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Lowering medium pH improves tolerance of tomato (*Lycopersicon esculentum*) plants to long-term salinity exposure

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ABSTRACT

Although salinity stress adversely affects plant function, manipulation of the rhizosphere may alleviate those negative impacts. We examined whether adjustment of rhizosphere pH, unadjusted control (~pH 8.5–9), pH 5.5, and pH 4.5 would mitigate adverse effects of salinity on tomato plants (cv. Mobil) in hydroponics. Plants were evaluated based on the leaf chlorophyll parameters, plant survival, leaf water relations, and yield. Chlorophyll fluorescence parameters were lowest at 28 days after salinity onset (DAS). The maximum PSII quantum yield (F_v'/F_m') and operating efficiency (ΦPSII) were recorded in plants grown in pH 4.5 at 56 DAS. At 28 DAS, the linear electron transport rate (*J*) was decreased by 10 and 13%, in control and pH 5.5, respectively, compared with the day zero. The fraction of photons used in photochemistry (%*P*) was suppressed at 28 DAS, but %*P* was the greatest under 4.5 pH at 56 DAS. Stomatal conductance and leaf osmotic potential (Ψ_O) were negatively correlated. Plants grown at pH 5.5 had the greatest fresh fruit weight and plant dry weight compared with the other pH levels. Although salinity adversely affected plant performance, lowering rhizosphere pH alleviated the adverse impacts of salinity. It seems that the tomato variety 'Mobil' used to measure leaf chlorophyll fluorescence parameters in this study had a salinity tolerance to which was enhanced at more acidic pH.

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Fruit weight; hydroponics; light-adapted chlorophyll fluorescence; photochemistry; quantum yield of PSII; rhizosphere acidity

Introduction

Tomato (*Lycopersicon esculentum*), belongs to the nightshade (*Solanaceae*) family and dicot order, is one of the most important fruit vegetables that is extensively cultivated for its edible fruits and accounts for 25% of the world vegetable production. Tomato is a good source of vitamins A, B1, B2, C, and niacin, as well as the phytochemical lycopene (Jones, 2007). Due to its well-known genetics and easy transforming capabilities, tomato is known as one of the best crops to study stress tolerance in the dicotyledonous crops (Yin et al. 2017). With the ability of ionic homeostasis and regulating leaf water potential, tomato is moderately tolerant to salinity (Martinez-Rodriguez et al. 2008). Seed germination, growth, and fruit development of tomato are adversely affected by high salinity (Cuartero et al. 2006).

With a cultivation area of 159,000 ha, Iran is ranked 15th in tomato production in Asia (Faostat 2018). However, tomato yield is diminished due to exposure to salinity stress in this arid region (Feleafel and Mirdad 2014). Soil salinity is becoming a significant problem that occurs in all climates. Yearly, around 0.3 to 1.5 Mha of farmlands are projected to salinity and are

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becoming less productive so that it has reduced the crop production by 20% each year (FAO, 2015; Porcel, Aroca, and Ruiz-Lozano 2012), and also another 20–46 MHa are prone to lose their production capacity by salinity. On the other hand, the earth population is increasing by the rate of 1.09% per year (United-Nations 2018). Hence, population growth and increasing demand for food require approaches to lessen the negative effects of environmental stresses. Such circumstances have led crop producers to the use of unconventional waters for irrigation. Besides, due to the scarcity of freshwater and the existence of low-quality water resources (saline and semi saline water), vegetable crop management has received a great deal of attention worldwide due to saline conditions (Malash et al. 2000).

Salinity stress primarily induces osmotic and ion effects, causing secondary stresses such as oxidative and nutrient deficiency (Chinnusamy, Jagendorf, and Zhu 2005). Proper acidity of nutrient solution optimizes nutrient uptake, increases photosynthetic system efficiency, and ultimately, maximizes plant growth (Hamlin and Barker 2006). By decreasing the nutrient solution's acidity, the solubility of some nutrients in water, and consequently, plant access to these elements increase (Wan, Cao, and Tibbitts 1994). In hydroponics, the acidity of nutrient solution and the rhizosphere are important in two respects; the first is that it affects the oxidation–reduction equilibrium, the solubility, and the ionic form of elements. Second, it affects the uptake of ions by the effect of H^+ and OH^- ions on the plant root, especially the membrane of ion transporting cells. Researchers have found that reducing the acidity of nutrient solution is an effective factor in reducing stomatal conductance in plants, with 29% and 4% decrease in stomatal conductance and transpiration rate, respectively, by decreasing acidity from 5.6 to 1.8 in bean (*Phaseolus vulgaris*) plants (Velikova et al. 1998). Those reductions can be due to a decrease in the pressure potential of the leaves.

Chlorophyll fluorescence is a widely used plant physiology technique to measure the photosystem II (PSII) activity. As a noninvasive method, it also provides a low cost and easy way to study the state of PSII under different conditions (Murchie and Lawson 2013; Ahmadi-Lahijani et al. 2018). The use of chlorophyll fluorescence has recently increased due to its application in crop improvement, particularly for screening favorable plant traits and connecting the genomic information with physiological and phenological responses (Baker and Rosenqvist 2004; Furbank et al. 2009). Measurement of chlorophyll fluorescence can provide a key technique for evaluating the plant response to environmental changes and studying the photosynthetic apparatus under different conditions. The demand for a high number of measurements in a short time, and fast protocols for screening photosynthesis that provides accurate information concerning plant status, have made chlorophyll fluorescence a widely used method in plant physiology studies (Montes, Melchinger, and Reif 2007; Furbank et al. 2009; Murchie and Lawson 2013).

Fluorescence quenching, the decline in the initial rise in fluorescence after applying actinic light, can be done through a combination of two processes. First, photochemical quenching (*qP*) consumes the electrons derived from the light-dependent processes in the photosynthetic pathway. This process is affected by any factor that favors the electrons being used in photosynthesis (N_p), such as the opening of stomata that enhances the CO_2 availability for Rubisco or the light activation of key enzymes in the Calvin cycle to achieve full activity (Buchanan and Balmer 2005; Lawson, Kramer, and Raines 2012). Second, the photoprotective process helps dissipation excess excitation energy within chlorophyll-containing complexes to prevent the formation of free radicals, which is called nonphotochemical quenching (NPQ). Depending on the species and conditions, NPQ acts as a '*safe*' mechanism to remove substantial chlorophyll excitation energy levels and compete with *qP* and fluorescence (Demmig-Adams and Adams III, 2006).

