

PHENOTYPING ROOT SYSTEM ARCHITECTURE OF COTTON (*GOSSYPIUM BARBADENSE* L.) GROWN UNDER SALINITY

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Soil salinity causes an annual deep negative impact to the global agricultural economy. In this study, the effects of salinity on early seedling physiology of two Egyptian cotton (*Gossypium barbadense* L.) cultivars differing in their salinity tolerance were examined. Also the potential use of a low cost mini-rhizotron system to measure variation in root system architecture and shoot biomass, accumulated lower Na⁺ ratio through a higher Na⁺ exclusion from both roots and leaves as well as synthesized higher proline contents compared to salt sensitive 'Giza 45' cultivar. Measuring RSA in mini-rhizotrons contain superior values of main root growth rate, total root system size, main root length, higher number of lateral roots and average lateral root length in 'Giza 90' under salinity. Higher lateral root density and length together with higher root tissue tolerance of Na⁺ ions in 'Giza 90' give it an advantage to be used as donor genotype for desirable root traits to other elite cultivars.

Key words: *Gossypium barbadense* L., salinity stress, phenotyping, root system architecture

Soil salinity is estimated to cause losses in crop production of about 27.3 billion US dollars annually (Qadir et al. 2014). The effects that excess Na⁺ cations present in saline soils have on plant physiology are devastating, ranging from ion-toxicity and physiological drought to reactive oxygen species (ROS) formation and cell death (Munns et al. 2003; Aboukheir et al. 2008). However, not all plants are equally tolerant to salinity. Although plants have developed a variety of strategies to tolerate salinity stress (Roy et al. 2014), the majority of economically important crop plants are considered glycophytes and are severely affected by high Na⁺ concentration with an evident trade-off between yield and salinity tolerance. Plant root system architecture (RSA), the spatial distribution of the root system within the rooting zone, is an important trait for salinity tolerance (Abul- Naas & Omran 1974). Phenotypic variability in RSA traits such as lateral root length and density but also assessing its available variability in Egyptian cotton (*G. barbadense*), an economically valuable species, is lacking.

Salinity tolerance among cotton germplasm varieties is highly variable. In this study, the effects of salinity on early seedling physiology of two Egyptian cotton (*Gossypium barbadense* L.) cultivars differing in their salinity tolerance were examined. Also the potential use of a low cost mini-rhizotron system to measure variation in root system architecture and shoot biomass, accumulated lower Na⁺ ratio through a higher Na⁺ exclusion from both roots and leaves as well as synthesized higher proline contents compared to salt sensitive 'Giza 45' cultivar. Measuring RSA in mini-rhizotrons contain superior values of main root growth rate, total root system size, main root length, higher number of lateral roots and average lateral root length in 'Giza 90' under salinity. Higher lateral root density and length together with higher root tissue tolerance of Na⁺ ions in 'Giza 90' give it an advantage to be used as donor genotype for desirable root traits to other elite cultivars.

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nutrients uptake and abiotic stress tolerance. Root system morphology and architecture. The identifying RSA traits was reported to contribute in improving grain yield and drought tolerance (Steele et al. 2013; Uga et al. 2013). Nevertheless, studying RSA in a mini-rhizotron used in our experiments consisted of two glass sheets of 30x30 cm separated by a 3 mm wide glass separator. The inner space available for culture substrate was approximately 250 cm². Experimental design and plant growth conditions. Experiments were arranged as a randomized design with 3–5 replicates, and were repeated two times. Experiments were performed using this mini-rhizotron in the present research work as follows:

Experiment 1
The substrate of this experiment included peat and perlite. Two glass sheets were placed over each other and sealed from the corners and below with paper clips and sellotape to keep substrate from being lost and was perforated at the bottom to allow drainage. Mini-rhizotrons were kept in a growth chamber under the following conditions: 25°C, 60% humidity, photon irradiance of 100 µE/m²/s and 16/8h light/dark cycle. Mini-rhizotrons were placed vertically under the angle of 70° in the growth chamber and covered with black plastic bags to provide dark conditions for roots.

Experiment 2

The substrate placed in mini-rhizotrons of this experiment consisted of sucrose-free ¼ strength MS medium (Murashige & Skoog 1962) supplemented with agarose gel 1.2% and pH was adjusted to 5.8. The same growing conditions were maintained as in experiment 1.

