pots. All labeled tomato fruits at the deep red ripe stage (about 3–5 fruits per plant) were harvested simultaneously.

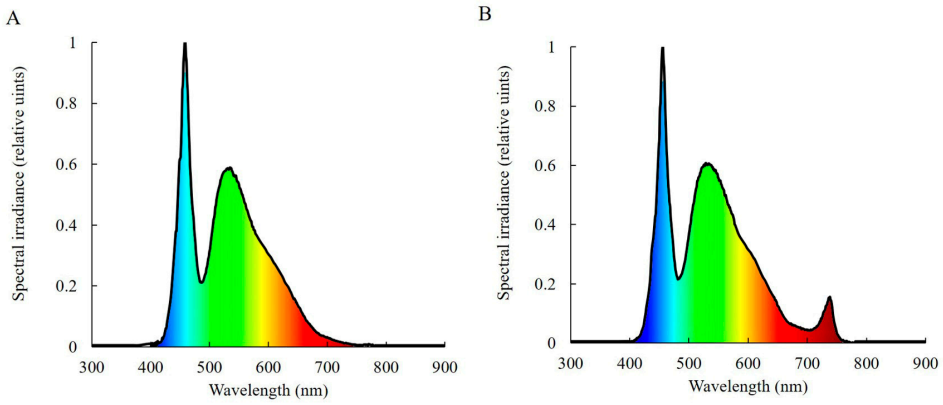

Figure 1. Relative spectral distribution of light quality treatments. (**A**) R/FR = 7; (**B**) R/FR = 0.7. The different colors correspond to different light quality.

2.2. Determination of Experimental Indexes

2.2.1. Determination of Plant Growth Parameters

After tomato fruits ripened, plant height was measured and leaf area was determined by using an LA-S leaf area meter (Hangzhou Wanshen Detection Technology Co., Ltd., Hangzhou, China). After the plants were fully dried at 80 °C in an oven, the whole-plant dry weight was determined. Each treatment was determined with four biological replications and replicated three times to ensure statistical validity.

2.2.2. Determination of Tomato Fruit Quality Parameters

Single-fruit weight was determined, and fruit firmness was measured with a GI-1 fruit firmness tester (Zhengzhou Hongchuang Environmental Protection Technology Co., Ltd., Zhengzhou, China). Fruit shape index was calculated as the longitudinal diameter to transverse diameter ratio. Total soluble solids content was determined with a DR101 digital sugar meter (Xingtai Deyan Technology Co., Ltd., Xingtai, China). Fruit color parameters were determined by using a Konica Minolta CM-700d color difference meter (Konica Minolta, Tokyo, Japan). Intrinsic quality parameters, including soluble sugar, sucrose, fructose, organic acid, total phenol, total flavonoid, lycopene, carotenoid and free amino acid contents, were assayed according to Li [22] and Toor and Savage [23]. Each treatment was determined with four biological replications and replicated three times to ensure statistical validity.

2.2.3. Metabolite Extraction and Profiling Analysis of Tomato Fruits

Metabolite extraction and profiling analysis were performed as previously described [24]. Briefly, a 60 mg sample from ripe tomato fruit was mixed with 40 μL of L-2-chloro-phenylalanine (0.3 mg·mL^{-1}) and 360 μL of cold methanol, then placed (−20 °C, 5 min) and fully ground (60 Hz, 2 min). The sample was ultrasonically extracted, vortex-shook, ultrasonically extracted (30 min) and centrifuged (13,000 r, 4 °C, 10 min). After being fully dried, the sample was added with 80 μL of methoxyamine hydrochloride pyridine solution (15 mg·mL^{-1}), vortex-shook and placed in a shaking incubator (37 °C, 90 min) to perform oximation reaction. The sample was added with 50 μL of BSTFA derivatization reagent, 20 μL of n-hexane and 10 μL of internal standard, vortex-shook for 2 min and reacted at 70 °C for 60 min.

The sample was analyzed with GC-MS metabolomics analysis. The derivatives in samples were separated in an Agilent 7890B gas chromatography system (Agilent Technologies Inc., Santa Clara, CA, USA) with a DB-5MS fused-silica capillary column. The injection temperature, volume and solvent delay were 300 °C, 1 μL and 5 min, respectively. The GC-MS data were recorded and pre-processed by MS-DIAL [25]. Each treatment was determined with four biological replications and replicated three times.

