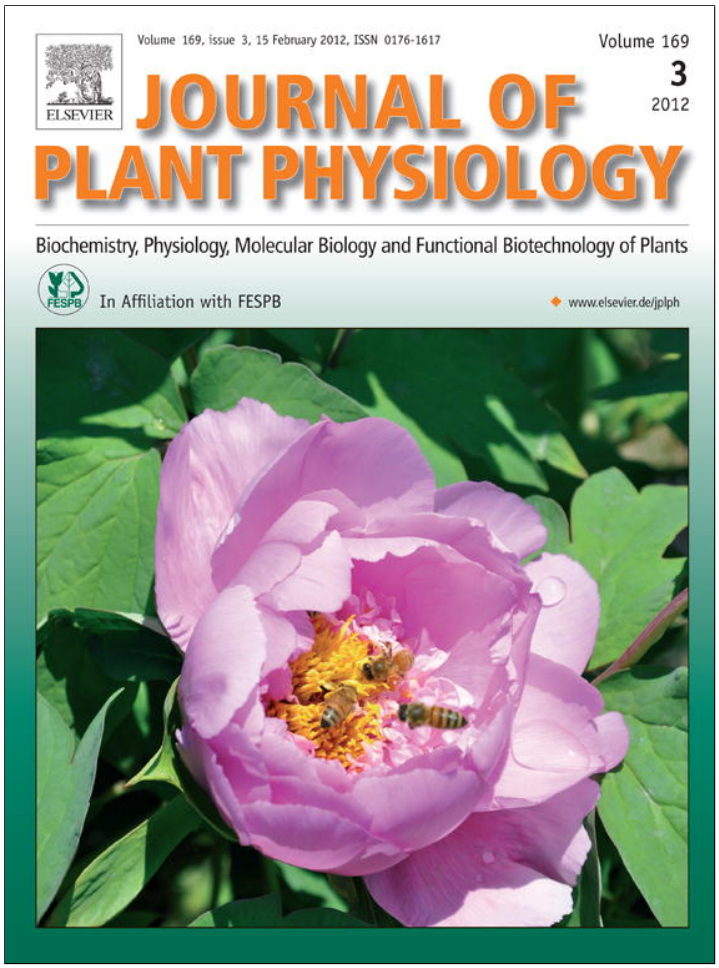

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Abscisic acid root and leaf concentration in relation to biomass partitioning in salinized tomato plants

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ABSTRACT

Salinization is one of the most important causes of crop productivity reduction in many areas of the world. Mechanisms that control leaf growth and shoot development under the osmotic phase of salinity are still obscure, and opinions differ regarding the Abscisic acid (ABA) role in regulation of biomass allocation under salt stress. ABA concentration in roots and leaves was analyzed in a genotype of processing tomato under two increasing levels of salinity stress for five weeks: 100 mM NaCl (S10) and 150 mM NaCl (S15), to study the effect of ABA changes on leaf gas exchange and dry matter partitioning of this crop under salinity conditions. In S15, salinization decreased dry matter by 78% and induced significant increases of Na^+ and Cl^- in both leaves and roots. Dry matter allocated in different parts of plant was significantly different in salt-stressed treatments, as salinization increased root/shoot ratio 2-fold in S15 and 3-fold in S15 compared to the control. Total leaf water potential (Ψ_w) decreased from an average value of approximately −1.0 MPa, measured on control plants and S10, to −1.17 MPa in S15. In S15, photosynthesis was reduced by 23% and stomatal conductance decreased by 61%. Moreover, salinity induced ABA accumulation both in tomato leaves and roots of the more stressed treatment (S15), where ABA level was higher in roots than in leaves (550 and 312 ng g^{-1} fresh weight, respectively). Our results suggest that the dynamics of ABA and ion accumulation in tomato leaves significantly affected both growth and gas exchange-related parameters in tomato. In particular, ABA appeared to be involved in the tomato salinity response and could play an important role in dry matter partitioning between roots and shoots of tomato plants subjected to salt stress.

Introduction

Soil salinization is currently one of the most important causes of crop productivity reduction in many areas of the world (Paranychianakis and Chartzoulakis, 2005). According to the United Nations Food and Agriculture Organization, about 20% of irrigated surface is affected by increasing salinity (Rozema and Flowers, 2008).

Salinity has a strong impact on crop yields both by reducing leaf growth and inducing leaf senescence (Albacete et al., 2008). This in turn reduces plant photosynthetic activity, limiting its ability to produce further growth or harvestable biomass (Yeo, 2007). The salinity response of plants occurs in two phases (Munns, 1993). During the first phase (days to weeks), the osmotic effect is prevalent, while during the second phase (weeks to months), growth is regulated by toxic effects due to the high salt accumulation in leaf tissues. Mechanisms that control leaf growth and shoot development under the osmotic phase of salinity are still obscure (Albacete et al., 2008).

It has been suggested that, during the osmotic phase, inhibition of plant growth could be regulated by hormones or their precursors (Munns and Tester, 2008). The plant's ability to adapt to environmental conditions likely involves long-distance signals between different organs (e.g., between root and shoot) mediated by phytohormones (Sachs, 2005; Albacete et al., 2008; Perez-Alfocea et al., 2010). In particular, abscisic acid (ABA) plays an important role in the whole plant response to drought and salt stress (Zhang et al., 2006). Under adverse environmental conditions, ABA acts as a general inhibitor of growth and metabolism, and negatively affects the synthesis of proteins and nucleic acids, although though these effects are species- and tissue-specific, and they can vary with the developmental stage (Srivastava, 2002). The role of ABA in growth regulation is particularly controversial (Albacete et al., 2008), as some authors have asserted that it inhibits plant growth (Dodd and Davies, 1996; Zhang and Davies, 1990b), while others have demonstrated exactly the opposite (Sharp and LeNoble, 2002).