Seed sterilization and cultivation

Seeds were sterilized in commercial sodium hypochlorite solution 1% for 10 min and then rinsed three times with tap water, and then left to germinate for two days in Petri dishes lined with water-soaked filter paper. Seed from cultivar Giza 90 was planted at approximately equal spacing from the other cultivar Giza 45 per mini-rhizotron.

Salinity stress treatment

In Experiment 1, two days old seedlings were transferred to mini-rhizotrons and randomly divided

MATERIAL AND METHODS

The present study was carried out during January–July 2016 in the Plant Physiology division, Department of Agricultural Botany, Faculty of Agriculture, Cairo University, Egypt.

Plant material

Egyptian cotton (*Gossypium barbadense* L.) cultivars ‘Giza 90’ (salt tolerant) and ‘Giza 45’ (salt sensitive) were used in our experiments, both obtained from the Cotton Research Institute, Agricultural Research Centre, Giza, Egypt.

Mini-rhizotron description

Mini-rhizotron system allows a non-destructive study of root development during early stages of seedling growth. It usually contains a thin layer of substrate that directs the roots to grow in 2D conditions, facilitating the monitoring and measurement

was watered with 100 ml of ¼ MS medium every two days during the two weeks. The second group was treated with ¼ MS medium containing 150 mM NaCl every two days also for two weeks.

In Experiment 2, using mini-rhizotron containing solid MS nutrient medium, salinity stress was imposed from the beginning using solid ¼ strength MS medium containing 150 mM NaCl, where 2 days old seedlings of both cotton cultivars were transferred to four mini-rhizotrons. In the case of control conditions, another four seedlings of both cultivars were transferred to NaCl free solid ¼ strength MS medium.

Salinity tolerance physiological traits

Leaf relative water content (RWC) was calculated according to Weatherly (1950). Fresh and dry weights were determined with the accuracy of 0.001 g on the regular lab scale. Dry weight of root and shoot tissues were measured after drying the material for 48 h at 70°C. Free proline concentration in leaves was determined according to Bates (1973) using 0.5 g dry weight samples. Na and K cation contents of shoot or root dry weight samples were extracted by 0.1 M HCl solution (Garcia del Moral et al. 2003). Determination of Na and K contents of shoot or root dry weight samples were extracted by 0.1 M HCl solution (Garcia del Moral et al. 2003). Determination of Na and K contents of shoot or root dry weight samples were extracted by 0.1 M HCl solution (Garcia del Moral et al. 2003).

Image capturing and analysis of RSA

Mini-rhizotrons were scanned with a Canon MG2400 series Scanner at 200 dpi at 14 days plant age. Scanned images RSA parameters were processed using ImageJ (Schneider et al. 2009). Data were collected from 3 individual seedlings per treatment per experiment. RSA parameters of control conditions were not significantly different from salinity stress conditions (= 5 KL]R VRIWZDUH WR GHWHFV \$OO GPWD ZHUH FOHDUHG from outliers.

Statistical analysis of data

Differences among means were tested by a two way ANOVA followed by Duncan post hoc test in the case of RSA parameters, differences between means were tested by t-test. Differences were considered significant if $P < 0.05$ in all analyses. Both statistical analyses were carried out using IBM SPSS Statistics V. 20 (IBM, USA).

RESULTS

Cv. 'Giza 90' accumulates lower Na and higher proline contents than 'Giza 45'

Under 150 mM NaCl treatment in both cultivars but with no differences between them (Table 1). Nevertheless, content of Na but not K in both shoots and roots as compared to plants under control conditions. These increases in Na FRQFHQWUDWLRQV ZHUH KLVKHU LQ FY μ*L]D ¶ PDNLQJ L]D cv. 'Giza 90' in eliminating Na to the outside of URRW FHOOV 7KLV ZDV UHÀHFWH decrease in K/Na⁺ ratio in cv. 'Giza 90' roots under salinity. However, cv. 'Giza 90' showed similar values to "Giza 45" under control conditions. In addition, the ability to synthesize proline under salinity W\ VWUHV LQ FY μ*L]D ¶ ZDV IRU cv. 'Giza 90' were one-fold higher than cv. 'Giza 45' under salinity stress, being 1.93 and 4.17 mg/g leaf dry weight basis in cvs. 'Giza 45' and 'Giza 90', respectively. Surprisingly, the synthesis of proline in cv. 'Giza 90' leaves under control conditions was similar to the value of cv. 'Giza 45' leaf proline under salinity conditions.

