Journal of Soil Science and Plant Nutrition
https://doi.org/10.1007/s42729-023-01449-3

ORIGINAL PAPER

Acidic Medium pH Mitigates the Effects of Long-Term Salinity on the Physiology, Biochemistry, and Productivity of Tomato (*Solanum lycopersicum* L.) Plants

Jafar Nabati[1] · **Mohammad Javad Ahmadi-Lahijani**[2] · **Armin Oskoueian**[2] · **Zahra Nemati**[3]

Received: 1 March 2023 / Accepted: 21 August 2023

Abstract
Salinity is one of the destructive abiotic stresses that limit the production of agricultural products. The medium acidity can impact ion uptake, the oxidation-reduction balance, and the solubility of the elements. The alleviative effects of the medium pH adjustment (unadjusted as control [pH ~ 8.5–9], pH 5.5, and pH 4.5) on adverse effects of salinity in tomato plants (*cv.* Mobil) were examined in soilless culture. Plant growth, biochemical traits, and fruit attributes were evaluated. Leaf chlorophyll content (*chla+b*) was increased at pH 5.5, decreased at pH 4.5, and remained constant in the control plants. The highest leaf *chla+b* was recorded at pH 5.5, 42 days after stress onset (DAS). Lowering the medium pH reduced leaf DPPH and leaf phenol content by ~ 55 and 45%, respectively, compared with the control. The highest root K^+ content and the lowest root Na^+/K^+ ratio were observed in plants grown at pH 5.5. The greatest leaf area, shoot and root dry weight (DW), and root length were observed at pH 5.5, increasing by 100, 23, 8, and 32%, respectively, compared with the control. Plants grown under pH 5.5 showed the highest number of fruits and fruit dry weight; lowering the medium pH increased the number of fruits and fruit DW by 77 and 32%, respectively, compared with the control. Generally, the medium pH adjustment at 5.5 enhanced the salinity tolerance of tomato plants. The results showed that lowering the medium pH could be a feasible approach to ameliorate the adverse effects of salinity on the growth and yield of tomato plants.

Keywords DPPH · Na^+/K^+ ratio · Phenol · Medium pH · Shoot/root ratio · Soilless culture

1 Introduction

Soilless culture is a method of growing plants without soil in which minerals are provided to the roots through irrigation water. The soilless cultures provide a more efficient water and minerals consumption and make it easier to adjust the medium (Sajjadinia et al. 2010). In hydroponic systems, it is possible to achieve the maximum yield and quality with proper and sufficient use of water and nutrients; however, the quality of the supplied water is of great importance. The hydroponic culture systems provide the possibility of a proper medium solution adjustment. The medium acidity is critical mainly due to its impacts on cell membrane ion transporters, the oxidation-reduction balance, and the solubility of the elements (Epstein and Bloom 2005).

Plant growth is inhibited by high salinity in the rhizosphere, which reduces the soil water potential and makes it hard for roots to absorb water. Salinity stress interrupts the plant water status and hinders the physiological and biochemical processes (Raza et al. 2022). Salt stress affects major processes such as germination, root and shoot dry weight, and Na^+/K^+ ratio. Salinity affects the concentration of nutrients and their transport in roots, shoots, and fruits (Fang et al. 2021; Raza et al. 2022). The concentration of various acids and vitamins in tomato fruits can be influenced by salinity. Salinity, through stimulating the biosynthesis of growth regulators such as ethylene and abscisic acid, accelerates leaf aging and reduces the length of the fruiting period in tomato plants (Ghanem et al. 2008). Salinity disturbs the balance of the absorption of nutrients such as

---

✉ Mohammad Javad Ahmadi-Lahijani
mjahmadi@um.ac.ir

[1] Department of Legume, Research Center for Plant Sciences, Ferdowsi University of Mashhad, Mashhad, Iran

[2] Department of Agrotechnology, Faculty of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran

[3] Department of Horticultural Science, Faculty of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran

nitrogen, potassium, and phosphorus. It causes a decrease in the initial growth of tomato plants and fruit production (Signore et al. 2016).

Reduction of water flow to growing fruits, fruit respiration, and fruit dry matter and the accumulation of sodium and proline in leaves are among the other effects of salt stress in tomatoes (Plaut et al. 2004; Putra and Yuliando 2015). Salt stress in the root zone of tomato (*Solanum lycopersicum* L.) plants decreased fruit yield, which was related to a decrease in fruit weight, while the number of fruits was not changed (Li et al. 2001). Kiferle et al. (2022) also observed that plant height, shoot fresh and dry weight, and fruit production were considerably decreased in 150 mM NaCl-treated plants. However, the positive effects of mild salt stress on the quality of tomato fruit have also been reported. The results of a study on tomato (*Lycopersicon esculentum* Mill. *cv*. Falkatoin) plants under soilless cultivation showed that with increasing the nutrient solution salinity, leaf area index, fruit weight, and yield were significantly decreased, whereas the fruit dry matter percentage was increased (Layegh et al. 2009).

Tomato (*Solanum lycopersicum* L.) belongs to the Solanaceae family and is the second most important vegetable in the world. Tomato is rich in minerals, vitamins, antioxidant compounds, and lycopene, and it is considered one of the most important crops in the world concerning human health and nutrition (Jones Jr 2007). The global production of tomato products is ~ 186 million tons of fruits harvested from 5 million hectares (FAO 2022). In Asia, with a production quantity of 15.7 m ton, Iran is ranked 4th after China, India, and Turkey. The ability to regulate leaf water potential and ionic homeostasis has made tomatoes relatively resistant to salinity (Martinez-Rodriguez et al. 2008). Nevertheless, the high salinity of soil and water in arid and semi-arid regions of the world adversely affects tomato yield (Feleafel and Mirdad 2014).

The increase in population, the need for more agricultural and food production, and the limitation of water resources due to climatic changes have led humankind to use low-quality water resources (unconventional water). Salinity is a worldwide agricultural concern, and many regions of the world, including Iran, are subjected/prone to saline water and soil, which limits the growth and development of plants. Usually, the irrigation water salinity in such areas is high and causes plant damage. Many farmers are reluctant to expand the greenhouse cultivations due to the high salinity of the irrigation water and the costs of lessening the salinity level. Under those situations; therefore, crop production might be unprofitable, and greenhouse cultivation sometimes might be under question. With reliable knowledge, however, the economic justification of greenhouse cultivations with saline water can be evaluated, and more accurate recommendations for farmers and plant breeders can be provided. Thus, investigating the approaches to reduce the effects of salinity in tomato cultivation systems is desired.

Salinity increases the medium pH and reduces the availability of some nutrients. Lowering the medium pH by increasing the nutrient solubility would enhance the plant nutrient absorption under saline conditions (Nabati et al. 2021). Furthermore, a lower pH by the acidification of the thylakoid lumen reduces the inhibitory effect of salinity on leaf physiology and biochemistry due to the accumulation of protons in the thylakoid lumen that form a ΔpH (Ruban et al. 2012). Hence, it was evaluated whether the medium pH adjustment might mitigate the adverse effects of salinity on the morphophysiological, biochemical, growth parameters, and fruit yield of tomato plants.

2 Materials and Methods

2.1 Experimental Procedure and Treatments

The study was conducted at the research greenhouse of the Department of Agriculture, the Ferdowsi University of Mashhad, in 2018. The medium pH (unadjusted as control [~ 8.5–9], 5.5, and 4.5) and sampling times (just before the onset of salinity stress; zero, 14, 28, 42, and 56 days after the onset of salinity stress; DAS) were considered as the experimental factors. The plants were grown under day/night temperatures of 25/18 ± 2 °C, respectively, with a relative humidity of 50 ± 5% and natural photoperiod (spring).

