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Salt stress affects mineral nutrition in shoots and roots and chlorophyll *a* fluorescence of tomato plants grown in hydroponic culture

Aicha Loudari[a], Chahinez Benadis[a], Rachida Naciri[a], Aziz Soulaimani[a], Youssef Zeroual[a], Mohamed El Gharous[a], Hazem M. Kalaji[b] and Abdallah Oukarroum[a]

[a]University Mohammed VI Polytechnic (UM6P), Ben Guerir, Morocco; [b]Department of Plant Physiology, Institute of Biology, Faculty of Agriculture and Biology, Warsaw University of Life Sciences – SGGW, Warsaw, Poland

ABSTRACT

Salt stress is considered one of the major constraints limiting plant growth. Here, tomato plants were grown in hydroponic culture with two salt sodium chloride concentrations (S1 = 2.8 dS m^{-1} and S2 = 4.8 dS m^{-1}). Under salt treatment, a significant decrease in chlorophyll content index and shoot and root dry weight were observed. We found that copper (Cu) was accumulated significantly in the shoot and sodium (Na) was significantly accumulated in the root. Furthermore, a significant nutrient imbalance indicated by a decrease in phosphorus (P), and potassium (K) uptake was measured. These decreases were accompanied by an increase in Na and Cu contents. A decrease in chlorophyll fluorescence yield was also observed indicating an inhibition at photosystem I acceptor sites. It seems that the downregulation of the electron transport between photosystem II and photosystem II under salt stress could be due to an imbalance in nutrient uptake.

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KEYWORDS
Mineral content; nutrients uptake; photosystem; root morphology

Introduction

Salinity constraint is a major abiotic stress to plant health and soil quality as it affects the productivity of most crops. This serious problem has drastically increased in recent years mainly in arid and semi-arid areas (Munns 2002; Mętrak et al. 2017; Bünemann et al. 2018). Salt stress influences a series of some major physiological processes such as photosynthesis, ion partitioning as well as Na^+/K^+ ratio, Reactive Oxygen Species (ROS) and hydraulic conductivity which affects the bioenergetic processes of electron transport chain (Kalaji and Pietkiewicz 1993; Neumann 1995; Steudle 2000; Munns 2002; Allakhverdiev and Murata 2008; Conde et al. 2011; Kalaji et al. 2011; Fakhrfeshani et al. 2015; Oukarroum et al. 2015; Almeida et al. 2017). Furthermore, salt stress seems to affect root anatomy and morphology parameters (Rivero et al. 2014; Robin et al. 2016).

Changes in morphological appearance in response to salinity stress are not enough to determine the effect and subsequently design the management strategies. It is therefore important to identify key physiological and biochemical factors for improving the salinity tolerance of plants (Munns and Tester 2008; Ahanger and Agarwal 2017; Ahanger et al. 2020). To date, three main mechanisms contributing to shoot tissue tolerance to salinity have been targeted: accumulation of Na^+ in the vacuole, synthesis of compatible solutes and production of enzymes catalyzing detoxification of ROS. Increasing the abundance of vacuolar Na^+/H^+ antiporters (NHX), vacuolar H^+ pyrophosphatases e.g. Pyrophosphate-energized vacuolar membrane proton pump 1, proteins involved in the synthesis of compatible solutes (such as proline and glycine betaine) and enzymes responsible for the detoxification of ROS had differing degrees of success in improving crop salinity tolerance.

Salt stress causes accumulation of ROS (Achard et al. 2008; Miller et al. 2010), which secondarily induced oxidative damage hampers the redox homeostasis resulting in declined photosynthetic efficiency (Miller et al. 2010; Xie et al. 2011; Khan et al. 2014), alters nitrogen and osmolyte metabolism (Ahanger and Agarwal 2017; Ahanger et al. 2020), mineral assimilation, phytohormone profile and expression of genes (Fallah et al. 2017; Ma et al. 2018). To avert the negative effects of salinity, plants have certain existing mechanisms like antioxidant system, osmotic adjustment and the efficient salt exclusion at root and vacuole level (Horie et al. 2012; Deinlein et al. 2014; Ahanger et al. 2020).

Most studies that show salinity-altered nutrient concentrations such as phosphorus (P) in plant tissues were conducted in soils. The interaction between salinity and nutrition of plants is highly dependent upon the plant species, plant developmental age, the composition and level of salinity and the concentration of macro and microelements in the substrate (Loupassaki et al. 2002; Shahriaripour et al. 2011). Plants synthesize proline, soluble sugars, glycine betaine, and other osmolytes to promote osmotic balance at the cellular level (Garg et al. 2002). Biosynthesis of osmoprotectants has been reported as an adaptive strategy to mediate salt stress. In addition to acting as osmo-solutes, they also act as N storage compounds and/or hydrophobic protectants for enzymes and cellular structures (Sami et al. 2016). It should also be noted that crops differ in their tolerance and ability to accumulate a high concentration of salts in their tissues. Thus, depending upon experiment conditions and selected plants, different results can be obtained. Salinity has been reported to affect phosphorus (P) mobility and bioavailability in the plant-soil system, and therefore root uptake (Grattan and Grieve 1992; Eisechie and Rodriguez