Salinity stress severely hinders root growth rate of cv. 'Giza 45'

Hidden lateral roots in the thin layer of substrate (Figure 1) made possible to only examine and measure growth of the main root of both cotton cultivars. SRR (= 5 KL]R VRIWZDUH WR GHWHFV \$OO GPWD ZHUH FOHDUHG hindered under 150 mM NaCl treatment compared with control (Table 1). Nevertheless, root system of cv. 'Giza 45' was apparently more sensitive to salinity as the decrease in its main root growth rate was PRUH VLJQL]D FDOV WKDQ FY μ*L]D NaCl, giving values of approximately 11.1 and 16.6 mm/day, respectively.

Cv. 'Giza 90' gives higher root and shoots biomass under salinity

Harvesting intact root system from peat moss/vermiculite substrate was not possible in mini-rhizotrons containing solid MS medium, the whole in

tact root system was easily harvested and washed. The effect of 150 mM NaCl on lateral roots of cv. 'Giza 45' was more profound and more detrimental to shoots of both cultivars (Table 1) being more significant. Root system architecture (RSA) traits under salinity of cv. 'Giza 90' is highly superior than 'Giza 45' Solid MS media in mini-rhizotrons permitted a clear and accurate measurement of the whole root system of both cotton cultivars (Figure 2). Nonetheless, the vigorous growth under control treatment led to overlapping of lateral roots of both cultivars

image analysis software (Figure 2 and Supplementary Figure 1). This, however, was not the case under 150 mM NaCl, where root growth was slower and less dense. Results in Table 2 show the effect of salinity on RSA of both cultivars. Overall, the morphology of cv. 'Giza 90' was considerably superior under both control and 150 mM NaCl conditions (Figure 2). The total root system size of cv. 'Giza 90' was 2.5 folds over cv. 'Giza 45' under 150 mM NaCl. Main root length of cv. 'Giza 90' as compared to cv. 'Giza 45' as well as almost a 2.5 folds bigger cumulative lateral roots length. This might imply that

the effect of 150 mM NaCl on lateral roots of cv. 'Giza 45' was more profound and more detrimental. Root system architecture (RSA) traits under salinity of cv. 'Giza 90' is highly superior than 'Giza 45' Solid MS media in mini-rhizotrons permitted a clear and accurate measurement of the whole root system of both cotton cultivars (Figure 2). Nonetheless, the vigorous growth under control treatment led to overlapping of lateral roots of both cultivars

DISCUSSION

Assessing salinity tolerance of 'Giza 90' and 'Giza 45' cotton cultivars to their salinity tolerance into three groups; salt sensitive, moderate salt tolerant and salt tolerant (Ashour & Abd-El'Hamid 1970). Curiously, early reports classify 'Giza 90' as salt sensitive (El-Kader et al. 2006). Thus, it was important in our work to assess the degree of seedling stage salinity tolerance of 'Giza 45' and 'Giza 90'

T a b l e 1

Salinity tolerance traits studied in cvs. 'Giza 90' and 'Giza 45' cotton plants (14 days age) under control and 150 mM NaCl treatment (Experiments 1 and 2)

Experiment	Trait	Control		150 mM NaCl	
		'Giza 90'	'Giza 45'	'Giza 90'	'Giza 45'
1	Leaf RWC [%]	82.1 ± 1.8	83.2 ± 1.5	73.5 ± 1.3	77.5 ± 0.5
	Root growth rate [cm/d]	28.0 ± 2.0	19.0 ± 1.9	16.6 ± 2.5	11.1 ± 1.0
	Leaf proline [mg/g]	2.22 ± 0.12	1.53 ± 0.20	4.17 ± 0.32	1.93 ± 0.03
	Leaf Na ⁺ [nmol/mg]	89.8 ± 9.4	60.6 ± 7.1	430.8 ± 37.2	648.4 ± 44.4
	Root Na ⁺ [nmo/mg]	310.5 ± 21.6	438.1 ± 61.5	716.6 ± 35.9	891.3 ± 57.3
	Leaf K ⁺ [nmol/mg]	282.2 ± 44.5	247.5 ± 53.8	302.2 ± 28.5	301.4 ± 29.2
	Root K ⁺ [nmol/mg]	251.1 ± 40.0	300.5 ± 16.2	394.4 ± 61.0	343.4 ± 5.8
	Leaf K ⁺ /Na ⁺	3.3 ± 0.9	4.2 ± 1.0	0.7 ± 0.0	0.5 ± 0.0
	Root K ⁺ /Na ⁺	0.8 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	0.4 ± 0.0
2	Shoot DWT [mg]	186.5 ± 2.6	92.7 ± 4.2	68.2 ± 10.3	25.3 ± 6.9
	Root DWT [mg]	126.2 ± 1.0	20.7 ± 1.4	104.7 ± 11.4	14.1 ± 2.7
	Shoot/Root	1.5 ± 0.7	4.5 ± 0.5	1.3 ± 0.6	2.4 ± 0.6