Tomato seeds (*cv*. Mobil) were grown in the seedling trays in a mist room and were transferred to a soilless culture system after 2 weeks. Plants were grown in pots (30 cm in diameter, each per pot and 1 m apart) filled with perlite as the culture medium under a closed hydroponic system. The Hoagland nutrient solution was used as the fertilizer, and the solution was circulated continuously (Hoagland and Arnon 1950). The salinity (NaCl) of the irrigation water was gradually increased (starting from one month after plant establishment) at the rate of 4 dS m^{-1} per week to reach 20 dS m^{-1} and continued to the end of the growing season. The solution for each pH treatment was circulated with a separate pump (three pumps). The acidity of the nutrient solution was adjusted daily using sulfuric acid (H_2SO_4) and was changed weekly (Nabati et al. 2021).

2.2 Measurements

The salinity levels were zero, 8, 16, 20, and 20 dS m^{-1} at day 0, 14, 28, 42, and 56 DAS, respectively. The measurements during the plant growth period were performed once before the onset of salinity stress and 14, 28, 42, and 56 DAS, and the rest were measured after harvesting (Nabati et al. 2021). Two plants per replication were analyzed ($n = 6$).

2.3 Biochemical Analysis

2.3.1 Leaf Pigments Content

One hundred milligram of leaf fresh weight was homogenized in 98% ethanol using a mortar and pestle. The data were recorded at 648, 664, and 470 nm using a spectrophotometer (Unico 2100, USA) (Lichtenthaler and Wellburn 1983).

2.3.2 Leaf Soluble Carbohydrates Content (SC)

The method of Dubois et al. (1956) was used to measure the leaf SC. Leaf fresh weight (100 mg) was homogenized in 70% ethanol using a mortar and pestle. The soluble carbohydrate content was quantified using a glucose standard curve.

2.3.3 Leaf DPPH Assay

2,2-Diphenyl-1-picrylhydrazyl (DPPH) assay is the most commonly used antioxidant assay for plant extract. To measure DPPH (1,1-diphenyl-2-picrylhydrazyl) activity, the absorption was read at a wavelength of 517 nm spectrophotometrically. The rate of inhibition of radical activity was calculated using the standard curve of ascorbic acid solution (Abe et al. 1998).

2.3.4 Leaf Phenol Content

The method of Singleton and Rossi (1965) was used to measure leaf phenol content. The total phenol content was determined based on absorbance in A765 nm and gallic acid standard and reported as mg g^{-1} dry weight.

2.3.5 Ion Assay

The Na^+ and K^+ contents were determined by the standard Na^+ and K^+ solutions using a flame photometer (Jenway, UK). The ratio of sodium to potassium (Na^+/K^+) was also measured (Kapur et al. 2012; Tandon and Tandon 1993).

2.3.6 Fruit Vitamin C and Lycopene Content

Five grams of fruit samples were homogenized with 25 mL of metaphosphoric acid-acetic acid solution to determine fruit vitamin C content. A colored solution absorbance was taken at 521 nm (Kapur et al. 2012). The method of Munhuewyi (2012) was used to assay the lycopene quantification. The absorbance at (502 nm) was determined spectrophotometrically (Unico 2100, USA). The total lycopene was calculated using the following equation:

$$Total\ lycopene = \frac{OD502 \times 3.12}{mass\ of\ the\ sample\ (g)} \times 1000 \tag{1}$$

2.4 Harvesting and Fruit yield

At physiological ripening (86 days after planting), plants were harvested, and plant height, shoot and root dry weight (DW), root length and volume, shoot-to-root ratio (Sh/R), and leaf area (Li-3100 area meter; LICOR, Lincoln, NE) were measured. The number of fruits per plant, fresh and dry weight, and moisture content were also measured.

2.5 Statistical Analysis

The experiment was conducted in a factorial arrangement (three pH levels and five measurement times) based on a completely randomized design (CRD) with three replications. Statistical analysis was performed using SAS *v*. 9.4. The means were compared using the LSD test at 5% probability.

3 Results

3.1 Leaf Pigments Content

Leaf pigments content was assayed at 14-day intervals just before the onset of salinity and after 14, 28, 42, and 56 DAS at different pH levels (Fig. 1). Generally, the highest content of leaf chlorophyll *a* (*chla*) was recorded at pH 4.5 at day 0 but significantly decreased to 56 DAS (Fig. 1A). Leaf *chla* was the lowest in pH 4.5 at 56 DAS, which was less than the half value for pH 5.5 and ~ 85% lower than the control. However, at 56 DAS, the highest leaf chla was observed at pH 5.5 (Figs. 1A and 5). Although the salinity stress reduced leaf *chlb* to 56 DAS, the pH 5.5-treated plants showed the highest leaf *chlb* compared with pH 4.5 and the control (Fig. 1B).

Leaf chlorophyll *a/b* (*chla/b*) was the highest in pH 4.5 at zero and 14 DAS; however, it decreased to be the lowest at 56 DAS and was ~ 30% lower than pH 4.5 and 5.5. The pH 5.5-treated plants showed a constant leaf *a/b* at all times and had the highest value at 56 DAS (Fig. 1D). The interaction of pH × Time significantly affected leaf chlorophyll *a and b* (*chl a and b*) (Fig. 1E). Leaf *chl a and b* was decreased to 28 DAS, while it showed different behavior to 56 DAS; leaf *chl a and b* remained constant in the control plants, decreased in pH 4.5, and increased in the pH 5.5-treated plants to 56 DAS. The