CONTACT Abdallah Oukarroum abdallah.oukarroum@um6p.ma, abdallah.oukarroum@gmail.com University Mohammed VI Polytechnic (UM6P), Lot-660 Hay Moulay, Rachid, Ben Guerir 43150, Morocco
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1999; Xie et al. 2017; Meena et al. 2018). In saline soils, mineral nutrients such as P availability are reduced because ionic strength effects, sorption processes in soil solution and low-solubility of Ca-P minerals in the soil. Since the solubility of P in saline soil solutions with high levels of Ca^{2+} is controlled by sorption processes on the solid phase of Ca-P minerals (Navarro et al. 2000).

Tomato plant is considered an important greenhouse crop in many semi-arid regions such as in the Mediterranean region where salinity has been considered a major constraint in crop production. We hypothesize that saline conditions affect nutrient uptake in hydroponic culture by tomato plants and alter the photosynthetic electron transport chain. In this work, physiological responses of tomato plants to two NaCl salt concentrations, S1 = 2.8 dS m^{-1} and S2 = 4.8 dS m^{-1}, were investigated. We emphasized the change in chlorophyll *a* (Chl *a)* fluorescence, chlorophyll content index (CCI), root morphology parameters and accumulation of some mineral nutrients (Na, P, Cu, and K).

Materials and methods

Plant material and growth conditions

Tomato seeds (*Lycopersicon esculentum* var CAMPBELL 33 TECHNI) were germinated in the peat in darkness at a temperature-controlled (23°C). Similar size seedlings were placed in a culture chamber with a relative humidity between 70 and 80% and an ambient temperature of 23 ± 2°C during the day / 18 ± 2°C at night. The total photoperiod was 16 h/day. Plants were irrigated by distilled water. Twenty-three days after germination (DAG), seedlings were transferred to a plastic container (six seedlings per container) containing 4L of half-concentrated nutrient solution, without any treatment (to confer at plant adaptation period). The nutritive solution used Hoagland and Arnon (1950). Nutrient solution (Table 1 in supplementary materials) consists of the following composition (ppm): N (270), K (234), Ca (200), Mg (49), Zn (0.48), Cu (0.02), B (0.45), Mn (0.5), Mo (0.01), and Fe (2.8). Phosphorus (P) was added to the nutrient solution as KH_2PO_4 at a concentration of 31 ppm P. Six days later, seedlings were exposed to two salinity (S) treatments (S1 = 2.8 dS m^{-1} and S2 = 4.8 dS m^{-1}).

The pH of the solution was daily monitored and adjusted to 5.5 with either H_2SO_4 or KOH supply. The nutrient solution in each container was changed weekly. The containers were completely randomized and re-positioned weekly to minimize environmental effects. The growth continued for 45 days after germination or for 15 days-treatment and chlorophyll a fluorescence and some related fluorescence parameters, chlorophyll content index, root morphology, dry weight, and mineral content were analysed. Electrical Conductivity Meter (EC meter) was used to measure the salinity of the nutrient solution.

Leaf chlorophyll a fluorescence

Tomato plants kept in dark for 15 min before the measurements were started (for each treatment, 15 measurements were made by Handy PEA+, Hansatech instruments). The measurement consisted of a single strong 1 s light pulse (3000 µmol s^{-1} m^{-2} which is an excitation intensity to ensure closure of all Photosystem II (PSII) reaction centers) provided by an array of six light-emitting diodes (peak 650 nm). The Chl *a* fluorescence transients (ChlF) were digitized between 10 µs to 1 s by the instrument. From the fluorescence transient measured during the first second of illumination, following fluorescence parameters were calculated:

The maximum quantum yield of primary photochemistry

$$jPo = [1 - (F_o/F_m) = F_V/F_m)]$$

F_o ($F_{20\mu s}$) and F_m correspond to the initial and maximum Chl *a* fluorescence. F_V corresponds to the maximum variable Chl fluorescence;

Performance index (PI)

$$PI = [g_o/(1 - g_o)].[j_{Po}/(1 - j_{Po})].[y_o/(1 - y_o)]$$

φ_{Po} corresponds to the efficiency by which an absorbed photon will be trapped by PSII reaction centers (RC).

The expression $\gamma_o/(1-\gamma_o)$ is estimated by JIP-test as equal to the ratio of reaction centers and the absorbance (RC/ABS). Therefore: The expression ψ_o (=1−V_J) is the fraction of electrons transported beyond Q_A^- per exciton trapped by the reaction centers (RC) of PSII. It is the probability that the energy of a trapped exciton is used for electron transport beyond Q_A. Q_A is the primary quinone electron acceptor of photosystem II.