2.3. Data Analysis

Metabolomic data were normalized and imported into R to perform principal component analysis (PCA), partial least squares discriminant analysis (PLS-DA), orthogonal partial least squares analysis (OPLS-DA) and univariate analysis. The threshold values were VIP > 1, difference multiplier FC > 1.2 or <0.87, and *p*-values < 0.05. Metabolic pathway analysis was conducted on the KEGG website (https://www.kegg.jp/, accessed on 17 March 2022.). The plant growth and fruit quality parameters were conducted by one-way ANOVA and Duncan's test ($p < 0.05$) in SPSS 21 software (IBM Corporation, Armonk, NY, USA).

3. Results

3.1. Low R/FR Alleviated the Adverse Effects of Salt Stress on Tomato Plant Growth and Fruit Quality

Generally, compared to CK, most tomato leaves turned yellow and withered in Na treatment, and tomato leaves were slightly chlorotic in Na+L treatment (Figure 2A). Meanwhile, compared to CK, L treatment significantly enhanced plant height, total leaf area and whole-plant dry weight by 14.00%, 36.15% and 31.82%, respectively, but dramatically decreased fruit hardness by 17.50%. Na treatment severely decreased total leaf area, whole-plant dry weight and single-fruit weight by 56.92%, 30.11% and 17.32%, respectively. Na+L treatment significantly enhanced plant height by 7.77% (Figure 2B–G). Interestingly, compared to Na, Na+L treatment significantly improved plant height, total leaf area and whole-plant dry weight by 13.54%, 85.93% and 37.19%, respectively. It was illustrated that low R/FR accelerated tomato plant growth under salt stress.

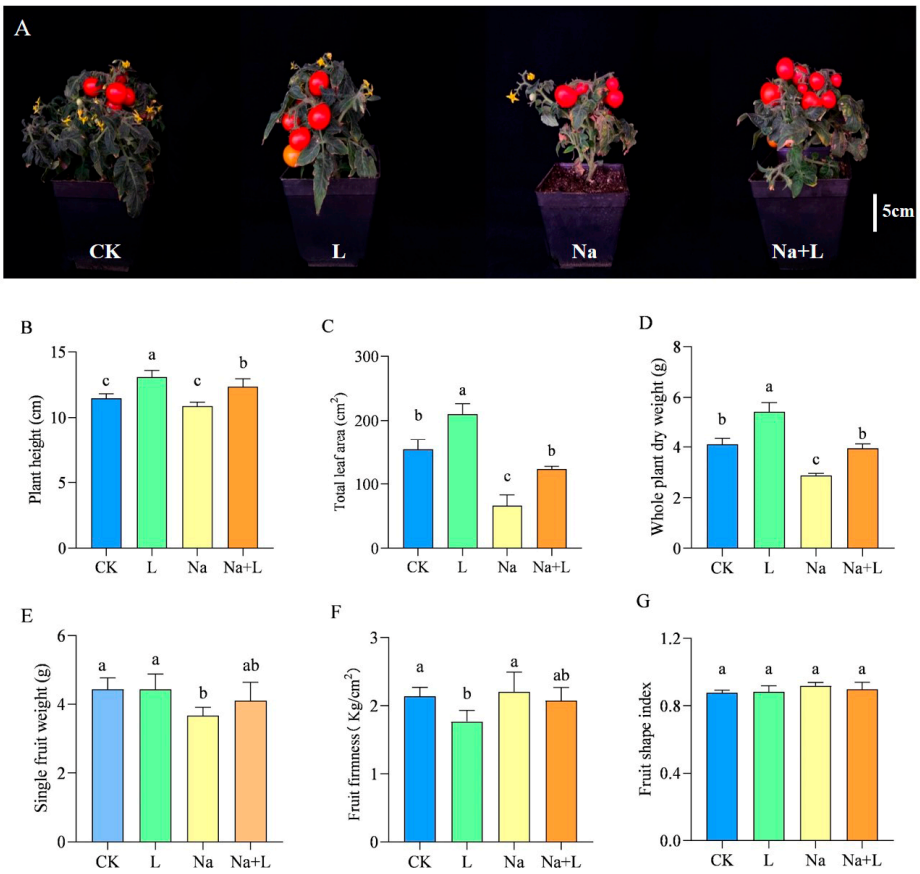

Figure 2. R/FR improved plant growth and fruit parameters in salt-stressed tomato plants. (**A**) Photographs of tomato plants; (**B**) plant height; (**C**) total leaf area; (**D**) whole-plant dry weight; (**E**) single-fruit weight; (**F**) fruit firmness; (**G**) fruit shape index. CK, R/FR = 7; L, R/FR = 0.7; Na, R/FR = 7 and 100 mmol·L^{-1} NaCl; Na+L, R/FR = 0.7 and 100 mmol·L^{-1} NaCl. Note: Lowercase letters represent statistically significant differences ($p < 0.05$).