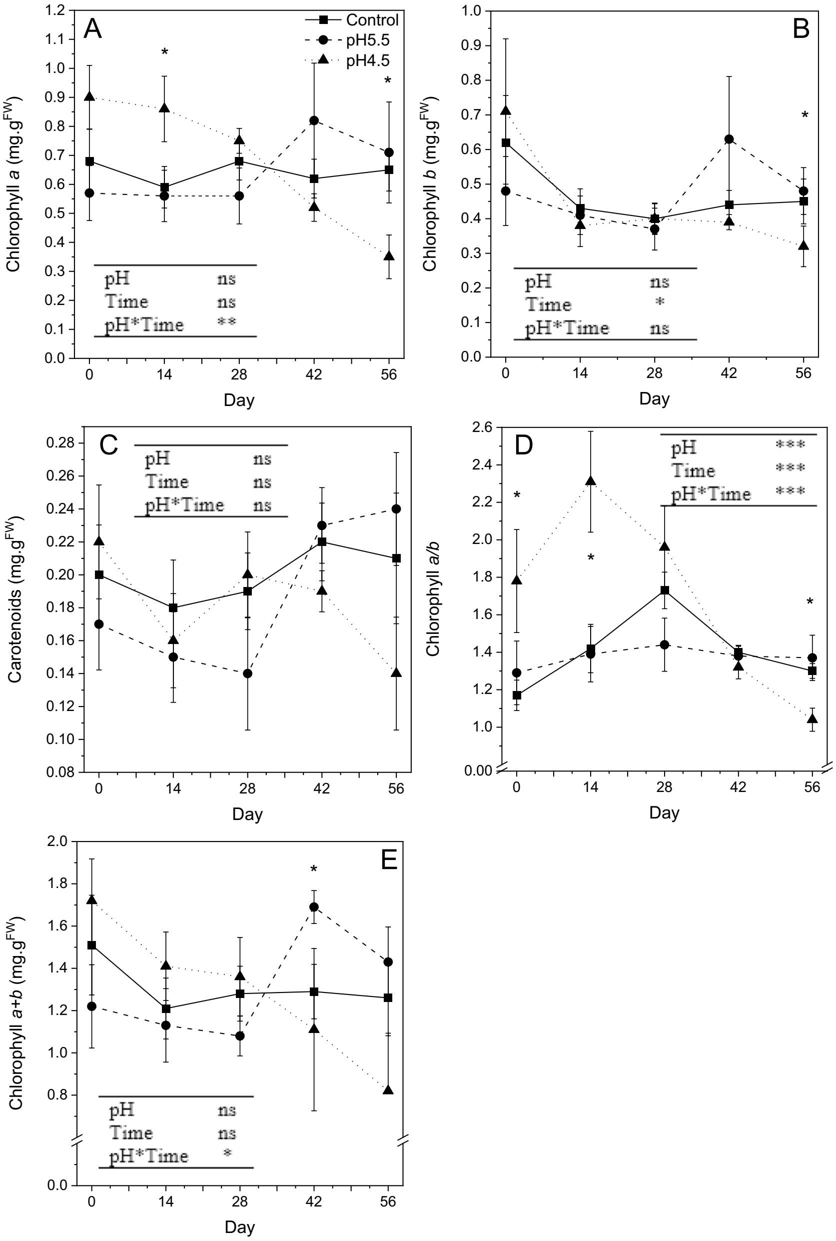

Fig. 1 Leaf **A** chlorophyll a, **B** chlorophyll b, **C** carotenoids, **D** chlorophyll a/b, and **E** chlorophyll a+b content of tomato plants grown at different medium pH under salinity stress. Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$, and vertical bars represent the differences between the control values and different measurement times. Data are means of six measurements ± SE. *, **, ***, and ns: significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$, and non-significant

highest leaf *chl a and b* was recorded in plants treated with pH 5.5 at 42 DAS by a 56% increase compared with 28 DAS (Figs. 1E and 5).

3.2 Leaf Soluble Carbohydrates Content (SC)

Leaf SC was affected by the time (Fig. 2A). Generally, leaf SC was decreased by increasing the intensity of salinity stress; for instance, leaf SC was decreased by ~ 100% from day 0 to 56 DAS. However, after a drastic decrease from day 0 to 14 DAS, leaf SC was increased by ~ 2-fold in pH 4.5 and the control to 28 DAS (Figs. 2A and 5). At 28 DAS, plants treated with pH 4.5 showed the highest leaf SC (Fig. 2A).

3.3 Leaf DPPH Activity

Leaf DPPH activity was significantly increased to 56 DAS (Fig. 2B). The control plants showed the highest leaf DPPH by ~ 55% greater activity at 28 DAS than at pH 5.5 and 4.5 (Fig. 5). Acidic pH-grown plants showed the lowest leaf DPPH activities at 28, 42, and 56 DAS, indicating the effects of lowering medium pH to ameliorate the salinity effects. The highest leaf DPPH activity at all pH levels was obtained from 42 DAS; however, it decreased to 56 DAS.

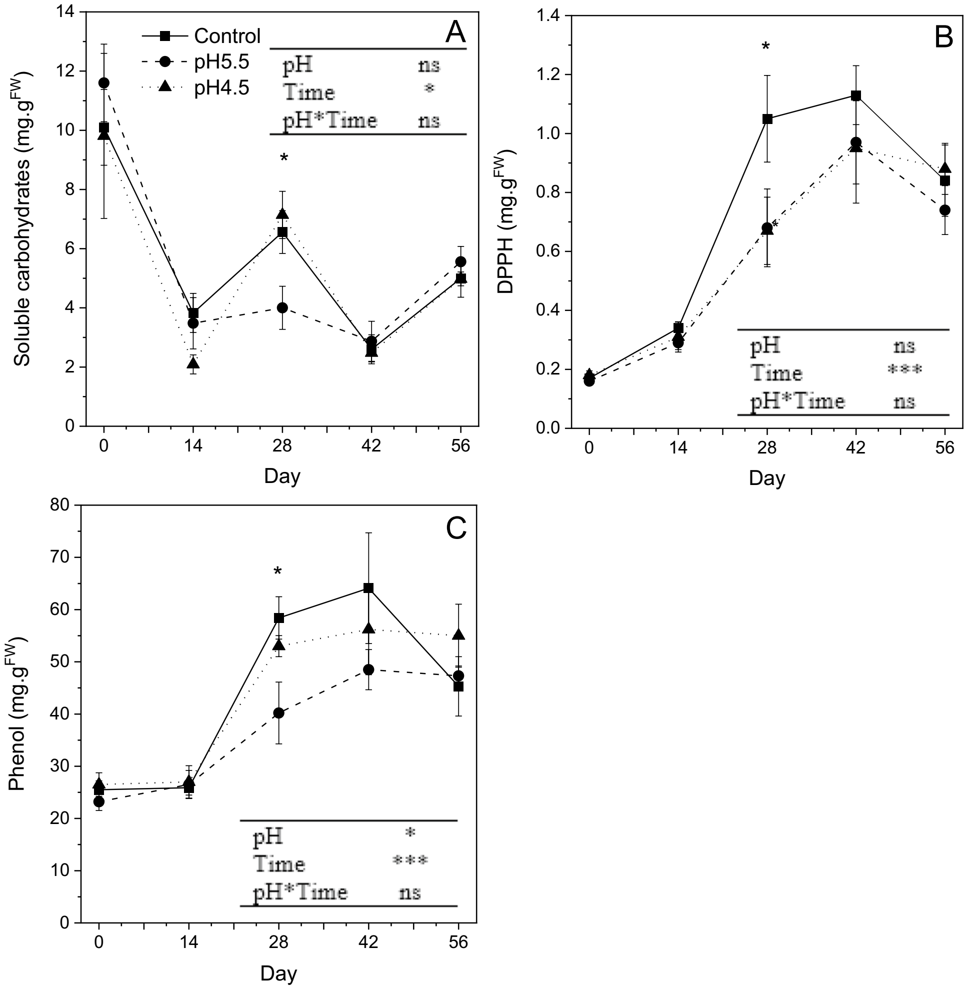

Fig. 2 Leaf **A** soluble carbohydrates, **B** 2,2-diphenyl-1-picryl-hydrazyl (DPPH), and **C** phenol content of tomato plants grown at different medium pH under salinity stress. Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$, and vertical bars represent the differences between the control values and different measurement times. Data are means of six measurements ± SE. *, **, ***, and ns: significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$, and non-significant

3.4 Leaf Phenol Content

Time and the medium pH affected leaf phenol content (Fig. 2C). Similar to the DPPH activity, leaf phenol content also showed an ascending trend to the last measurement time. The highest leaf phenol content at all pH levels was obtained from 42 DAS; however, it decreased to 56 DAS. The highest leaf phenol content was recorded at 28 DAS in the plants grown under the control pH by an increase of 45% compared with pH 5.5 (Fig. 5). The plants grown at pH 5.5 showed the lowest leaf phenol content, which was significantly lower compared with pH 4.5 and the control at 28 DAS.