The efficiency with which an electron can move from the reduced intersystem electron acceptors to the Photosystem I (PSI) end electron acceptors δ_{Ro} (parameter related to electron transfer rate at PSI acceptor side):

$$\delta_{Ro} = (1 - V_I)/(1 - V_J)$$

V_t is defined as relative variable Chl *a* fluorescence at time t corresponding to $(F_t - F_o)/(F_M - F_o)$ and this expression can be taken as a measure of the fraction of the primary

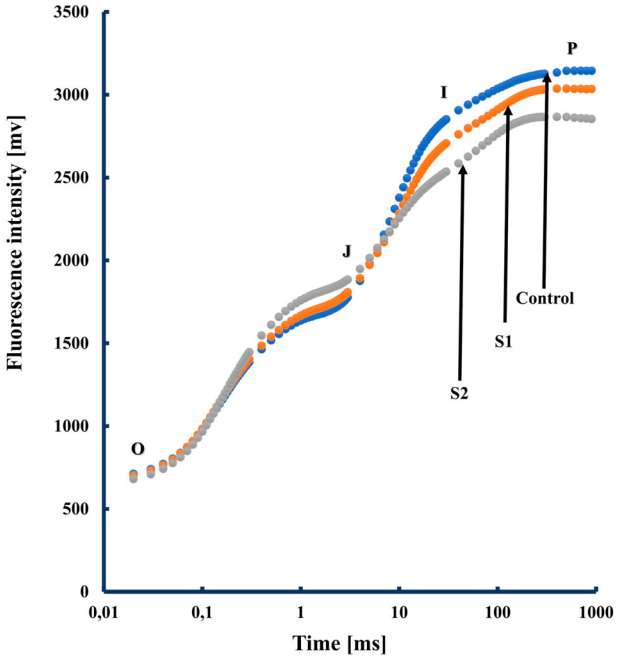

Figure 1. A typical Chlorophyll *a* polyphasic fluorescence rise OJIP, exhibited by salt-stressed tomato plants. The transients are plotted on a logarithmic time scale. the marks indicate the time points used by the JIP-test for the calculation of structural and functional parameters. The signals are the fluorescence intensity F_o (at 20 µs); the fluorescence intensities F_J (at 2 ms) and F_I (at 30 ms); the maximal fluorescence intensity, $F_P = F_M$. Each transient represents the mean of 15 measurments.

quinone electron acceptor of PSII in its reduced state [Q_A^-/$Q_{A\ (total)}$].

The relative contribution of the I-P phase is expressed as delta $V_I = [(F_m - F_I)/(F_m - F_o)]$ and it is related to photosystem I content (Oukarroum et al. 2009)

Chlorophyll content

The chlorophyll content index (CCI) was measured from the middle part of the leaf by using CL-O1 chlorophyll meter (Hansatech instruments).

Roots morphology parameters

Roots were carefully spread over a plastic box and scanned using an Epson Perfection LA2400 scanner. Data of total root length, root average diameter, volume and root surface area were acquired by processing the scanned root images using the WinRHIZO image analyzing system (Regent Instructions, Quebec, Canada).

Dry weight determinations and chemical analysis

Shoots and roots of control and treated plants were dried in an oven at 70°C for 2 days to determine dry weights. Also, elemental concentrations of Na, P, K, and Cu. Chemical