3.2. Metabolomics Analysis

3.2.1. Identification of Differentially Expressed Metabolites

GC-MS-based metabolomics identified 362 metabolites in tomato fruits. In total, 42 differentially expressed metabolites (DEMs), including carbohydrates, organic acids, phenolics, amino acids, lipids, nucleosides and organoheterocyclic, were differentially regulated in tomato fruits under different treatments (Figure 3A, Table S1). Compared to CK, there were 42 DEMs (36 up-regulated and 6 down-regulated metabolites) and 32 DEMs (25 up-regulated and 7 down-regulated metabolites) in L and Na treatment, respectively (Figure 3B,C, Table S2). Meanwhile, 25 DEMs (19 up-regulated and 6 down-regulated metabolites) were observed in the Na+L/Na comparison group.

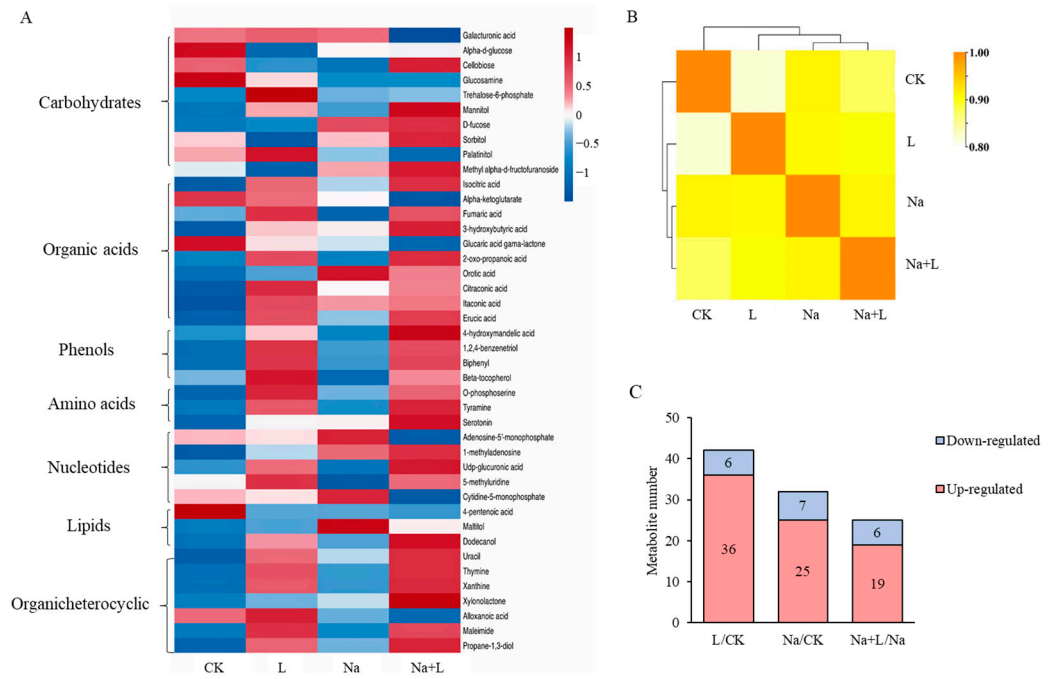

Figure 3. Metabolome analysis of tomato fruits. (**A**) Heat map of differentially expressed metabolites (DEMs). The colors indicate DEM relative level content from low (blue) to high (red). (**B**) The Spearman correlation coefficient analysis of metabolomic data; (**C**) the numbers of DEMs.

3.2.2. Low R/FR Enhanced the Contents of Carbohydrates and Organic Acids in Salt-Stressed Tomato Fruits

Metabolomic analysis suggested that R/FR influenced the accumulation of metabolites involved in carbohydrate and organic acid metabolism in tomato fruit under salt stress (Figure 4A,B). Compared to CK, L treatment significantly decreased most carbohydrate, including α-d-glucose (55.17%), glucosamine (42.81%), cellobiose (26.97%), sorbitol (18.51%) and methyl α-D-fructofuranoside (51.55%), but increased most organic acid, including fumaric acid (82.06%), citraconic acid (239.79%), itaconic acid (156.22%), 2-oxo-propanoic acid (105.05%), 3-hydroxybutyric acid (33.33%), isocitric acid (100.00%) and erucic acid (300.00%). Na treatment dramatically down-regulated glucosamine content by 69.78% but up-regulated D-fucose (44.51%) and most organic acids, including orotic acid (117.74%), citraconic acid (116.20%), itaconic acid (114.24%), 3-hydroxybutyric acid (33.33%), isocitric acid (58.21%) and erucic acid (300.00%) when compared to CK. However, compared to Na, Na+L treatment notably up-regulated methyl α-D-fructofuranoside, mannitol, fumaric acid, 2-oxo-propanoic acid, 3-hydroxybutyric acid and isocitric acid contents by 53.65%, 40.30%, 174.80%, 125.13%, 25.00% and 42.45%, respectively, but down-regulated galacturonic acid content by 69.51%.