Abbreviations: ABA, abscisic acid; A, photosynthesis; E, transpiration; gs, stomatal conductance; Ψ_w, total leaf water potential; Ψ_π, osmotic leaf potential; Ψ_p, pressure potential.

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Consequently, several different opinions exist on the role of ABA in the regulation of biomass allocation under salt stress (Sachs, 2005).

In this work, ABA levels in both roots and leaves were analyzed in a cultivated genotype of processing tomato submitted to two increasing levels of salinity stress (100 and 150 mM NaCl for five weeks), to study the effects of salt stress-mediated changes in ABA concentration on growth dynamics, gas exchange and ion accumulation of this crop under salinity conditions.

Materials and methods

Plant material and growth conditions

The experiment was carried out at the University of Basilicata, Italy (40°N, 15°E) in a temperature-controlled glasshouse in rounded plastic pots (1 m diameter × 0.38 m height) with a volume of 250 L. On the 20th of May 2010, processing tomato plants (cv Perfectpeel) at the stage of two fully expanded leaves were transplanted in plastic pots filled with aerated Hoagland nutrient solution (EC = 2.5 dS m^{-1}; pH 6.0) (Hoagland and Arnon, 1950). The solution contained the following nutrients as mmol L^{-1}: NO_3^- 13.5; NH_4 1.5; PO_4^{3-} 1.0; K^+ 6.0; Ca^{2+} 5; Mg^{2+} 2.0; SO_4^{2-} 2.0. Loss of nutrient solution was compensated weekly. Salinization treatment began 10 days after transplantation. An automated heating system started working each time air temperature dropped under 18 °C, and the greenhouse roof opened as soon as the temperature exceeded 25 °C.

During the entire experimental period, meteorological data were recorded by an automatic weather station placed in the greenhouse. The parameters measured were mean air temperature, air humidity and global radiation; they were acquired every 10 s, averaged and registered every 30 min by a Sky "data logger" (Sky DataHog2, type SDL 5400, Skye, Powys, UK). All data were downloaded from the data logger by a laptop and processed in order to obtain the daily averages.

Tomato plants underwent two salinity levels, 10 and 15 dS m^{-1}, through NaCl addition (commercial salt), corresponding to 100 and 150 mM NaCl. Experimental plan foresaw a control treatment maintained at a 2.2 dS m^{-1} salt level. Each experimental treatment was replicated twice arranging the pots according to a randomized block factorial scheme. In each pot, there were 6 plants, yielding a total of 12 plants per experimental treatment. Salt addition to the nutrient solution occurred 7 days after transplant to avoid osmotic shock to plants. The nutrient solution pH was daily adjusted to 6.0 for all the treatments. Beginning at 7 days after transplant and up to the beginning of the flowering stage, measurements were carried out at 6- or 7-day intervals between 12:00 and 14:00 h under conditions of high photosynthetically active radiation (PAR > 1500 μmol photons m^{-2} s^{-1}).

Growth parameters

Leaf area was monitored weekly through nondestructive sampling and, at the end of the experimental trial (37 days after transplanting), by a surface electronic detector (Model 3100, LI-Cor, Inc., Lincoln, NE, USA). At tomato harvesting (37 days after transplanting) dry matter and leaf number were obtained and counted, respectively. Total dry matter (hypogeous and epigeous, DM) was obtained drying the samples in a ventilated oven at 75 °C until constant weight.

Gas exchange

The measurements of net assimilation (A), transpiration (E), stomatal conductance (gs) and intercellular CO_2 concentration (Ci) were carried out every 7 days for all plants of the 3 compared experimental treatments, on apical mature leaves, well exposed to radiation, belonging to five plants representative of each experimental treatment. An open-type portable measurement system (Li-Cor, Inc., mod. 6400, Lincoln, NE, USA) was used. Water use efficiency (WUE) was calculated as the ratio between assimilated CO_2 and transpiration flow.

Determination of Na and Cl

All chemicals for the preparation of the ionic chromatography (IC) eluents and standard solution at analytical reagent grade were purchased from Aldrich (St. Louis, MO, USA). Deionized water at 18 MΩ was used to prepare all of the solutions, and obtained using a water purification system (Millipore, Bedford, MA, USA). For Cl and Na elution at flow rate of 1 mL min^{-1} a solution of 0.5 mM Na_2CO_3/$NaHCO_3$ (1:1, v:v, NaOH 1 mM) and a solution of 25 mM methanesulphonic acid were used. Eluents were filtered through an Aldrich 0.22 μm pore size membrane filter (Millipore, Bedford, MA, USA), and degassed prior to use.

All of the samples were dried, frozen in liquid nitrogen, ground to powder and lyophilized. 25.0 mg of the sample was suspended in 10 mL of water then shaken for 30 min and centrifuged at 3000 rpm for 15 min. The suspensions containing Na and Cl extracted from different parts of the tomato were analyzed after filtering through an Aldrich membrane filter (0.22 μm) just prior to injection in the IC system.

A Dionex DX 100 IC system (Sunnyvale, CA, USA) composed of a GP20 isocratic pump and a CD20 conductivity detector was used. The Cl and Na determinations were performed on a Dionex IonPac AS14 column (250 mm × 4 mm i.d.) protected by an IonPac AG14 guard column (50 mm × 4 mm i.d.) and an IonPac CS column (250 mm × 4 mm i.d.) protected by an IonPac CG12A guard column (50 mm × 4 mm i.d.), respectively. The detector was preceded by a self-regenerating suppressor system (Dionex, Sunnyvale, CA, USA) operating in recycle mode was used to reduce the background eluent conductivity that can provide detection limits up to 10 times lower than not-suppressed technique.