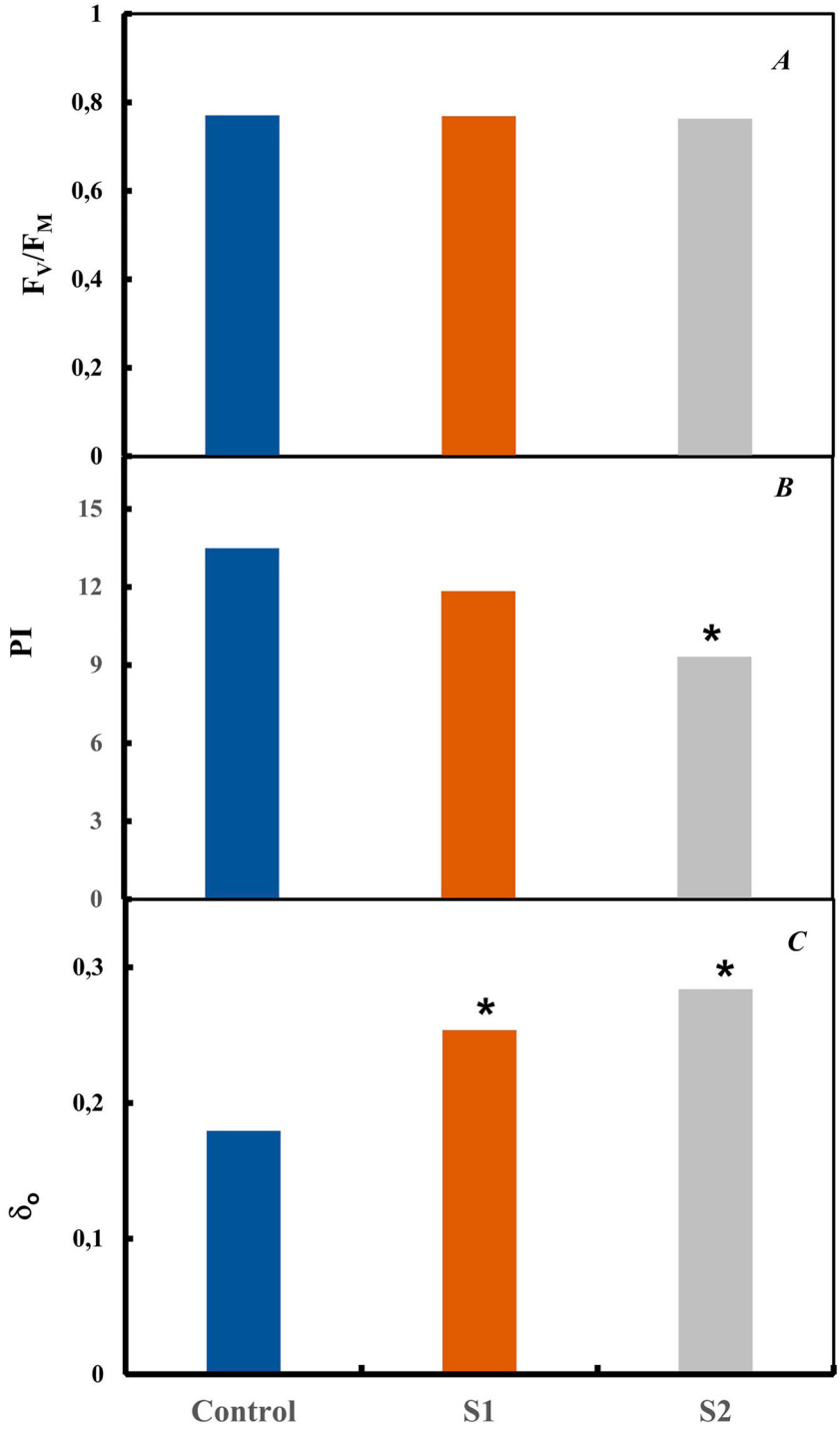

Figure 2. Maximum quantum yield of primary photochemistry (Fv/Fm), Performance index (PI) and the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors δ_{Ro}. Each value represents the mean of five independent experiments with about 15 repetitions.

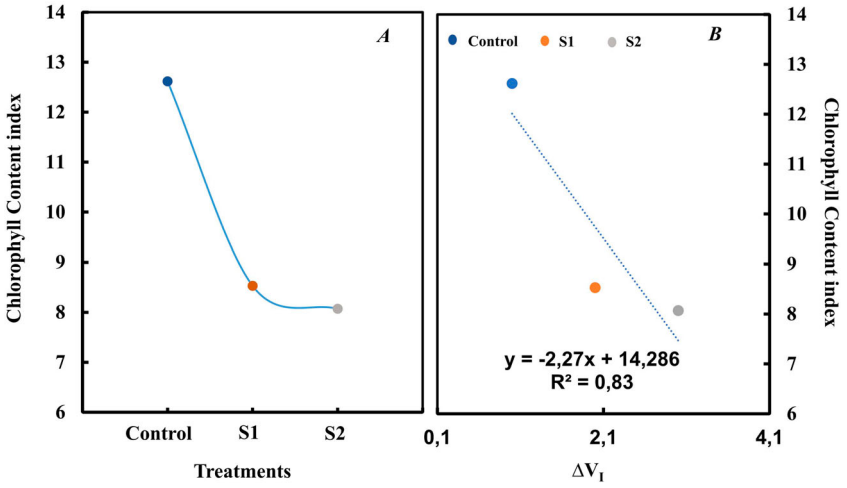

Figure 3. Change in chlorophyll content index and correlation between delat V_I and chlorophyll content index. Each value represents the mean of three independent experiments with about 15 repetitions.

elements were analyzed on a dry-weight basis using Inductively Coupled Plasma Optical Emission Spectrometry (Agilent 5110 ICP-OES, USA).

Statistical analysis

Data were subjected to analysis of variance (ANOVA) in SPSS 13.0 (SPSS Inc., USA) to examine the impacts of salinity on ChlF parameters, dry matter, chlorophyll content, root morphological traits, and macro and microelement concentrations.