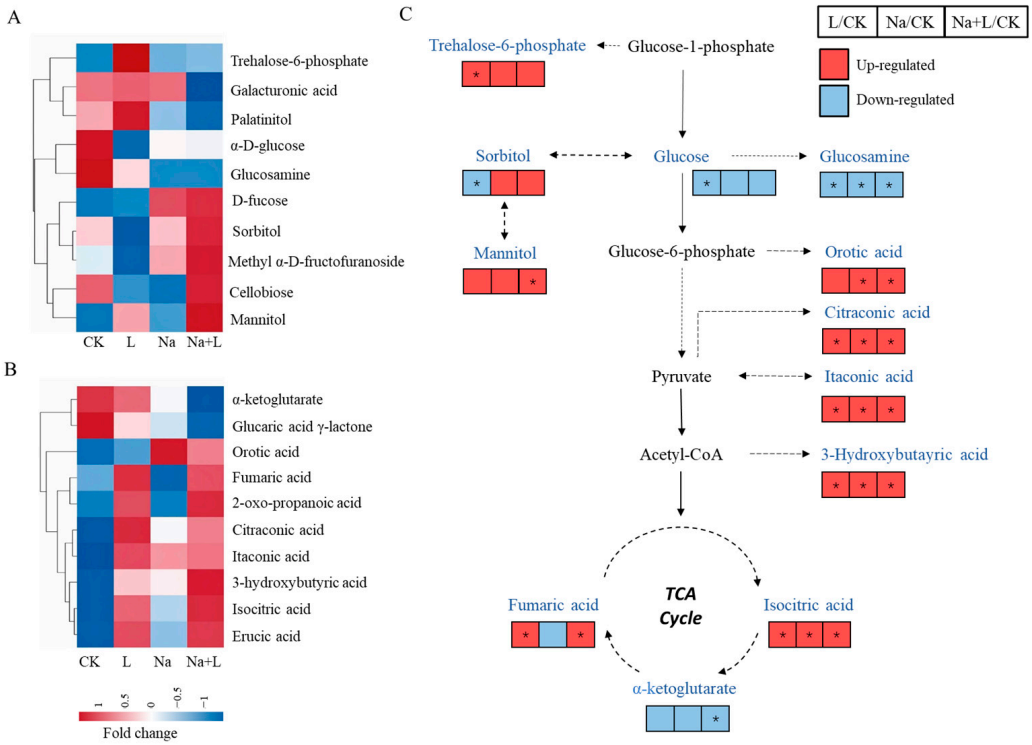

Figure 4. Low R/FR enhanced carbohydrate and organic acid metabolites in salt-stressed tomato fruits. (**A**) Heat map of the DEMs involved in carbohydrate metabolism; (**B**) Heat map of the DEMs involved in organic acid metabolism; (**C**) Schematic diagram of sugar and organic acid metabolism in tomato fruit. Blue letters indicate DEMs, red and blue boxes indicate significant increase and decrease in metabolite contents, respectively. Note: Asterisks indicate statistically significant differences ($p < 0.05$).

In order to further investigate the changes in carbohydrates and organic acids metabolism, KEGG enrichment analysis was conducted and suggested that all DEMs were enriched in 12 differential metabolic pathways ($p < 0.05$), including citrate cycle (TCA cycle), C5-branched dibasic acid metabolism, butanoate metabolism, fructose and mannose metabolism, pentose and glucuronate interconversions, pyrimidine metabolism, arginine biosynthesis, alanine, aspartate and glutamate metabolism, amino sugar and nucleotide sugar metabolism, galactose metabolism, ascorbate and aldarate metabolism, synthesis and degradation of ketone bodies (Table S3). Compared to CK, both Na and L treatments induced 12 carbohydrates and organic acids metabolic pathways perturbation, respectively. However, Na+L treatment perturbed only 11 metabolic pathways except ascorbic acid and uronate metabolism when compared to Na treatment (Figure 4C).