The most sensitive part of the photosynthetic apparatus to abiotic and biotic stress is PSII (Murchie and Lawson 2013). The quantum efficiency of PSII electron transport in the light (*Fq'/Fm'*), also known as ΦPSII, has widely been used as an indicator of PSII efficiency mainly due to its accuracy and ease of measurement in the light (Murata 1992; Maxwell and Johnson 2000;

Baker 2008), and a rare or small contribution of PSI below 700 nm wavelengths, and multiple turnovers of PSII during saturation pulse (Baker 2008). It has been observed that under a controlled environment, ΦPSII was positively correlated with the CO_2 assimilation rate (Genty, Briantais, and Baker 1989; Genty, Wonders, and Baker 1990; Cornic and Massacci 1996). This correlation seems logical because ATP and NADPH, the linear electron transport products, are directly utilized in photosynthesis in known values (Murchie and Lawson 2013). These observations have extended the possibilities of using this technique to measure the photosynthetic rate and have advanced the understanding of photosynthetic alterations. The energy of light absorbed by chlorophyll molecules can be used in the photochemistry pathway (drive photosynthesis) and re-emitted as heat or light (fluorescence). These processes compete and cannot be isolated from each other. Therefore, the chlorophyll fluorescence yield provides useful information about heat dissipation and the photochemistry quantum efficiency (Murchie and Lawson 2013). Given that the photochemistry supply energy for plants for CO_2 assimilation, this can be important for evaluating plant photosynthesis and productivity and yield.

The cultivation area in Iran for tomato is reduced due to high water and soil salinity and high initial costs to reduce salinity. Many farmers are reluctant to cultivate in greenhouses due to less profitable production in saline and semisaline water sources. Therefore, widespread greenhouse cultivation is under question. However, with reliable information, it is possible to evaluate the economic justification of greenhouse cultivation by saline water and provide detailed recommendations for the farmers to lessen salinity effects on plants. Therefore, it was hypothesized that the medium pH adjustment might alleviate the adverse effects of salinity on gas exchange and chlorophyll fluorescence parameters and fruit yield of tomato plants.

Materials and methods

Experimental site and procedure

The experiment was carried out at the research greenhouse of the Department of Agriculture, Ferdowsi University of Mashhad, in 2018. Tomato cultivar (*cv*. Mobil) were studied under salinity stress conditions at three acidity levels (pH) (Unadjusted as Control [~8.5–9], 5.5, and 4.5) and five measurement time (just before the onset of salinity stress (0), 14, 28, 42, and 56 days after the onset of salinity stress; DAS) every 14 days.

The seeds were first sown in the seedling trays in a mist room and, after 2 weeks, transferred to a hydroponic system. Each plant was sown in a pot (30 cm in diameter) one m apart. The culture medium was perlite, and a closed hydroponic system was used. The plants were fertilized using the Hoagland nutrient solution (Hoagland and Arnon 1950), and the solution was circulated continuously. One month after plant establishment, the salinity (NaCl) stress was applied gradually, at four dS m^{-1} per week. Electrical conductivity increased to 20 dS m^{-1} and then applied until the end of the growing season. Each pH treatment was facilitated with a separate pump (three pumps) to circulate the solution. The nutrient solution was changed weekly, and the nutrient solution's acidity was adjusted daily using sulfuric acid (H_2SO_4). The photoperiod inside the greenhouse was adjusted according to the natural daylength (spring) and the temperature of day and night was 25 ± 2 and 18 ± 2 °C, respectively.

Measurements

The measurements were performed once before the onset of salinity stress and 14, 28, 42, and 56 days after stress onset (DAS). The first day's salinity level and 14, 28, 42, and 56 DAS were zero, 8, 16, 20, and 20 dS m^{-1}, respectively. Two plants per replication were analyzed ($n = 6$).

Chlorophyll fluorescence

The leaf chlorophyll fluorescence including the steady-state value of fluorescence in the light (F_t), the light-adapted minimum chlorophyll fluorescence (F_o'), light-adapted maximum chlorophyll fluorescence (F_m'), variable fluorescence (F_v'), maximum efficiency of PSII photochemistry in the light when all centers are open (F_v'/F_m'), PSII operating efficiency; the quantum efficiency of PSII electron transport in the light (F_q'/F_m', also known as ΦPSII), photochemical quenching (F_q'/F_v', also known as qP), the proportion of closed reaction centers ($1–F_q'/F_v'$ or $1–qP$), and estimation of the fraction of open PSII centers (qL) were measured from the youngest fully developed leaf on each plant per pH ($n = 3$) using a fluorometer (MINI-PAM Portable Chlorophyll Fluorometer, WALZ, Germany). Measurements were performed at 9:00–10:00 h. 30 min before measurements, light intensity was reduced to 50% using shades. The fraction of absorbed radiation that utilized in PSII photochemistry (%P), dissipated in the antenna (%D), and neither dissipated in the PSII antennae nor used in photochemistry (%X) was estimated according to Demmig-Adams et al. (2008):

$$\%P = (Fv'/Fm') - qP \times 100 \quad (1)$$

$$\%D = 1 - (Fv'/Fm') \times 100 \quad (2)$$

$$\%X = (Fv'/Fm')\ (1 - qP) \times 100 \quad (3)$$

The linear electron transport rate (J) described as in Equation (4) (Genty, Briantais, and Baker 1989):

$$J = \Phi PSII \times PFDa \times (0.5) \quad (4)$$

PFDa is absorbed light (μmol m^{-2} s^{-1}), and 0.5 is a factor (accounts for the partitioning of energy between PSII and PSI. It is generally not practical to measure the light absorbed by a leaf; therefore, relative changes in J can usefully be monitored by merely multiplying ΦPSII by incident light (Maxwell and Johnson 2000). Therefore, equation four can be modified as:

$$J = \Phi PSII \times PFDi \quad (5)$$

Stomatal conductance

Stomatal conductance (g_s) was measured using a leaf porometer (Decagon Devices, Inc., USA) from the leaves used for the chlorophyll fluorescence at the same time.

SPAD. Total chlorophyll content was measured in intact leaves using a portable chlorophyll meter (CCM-200, Opti-Science, USA). At least three leaves per replicate were measured from the same leaves where the chlorophyll fluorescence was measured. Readings were taken from three plants per replicate in the middle of leaf lamina and averaged. CCM-200 estimates chlorophyll in two wavelengths (653 and 931 nm).