Plant water status

Plant water status was determined at the end of the experiment, 37 days after transplant. Total leaf water potential (Ψ_w) and osmotic leaf potential (Ψ_π) were measured on the youngest uppermost fully expanded leaf and on mature expanded leaves using a Peltier-cooled thermocouple psychrometer (Tru Psi SC10X; Decagon Devices, Pullman, WA, USA) in the psychrometric mode. Leaf discs were removed from one side of the midrib of the lamina and sealed in the psychrometer chamber in less than 15 s. Samples were allowed to equilibrate for 2 h before Ψ_w and Ψ_π readings were carried out. All microvolt equilibration readings were corrected for temperature to 25 °C. Leaf discs were then frozen in a cold room at −20 °C for 24 h to rupture cell membranes, and returned to the chamber to measure Ψ_π. Pressure potential (Ψ_p) was estimated as the difference between Ψ_w and Ψ_π assuming a matric potential equal to 0.

ABA extraction and analysis

At the end of the experiment, 37 days after transplant, leaves and roots were sampled. Both for leaves and root tissues, an aliquot of 250 mg of shoot or root tissue was ground into powder with liquid nitrogen with a mortar and pestle, and put in a tube. 2.5 mL extraction solvent (2-propanol/H_2O/HCl 37%; 2:1:0.002, v/v/v) was added to each tube. The tubes were shaken at a speed of 100 rpm for 30 min at 4 °C. 2.5 mL of dichloromethane was added to each tube, and then the samples were shaken for 30 min at 4 °C

Table 1
Total leaf water potential (Ψ_w), osmotic leaf potential (Ψ_π) pressure potential (Ψ_p) measured in leaves of tomato plants subjected to two levels of salt stress. Mean values ($n = 5$) within a column followed by different lowercase and uppercase letters are significantly different at $P < 0.05$ and $P < 0.01$, respectively, according to Duncan's multiple range test.

Treatments	Ψ_w (MPa)	Ψ_π (MPa)	Ψ_p (MPa)
Control (EC = 2.5 dS m^{-1})	−0.99 A	−1.24 A	0.25 a
S10 (EC = 10 dS m^{-1})	−0.95 A	−1.20 A	0.25 a
S15 (EC = 15 dS m^{-1})	−1.17 B	−1.57 B	0.40 b

and centrifuged at 13,000 × g for 5 min. After centrifugation, two phases were formed, with plant debris between the two layers, so 1.0 mL of the solvent from the lower phase was transferred using a Pasteur pipette into a screw-cap vial, and the solvent mixture was concentrated using an evaporator with nitrogen flow. Finally, the samples were re-dissolved in 0.1 mL methanol and stored at −20 °C before quantitative analysis. The quantitative determinations of abscisic acid (ABA) were carried out by a competitive enzyme-linked immunosorbent assay (ELISA) using the Phytodetek® ABA Test Kit (Agdia Biofords, Evry, France) (Quarrie et al., 1988). The means of the optical densities and binding percentage of duplicate standards or samples (100 μL) were calculated and plotted in a semi-logarithmical scale, in order to linearize the equation.

Statistical analysis

Experimental results underwent variance analysis (ANOVA) using Sigma Plot 11.0 for Windows (Systat Software Inc., San Jose, CA, USA). Significant differences were identified by Duncan's test with 5% and 1% significance.

Results

Plant growth and water relations

The number of leaves per plant decreased in the saline stressed treatment from 72 to 52 in control and in S10 treatment, respectively, and reached 40 leaves per plant in the S15 treatment (Fig. 1a). Moreover, salinity strongly reduced leaf area, as at the end of the experiment, leaf area was 12879 cm^2 in control, 6985 cm^2 in the S10 treatment and 3036 cm^2 in the S15 treatment (Fig. 1b).

Salinization decreased dry matter by 78% in the more stressed treatment (S15). In fact, total dry matter decreased progressively in two salt stressed treatments compared to the control (43, 106 and 196 g plant^{-1}, respectively (Fig. 2a). Salt stress decreased leaf and stem dry matter, while root dry matter was not affected (Fig. 2a). Dry matter allocated in different parts of the plants was significantly different in salt stress treatments. Taking into account the total plant dry matter, its amount in roots was greater in S15 than in S10. Salinization increased the root/shoot ratio 2-fold in the S10 treatment when compared to the control, reaching the highest value in S15 (0.56 g g^{-1}) (Fig. 2b).

Salt stress applied to tomato plants during the experiment resulted in a progressive reduction of plant tissue water status exclusively in the more stressed treatment (S15). At the end of the experiment, Ψ_w decreased from an average value of −0.98 MPa, measured on control and S10 treatment, to −1.17 MPa in S15 treatment. Similarly, Ψ_π passed from an average value of −1.22 MPa, measured on control and S10 plants, to −1.57 MPa measured on tomato plant under S15 treatment (Table 1). Conversely, turgor Ψ_p increased from 0.25 MPa in control plants and S10 to 0.40 MPa in S15 (Table 1).