To further confirm the metabolic results, carbohydrate and organic acid levels were investigated in tomato fruits. Compared to CK, L treatment largely increased sucrose content by 158.99%, Na treatment dramatically enhanced sucrose content by 75.90%, Na+L treatment significantly increased total soluble solid (TSS), sucrose and organic acid contents by 9.54%, 87.05% and 27.65%, respectively (Figure 5). Compared to Na treatment, Na+L treatment significantly increased total soluble solid and soluble sugar contents by 6.88% and 15.44%, respectively.

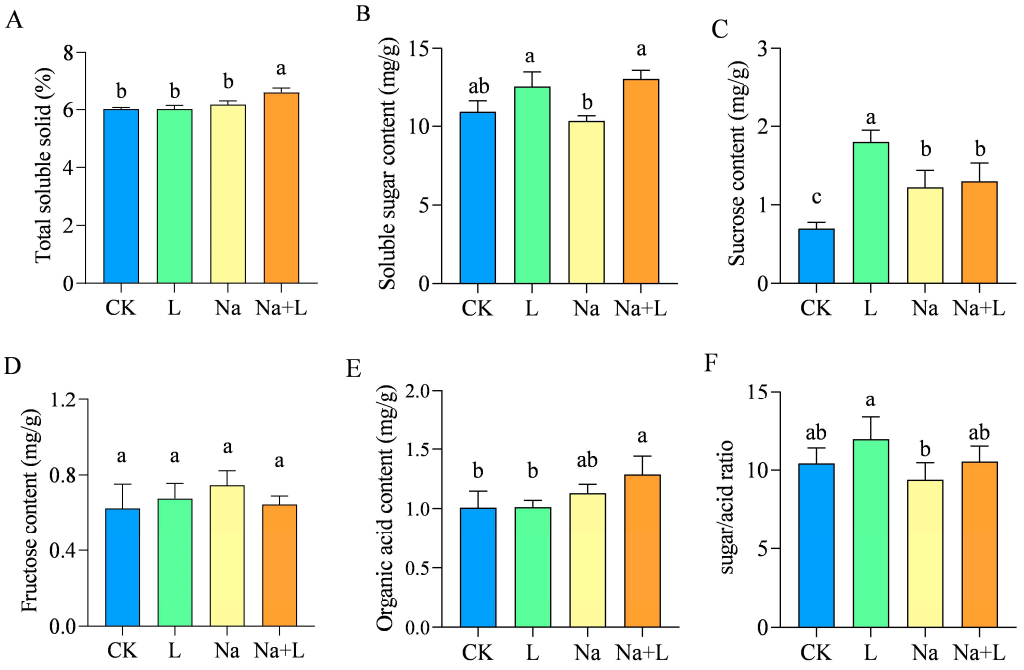

Figure 5. Low R/FR increased carbohydrate and organic acid contents in salt-stressed tomato fruits: (**A**) total soluble solid; (**B**) soluble sugar content; (**C**) sucrose content; (**D**) fructose content; (**E**) organic acid content; (**F**) sugar/acid ratio. Note: Lowercase letters represent statistically significant differences ($p < 0.05$).

3.2.3. Low R/FR Improved the Contents of Phenols and Amino Acids in Tomato Fruits under Salt Stress

According to metabolomic analysis, low R/FR promoted phenols (1,2,4-benzenetriol and biphenyl) and amino acids (serotonin, O-phosphoserine and tyramine) accumulation in salt-stressed tomato fruits (Figure 6A,B). Compared to CK, L treatment significantly enhanced total phenol, total flavonoid, lycopene and free amino acid contents by 41.85%, 22.37%, 23.98% and 23.81%, respectively. Compared to CK, Na treatment dramatically increased free amino acid content by 28.21% but decreased lycopene content by 34.43%; moreover, Na+L treatment notably increased total phenol, total flavonoid and carotenoid contents by 43.96%, 41.61% and 57.27%, respectively (Figure 6C–H). It was noteworthy that compared to Na treatment, Na+L treatment significantly enhanced accumulation of phenols, including total phenol (28.07%), total flavonoid (25.99%), carotenoid (26.36%) and lycopene (42.86%) contents.

Compared to CK, L treatment largely reduced yellowness (b*) by 10.40%, Na treatment dramatically increased lightness (L*) and b* by 9.50% and 9.60%, respectively; moreover, Na+L treatment notably increased L* by 4.50% (Figure 7A–C). Interestingly, compared to Na treatment, Na+L treatment significantly reduced L* and b* but enhanced redness (a*).