Each value represents the mean ± SD. Different letters indicate significant differences (P > 0.05) according to Duncan test. (Abbreviations: RWC – relative water content; DWT – dry weight)

cultivars using simple physiological measurements. cv. 'Giza 90' was detected. This is an important trait to protect the leaves photosynthetic machinery from damage induced by excessive Na⁺ involving several mechanisms such as Na⁺ loading, Na⁺ retrieval from the xylem and Na⁺ retrieval from the shoots (Karley et al. 2000; Davenport et al. 2007). The lower Na⁺ concentration in the leaves is usually expressed in more salinity tolerance. Furthermore, the root system morphology under salinity makes the uptake more problematic, causing a massive elongation of the taproot of cotton plants by 60% (Shabala & Cuin 2008). Nevertheless, the results of this level of salinity on the water relations of both cultivars was assessed by measuring the relative water content (RWC) in leaves (Table 1) and in shoots, indicating that stress level imposed was not very severe (Table 1). Under salinity, cells adjust their osmotic potential by accumulating many compatible solutes which also perform many other important functions. Osmotic potential might depend on the level of transcription of osmotic potential regulators and activity of responsible transporters such as SOS1 and NHX (Harris & Hildebrand 1988) reported that cotton has more osmotic adjustment capabilities than other cotton cultivars for osmotic potential exist, suggesting that genotypic variation for osmoregulation in cotton is wide (Quisenberry et al. 1982). All in all, it is extensively reported that proline concentration increases in cotton with increasing soil salinity (He et al. 2007). It is apparent that under our experimental conditions, proline content of cv. 'Giza 90' giving it a superior ability to maintain its turgor under salinity, results similarly reported by El-Kadi et al. (2006).

High salinity reduces vegetative and reproductive growth of cotton (Gorham et al. 2010). Both plant height and leaf expansion are negatively affected in saline soils where the differentiation of nodes is suppressed (Ahmed 1994). These effects are however less accentuated in tolerant as in case 'Giza 90' where both its shoot and root biomass are expressed in more salinity tolerance. Furthermore, the root system morphology under salinity makes the uptake more problematic, causing a massive elongation of the taproot of cotton plants by 60% (Shabala & Cuin 2008). Nevertheless, the results of this level of salinity on the water relations of both cultivars was assessed by measuring the relative water content (RWC) in leaves (Table 1) and in shoots, indicating that stress level imposed was not very severe (Table 1). Under salinity, cells adjust their osmotic potential by accumulating many compatible solutes which also perform many other important functions. Osmotic potential might depend on the level of transcription of osmotic potential regulators and activity of responsible transporters such as SOS1 and NHX (Harris & Hildebrand 1988) reported that cotton has more osmotic adjustment capabilities than other cotton cultivars for osmotic potential exist, suggesting that genotypic variation for osmoregulation in cotton is wide (Quisenberry et al. 1982). All in all, it is extensively reported that proline concentration increases in cotton with increasing soil salinity (He et al. 2007). It is apparent that under our experimental conditions, proline content of cv. 'Giza 90' giving it a superior ability to maintain its turgor under salinity, results similarly reported by El-Kadi et al. (2006).