Leaf relative water content (RWC)

Leaf relative water content (RWC) was measured according to Smart and Bingham (1974). The leaf samples were collected from the central rows of each plot, and RWC was calculated as Equation (2):

$$RWC = \left[\frac{FW - DW}{TW - DW}\right] \times 100 \quad (6)$$

Here, DW, FW, and TW are the leaf dry and fresh weight and turgid weight, respectively.

Leaf osmotic potential (ψ_O)

The leaf ψ_O was determined according to the freezing point depression method using an osmometer (Wogel, model OM802.D). The leaf osmolytes content was calculated based on the van't Hoff equation, and the leaf water content was measured by the Equation (7):

$$\frac{mMol}{g} = \left[\left(-\frac{Op}{RT} \times \frac{WC}{1-WC}\right)\right] \tag{7}$$

where the osmolytes content is based on mM g^{-1} dry weight, R is the gas constant (0.083), T is the temperature (°K), O_p is the leaf osmotic potential (MPa), and WC is the leaf water content.

Survival

The percentage of the survived plants was determined according to Equation (8):

$$\%\ Survival = \left[\frac{number\ of\ plants\ at\ day\ 56}{number\ of\ plants\ at\ the\ first\ day} \times\ 100\right] \tag{8}$$

Statistical analysis

The experiment was carried out 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.* 9.1 and Excel software. The mean comparison was made using the LSD test at 5% of probability.

Results

Chlorophyll-a fluorescence parameters

Chlorophyll-*a* fluorescence was analyzed just before the onset of salinity and after 14, 28, 42, and 56 DAS at different pH levels. Generally, the lowest values for the Chl-*a* fluorescence was observed at 28 DAS (Figure 1). The maximum light-adapted quantum yield of PSII photochemistry, F_v'/F_m', was recorded in pH 4.5 plants at 56 DAS with a significant difference and percentage increase of 11% compared with the control (pH–8.5–9) (Figure 1a). Similarly, the greatest PSII operating efficiency in the light, ΦPSII, was observed at 56 DAS, although no difference was observed between the two acid pH levels (Figure 1b).

There was no significant difference in photochemical quenching, *qP*, between the pH treatments at different measurement times except for 28 DAS, in which the plants grown at pH 5.5 had the greatest *qP* compared with the other pH levels (Figure 1c). The linear electron transport rate, *J*, was decreased at 28 DAS in the control and pH 5.5 levels by 10 and 13%, respectively, compared with the day zero; however, *J* tended to increase afterward. So that the greatest *J* was recorded at 56 DAS at 4.5 pH level (Figure 1d). Salinity stress decreased 1–*qP*, the proportion of closed reactions centers, at 28 and 56 DAS, especially in pH 5.5 compared with the control (Figure 1e). The greatest 1–*qP* was recorded at pH 4.5 at all measurement times. At 56 DAS, it was 1.5 and 1.8 times greater than the control and pH 5.5, respectively. Although the estimated fraction of open PSII centers, *qL*', was greater in the control and pH 4.5 at day zero and 42 DAS, no significant difference was observed at the end of the experiment (Figure 1f).

The steady-state value of fluorescence in the light (F_s'), F_o', and F_m' showed the same trend at different measurement times, in which there was a significant decline at 56 DAS compared with the control (Table 1). F_s'/F_o' neither affected by salinity stress nor by pH levels; however, a declining trend was observed by increasing salinity exposure (Table 1).

The fraction of photons absorbed by PSII antennae used in photochemistry (%*P*) and the fraction thermally dissipated in the antennae (%*D*) were affected by the time of measurement