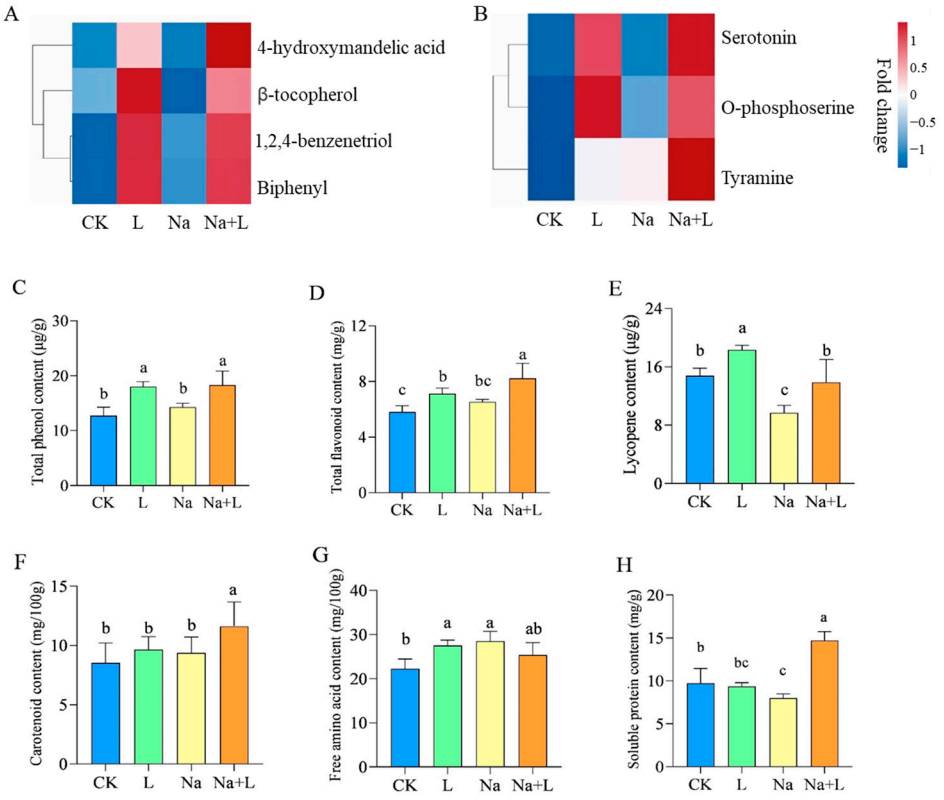

Figure 6. Low R/FR promoted phenol, pigment and amino acid contents in salt-stressed tomato fruits: (**A**) heat map of DEMs involved in phenol metabolism; (**B**) heat map of DEMs involved in amino acid metabolism; (**C**) total phenol content; (**D**) total flavonoid content; (**E**) lycopene content; (**F**) carotenoid content; (**G**) free amino acid content; (**H**) soluble protein content. Note: Lowercase letters represent statistically significant differences ($p < 0.05$).

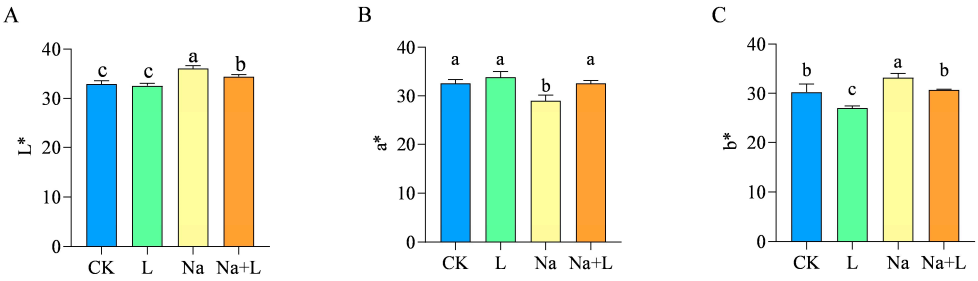

Figure 7. Low R/FR promoted pericarp color in salt-stressed tomato fruits: (**A**) lightness (L*); (**B**) redness (a*); (**C**) yellowness (b*). Note: Lowercase letters represent statistically significant differences ($p < 0.05$).

4. Discussion

Salt stress becomes a serious threaten to tomato cultivation; it not only inhibits plant growth but also adversely affects fruit quality and yield [3,7]. The plant biomass is a crucial index for evaluating plant responses and tolerance to environmental stresses [26]. In this study, salt stress induced leaf chlorosis and significantly reduced total leaf area, whole-plant dry weight and single-fruit weight, implying that salt stress severely impeded plant growth (Figures 2 and 8). However, low R/FR largely improved leaf area and whole-plant dry weight, dramatically alleviating these adverse effects. Similar observations were reported in lettuce, soybean and geranium [27–29]. Low R/FR was conducive to the increase in leaf area mainly through increasing cell wall elongation; it also dramatically improved photosynthetic characteristics, finally improving plant biomass [9,30].