Results

Understanding the physiological and biochemical mechanisms of salt stress is an important way to counter the negative effects of salinity and detect sensitive and tolerant traits in plants. Salt stress can, directly or indirectly, affect the photosynthetic activity of plant which is considered as one of the most important metabolic processes in plants. Reduction in photosynthetic activity alters also ChlF kinetics (Strasser et al. 2004 and references therein). Tomato leaves exhibit the typical ChlF transient OJIP during the first second of illumination in control and in salt

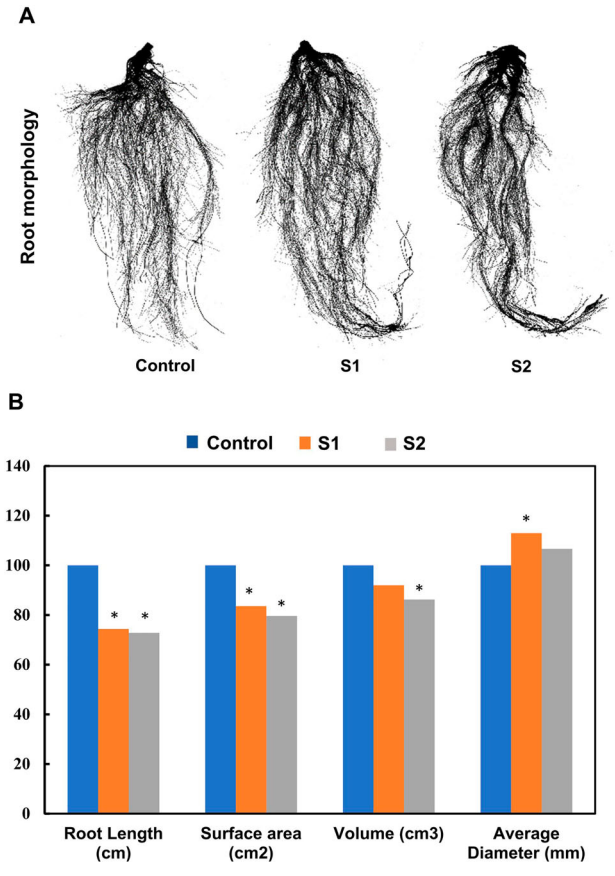

Figure 4. Change in root length, root average diameter, volume and root surface in salt-stressed plants. Each value represents the mean of three independent experiments.

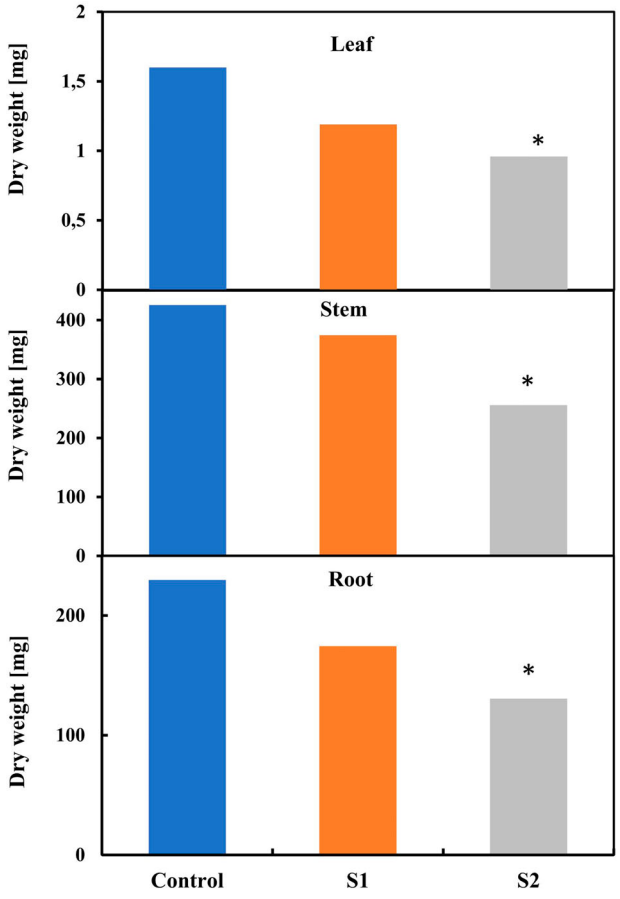

Figure 5. Change in leaves (*A*), stem (*B*) and root weights (*C*) in salt-stressed plants. Each value represents the mean of three independent experiments.