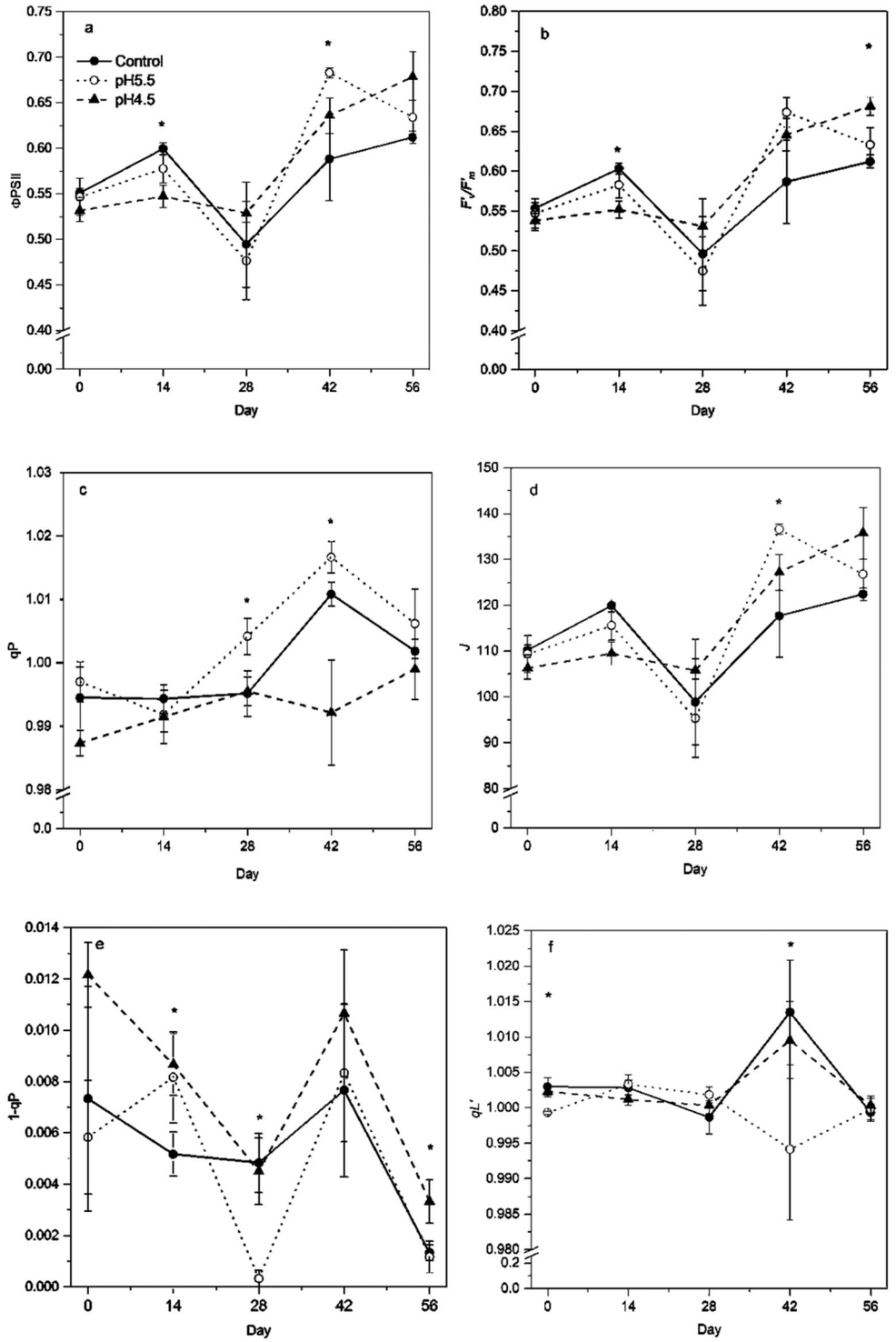

Figure 1. Light-adapted leaf fluorescence parameters: (a) PSII operating efficiency (ΦPSII), (b) Maximum efficiency of PSII photochemistry in the light (F_v'/F_m'), (c) Photochemical quenching (*qP*), (d) Linear electron transport rate (*J*), (e) The proportion of centers that are closed 'excitation pressure' on PSII (1–*qP*), and (f) Estimates the fraction of open PSII centers (*qL'*). Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$ and vertical bars represent the difference between the control and different measurement times values. Data are means of six measurements ± SE.

Table 1. Fluorescence chlorophyll parameters of tomato plants under actinic light.

			Fs′		
pH	0	14	28	42	56
Control	371 ± 3.04	325 ± 11.2	351 ± 6.09	336 ± 10.5	288 ± 9.84
5.5	393 ± 6.44	343 ± 23.0	365 ± 12.1	315 ± 12.9	277 ± 5.73
4.5	421 ± 11.7	341 ± 11.1	417 ± 3.37	437 ± 31.7	254 ± 15.0
			F_o'		
Control	365 ± 2.67	322 ± 10.1	350 ± 6.26	335 ± 13.7	289 ± 9.94
5.5	393 ± 7.03	339 ± 21.5	366 ± 11.8	325 ± 24.2	279 ± 6.95
4.5	415 ± 11.2	337 ± 9.89	415 ± 6.38	433 ± 36.7	268 ± 9.43
			F_m'		
Control	819 ± 9.74	813 ± 26.9	725 ± 57.9	857 ± 56.8	748 ± 21.3
5.5	926 ± 45.3	821 ± 67.4	734 ± 80.3	999 ± 48.2	771 ± 33.0
4.5	940 ± 34.0	753 ± 11.8	910 ± 67.7	1244 ± 91.5	857 ± 17.3
			F_s'/F_o'		
Control	1.007 ± 0.0043	1.008 ± 0.0008	1.003 ± 0.0017	1.004 ± 0.0123	0.998 ± 0.0033
5.5	1.002 ± 0.0032	1.012 ± 0.0042	0.997 ± 0.0022	0.981 ± 0.0368	0.998 ± 0.0067
4.5	1.014 ± 0.0024	1.009 ± 0.0044	1.004 ± 0.0023	1.014 ± 0.0153	0.951 ± 0.0608

0, 14, 28, 42, and 56 days after the onset of salinity stress. Values are mean ± SE of three replicates ($n = 3$).

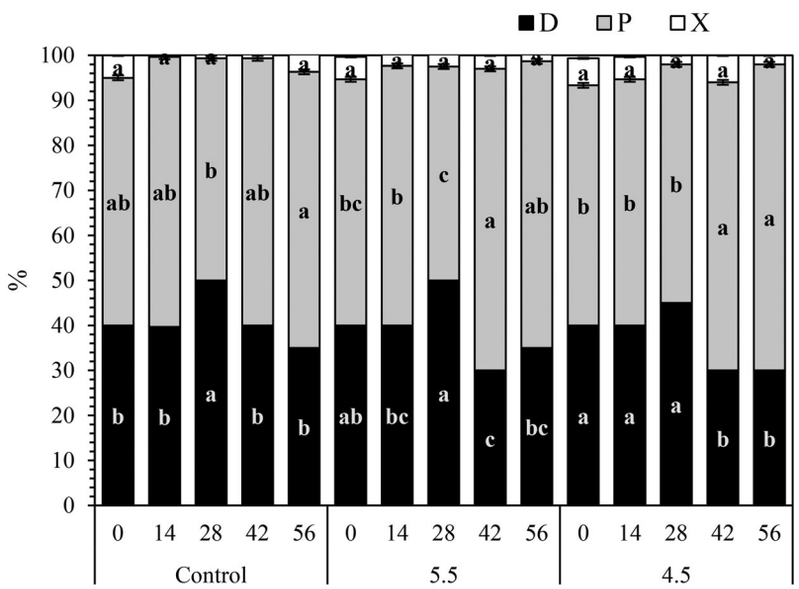

Figure 2. The fraction of photons that dissipated in the antenna (%*D*), utilized in PSII photochemistry (%*P*), and absorbed by PSII neither used in photochemistry nor dissipated in the PSII (%*X*). Letters represent the difference between the control and different measurement times at each pH level. Data are means of six measurements ± SE.

(Figure 2). The fraction of photons absorbed by PSII antennae used in photochemistry (%*P*) was suppressed at 28 DAS, but %*P* increasing to 56 DAS. The greatest %*P* was at 56 DAS under pH 4.5 pH (Figure 2). The greatest %*D*, recorded at 28 DAS, was greater at pH 4.5 and 5.5 than the control, while %*P* was greatest at 42 and 56 DAS. The fraction neither used in photochemistry nor dissipated in the antennae (%*X*) was affected by pH levels and showed a significant increase at pH 4.5 (increased by 30 and 60%, respectively, compared with pH 5.5 and the control (Figure 2).