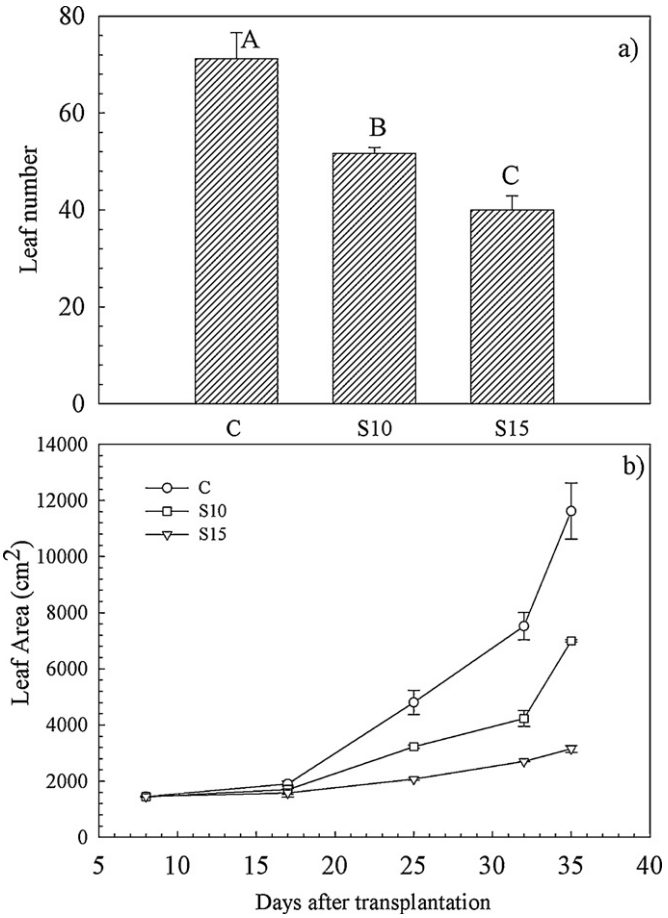

Fig. 1. (a) Leaf number, and (b) leaf area measured in tomato plants subjected to two levels of salt stress. Mean values ($n = 5$) ± S.E. within a column followed by different letters are significantly different at $P < 0.01$, according to Duncan's multiple range test.

Gas exchange

Photosynthesis did not differ between control and moderate salt treatment (S10 treatment) (Fig. 3a), while it decreased by 23% in more severe treatment compared to controls, showing values of 24.1 and 31.3 μmol CO_2 m^{-2} s^{-1}, respectively, at 37 days from transplantation (Table 2). Conversely, transpiration was significantly lower in both salt stress treatments than in the control (Fig. 3b), and was 55% lower than control at the end of salt stress treatment (Table 2).

Salt stress conditions had a strong impact on stomatal conductance, as it decreased progressively in agreement with the salinity level (Fig. 4a). At the end of the experiment, stomatal conductance was reduced by 19% in the S10 treatment and by 61% in the S15 treatment compared to controls (Table 2). For intercellular CO_2, the concentration time trend was in agreement with the stomatal conductance trend (Fig. 4b). At the end of the experimental period, intercellular CO_2 concentration decreased by 7% in the S10 treatment and by 30% in S15 (Table 2). Water use efficiency increased significantly only in S15 (4.25 μmol CO_2 mol H_2O^{-1}), while in S10 and controls, its average was 3.05 μmol CO_2 mol H_2O^{-1}.

Ion content

Sodium and chloride concentrations in salinized tomato plants varied according to the salinity level applied, and different ion accumulations among plant portions were observed (Fig. 5). Na^+ concentration was below 1.0 g kg^{-1} dry weight in all the tissues of

Table 2
Photosynthesis (A), transpiration (E), stomatal conductance (gs), intercellular CO_2 concentration (Ci), and water use efficiency (WUE), measured at the end of the experiment (37 days after transplantation) in leaves of tomato plants subjected to two levels of salt stress. Mean values ($n = 5$) within a column followed by different lowercase and uppercase letters are significantly different at $P < 0.05$ and $P < 0.01$, respectively, according to Duncan's multiple range test.

Treatment	A (μmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	gs (mol H_2O m^{-2} s^{-1})	Ci (μmol CO_2 m^{-2} s^{-1})	WUE (μmol CO_2 mmol H_2O^{-1})
Control (EC = 2.5 dS m^{-1})	31.3 a	10.6 A	0.6 A	292 A	2.9 B
S10 (EC = 10 dS m^{-1})	29.4 ab	9.7 A	0.5 B	272 A	3.2 B
S15 (EC = 15dS m^{-1})	24.1 b	5.8 B	0.2C	204 B	4.3 A

control plants (Fig. 5a). Regarding the two salt treatments, Na^+ level was 14–43 g kg^{-1} dry weight in S10 and S15, respectively (Fig. 5a). In general, the Cl^- concentration was higher than the Na^+ concentration in salinized tomato plants. The highest Cl^- concentration in the control treatment was 14 g kg^{-1} weight, measured in control roots. The Cl^- plant tissue concentration was higher in both salt treatments than the control treatment. The maximum Cl^- concentration was measured in roots of S15 (111 g kg^{-1} dry weight). In S10, the Cl^- level (48 g kg^{-1}) was not significantly different from stem Cl^- concentration (Fig. 5b).

Abscisic acid

In leaf tissues, ABA was inversely correlated to the degree of stomata opening, as the stomatal conductance and ABA concentration relationship clearly show (Fig. 6a; $y = -592x + 460$; $R^2 = 0.7$). Salinity induced ABA accumulation in both tomato leaves and roots (Fig. 6b). Under moderate salinity (S10), ABA concentration was not different between leaves and roots (263 and 165 ng g^{-1} fresh weight, respectively), while with more severe treatment, the ABA concentration was significantly higher in roots than leaves (550 and 312 ng g^{-1} fresh weight, respectively) (Fig. 6b). Very low ABA concentrations (below 50 ng g^{-1} fresh weight) were measured in leaves and roots in control plants.

In leaf and root tissues, ABA was directly correlated to the sodium and chloride concentrations (Fig. 7). Higher Na^+ and Cl^- concentrations measured in roots corresponded to the higher ABA