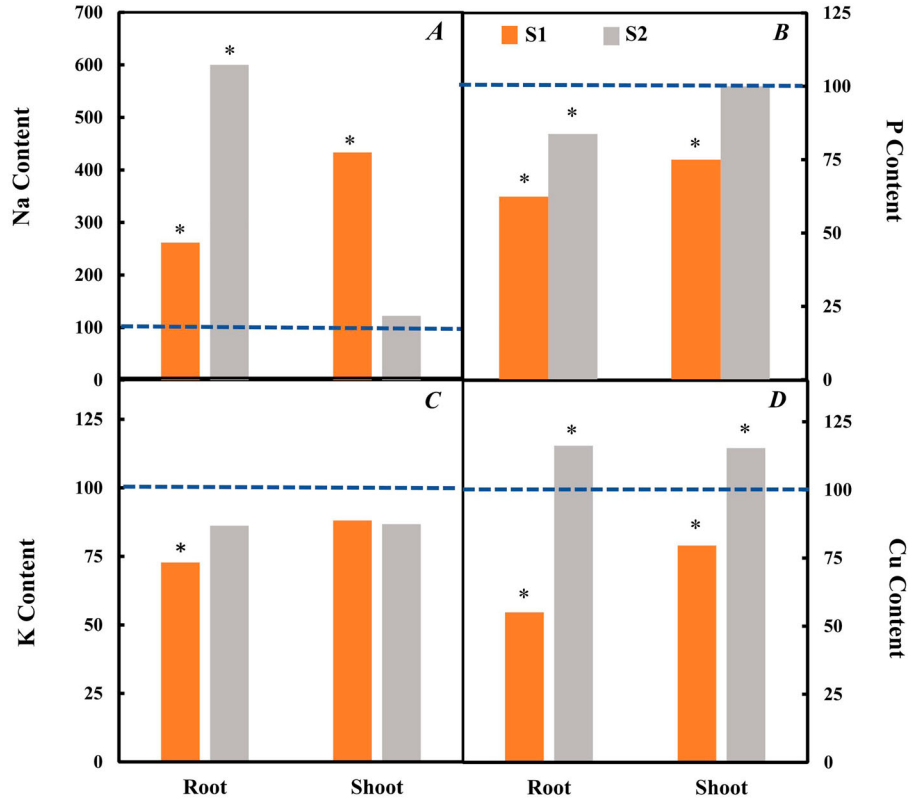

Figure 6. Change in Na (*A*), P (*B*), K (*C*) and Cu (*D*) contents (ppm) in shoot and root of salt-stressed plants, stem and root weight in salt-stressed plants. Data were normalized to control. Each value represents the mean of three independent experiments.

treatments (Figure 1). ChlF is used for understanding the reduction of the electron flow through PSII and PSI under two salt concentrations. The polyphasic fluorescence intensity increases from a minimum fluorescence intensity (Fo) to maximum fluorescence intensity (Fm) with two interval phases: the photochemical phase O-J and the thermal phase J-I-P (Strasser et al. 1995). We noticed here that the J-to-I-rise can be associated with the reduction of the PQ-pool (Schansker et al. 2003) and the I-to-P-rise with electron flow through PSI (Schreiber et al. 1989; Schansker et al. 2003).

To further investigate how the electron transport chain is changed under salt treatment, the changes in PSII photochemistry were investigated in tomato plants kept in dark. According to JIP-test (Strasser et al. 2004; Oukarroum et al. 2007, 2015), the behavior of PSII under different stress conditions is quantified through functional and structural parameters derived from the fluorescence transients (O–J–I–P). To translate ChlF transient on quantitative fluorescence parameters, the maximum yield of primary photochemistry of PSII (Fv/Fm) was calculated and appeared to be not affected by salt treatment (Figure 2).

The effect of salt treatment on changes that occurred in the performance index (PI) in fully expanded tomato leaves is shown in Figure 2. In this work, a significant decrease in PI parameter was significantly pronounced after 2 weeks of S2 treatment. The reduced electron transport chain resulted from PSII to PSI function could indicate the observed decrease in PI. However, and as an unexpected result, the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end-electron acceptors (δ_{Ro}) showed a significant increase compared to control ($P < 0.05$) for salt treatment.

Exposure of tomato plants to salt treatment induced a significant decrease of Chl content index (Figure 3). After 2 weeks of salt treatments, Chl content index decreased by 36% and 38% compared to control ($p < 0.05$) respectively at S1 and S2. Comparing Chl content index with the parameter ΔV_I, a linear correlation was observed (Figure 3). We noted here that the relative reduction in ΔV_I has been reported to be related to a loss of PSI reaction centers. In a previous study, in drought-stressed barley plants, it has been shown that I-P-loss seems to be correlated to a loss of PS I reaction centers content as determined by 820 nm transmission measurements (Oukarroum et al. 2009).

In this work and after two weeks of salt treatment, the morphology, length, surface, volume and diameter of the root were studied (Figure 4). These characteristics showed a significant reduction compared to the control except for the diameter parameter for treatment S1 where a significant increase was noticed (Arif et al. 2019; Dinneny 2019; Terletskaya et al. 2019). In previous works, Céccoli et al. (2011) and Neumann (1995) reported also that salinity alters anatomical and morphology of roots such as diameter and length parameters.

In Figure 5, a significant decrease in the dry weight of the leaves, stem, and root was also observed for the highest salt treatment. It seems that physiological shoot growth is less influenced compared to those of root growth, this result is in concordance with the results obtained by Céccoli et al. (2011). Our results showed that S2 treatment was the treatment that significantly affected plants.

Plant mineral content affected by salt stress has been reported in previous studies (Hasana and Miyake 2017; Thu et al. 2017). Here, to determine how nutrients uptake was affected by the salt treatment in hydroponic culture,

chemical elements Na, P, K and Cu were analyzed at the end of this experiment in the root and aerial part (Figure 6). Our results show that significant accumulation of Na was observed for treatment S2 in the root whereas, after 2 weeks of salt treatment, it was in the aerial part at S1 where the accumulation of Na was observed.