Stomatal conductance and SPAD

Time of measurement and the medium pH interacted to affect g_s. Generally, g_s was suppressed by increasing salinity stress and pH levels. Although the greatest g_s was observed in plants at pH 4.5 on the first day, 31% greater than at control pH, it decreased to 56 DAS. The lowest g_s was in

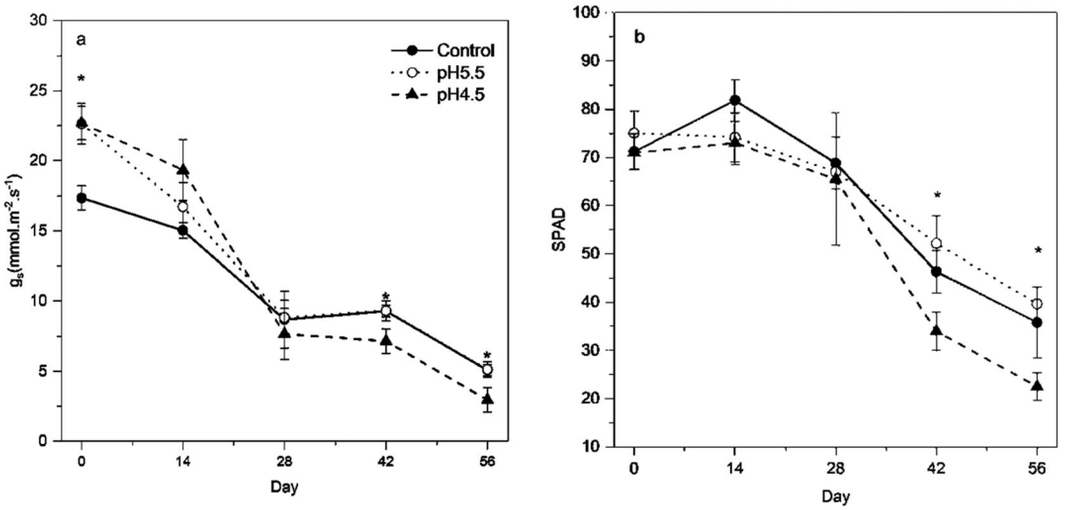

Figure 3. (a) Leaf stomatal conductance (g_s), and (b) SPAD values. Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$ and vertical bars represent the difference between the control and different measurement times values. Data are means of six measurements ± SE.

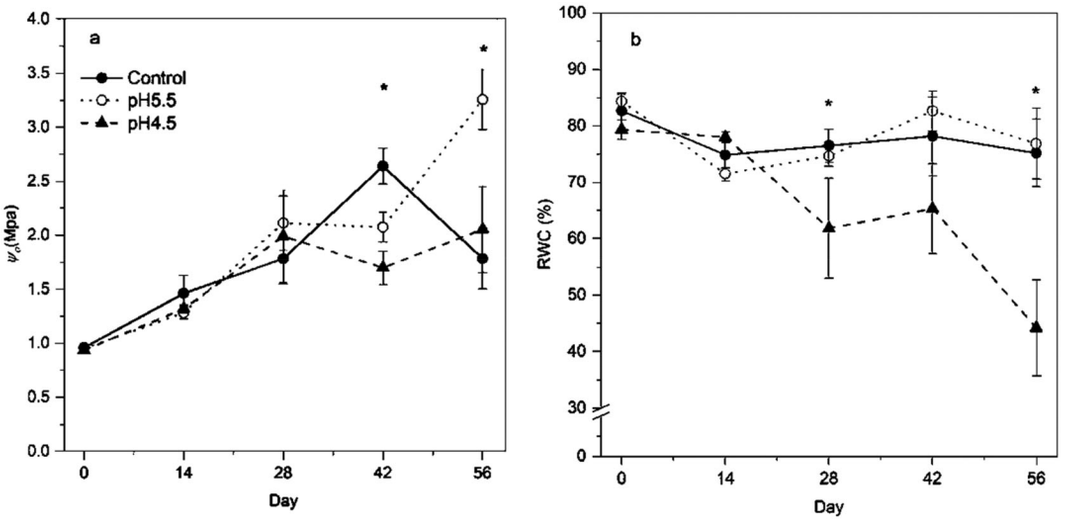

Figure 4. (a) Leaf osmotic potential (Ψ_O), and (b) relative water content (RWC). Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$ and vertical bars represent the differences between the control values and different measurement times. Data are means of six measurements ± SE.

plants at pH 4.5 on 56 DAS, decreasing 41% compared to control pH (Figure 3a). Leaf SPAD values also showed a decreasing trend to 56 DAS (Figure 3b). The lowest SPAD value was observed at 56 DAS in plants at pH 4.5, 2.5 times lower than plants in the control pH.

Leaf RWC and Ψ_O

The leaf Ψ_O was increased by decreasing RWC. The greatest leaf Ψ_O was recorded at 56 DAS in the plants grown at pH 5.5 by an increase of 82% compared with the control pH (Figure 4a). The leaf RWC showed a decreasing trend either by increasing salinity or decreasing pH (Figure 4b). The greatest decline in the leaf RWC was observed at pH 4.5 after 56 days of salinity stress by 70% compared with the control pH.

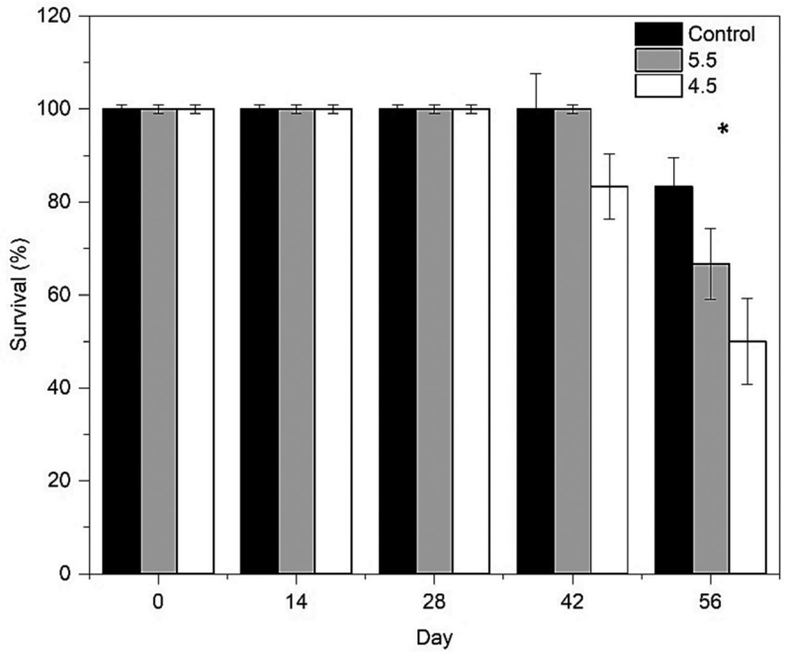

Figure 5. Plant survival percentage of tomato plants. Day; days after stress onset. Asterisks denote significant differences between the pH levels at $p \leq 0.05$ and vertical bars represent the differences between the control and different measurement times values. Data are means of six measurements ± SE.

Survival percentage

Although there was no significant difference between the pH levels and time of measurement to 42 DAS, the plant survival was significantly decreased at 56 DAS in all pH levels. For instance, the survival on day 56 for plants grown in control pH, pH 5.5, and pH 4.5, was 84, 67, and 50%, respectively (Figure 5).