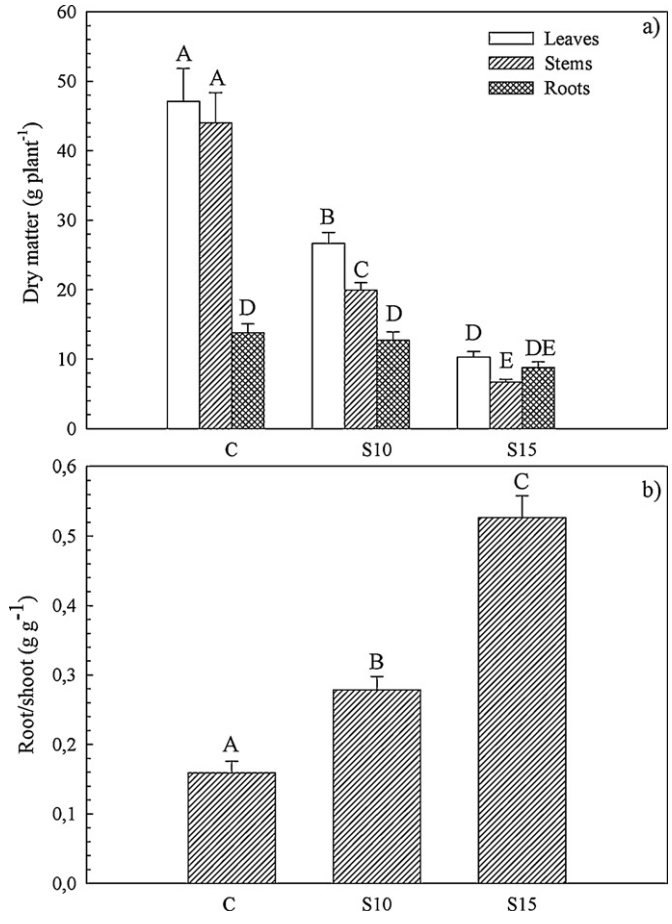

Fig. 2. (a) Dry matter, and (b) root/shoot ratio measured in tomato plants subjected to two levels of salt stress. Mean values ($n = 5$) ± S.E. within a column followed by different letters are significantly different at $P < 0.01$, according to Duncan's multiple range test.

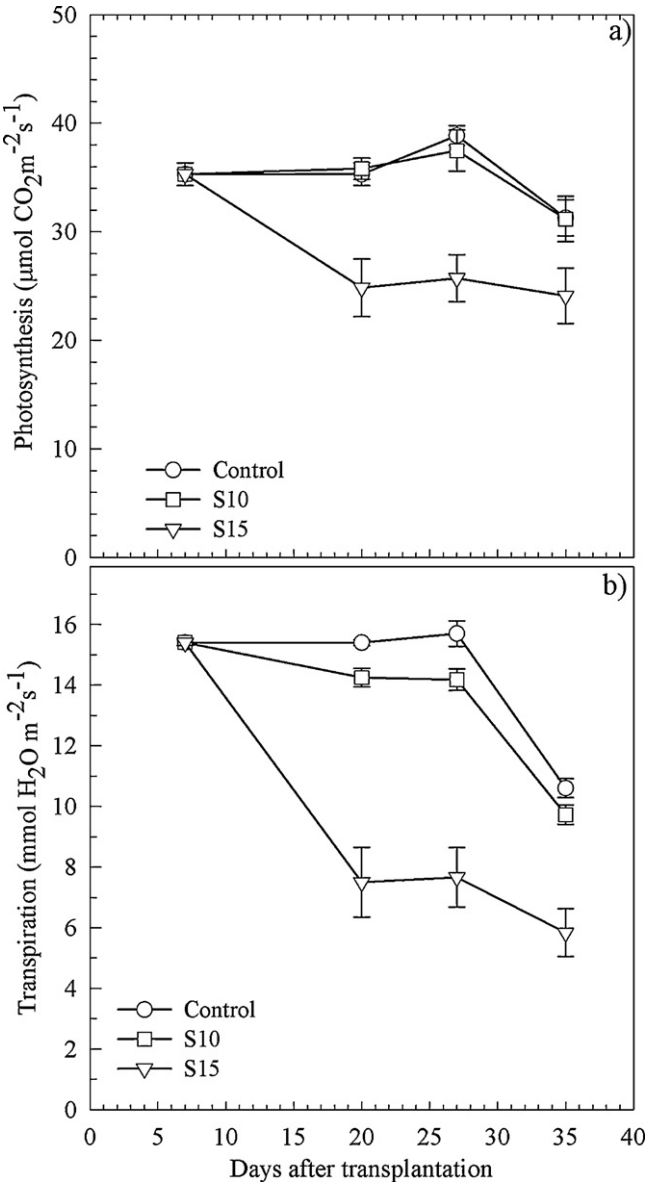

Fig. 3. (a) Photosynthesis, and (b) transpiration trends measured in tomato plants subjected to two levels of salt stress. The values represent means ($n = 5$) ± S.E.