A different partitioning of Na^+ ions between root and shoot was reported (Ochiai and Matoh 2002; Keisham et al. 2018). However, it was observed that P presents a significant decrease for the two treatments except during treatment S2 in the aerial part. It is well documented that P is a major element for the shoot and root growth and low-P uptake under salt stress could induce a reduction in biomass development (Navarro et al. 2001; Demiral 2017; Khan et al. 2018). Also, it has been reported that reduction in growth under salt stress could be attributed to a nutritional imbalance and excessive Na^+ uptake (Hand et al. 2017; Isayenkov and Maathuis 2019).

Discussion

Plant growth is related to photosynthetic performance and changes in carbon economy under saline conditions (Webster et al. 2016; Asrar et al. 2017). Salinity stress often results in biomass reduction as a survival strategy of plants which is related with failure in carbon assimilation (Fall et al. 2017; Pompeiano et al. 2017). In such situations, plants distribute higher assimilated carbon to energy and maintenance rather than development of plant parts (Asrar et al. 2017). Photosynthetic rates are reported to be dependent to salinity concentration and duration of salt exposure (Fall et al. 2017; Pompeiano et al. 2017). A decrease in net CO_2 assimilation is related to stomatal closure to regulate transpiration rate and water use efficiency (Liu et al. 2011). Long term salinity alters biochemical reactions (like Rubisco carboxylase/oxygenase activity and regeneration of Ribulose-1,5-bisphosphate (RuBP) and triose phosphates) that regulate gas-exchange. Moreover, it is reported that the major functional chloroplast protein complexes, i.e. PSI, PSII, ATP-synthase and $Cytb_6f$, involved in harvesting light energy (Dekker and Boekema 2005) are altered under saline conditions along with Rubisco protein (Xu et al. 2010; Li et al. 2011).

In our work and under salt treatment, a decrease of J-I-P fluorescence yield was observed, and this change was found to be related to the downregulation of the electron transport chain (Stirbet and Govindjee 2011, 2012). These findings suggest a limitation of both donor and accepter-side of PSI (decrease in J-I-P yield). However, the maximum yield of primary photochemistry of PSII (Fv/Fm) appeared to be not affected by salt treatment and this result confirms the high stability of the potential PSII photochemical efficiency. We noted here that some previous studies demonstrate that salt stress may affect this fluorescence parameter Fv/Fm, this contradictory result appears to be depending on the studied plant species and the specific experimental conditions. That means that salt treatment in tomato leaves induced regulation of the intersystem electron transport between PSII and PSI and may indicate a cellular adaptation to counter the negative effect of salinity and ensure equilibrium in photosynthetic electron transport. These insights indicate the adaptation complexity of the plant adaptation to salt stress.

We noted here a decrease in the amount of K in the root and shoot part in salt-stressed plants. Interestingly, it has bed reported that salinity induced Na^+ injury, which affects K^+ uptake by root cells (Conde et al. 2011). Furthermore, Na^+ accumulation inactivates both photosynthetic and respiratory electron transport (Allakhverdiev et al. 2000), which was observed in our work by a decrease in the photosynthetic performance index (PI) and I-P phase (loss of PSI reaction centers).

Our results were coherent with the literature published previously. However, It is in our interest to note that, nutrients P and K decrease with high salt concentration is accompanied by a significant increase in Na and Cu contents in root and shoot (Demiral 2017; Hand et al. 2017; Thu et al. 2017). It should also be noted that the quantity of Cu varies according to the plant parts of accumulation. Indeed, a significant reduction was observed in the root and an increase in the aerial part for the two salt treatments. In conclusion, the observed reduction in studied physiological parameters could be due to a negative change in nutrient uptake affect disequilibrium on ion homeostasis and then a cascade of changes in physiological and biochemical processes. Interaction of salinity and Cu and plant Cu uptake change might play a significant role in the response and adaptation of plants to salt stress.

Acknowledgements

A.L., and A.O conceptualized the lab studies; A.L., C.B., and R.N., designed the lab studies; H.K., A.S., M.G., performed the studies, analyzed the samples and data; A.L., Y.Z., and A.O., wrote the paper. All authors discussed the results and commented on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Notes on contributors

Aicha Loudari is currently a PhD student in the SoilPhorLife project set up between the Mohamed VI Polytechnic University of Benguerir (Morocco) and the University of Liège, she is studying the interactions between salinity and availability of Phosphorus in the plant-soil system and seeks to develop a model of these interactions. Before that, she obtained her bachelor's degree in cellular and molecular biology in 2014 at the Moulay Ismail University in Meknes (Morocco) and her Master in Plant Biotechnology in 2016 at the Mohammed V University in Rabat (Morocco) where she worked on the in vitro culture of saffron and its bioactive molecules.