Fruit yield and plant dry matter

Tomato fruit yield and plant dry matter were influenced by pH treatments (Figure 6). Although there was no significant difference between the control and pH 4.5, plants grown at pH 5.5 had the greatest FW and DM compared with the other pH levels (Figure 6). However, decreasing pH to 4.5 decreased both FW and DM by 36% compared with the pH 5.5.

Discussion

Leaf chlorophyll fluorescence is a fast and accurate method to study the effect of environmental stress on plants (Calatayud et al. 2006; Murchie and Lawson 2013). Since the operational photosynthesis in a growth environment is important to raise the outcome, light-adapted fluorescence parameters provide valuable information to evaluate the medium salinity and acidity effects on tomato photosynthetic performance. F_o' (light-adapted) and its equivalent F_o (dark-adapted) are fundamental for fluorescence analysis, which can be measured exposed to a far-red (FR) light. PSI is stimulated by FR and draws electrons from PSII to fully oxidizing Q_A (Murchie and Lawson 2013). We found an ascending trend in F_o' by decreasing the pH level to 42 DAS. Any increases in the F_o' values indicate damage to and inactivation of *D1* protein (Murchie and Lawson 2013). However, it seems the plants tried to adapt to the stressed conditions so that F_o'

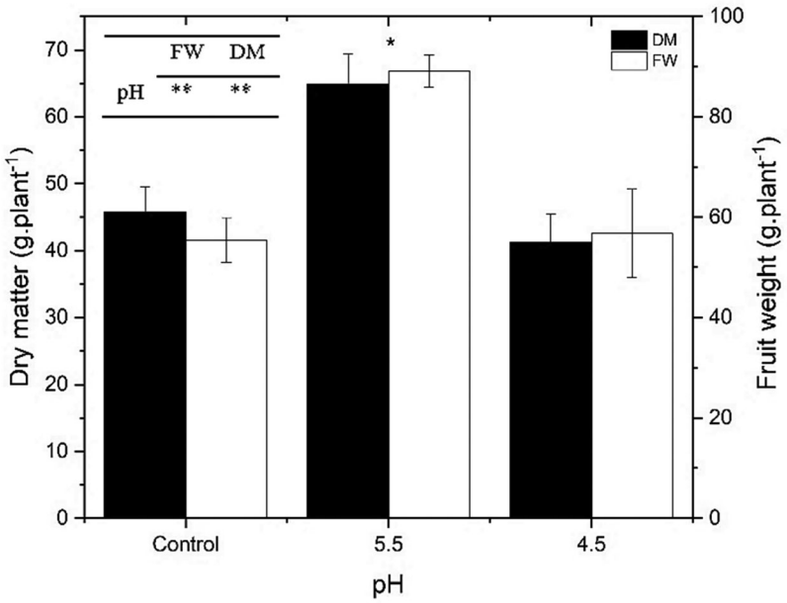

Figure 6. Fruit fresh weight (FW) and plant dry matter (DM) of tomato plants. Asterisks denote significant differences between the pH levels at $p \leq 0.05$ and vertical bars represent the differences between the control and different measurement times values. Data are means of six measurements ± SE.

was decreased at 56 DAS. A positive correlation was found between plant survival and F_o' (Figure 7). Besides, the lowest F_o' recorded in pH 4.5 at 56 DAS probably indicates a mitigating role of acidic pH under saline conditions.

The maximum light-adapted fluorescence, F_m', which is less than its dark-adapted equivalent (F_m), can be measured using a saturating pulse under actinic illumination that transiently closes all reaction centers. Many parameters can be calculated using those parameters (Murchie and Lawson 2013). PSII maximum efficiency (F_v'/F_m') describes the maximum light-adapted PSII operating efficiency. Any decrease in F_v'/F_m' reflecting an increase in NPQ. Therefore, it is possible to determine NPQ using the changes in F_v'/F_m', in which the two parameters will coincide nonlinearly (Murchie et al. 1999). Although g_s was significantly decreased by salinity stress, F_v'/F_m' did not show a declining trend under such conditions. Stomatal closure does not substantially decrease F_v'/F_m' by itself. Photosynthesis is regulated by both stomatal and nonstomatal factors; hence, it seems salinity stress only suppressed the stomatal factor, and the leaf photochemistry was not affected, which might be due to the alleviating effect of lower pH at high saline level. F_v'/F_m' was adversely affected (with significant differences) by salinity after 28 DAS, with a decline of 10 and 16% in the control and pH 5.5, respectively, compared with day zero. A decline in this ratio was mostly due to a decrease in the maximum Chl fluorescence yield in light-adapted leaves (F_m').

PSII maximum efficiency is correlated with leaf photosynthesis efficiency (Shu et al. 2012). A decline in this ratio indicates photoinhibition damage caused by the incident photon flux density when plants are subjected to a wide range of environmental stresses (Shu et al. 2012). A reduction in F_v and an increase in F_o is considered an inhibition of the acceptor side of PSII (Tezara et al. 2005). The reduction in F_v/F_m and qP were correlated with an increase in NPQ, suggesting the drought-induced dissipation of damaging excessive energy (Calatayud et al. 2006).

Decreasing the medium pH reduced the adverse effect of salinity stress on chlorophyll fluorescence and improved F_v'/F_m' and qP. Nonphotochemical quenching, as a '*safe*' process, is regulated by the acidification of the thylakoid lumen due to the accumulation of protons in the thylakoid lumen that form a ΔpH (Horton et al. 2008; Ruban, Johnson, and Duffy 2012). Hence, a lower

pH seems to reduce the inhibitory effect of salinity on leaf photochemistry. The increasing level of F_v'/F_m' and qP of tomato plants showed a remarkable ability of this variety to dissipate excess light energy as heat and prevent harmful ROS formation. The leaves under salinity stress increased their linear electron transport rate (J) 28 DAS afterward, which might be due to an increase in the ability for NPQ to protect the photosynthetic apparatus.

A decrease in the proportion of excitation energy used in photochemistry was correlated with a reduction in ΦPSII and qP (Havaux, Strasser, and Greppin 1991). Under such circumstances, NPQ increases to guarantee the dissipation of excitation energy. After 42 days under salinity stress, the capacity for photochemical quenching was stimulated. Plants grown at pH 5.5 showed greater qP values than the other pH levels that the difference was significant at 28 and 42 DAS. The maximum value was increased, and the quenching relaxation was more than that of day zero. This may be due to higher linear electron transport rate associated with an increased ability to establish ΔpH across thylakoid membranes by lower pH levels. Other factors, i.e., increased zeaxanthin content, might also be associated (Calatayud et al. 2006).