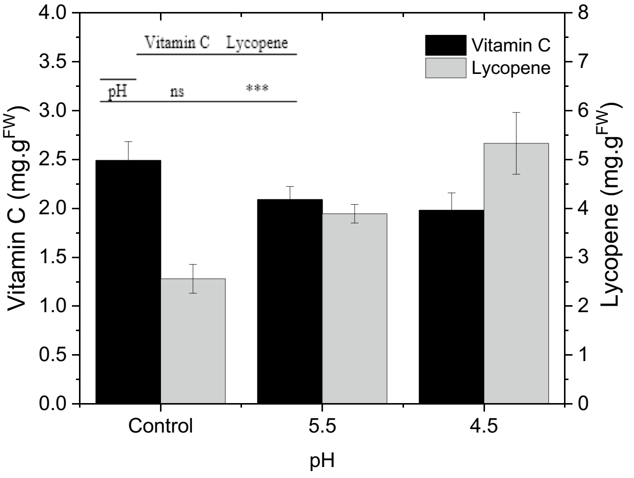

Fig. 3 Fruit vitamin C and lycopene content of tomato plants grown at different medium pH under salinity stress. Vertical bars represent significant differences between the pH levels at $p \leq 0.05$. ± SE. Data are means of six measurements. ***, and ns: significant at $p \leq 0.001$, and non-significant

3.5 Fruit Vitamin C and Lycopene Content

Although fruit vitamin C was not affected by the medium pH, it showed a descending trend by lowering the pH (Fig. 3). Fruit lycopene content was affected by the medium pH. Fruit lycopene content, in comparison, increased by lowering the medium pH. The highest fruit lycopene content was obtained from pH 4.5, which was ~ 110 and 37% higher than the control and pH 5.5, respectively (Fig. 5).

3.6 Ion Assay

The results indicated that shoot and root K^+ content and root Na^+/K^+ ratio were affected by the medium pH (Table 1). Lowering the medium pH increased the shoot and root K^+ content; however, Na^+ content was not affected by the pH treatments. It indicated that the alteration in the Na^+/K^+ ratio was mainly due to the changes in K^+ content. The highest shoot K^+ content was recorded in pH 4.5 by a 26% increase compared with the control. However, plants grown under pH 5.5 showed the highest root K^+ content and the lowest root Na^+/K^+ ratio by 72 and 33%, respectively, compared with the control (Fig. 5).

3.7 Growth Parameters

Leaf area, shoot and root dry weight, and root length were affected by the medium pH (Table 2). The highest leaf area, shoot and root DW, and root length were observed in pH 5.5, which were 100, 23, 8, and 32%, respectively, greater than the control (Fig. 5). Lowering the medium pH to 4.5 reduced the growth parameters to values less than the control.

3.8 Fruit Yield

The medium pH affected the number of fruits and fruit DW. Nevertheless, the fresh weight and moisture percentage of fruits were not influenced by the medium pH (Fig. 4). Plants grown under pH 5.5 showed the greatest number of fruits and fruit DW. Lowering the medium pH to 5.5 increased the number of fruits and fruits DW by 77 and 32%, respectively, compared with the control (Figs. 4 and 5). However, the number of fruit was significantly reduced at pH 4.5.

4 Discussion

Salinization profoundly affects nutrient behavior and the electrochemical properties of soils. Salinity increases ionic strength, which consequently suppresses the activity coefficients of ions in solution, leading to increasing the pH values. Higher pH directly reduces root activity, leaf water content, and nutrient absorption (Kaiwen et al. 2020). In a

Table 1 Leaf and root sodium (Na^+) and potassium (K^+) content and sodium to potassium ratio (Na^+/K^+) of tomato plants grown at different medium pH levels under salinity stress

	Shoot Na^+	Shoot K^+	Shoot Na^+/ K^+	Root Na^+	Root K^+	Root Na^+/ K^+
pH	(mg.g^{DW-1})	(mg.g^{DW-1})		(mg.g^{DW-1})	(mg.g^{DW-1})	
Control	13.6 ± 1.30	16.6 ± 0.86	0.84 ± 0.11	17.1 ± 1.80	7.49 ± 0.57	2.32 ± 0.24
5.5	14.8 ± 0.73	19.7 ± 0.62	0.75 ± 0.04	19.2 ± 1.65	12.9 ± 1.31	1.54 ± 0.12
4.5	16.4 ± 2.79	20.9 ± 1.07	0.83 ± 0.17	16.1 ± 1.76	8.27 ± 0.65	2.09 ± 0.33
$LSD_{0.05}$	5.3	2.57	0.35	5.1	2.67	0.72
ANOVA						
pH	ns	**	ns	ns	***	*
CV (%)	16.3	6.4	12.8	13.6	12.4	13.4

*, **, ***, and ns: significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$, and non-significant. *CV*, coefficient of variation

Table 2 Growth parameters and fruit yield traits of tomato plants grown at different medium pH levels under salinity stress

	Plant height	Leaf area	Shoot DW	Root length	Root volume	Root DW	Shoot/root
pH	(cm)	(m^2.plant^{-1})	(g.plant^{-1})	(cm)	(cm^3.plant^{-1})	(g.plant^{-1})	
Control	54.0 ± 2.49	10.7 ± 0.77	50.8 ± 3.59	34.7 ± 1.66	38.1 ± 3.40	4.6 ± 0.44	11.2 ± 0.72
5.5	59.3 ± 2.40	21.9 ± 6.22	62.7 ± 3.68	37.5 ± 1.64	44.3 ± 1.75	6.1 ± 0.34	10.3 ± 0.47
4.5	50.5 ± 3.49	13.5 ± 0.53	42.6 ± 3.45	31.1 ± 1.41	36.8 ± 4.00	4.4 ± 0.49	9.9 ± 0.50
$LSD_{0.05}$	8.1	10.6	10.5	4.6	9.3	1.2	1.6
ANOVA							
pH	ns	*	**	*	ns	*	ns
CV (%)	7.5	23.7	9.8	6.3	11.3	11.3	7.3

*, **, ***, and ns: significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$, and non-significant. *CV*, coefficient of variation

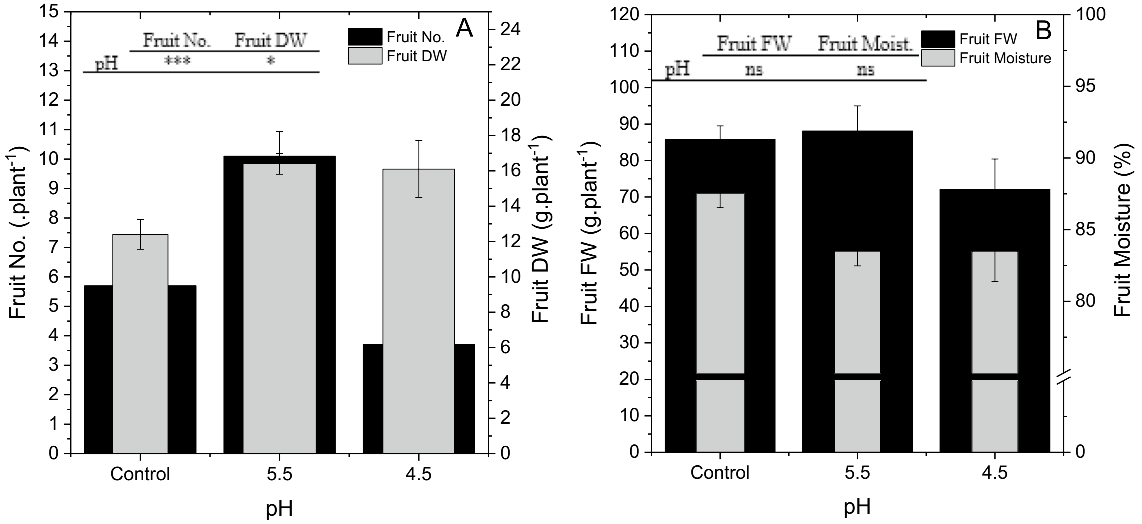

Fig. 4 Fruit yield parameters of tomato plants grown at different medium pH under salinity stress. Vertical bars represent significant differences between the pH levels at $p \leq 0.05$. ± SE. Data are means of six measurements. *, ***, and ns: significant at $p \leq 0.05$, $p \leq 0.001$, and non-significant. CV, coefficient of variation. No: number; DW: dry weight; FW: fresh weight; moist: moisture

hydroponic environment, the acidity of nutrient solutions and growth medium is important in two respects; first, it affects the oxidation-reduction balance, solubility, and ionic form of the elements. Second, it affects ion uptake by affecting H^+ and OH^- ions in plant roots, especially cell membranes ion transporter (Epstein and Bloom 2005).