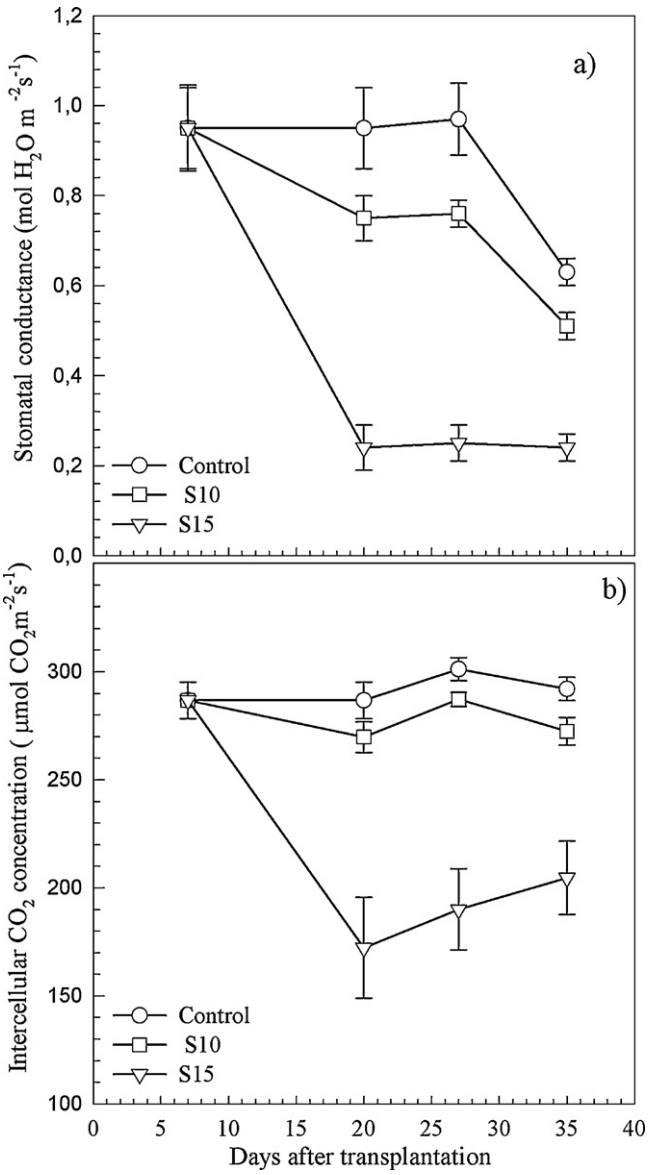

Fig. 4. (a) Stomatal conductance, and (b) intercellular CO_2 concentration measured in tomato plants subjected to two levels of salt stress. The values represent means ($n = 5$) ± S.E.

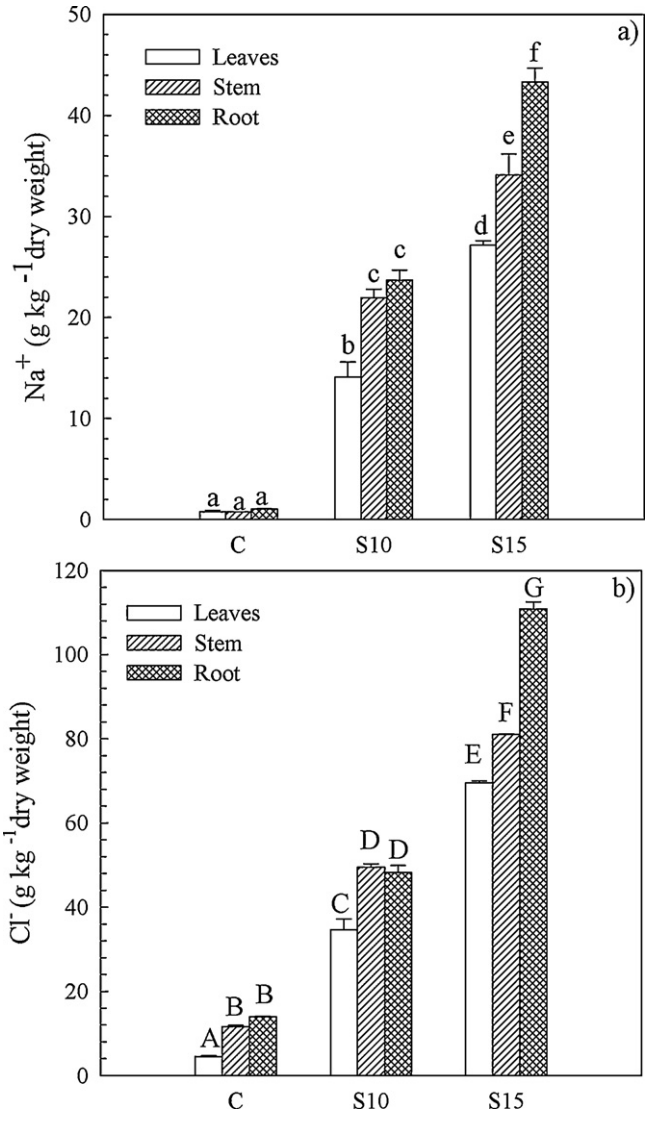

Fig. 5. Levels of Na^+ and Cl^- in leaves, stem and root of tomato plants subjected to two levels of salt stress. Vertical bars give standard error of the mean. Mean values ($n = 5$) within a column followed by different lowercase and uppercase letters are significantly different at $P < 0.05$ and $P < 0.01$, respectively, according to Duncan's multiple range test.

concentration (550 ng g fresh weight^{-1}), which was measured in the roots of the more stressed treatment (S15).

Discussion

It is known that the ratio between root and epigeous dry matter is usually constant, given that the root system and epigeous part grow at the same rate. This dimensional balance between different parts of the plant is guaranteed by the processes of assimilation and partitioning of carbohydrates, but it can be heavily affected by stress conditions (Erice et al., 2010). The ratio between root and epigeous dry matter increased with increasing salinity in the nutrient solution, rising from 0.16 to 0.28 g g^{-1} in control and S10 treatment, respectively, and getting 0.53 g g^{-1} in S15 treatment (Fig. 3b). Currently, opinions still differ on the physiological significance of the increase of the root-shoot ratio under salinity (Moya et al., 1999; Dalton et al., 2000).

Our results on plant growth parameters (Figs. 1 and 2) are in accordance with other authors on tomato crop behavior under salt stress (Albacete et al., 2008; Maggio et al., 2007b). According to those authors, the lower growth of the epigeous parts of the plant is caused by the end of new leaf appearance and a limited leaf growth. Actually, salinity slows cellular division and growth (Albacete et al., 2008). Moreover, under high salinity level, photosynthesis was significantly reduced (Table 2 and Fig. 3a), and thus stressed plants had a lower quantity of fixed carbon to be used for plant growth. Lower stomatal conductance and assimilation rate observed in S15 account for the lower leaf growth and subsequently for the smaller accumulation of dry matter observed in this treatment. With respect to the reductions in Ψ_w and Ψ_π (Table 2), they were proportional to the level of salinization (Table 1) and coupled with an accumulation of Na^+ and Cl^- ions (Figs. 5 and 7).