The results showed that the energy distribution in PSII was different among the treatments. The fraction of absorbed radiation utilized in PSII photochemistry (%P) was limited by 28 days exposed to salinity stress. Consequently, the energy fraction dissipated as thermal energy in the PSII antennae (%D) was increased at 28 DAS in all treatments. A positive correlation was found between J and %P, which indicated the fraction of photons absorbed in the PSII correlated with the linear electron transport chain (Figure 7). However, at 42 and 56 DAS, %P was increased, which positive correlations were observed between J, ΦPSII, and F_v'/F_m'. The fraction of absorbed radiation neither dissipated in the PSII antennae nor used in photochemistry (%X) was increased in leaves grown at pH 4.5 compared with the other pH levels. Demmig-Adams et al. (2008) believe that an increase in %X might lead to chlorophyll molecule de-excitation. It leads to a lower dissipation of energy in the PSII antennae and, consequently, a decrease in the fraction of the excitation energy used in photochemistry (Calatayud and Barreno 2004).

When plant capacity for dissipation of excitation energy is less than the amount of its absorption, damage to PSII reaction centers might occur (Demmig-Adams and Adams 1992). 1–qP denotes the proportion of closed reaction centers (Huner, Öquist, and Sarhan 1998; Huner et al. 2008). This parameter indicates the onset of photoinhibition and can be used to determine the photoprotective quenching level of fluorescence (Anderson, Chow, and Park 1995; Ruban and Murchie 2012). Calatayud et al. (2006) found that a lower qP observed in ozone-stressed plants was mainly due to decreased oxidizing Q_A capacity. Under such conditions, the pressure of excitation on PSII (1–qP) might be enhanced and caused the PSII reaction centers to be closed (Calatayud and Barreno 2001). In the present study, the positive correlation between 1–qP and g_s might indicate that the stomata closure reduced the CO_2 entrance into the leaves, and this affected the leaf capacity to drive the PSII reaction centers. A lower g_s is an important mechanism to protect the internal tissues against stress injury (Koch et al. 1998; Guidi et al. 2001). Salinity stress reduces leaf RWC and water potential; both limit the stomatal aperture. Eventually, the photosynthetic process will be inhibited, resulting in changes in ΦPSII (Baker and Rosenqvist 2004).

In this study, although an increase in salinity stress decreased F_v'/F_m' up to 28 DAS, we observed that F_v'/F_m' increased at 42 and 56 DAS. It seems that salinity stress initially adversely affected F_v'/F_m', but the plants tried to adjust to the conditions, probably by the osmotic adjustment. Shabala et al. (1998) have also found no immediate effects on PSII performance in maize (*Zea mays* L.) plants grown under a high concentration of NaCl, which was observed by the lack of change in F_v/F_m. Measurement of fluorescence parameters potentially can screen salt-tolerant varieties (Smillie and Nott 1982). It seems that the tomato variety (Mobil) used in our experiment has levels of salinity tolerance, where this tolerance was enhanced by decreasing the growing medium pH.

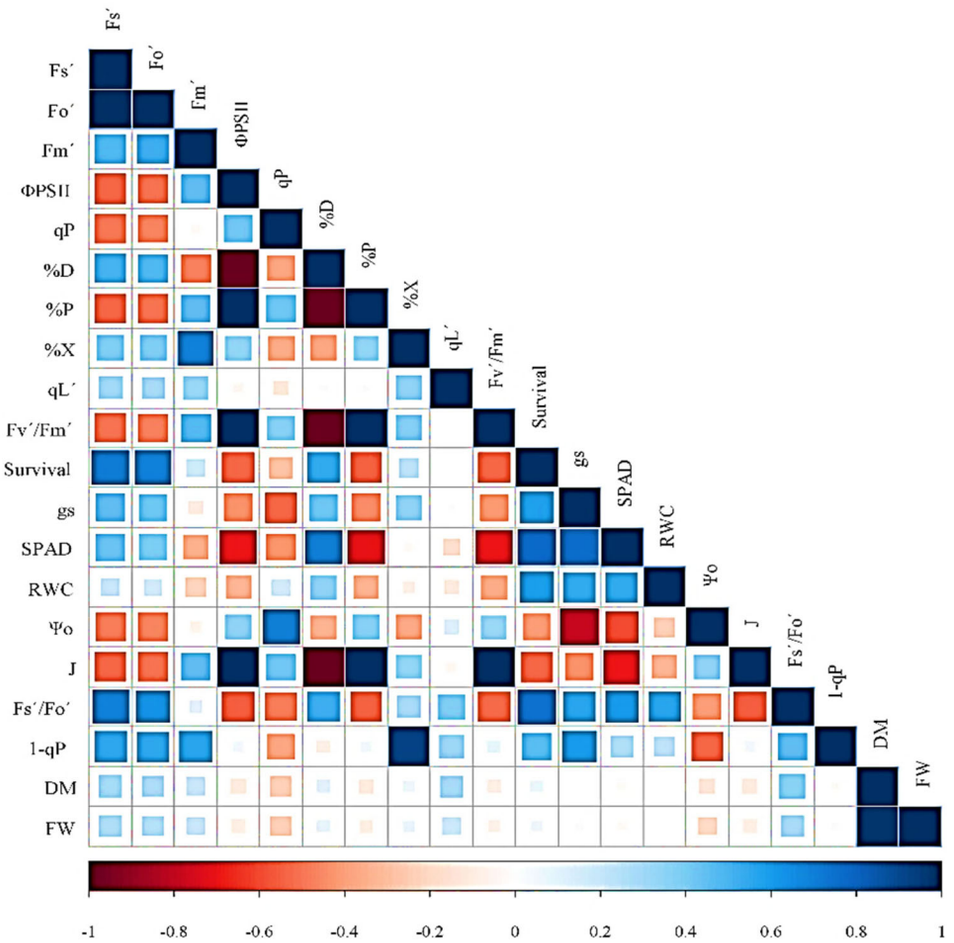

Figure 7. Corplot analysis of (F_s') light-adapted steady-state of chlorophyll fluorescence, (F_o') non-variable fluorescence, (F_m') maximal fluorescence, (ΦPSII) PSII operating efficiency, (*qP*) Photochemical quenching, (%*D*) the fraction of photons dissipated in the antenna, (%*P*) the fraction of photons utilized in PSII photochemistry, (%*X*) the fraction of absorbed photons by PS2 neither used in photochemistry nor dissipated in the PS2, (*qL'*) estimates the fraction of open PSII centers, (F_v'/F_m') maximum efficiency of PSII under actinic light, (survival) plant survival percentage, (g_s) stomatal conductance, (SPAD) leaf SPAD values, (RWC) leaf relative water content, (Ψ_O) leaf osmotic potential, (*J*) linear electron transport rate, (F_s'/F_o') F_s' normalized to light-adapted F_o' (1–*qP*) the proportion of centers that are closed, (DM) plant dry matter, and (FW) fruit weight of tomato plants under salinity stress and different medium pH levels.