The degradation rate of chlorophyll *a* has been reported under low acidity conditions, which is 2.5 times higher than that of chlorophyll *b* (Gunawan and Barringer 2000). Accordingly, in the present study, it was also observed that leaf *chla* was significantly decreased to day 56th under pH 4.5. Therefore, leaf *chla/b* was decreased by decreasing pH to 4.5. Leaf chlorophyll content was improved by lowering the medium pH under salinity stress. Plants treated with pH 5.5 showed the highest leaf *chl a and b*. Positive correlations were observed between leaf *chl a and b*, fruit number, and root and shoot DW (Fig. 6). Iron, zinc, and manganese shortage significantly decreased the contents of photosynthetic pigments in lettuce plants (Roosta et al. 2018). Fe, Zn, and Mn are directly implicated in the photosynthetic procedure. For instance, cytochrome and ferredoxin contain Fe, which participates in the electron transport chain, oxidation, and reduction reactions (Barker and Pilbeam 2015). Zn and Mn are also a part of enzymatic redox reactions and enable water splitting in PSII (Aravind and Prasad 2004; Roosta et al. 2018). Fe, Zn, and Mn deficiencies lead to the D_1 protein decomposition in the PSII reaction center (Bertamini et al. 2001). However, those elements are less available in alkaline pH and may adversely affect the chloroplast proteins, concentration of *Chl*, and photochemical efficiency. Leaf chlorophyll content is an important indicator of the rate of photosynthesis (Koca et al. 2007). Keshmiri et al. (2018) observed a positive correlation between leaf chlorophyll content and photosynthetic rate in potato plants. Lowering the medium pH diminished the negative effect of salinity on leaf chlorophyll fluorescence of tomato plants; it improved the maximum quantum yield and photochemical quenching, the fraction of photons used in photochemistry, and the efficiency of electron transport (Nabati et al. 2021).

Salinity stress imposes ion imbalance in plant cells (Munns and Tester 2008). In the present study, lowering the medium pH increased K^+ concentration in tomato roots and leaves under saline conditions. Although the high salinity in the medium enhanced the Na^+/K^+, lowering the medium pH to 5.5 reduced the Na^+/K^+ compared with the control resulting from the increased K^+ concentration in plant tissues. Salinity increases the medium pH, and some nutrients might be less available at alkaline pH. At high salt concentrations, alkaline pH damaged the leaf photosynthetic function and the root system of alfalfa (*Medicago sativa*) plants, which was mainly related to the greater damage of higher pH levels on roots and limitation of water and nutrients absorption rather than the increase of Na^+ absorption (Kaiwen et al. 2020).

Root K^+ showed a positive correlation with plant growth and fruit yield. Potassium (K^+) is an essential macronutrient that plays a critical role in stomatal opening adjustment, osmotic adjustment, enzyme activation, and cytoplasmatic pH homeostasis (Almeida et al. 2017; Barragán et al. 2012). The Na^+ and K^+ ions are similar in ionic radius and hydration energy. Na^+ competes with K^+ for binding the key metabolic processes in the cytoplasm, such as enzymatic reactions, protein synthesis, and ribosome functions, leading to the dysfunction of many enzymes that need K^+ for proper functioning (Almeida et al. 2017;

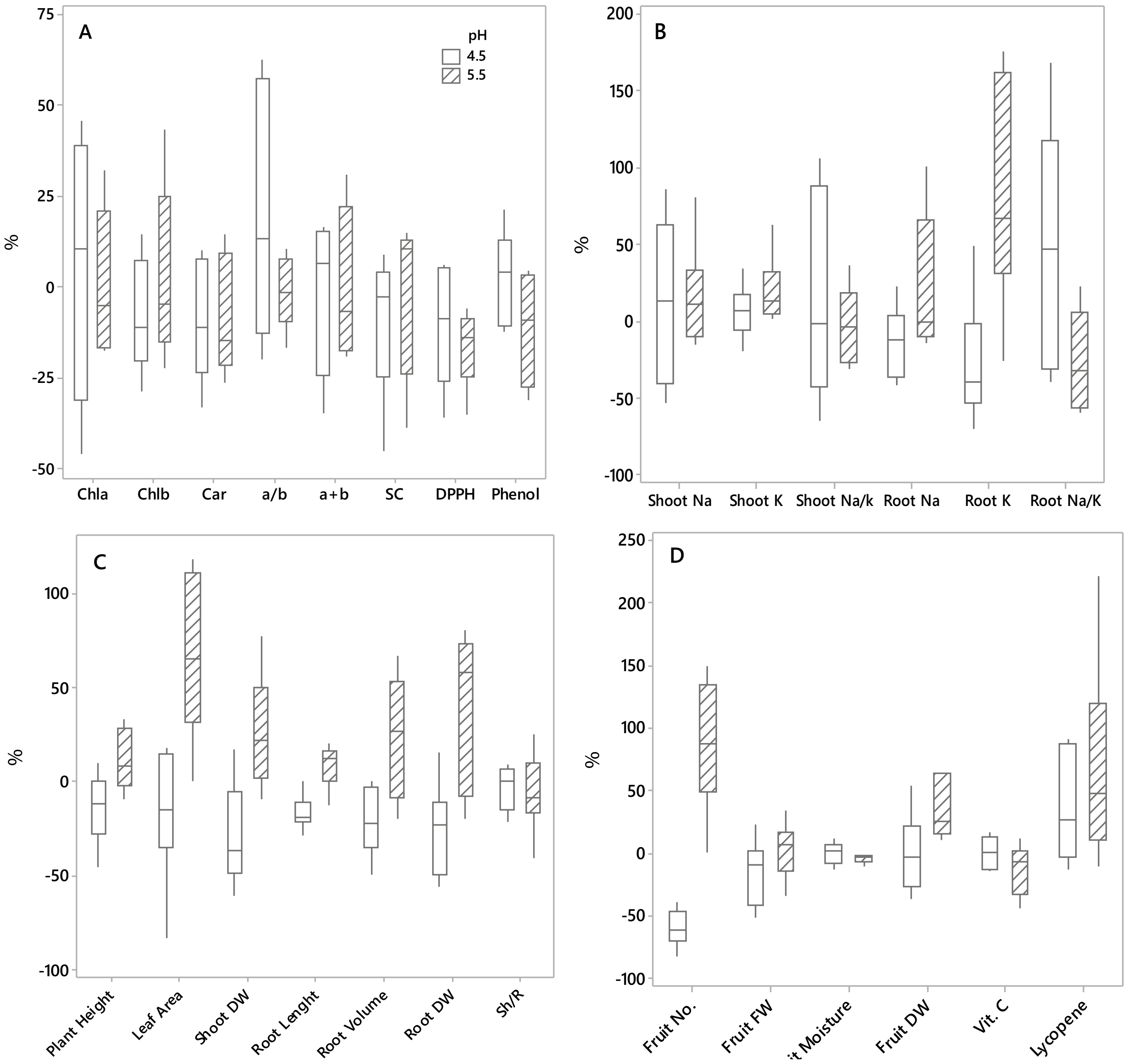

Fig. 5 Percent changes of biochemical and growth parameters of tomato plants affected by the medium pH compared to the control using the formula [(pH "5.5 or 4.5" − control)/(control)] × 100). Chla: chlorophyll a; Chlb: chlorophyll b; Car: carotenoids; a/b: chlorophyll a/b; a+b: chlorophyll a+b; DPPH: 2,2-diphenyl-1-picrylhydrazyl; DW: dry weight; Sh/R: shoot to root ratio; FW: fresh weight; Vit. C: vitamin C