The different leaf and root accumulation for Na^+ and Cl^- observed here (Fig. 5) are consistent with the existence of different mechanisms of accumulation and/or partitioning for these two ions in tomato plants (Maggio et al., 2007b). We know that Na^+ and Cl^- follow different patterns of partitioning in plant cells (Zhu, 2002). In particular, Na^+ enters root cells and is mainly compartmentalized into the vacuole (Shi et al., 2000, 2003; Zhang and Blumwald,

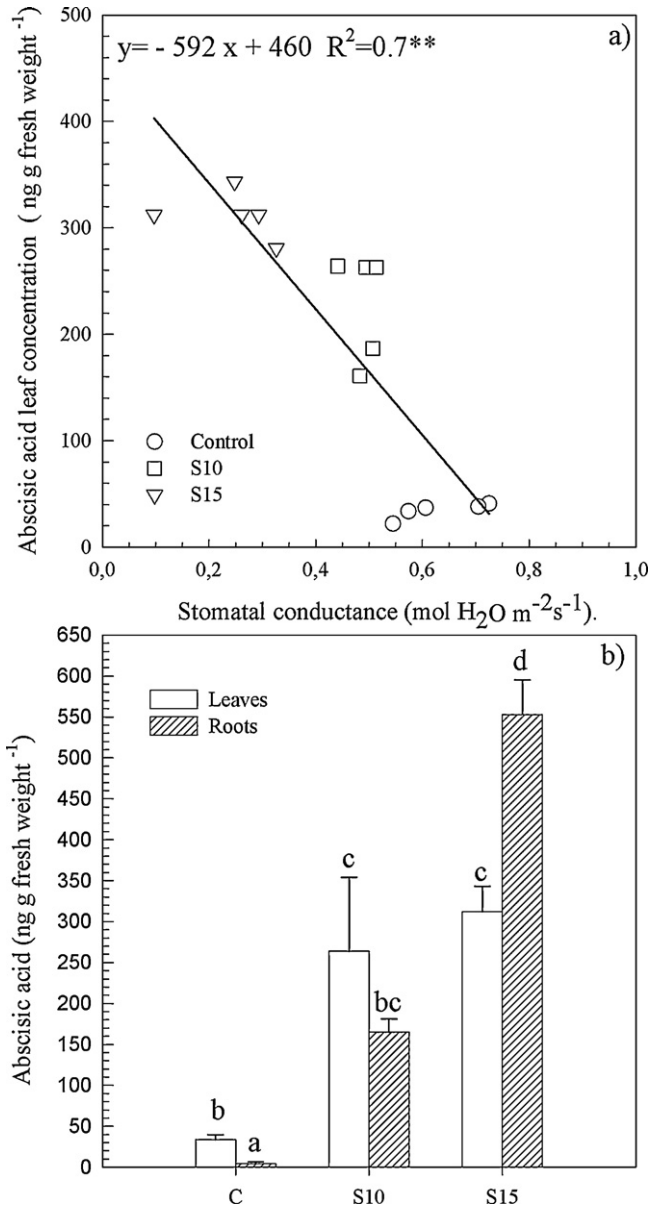

Fig. 6. (a) Relationship between leaf abscisic acid (ABA) and stomatal conductance, and (b) ABA concentration in leaves and roots in tomato plants subjected to two levels of salt stress. Mean values ($n = 5$) within a column followed by different letters are significantly different at $P < 0.05$, according to Duncan's multiple range test.

2001), but under high salinity levels, Na^+ is extruded from the cytoplasm into the apoplastic space, where it follows the transpiration water flux (Maggio et al., 2007b). However, since apoplastic or vacuole Na^+ concentrations were not assayed, Na likely$^+$ accumulated in S15 leaves more than in the less stressed S10 (Fig. 5a). Probably, the high Na^+ and Cl^- accumulation into the roots, together with the observed increase of root dry matter in S15, may be explained as a plant effort to strengthen the ion detoxification capability of roots (Huh et al., 2002; Maggio et al., 2007b).

ABA contributes to salt response during the osmotic phase through improvement of stomatal regulation (Hassine and Lutts, 2010). Indeed, a very strict relation between ABA leaf concentration and stomatal conductance occurred (Fig. 6a). Stomatal closure due to ABA accumulation in leaf tissues was a prolific research field for many years, but there are few data about ABA partitioning among the different plant organs (Assmann, 2004; Zhang et al., 2004). Changes in ABA concentrations between leaves and roots may explain the relative changes in growth ratios and biomass partitioning induced by salt stress (Figs. 1 and 2). Leaf and stem dry matter reduction can be associated with a reallocation of photosynthetates to the roots (Maggio et al., 2007b) mediated by ABA signaling (Albacete et al., 2008). The few available experimental data on tomato (Albacete et al., 2008; Ghanem et al., 2008) are in accordance with our results, but they are at variance with what has been reported by other authors (Mulholland et al., 2003; Maggio et al., 2007b). In tomato under advanced salinization, the high ABA tissue concentration could control organ adaptation processes, such as dry matter partitioning (Albacete et al., 2008) and functional modifications of the root/shoot ratio (Maggio et al., 2007b). Usually, in studies on plants subjected to salt stress, most attention has been directed to ion exclusion/compartmentalization and osmolytes accumulation, whereas other morphological traits of potential interest in stress adaptation, such as root and stomatal behavior, have received less focus (Maggio et al., 2007b). At present, information on root architectures/morphologies that can benefit stress adaptation under salt stress is currently unavailable (Maggio et al., 2011). However some authors have underlined that ABA seems to be involved in root system architecture and, therefore, in the response of plant to soil stresses as drought and salinity (Ghanem et al., 2011a; Wang et al., 2010).