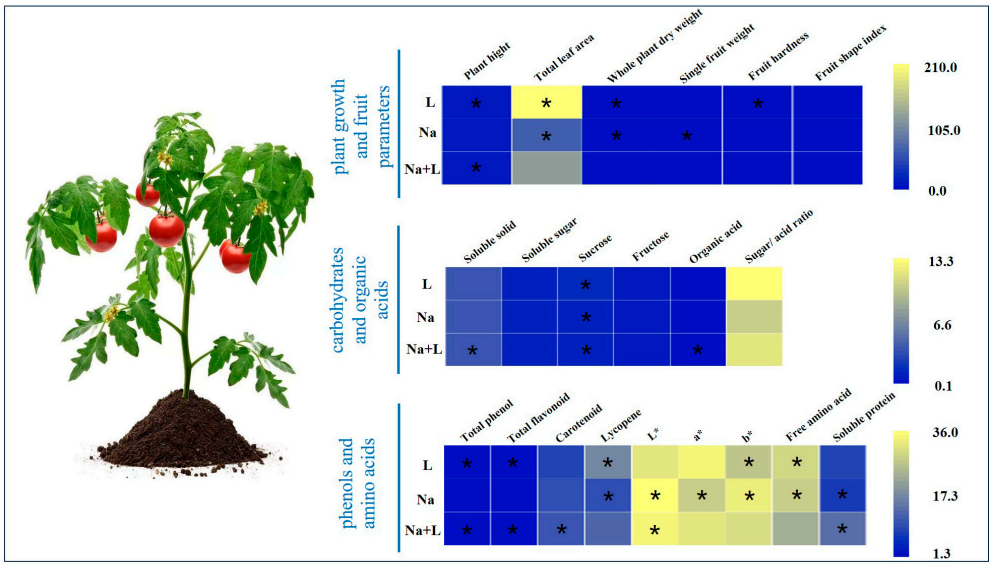

Figure 8. Low R/FR improved plant growth and fruit quality parameters in salt-stressed tomato plants. The heat map represents the fold change of each value compared to CK. Note: Asterisks indicate statistically significant differences ($p < 0.05$).

The fruit quality directly reflects its commercial characteristics [8,26]. Previous studies indicated that long-term salt stress significantly reduced pepper fruit length and dry weight [31]. In the present study, salt stress drastically decreased tomato fruit quality by reducing single-fruit weight, lycopene content and redness (Figures 2, 6 and 7). On one hand, high salt concentration decreased leaf photosynthesis and sugar accumulation, directly reduced single-fruit weight; on the other hand, it triggered rapid accumulation of ROS, including $O_2^{\cdot -}$, ·OH and H_2O_2, resulting in physiological metabolism disorder and decreased lycopene content [2]. Our data suggested that low R/FR enhanced redness, lycopene and carotenoid contents in tomato fruit under salt stress (Na+L vs. Na). When exposed to low R/FR, light-activated PHYA/B induced *HY5* gene expression and up-regulated *PSY* and *ZDS* gene expressions, leading to sharp rises in lycopene content and redness in tomato fruit [32].

Salt stress affects carbohydrate accumulation in tomato fruit. Carbohydrate is a key indicator of fruit sweetness and is also related to fruit quality, such as firmness and volatile aroma [33]. Numerous studies proved that under salt stress, low R/FR significantly promoted leaf photosynthesis and carbohydrate accumulation in cucumber plants [17]. Consistent with this, our study illustrated that low R/FR significantly increased TSS and soluble sugar contents in tomato fruit under salt stress (Na+L vs. Na, Figure 5). Soluble sugar is a major constituent of TSS. Under salt stress, low R/FR induced abundant soluble sugar, which not only provided ample carbon skeleton and energy for biosynthesis but also protected plants from osmotic stress [34,35]. This can be further proved by the changes in carbohydrate metabolites. Under salt stress, low R/FR up-regulated methyl α-D-fructofuranoside and mannitol levels by 53.65% and 40.30%, respectively, but down-regulated galacturonic acid level by 69.51% (Figure 4). Methyl α-D-fructofuranoside, a starting material for many carboxylates, is very common in horticultural fruits, such as Indian mulberry and sour star fruits [36,37]. Mannitol is a compatible solute and antioxidant which protects plant from biotic and abiotic stress [38]. In salt-stressed tomato fruit, low R/FR induced the accumulation of mannitol and methyl α-D-fructofuranoside, which accelerated biosynthesis, enhanced oxidation function, and finally improved plant tolerance to salt stress [39]. Galacturonic acid mainly comes from plant cell walls. Under salt stress, low R/FR led to a reduction in galacturonic acid, which sped up tomato fruit softening [40].