Marschner 2011). Chuamnakthong et al. (2019) found that rice plants accumulated more Na^+ at pH 8.0 than at pH 7.0 under saline-alkaline conditions, suggesting that high pH promotes Na^+ accumulation in rice. High pH under saline conditions reduced the K^+ absorption ability of rice (*Oryza sativa*) varieties, resulting from their effects on the expression levels of the genes encoding K^+ channels and transporters (*OsAKT1*, *OsHAK5*, *OsHAK7*, *OsHAK10*, and *OsHAK16*) (Nampei et al. 2021). Placing sodium in the vacuole and removing it from the cytosol by the Na^+/H^+ antiporters can maintain the sodium concentrations low in plant tissues (Zhu and Gong 2014). The lower vacuole pH (pH 5.5) and higher Ca^{2+} concentration led to a higher K^+/H^+ exchange activity over Na^+/H^+ (Yamaguchi et al. 2003).

Salinity, through instigating the membrane lipid peroxidation and oxidative damage, may increase ROS production (Kafi et al. 2021; Wang et al. 2013). Xing et al. (2015) observed that SOD and CAT activity significantly increased by increasing the salinity stress intensity. In the present study, leaf phenol and DPPH were increased by increasing

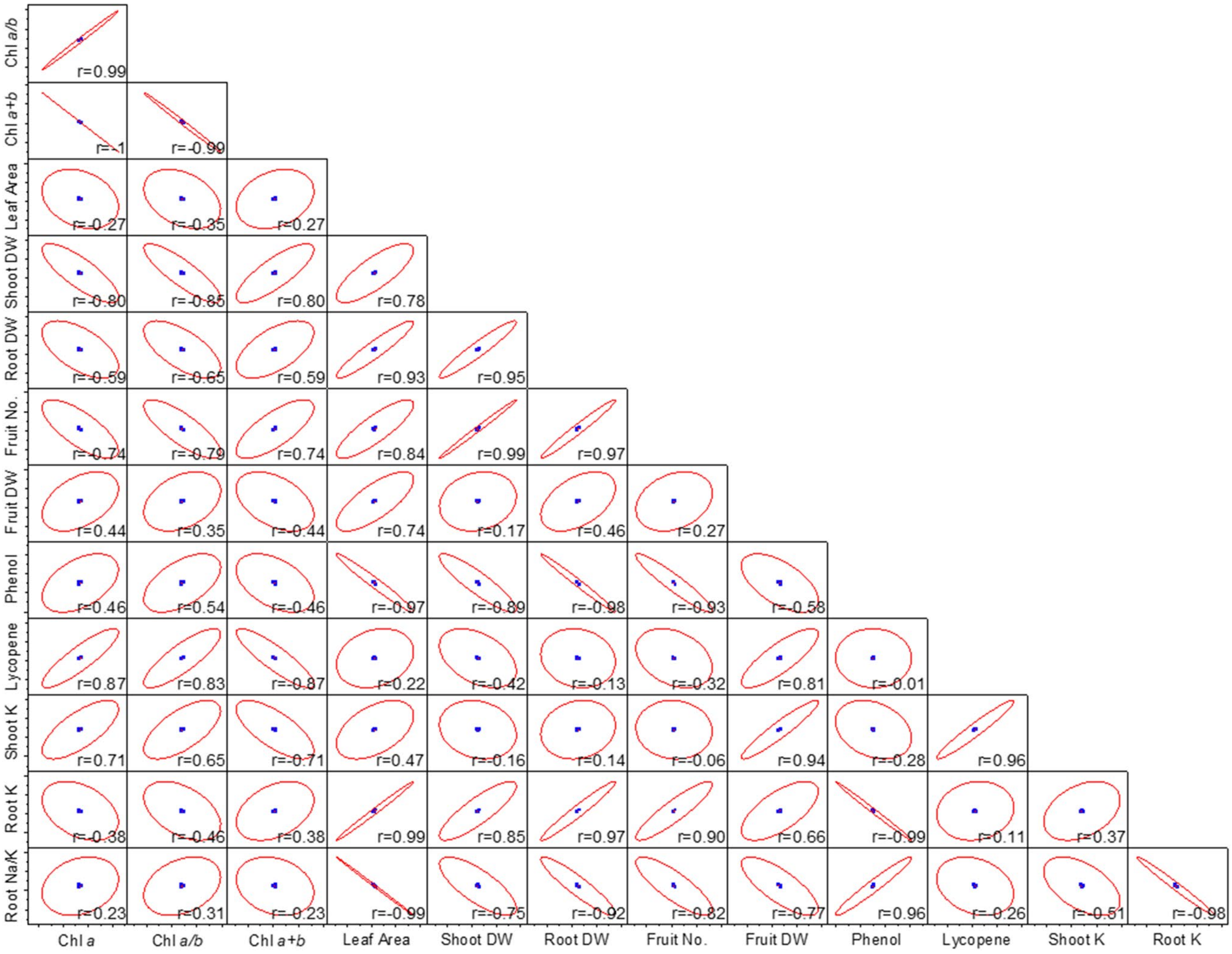

Fig. 6 Pearson's correlation coefficient of the biochemical and growth parameters of tomato plants at different pH under salinity stress. Chl: leaf chlorophyll; DW: dry weight; No: number; K: potassium

the salinity exposure and intensity; however, lowering the medium pH decreased their content and activities. DPPH assay is the most commonly used antioxidant assay for plant extract. Increasing the activities of antioxidants can indicate that the plants are under stress and require enhancing their defense systems to combat stressful conditions. The acidic medium pH could mitigate the adverse effects of salinity on lipid peroxidation and ROS production.

Leaf phenol content was negatively correlated with the shoot and root DW, leaf area, fruit number, and fruit DW (Fig. 6). Hejazi Mehrizi et al. (2012) observed that total phenolic content in rosemary (*Rosmarinus officinalis* L., Lamiaceae) leaves was greatly enhanced by salinity. They concluded that enhanced phenolic biosynthesis induced by salinity stress provided a further resource partitioning pattern for carbon and led to a reduction in plant growth. However, the DW and number of fruit were improved by lowering the medium pH, probably due to the decreased phenol content and increased C partitioning to vegetative and reproductive tissues. Bistgani et al. (2019) also observed that the total phenol content of *Thymus vulgaris* and *Thymus daenensis* increased under salinity stress compared with control plants. Phenolic compound production is influenced by environmental factors and plant genetics (Awika and Rooney 2004). The moderate salinity stress induces a saline tolerance pathway in plants by enhancing the total phenolic compounds (Salem et al. 2014). Phenolic compounds contribute to the antioxidant capacity of plants and play a critical role in the defense against biotic and abiotic stresses, and they can mitigate oxidative stress and scavenge the reactive oxygen species (ROS) as antioxidants in different plants tissues (Caprioli et al. 2018; Jabri Karoui et al. 2016; Kleinwächter and Selmar 2014).

The results showed that the leaf area decreased with increasing salinity intensity. Reducing leaf growth is the primary response of plants to salinity, resulting from the reduction of water content in plant tissues (Nabati et al. 2021). In other words, salinity increases the energy required to maintain the normal state of the cell; as a result, less energy is left for growth (Kafi et al. 2021). However, lowering the medium pH to 5.5 significantly increased leaf LA. Velikova et al. (1998) found that lowering the nutrient solution acidity from 5.6 to 1.8 reduced the transpiration rate of bean (*Phaseolus vulgaris*) plants, which increased the leaf water content, leading to higher cell pressure, expiation, and division. Leaf development was also slower at pH 7 compared with pH 6–5 in *Ambrosia artemisiifolia* L. (Gentili et al. 2018).