A significant negative correlation was observed between g_s and Ψ_O (Figure 7). Reducing stomatal aperture along with osmotic adjustment, led to an increase in the osmotic potential of leaves. On the other hand, a positive correlation between Ψ_O and *qP* indicated that a decrease in the leaf water potential provided conditions under which the photochemical quenching could maintain even under saline conditions. Lowering the nutrient solution acidity reduces the g_s of the plant effectively. In bean (*Phaseolus vulgaris*) plants, Velikova et al. (1998) found that a decrease in pH from 5.6 to 1.8 decreased the transpiration rate by 4%, which may have decreased the leaf pressure potential. Keshmiriet al. (2018) observed that stomatal conductance and transpiration rate were suppressed in potato (*Solanum tuberosum*) by a decrease in pH of the growing medium from 5.6 to 3. In their study, stomatal conductance and transpiration rate were decreased by 56 and 14%, respectively, at a pH of 3 compared to 5.6.

Flexas (2001) believed that the steady-state of chlorophyll fluorescence (F_s) could indicate leaf photosynthesis and stomatal conductance status under drought conditions. The light-adapted

steady-state of chlorophyll fluorescence, F_s', has also been identified as a good indicator of plant chlorophyll fluorescence status under drought stress (Flexas et al. 2002). We also found that F_s' was declined as salinity stress increased. The steady-state of chlorophyll fluorescence decreases when the antenna thermal dissipation increases as a competitive reaction with chlorophyll fluorescence and photochemistry. When plants are exposed to a stressful condition, thermal dissipation increases due to an increased ΔpH; this is due to a decrease in electron transport to CO_2 due to reduced g_s. The normalized F_s to F_o (F_s/F_o) indicate suppressed CO_2 assimilation, g_s, and an increased NPQ. Therefore, the relationship between stomatal conductance and F_s/F_o can be used to detect the stress effects on plants (Moya et al. 1998; Flexas et al. 2000). We found positive correlations between F_s'/F_o' and g_s, SPAD, RWC, and survival percentage (Figure 7). Flexas et al. (2002) also found correlations between F_s/F_o and N_p, g_s, NPQ, and ETR in drought-stressed grapevines. They found a substantial relationship between F_s/F_o and NPQ, indicating F_s/F_o is directly correlated with NPQ.

Proper acidity of the nutrient solution optimizes the absorption of nutrients and increases the photosynthetic system efficiency and, ultimately, the maximum plant growth (Hamlin and Barker 2006). The nutrient solution optimum acidity can maximize photosynthesis and plant growth by affecting the optimal uptake of nutrients (Hamlin and Barker 2006). In a hydroponic environment, the acidity of nutrient solutions; therefore, the rhizosphere acidity is important in two respects; first, it affects the oxidation–reduction balance, solubility, and ionic form of the elements. Second, it affects ion uptake through an effect on H^+ and OH^- ions by plant roots, especially ion transporter of cell membranes (Epstein and Bloom 2005). Decreasing the nutrient solution acidity increases the water solubility of some nutrients and plant access to those elements (Wan, Cao, and Tibbitts 1994). In the present study, decreasing the medium pH mitigated the adverse effects of salinity on tomato plants. Lower medium pH possibly provided the plants with greater nutrients. Some of the nutrients (especially micronutrients) tend to be less available when soil pH is above 7.5. Soil pH will rise (become alkaline) as the salinity increases. Therefore, reducing pH would make some nutrients more available for plants. Reducing the nutrient solution acidity from 5.6 to 3 decreased N_p; however, there was no significant difference between the acidity of 4 compared to 5.6 (Keshmiri, Kafi, Parsa, Nabati, and Zare-Mehrjerdi 2018).

Lowering the growing medium pH to 5.5 increased plant dry matter and fruit yield of tomato plants. Layegh et al. (2009) examined the effect of nutrient salinity on growth, yield, and quality of tomato fruits under soilless conditions. They showed that by increasing the nutrient solution electrical conductivity, the total yield, average fruit weight, and leaf area index decreased, while the percentage of fruit dry matter tended to increase. The tuber production in the potato plant increased by a decrease in the nutrient solution acidity to 5.5 compared to the control (Wan, Cao, and Tibbitts 1994). With the temporary and intermittent decrease in the nutrient solution acidity, the tuber production rate in potato plants increased by pH 5.5 compared with the control (Wan, Cao, and Tibbitts 1994; Keshmiri et al. 2018). However, greater availability of the nutrients by lowering the medium pH might stimulate the allocation of photoassimilates to the physiological sinks and thereby, plant productivity.

Conclusion

Chlorophyll fluorescence parameters represent alterations in the light reactions of photosynthesis. Photosynthesis can be regulated by both stomatal and nonstomatal factors, depending on the environmental conditions and plant species (Ahmadi-Lahijani et al. 2018). Salinity stress gradually decreased stomatal conductance over time, suggesting a sensitivity of g_s to salinity. A decrease in g_s was accompanied by a decrease in the leaf RWC and an increase in Ψ_O. Lowering the medium pH improved the leaf chlorophyll fluorescence and fruit fresh weight of tomato plants. The plant survival percentage was positively correlated with g_s, RWC, and SPAD, indicating the vital role of

leaf water and pigment content and the availability of CO_2 to photosynthetic performance. Furthermore, a positive correlation was also found between plant survival and F_s' that might be considered an easy and fast indicator of the stressed plants. Reducing stomatal aperture and osmotic adjustment led to an increase in the osmotic potential of leaves, which helped maintain more water in the plant. Although salinity adversely affected plant performance, lowering the rhizosphere pH could alleviate the negative impacts of salinity. It seems that the tomato variety (Mobil) used in this study has a salinity tolerance, which was enhanced by lowering the rhizosphere pH.

Declaration of interest statement

There is no conflict of interest.

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