Prolonged salt stress tended to induce a large accumulation of organic acids, which are important to tomato flavor [41]. In the present study, both the Na and Na+L treatments increased organic acid content (Figure 5). Metabolomic analysis also proved that Na and Na+L treatments significantly up-regulated most organic acids levels. Meanwhile, most organic acids levels were much higher in Na+L treatment when compared to Na treatment. Fumaric acid and isocitric acid are two main intermediate products in the TCA cycle (Figure 4). Under salt stress, low R/FR induced a large accumulation of fumaric acid and isocitric acid, which accelerated the TCA cycle, producing more adenosine triphosphate (ATP) and precursors for amino acid, fatty acid and cholesterol [20]. Furthermore, low R/FR induced the accumulation of organic acids, including 2-oxo-propanoic acid and 3-hydroxybutyric acid, which effectively stabilized intracellular pH and maintained osmotic pressure, eventually improving salt tolerance [34].

As an important secondary metabolite, phenol has a considerable effect on fruit quality, antioxidant capacity and stress tolerance in plants [42]. Our data suggested that compared to salt stress, low R/FR drastically enhanced total phenol and total flavonoid contents in tomato fruit (Na+L vs. Na, Figure 6). These can be further proved by the increase in phenol compounds, such as 1,2,4-benzenetriol and biphenyl. Tegelberg et al. [43] demonstrated that R/FR influenced the contents of phenols, including chicoric acid and caffeic acid in silver birch plants. Abundant phenols induced by low R/FR were beneficial for scavenging excess ROS and effectively alleviating the negative effects of salt stress [20].

As one of the most abundant primary metabolites, amino acids play positive roles in plant tolerance to abiotic stress [2]. Previous studies illustrated that salt stress and far-red light enhanced amino acids contents [30,44]. Numerous amino acids induced by low R/FR effectively decreased the osmotic potential of intracellular solutes, balanced osmotic intensity both inside and outside the protoplast, maintained structure and conformation of intracellular enzymes, finally alleviating the adverse impacts of salt stress [32]. Duan et al. [41] proved that high salt concentration induced more than 32 amino acids and their derivatives in *Salicornia europaea*. Our study suggested that both L and Na treatments significantly increased free amino acids content (Figure 6). This can be further proved by the similar trends in amino acids compounds (o-phosphoserine, tyramine and serotonin) in Na+L treatment. Serotonin, a curial mediator, is involved in plant growth and responses to adverse situations. Abundant serotonin induced by low R/FR improved plant tolerance to salt stress due to its powerful antioxidant capacity [45]. To our knowledge, the physiological importance of o-phosphoserine and tyramine have not yet been elucidated.

5. Conclusions

In summary, low R/FR significantly enhanced whole-plant dry weight and reduced fruit hardness and b*, and notably promoted plant growth and fruit quality. Salt stress decreased whole-plant dry weight, single-fruit weight and increased organic acid content, and severely inhibited plant growth and decreased fruit quality. The metabonomic analysis also revealed similar trends. However, low R/FR largely alleviated the adverse impacts of salt stress based on comparative physiological and metabolomic analysis. Low R/FR improved fruit quality by mainly enhancing the accumulation of metabolites involved in carbohydrates, organic acids, phenols, amino acids and promoting the TCA cycle in tomato fruit under salt stress. The results provided a theoretical foundation for enhancing tomato tolerance to salt stress with light quality regulation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14050983/s1, Table S1. Effects of R:FR on differential metabolites in tomato plant under salt stress; Table S2. The number of differentially expressed metabolites (DEMs) from tomato fruits exposed to different R/FR and salt stress; Table S3. Effect of R:FR on metabolic pathway in tomato fruit under salt stress.

Author Contributions: Conception and design of the research, Y.M.; investigation and methodology, R.L.; data curation and validation, C.L.; formal analysis and writing—original draft preparation,

X.Z.; writing—original draft preparation, X.X.; writing—review and editing, M.S.; supervision and visualization, L.B.; writing—review and editing, funding acquisition and project administration, L.H. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data are not readily available for public consumption due to privacy and other issues.

Conflicts of Interest: The authors declare no conflicts of interest.

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