Shoot and root DW were also increased by lowering the medium pH to 5.5. Working on *Citrus* spp., Long et al. (2017) also found that the highest plant dry weight was observed in sub-acidic pH (pH 5–6), which was due to higher N, P, K, Ca, and Mg availability for plants. Although the Sh/R was not affected by the medium pH, it showed a descending trend by lowering the pH, indicating that acidic pH reduced the shoot more than root growth. Salt accumulation in plant tissues restricts the CO_2 supply and inhibits the leaf photosynthetic rate (Mahmoud et al. 2019). Any decrease in leaf photosynthesis may interrupt the production of photoassimilates and adversely affect the biochemical processes. In *Arabidopsis thaliana*, a slower growth rate was correlated with reduced photosynthetic efficiency in different populations (Tessmer et al. 2013). Soil pH influences the availability and uptake of micronutrients; for instance, Mg is implicated in the plant's photosynthetic efficiency. At high pH, however, Ca and Mg tend to form less or not available compounds when reacting with P and many micronutrients (Dighton and Krumins 2014; Gentili et al. 2018).

The absorption of nutrients, photosynthetic efficiency, and plant growth could be optimized by the proper acidity of the nutrient solution (Nabati et al. 2021). The medium pH plays a significant role in the solubilization and availability of nutrients in the root zone. Microorganism activity and the water solubility of some nutrients are increased by lowering the nutrient solution pH (Gentili et al. 2018). The availability of micronutrients is reduced in alkaline pH and can adversely affect plant growth, including height, lateral spread, biomass, flower size and number, and pollen production (Jiang et al. 2016). Narrow-leaf lupine (*Lupinus angustifolius*) plants grown at acidic pH (4.5) had a higher specific root length compared with those grown at alkaline or neutral pH (Robles-Aguilar et al. 2019). This might be a beneficial trait to increase P uptake in acidic pH (Hill et al. 2006).

Saline conditions reduced the plant growth and fruit attributes. However, fruit number, DW, and lycopene content tended to increase by lowering the medium pH. It was observed that salinity decreased fruit yield, mean fruit weight, and leaf area index in tomato (*Solanum lycopersicum*) plants; however, the fruit dry matter percentage was increased (Layegh et al. 2009). Tuber production in potato (*Solanum tuberosum*) plants was increased by lowering the nutrient solution pH to 5.5 (Wan et al. 1994). Gentili et al. (2018) observed that the number and size of inflorescences of *A. artemisiifolia* were increased with plant dry weight at acidic pH. Decreasing the medium acidity might stimulate the photoassimilates allocation to the physiological sinks, and greater availability of nutrients can enhance plant productivity.

5 Conclusions

Saline conditions adversely affected tomato plant biochemistry, growth, and fruit attributes. However, the medium pH adjustment beneficially alleviated the effects of salinity on tomato plants. Lowering the medium pH diminished the adverse effects of salinity on such traits as leaf chlorophyll, phenol, DPPH, lycopene, Na^+/K^+, and fruit yield. Briefly, the ameliorating effects of the medium pH adjustment on tomato plant performance can be due to (a) the improved leaf chlorophyll content that affects the photosynthetic performance; (b) the lower root and shoot Na^+/K^+ ratio; (c) the lower detrimental effects of salinity on lipid peroxidation, which can be elucidated from the reduced leaf DPPH and phenol content under acidic pH; and (d) the increased fruit dry weight and fruit number resulting from improved salinity tolerance of the plants. Generally, lowering the medium pH to 5.5 enhanced the salinity tolerance of tomato plants. It can be considered to reduce the adverse effects of salinity on the growth and yield of tomato plants.

Data Availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Abe N, Murata T, Hirota A (1998) 'Novel 1, 1-diphenyl-2-picryhy-drazyl-radical scavengers, bisorbicillin and demethyltrichodimerol, from a fungus'. Biosci Biotechnol Biochem 62:61–662

Almeida DM, Oliveira MM, Saibo NJ (2017) Regulation of Na^+ and K^+ homeostasis in plants: towards improved salt stress tolerance in crop plants. Genet Mol Biol 40:326–345

Aravind P, Prasad M (2004) Zinc protects chloroplasts and associated photochemical functions in cadmium exposed *Ceratophyllum demersum* L., a freshwater macrophyte. Plant Sci 166:1321–1327

Awika JM, Rooney LW (2004) Sorghum phytochemicals and their potential impact on human health. Phytochem 65:1199–1221

Barker AV, Pilbeam DJ (2015) Handbook of plant nutrition. CRC press

Barragán V et al (2012) Ion exchangers NHX1 and NHX2 mediate active potassium uptake into vacuoles to regulate cell turgor and stomatal function in *Arabidopsis*. Plant Cell 24:1127–1142

Bertamini M, Nedunchezhian N, Borghi B (2001) Effect of iron deficiency induced changes on photosynthetic pigments, ribulose-1, 5-bisphosphate carboxylase, and photosystem activities in field grown grapevine (*Vitis vinifera* L. *cv*. Pinot noir) leaves. Photosynthetica 39:59–65

Bistgani ZE, Hashemi M, DaCosta M, Craker L, Maggi F, Morshedloo MR (2019) Effect of salinity stress on the physiological characteristics, phenolic compounds and antioxidant activity of *Thymus vulgaris* L. and *Thymus daenensis* Celak. Ind Crop Prod 135:311–320

Caprioli G et al (2018) Thymus lanceolatus ethanolic extract protects human cells from t-BHP induced oxidative damage. Food Funct 9:3665–3672

Chuamnakthong S, Nampei M, Ueda A (2019) Characterization of Na^+ exclusion mechanism in rice under saline-alkaline stress conditions. Plant Sci 287:110171

Dighton J, Krumins JA (2014) Interactions in soil: promoting plant growth, vol 1. Springer

Dubois M, Gilles KA, Hamilton JK, Pt R, Smith F (1956) Colorimetric method for determination of sugars and related substances. Anal Chem 28:350–356

Epstein E, Bloom A (2005) Mineral nutrition of plants: principles and perspectives Inc. Sinauer Assoc, Sunderland, UK

Fang S, Hou X, Liang X (2021) Response mechanisms of plants under saline-alkali stress. Front Plant Sci 12:667458

FAO (2022) Food and agriculture organization of the United Nations. Italy, Rome

Feleafel MN, Mirdad ZM (2014) Alleviating the deleterious effects of water salinity on greenhouse grown tomato. Int J Agric Biol 16

Gentili R, Ambrosini R, Montagnani C, Caronni S, Citterio S (2018) Effect of soil pH on the growth, reproductive investment and pollen allergenicity of *Ambrosia artemisiifolia* L. Front Plant Sci 9:1335

Ghanem ME et al (2008) Hormonal changes during salinity-induced leaf senescence in tomato (*Solanum lycopersicum* L.). J Exp Bot 59:3039–3050

Gunawan MI, Barringer SA (2000) Green color degradation of blanched broccoli (*Brassica oleracea*) due to acid and microbial growth. J Food Process Preserv 24:253–263

Hejazi Mehrizi M, Shariatmadari H, Khoshgoftarmanesh A, Dehghani F (2012) Copper effects on growth, lipid peroxidation, and total phenolic content of rosemary leaves under salinity stress. J Agric Sci Technol 14:205–212

Hill J, Simpson R, Moore A, Chapman D (2006) Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. Plant Soil 286:7–19

Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil, vol 347. Circular. California agricultural experiment station

Jabri Karoui I, Msaada K, Abderrabba M, Marzouk B (2016) Bioactive compounds and antioxidant activities of thyme-enriched refined corn oil. J Agric Sci Technol 18:79–91

Jiang Y, Li Y, Zeng Q, Wei J, Yu H (2016) The effect of soil pH on plant growth, leaf chlorophyll fluorescence and mineral element content of two blueberries, vol 1180. XI International Vaccinium Symposium, pp 269–276

Jones JB Jr (2007) Tomato plant culture: in the field, greenhouse, and home garden. CRC press

Kafi M, Nabati J, Ahmadi-Lahijani MJ, Oskoueian A (2021) Silicon compounds and potassium sulfate improve salinity tolerance of potato plants through instigating the defense mechanisms, cell membrane stability, and accumulation of osmolytes. Commun Soil Sci Plant Anal 52:843–858

Kaiwen G et al (2020) Effects of salt concentration, pH, and their interaction on plant growth, nutrient uptake, and photochemistry of alfalfa (Medicago sativa) leaves. Plant Signal Behav 15:1832373

Kapur A, Hasković A, Čopra-Janićijević A, Klepo L, Topčagić A, Tahirović I, Sofić E (2012) Spectrophotometric analysis of total ascorbic acid content in various fruits and vegetables. Glas Hem Tehnol Bosne Herceg 38:39–42

Keshmiri E, Kafi M, Parsa M, Nabati J, Zare Mehrjerdi M (2018) Effect of various levels of nitrogen fertilizer and the nutrient solution acidity on the physiological characteristics and mini tuber production of potato (*Solanum Tuberosum* L.). Crop Physiol 10:97–118

Kiferle C, Gonzali S, Beltrami S, Martinelli M, Hora K, Holwerda HT, Perata P (2022) Improvement in fruit yield and tolerance to salinity of tomato plants fertigated with micronutrient amounts of iodine. Sci Rep 12:14655

Kleinwächter M, Selmar D (2014) Influencing the product quality by applying drought stress during the cultivation of medicinal plants. In: Physiological mechanisms and adaptation strategies in plants under changing environment. Springer, pp 57–73

Koca N, Karadeniz F, Burdurlu HS (2007) Effect of pH on chlorophyll degradation and colour loss in blanched green peas. Food Chem 100:609–615

Layegh M, Pyvast GHA, Samie Zadeh HAK, M. (2009) Effect of nutrient solution salinity on growth, yield and quality traits in tomato soilless culture. J Hort Sci 40:11–21

Li YL, Stanghellini C, Challa H (2001) Effect of electrical conductivity and transpiration on production of greenhouse tomato (*Lycopersicon esculentum* L.). Sci Hortic 88:11–29

Lichtenthaler HK, Wellburn AR (1983) Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. Portland Press Ltd

Long A et al (2017) Effects of low pH on photosynthesis, related physiological parameters, and nutrient profiles of citrus. Front Plant Sci 8:185

Mahmoud AWM, Abdeldaym EA, Abdelaziz SM, El-Sawy MB, Mottaleb SA (2019) Synergetic effects of zinc, boron, silicon, and zeolite nanoparticles on confer tolerance in potato plants subjected to salinity. Agron 10:19

Marschner H (2011) Marschner's mineral nutrition of higher plants. Academic press

Martinez-Rodriguez MM et al (2008) The effectiveness of grafting to improve salt tolerance in tomato when an 'excluder'genotype is used as scion. Environ Exp Bot 63:392–401

Munhuewyi K (2012) Postharvest losses and changes in quality of vegetables from retail to consumer: a case study of tomato, cabbage and carrot. Stellenbosch University, Stellenbosch

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Ann Rev Plant biology 59:651

Nabati J, Ahmadi-Lahijani MJ, Goldani M, Nezami A, Oskoueian A, Hosinaiyan M, Mohammadi M (2021) Lowering medium pH improves tolerance of tomato (*Lycopersicon esculentum*) plants to long-term salinity exposure. J Plant Nutr 44:1853–1868

Nampei M, Jiadkong K, Chuamnakthong S, Wangsawang T, Sreewongchai T, Ueda A (2021) Different rhizospheric pH conditions affect nutrient accumulations in rice under salinity stress. Plant 10:1295

Plaut Z, Grava A, Yehezkel C, Matan E (2004) How do salinity and water stress affect transport of water, assimilates and ions to tomato fruits? Physiol Plant 122:429–442

Putra PA, Yuliando H (2015) Soilless culture system to support water use efficiency and product quality: a review. Agric Agric Sci Proc 3:283–288

Raza A et al (2022) Smart reprograming of plants against salinity stress using modern biotechnological tools. Crit Rev Biotechnol:1–28

Robles-Aguilar AA, Pang J, Postma JA, Schrey SD, Lambers H, Jablonowski ND (2019) The effect of pH on morphological and physiological root traits of *Lupinus angustifolius* treated with struvite as a recycled phosphorus source. Plant Soil 434:65–78

Roosta H, Estaji A, Niknam F (2018) Effect of iron, zinc and manganese shortage-induced change on photosynthetic pigments, some osmoregulators and chlorophyll fluorescence parameters in lettuce. Photosynthetica 56:606–615

Ruban AV, Johnson MP, Duffy CD (2012) The photoprotective molecular switch in the photosystem II antenna. Biochim Biophys Acta (BBA)-Bioenerg 1817:167–181

Sajjadinia A, Ershadi A, Roosta H (2010) Comparison of eco-physiological characteristics of pepper in hydroponic and aquaponic systems. J Soil Plant Interact-Isfahan Univ Technol 1:1–8

Salem N, Msaada K, Dhifi W, Limam F, Marzouk B (2014) Effect of salinity on plant growth and biological activities of *Carthamus tinctorius* L. extracts at two flowering stages. Acta Physiol Plant 36:433–445

Signore A, Serio F, Santamaria P (2016) A targeted management of the nutrient solution in a soilless tomato crop according to plant needs. Front Plant Sci 7:391

Singleton VL, Rossi JA (1965) Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. Am J Enol Vitic 16:144–158

Tandon HLS, Tandon H (1993) Methods of analysis of soils, plants, waters, and fertilisers. Fertiliser Development and Consultation Organisation, New Delhi

Tessmer OL, Jiao Y, Cruz JA, Kramer DM, Chen J (2013) Functional approach to high-throughput plant growth analysis. BMC Syst Biol 7:1–13

Velikova V, Yordanov I, Kurteva M, Tsonev T (1998) Effects of simulated acid rain on the photosynthetic characteristics of *Phaseolus vulgaris* L. Photosynthetica 34:523–535

Wan WY, Cao W, Tibbitts TW (1994) Tuber initiation in hydroponically grown potatoes by alteration of solution pH. HortSci 29:621–623

Wang Q, Liang X, Dong Y, Xu L, Zhang X, Kong J, Liu S (2013) Effects of exogenous salicylic acid and nitric oxide on physiological characteristics of perennial ryegrass under cadmium stress. J Plant Growth Regul 32:721–731

Xing Y, Chen W-h, Jia W, Zhang J (2015) Mitogen-activated protein kinase kinase 5 (MKK5)-mediated signalling cascade regulates expression of iron superoxide dismutase gene in Arabidopsis under salinity stress. J Exp Bot 66:5971–5981

Yamaguchi T, Apse MP, Shi H, Blumwald E (2003) Topological analysis of a plant vacuolar Na^+/H^+ antiporter reveals a luminal C terminus that regulates antiporter cation selectivity. Proc Natl Acad Sci 100:12510–12515

Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. Agron Sustain Dev 34:455–472