Chahinez Benadis was born and raised in ALGERIA. She holds a PhD on Biotechnology in 2015, from the faculty of science, Oran. Her PhD thesis focused on the valorization of rhizospheric microorganisms by producing biofertilizer to enhance legumes yield production. Broadly, her methodological research is oriented to develop sustainable agricultural system by introducing precision fertilization strategy. Winner of the 2015 L'Oréal-UNESCO For Women in Science Awards. Since 2019, she served as a post-doctoral researcher at Mohammed VI Polytechnic university. Recently, her researches are increasingly focused on plant agro-physiology and oriented towards the development of beneficial microorganisms for plants cultivation in order to select microorganisms and microalgae adapted to current biotic and abiotic constraints conditions.

Rachida Naciri is a Researcher Engineer, she has a master's degree in Agronomy from National School of Agriculture of Meknes (ENA), Morocco in 2015. Since 2019, she joined Mohammed VI Polytechnic University as R&D research engineer in plant improvement and physiology. Her research interests include plant stress physiology, plant nutrition, and plan histological techniques.

Aziz Soulaimani is a Researcher Engineer the Agricultural Innovation and Technology Transfer Center (A Network of Experimental Farms throughout Africa) at Mohammed VI Polytechnic University. He is responsible of the Plant and Soil analysis Laboratory and his research interests include soil, plant nutrition.

Dr. Youssef Zeroual, PhD in Microbiology and Biotechnology. He joined OCP in 2007 as Researcher in Biotechnology and Agronomy in R&D department and from 2019 he is in charge of soil management program in OCP Innovation department. His background is oriented to soil microbiology, interaction soil-plant- microbes, soil management, biofertilizers and Biostimulant , Biomass valorization.

Dr. Mohamed El Gharous professor at the School of Agriculture and environment and Director of the Agricultural Innovation and Technology Transfer Center (A Network of Experimental Farms throughout Africa) at Mohammed VI Polytechnic University. Dr. Mohamed El Gharous received his bachelor's degree option experimental sciences in 1976. He received his engineering degree in horticulture in 1980 from IAV Hassan II, Rabat and his master and Ph-D in Agronomy and Soil Science from Oklahoma State University, United States of America, respectively in 1987 and 1991. Dr. Mohamed El Gharous also served as Director of the Regional Center for Agricultural Research Settat for 16 years, board member of the Faculty of Science and Technology of Settat, member of the Joint Committee Franco-Moroccan Research Projects for Development (PRAD) and Chairman of different non-governmental associations.

Professor Mohamed Hazem Kalaji graduated in 1983 from Agricultural Faculty, Aleppo University, Syria. In 1993, at Warsaw University of Life Sciences (SGGW), he received a PhD degree in Agricultural Sciences in the field of Agronomy with specialization of Plant Physiology and later on, in 2013, he obtained Doctor of Science degree (Habilitation) in agronomy. Both degrees were distinguished (Honour level) by SGGW. In 2015, Associate professor Kalaji got the position of Extraordinary Professor at the same university. Kalaji belongs to a group of worldwide recognized specialists in the field of plant physiology, in particular in the field of photosynthesis. The conducted research concerns: functioning, bioenergetics and efficiency of photosynthetic apparatus of plants, productivity of plant assimilation apparatus, plant reactions to abiotic and biotic stressors, chlorophyll fluorescence and gas exchange of plants. In recent years, he has been conducting research towards the creation of innovative solutions for agriculture and environmental protection based on the combination of Plant talk and Machine Learning. As part of international contacts, he has established cooperation with several dozens of institutions and universities from around the world (e.g. India, China, Switzerland, USA, Brazil, Spain, Saudi Arabia, Italy and many others). Associate professor Kalaji reviewed several Polish and foreign postdoctoral and doctoral dissertations, over 700 national and international projects and over 100 scientific papers of international scientific journals. He is also the editor of several international journals. During 2012-2018, he was the most cited scientists in the field of chlorophyll fluorescence.

Dr. Abdallah Oukarroum is a plant physiologist with extensive experience with the study of the photosynthetic apparatus. During his master's degree at the University Ibn Zohr in Morocco. Through his Ph.D thesis, conducted at the University of Geneva in Switzerland, Abdallah Oukarroum acquired an extensive experience in study of alterations in photosynthetic apparatus of plants under environmental stress mainly drought, salt and heat stress. As well, he established two new indexes which rank plant varieties with respect to drought and heat tolerance. At University of Quebec in Montreal in Canada, Abdallah Oukarroum as a post-doc and as a Researcher/Lecturer studied inhibitory effects and bioaccumulation of metals and metallic nanoparticles at membrane and cellular level on aquatic plants. Currently Abdallah Oukarroum is associate professor at University Mohammed VI Polytechnic (UM6P) in Morocco. He is interested in the study of the physiological and biochemical responses to different abiotic stress of superior's plants (terrestrials and aquatic plants), microalga and lichens.

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