Our results regarding ABA increases in the leaves (Fig. 6b) are in agreement with earlier ABA synthesis in leaves in response to salt stress, which causes stomatal closure and, consequently, a reduction of leaf gas exchange (Maggio et al., 2007b). Similar to its action in the shoot, ABA increase may also be necessary to maintain root growth in salinized plants (Albacete et al., 2008). Sharp and LeNoble (2002) and Spollen et al. (2000) demonstrated that higher root growth under low water potential is related to high ABA accumulation in the roots, and that the keeping of root growth under low water potential depends on ABA accumulation in roots. The increase of ABA root concentration and root/shoot ratio measured under salt conditions (Figs. 2b and 6b) seems to confirm this hypothesis. The previous authors also supposed that ABA is involved in the inhibition of ethylene production, which is a growth inhibitor under stress. However, some authors (Ghanem et al., 2011b) showed that the root-localized induction of cytokinin biosynthesis significantly decreases both ABA and Na^+ accumulation in the root and other organs without altering root biomass under moderate salinity (100 mM NaCl). As Zhang et al. (2006) clearly reported, it is possible to assign to ABA a dual role in plant physiological regulation. That is an inhibitive role when it is accumulated in large amount under stress, and a promoting role when it is at low concentration. We measured high ABA root concentration in correspondence of higher Na^+ and Cl^- root concentration (Fig. 7), so it is possible to suppose its inhibition role, as other authors reported (Sharp and LeNoble, 2002). It is noteworthy that the slopes of the linear relationship between ABA and leaf and root ionic concentrations were higher for Na^+ than for Cl^- either in leaves and roots (Fig. 7).

In any case, higher root/shoot growth could be seen as part of a dynamic adaptation process in which plant physiological/metabolic responses evolve together with plant development, soil salinization and atmospheric parameters during the crop cycle (Maggio et al., 2011).

ABA is only one of the complex groups of hormonal signals which are involved in the tomato salinity response (Albacete et al., 2008), but the data presented in this study show that a different endogenous ABA and ion accumulation, both at the root and leaf levels, may play an important role in regulating growth, leaf gas exchange and dry matter partitioning of salt-stressed tomato plants. The increase of the root/shoot ratio in this species was confirmed to be an

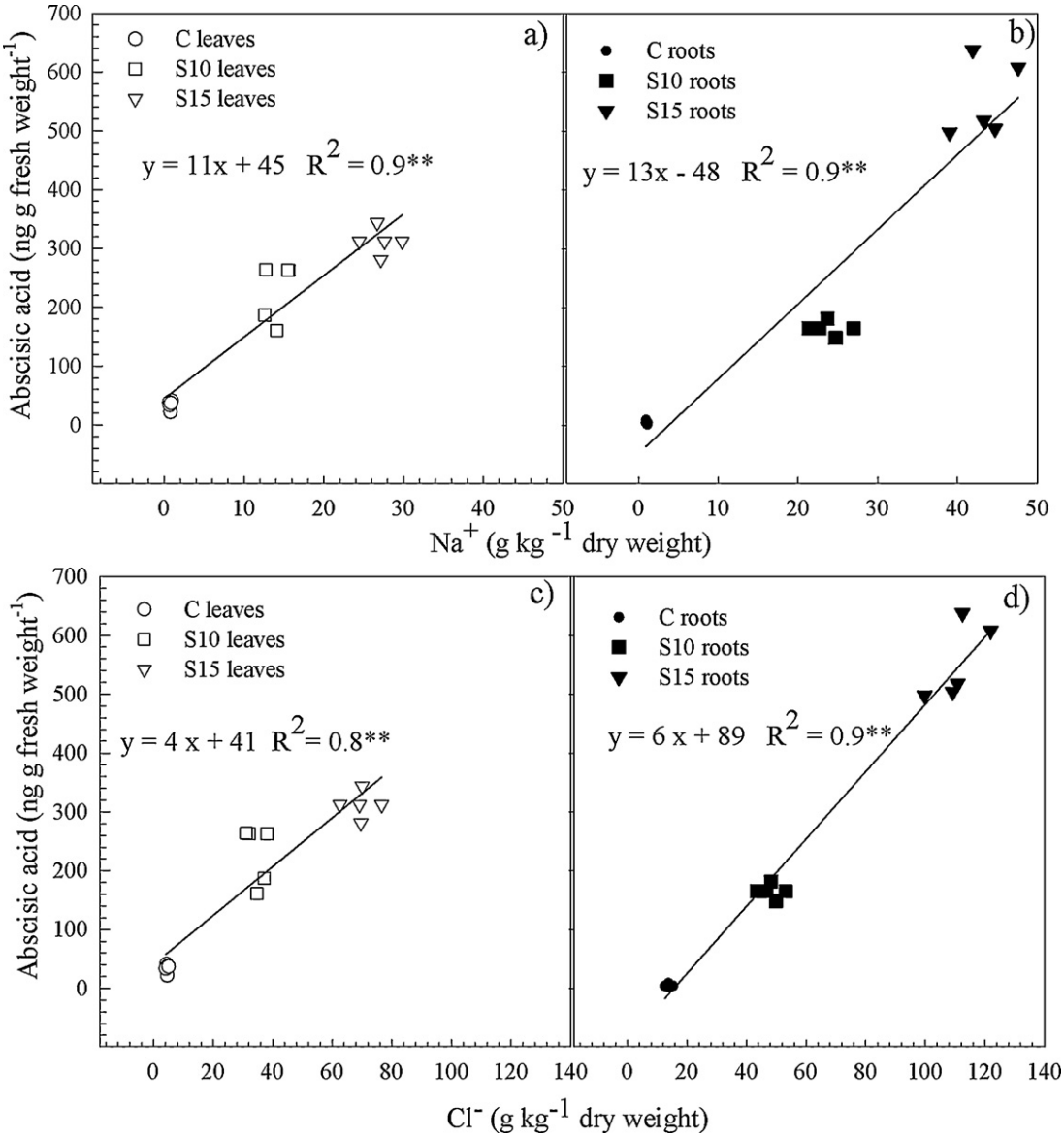

Fig. 7. (a) Relationship between leaf sodium and ABA concentrations, (b) relationship between root sodium and ABA concentrations, (c) relationship between leaf chloride and ABA concentrations, and (d) relationship between leaf chloride and ABA concentrations in tomato plants under two levels of salt stress.

effective physiological response to modulate ion accumulation under salinity conditions.

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