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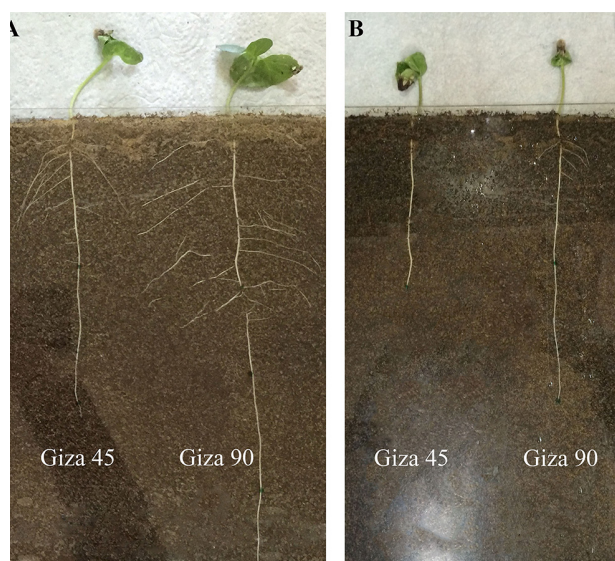


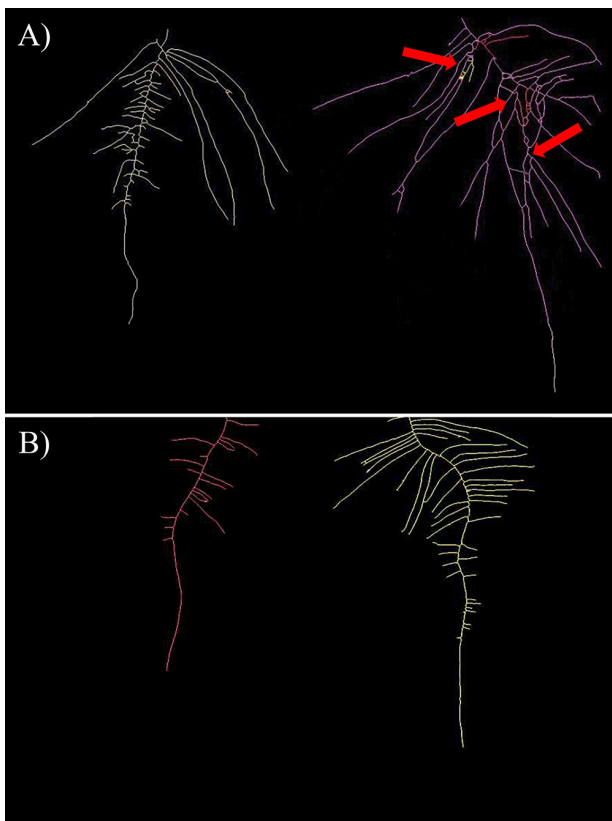
Figure 1. Root system morphology of cvs. 'Giza 90' and 'Giza 45' cotton plants (14 days age) under A) control and B) 150 mM NaCl conditions (Experiment 1)

Challenges in studying RSA of cotton

Root phenotype of plant seedling can be a sound predictor of later stages of plant development (Tupper & Peres 2002). However, a problem we faced in studying roots of early stage cotton plants in



Figure 2. Root system morphology of cvs. 'Giza 45' and 'Giza 90' cotton plants (14 days age) under A) 150 mM NaCl and B) control conditions (Experiment 2)



Giza 45

Giza 90

of root system morphology of cvs. 'Giza 90' and 'Giza 45' cotton plants (14 days age) under A) control and B) 150 mM NaCl conditions (Experiment 2). Red arrows indicate entangled regions erroneously detected by the software

mini-rhizotron, in contrast to other crops such as tomato (Darwish et al. 2016), was that some lateral roots were either hidden into the soil layer and not showing over neither the front nor back glass plates of the mini-rhizotron to be scanned for subsequent image analysis. Also, some lateral roots showed at back side only. The main cause of this problem is that the lateral roots of cotton emerge on the main

cy of studying RSA in 2D mini-rhizotrons, as in the case of our experiment. A possible solution to avoid this problem is to force the growth of lateral roots in an even more 2D growth by decreasing the spacing between the two mini-rhizotron glass plates even lower than 3 mm. This, however, will probably put a mechanical strain which might affect the main root growth making its growth pattern not be reliable to study. Thus, solid MS medium was used to provide a translucent environment needed to detect all lateral roots and study their RSA. Another problem we faced was that, under control conditions, the root growth was very vigorous and led to the overlapping and entanglement of lateral roots in many zones (Figure 2). This problem leads to a faulty detection of roots in Rhizo software and gave erroneous results (Supplementary Figure 1). This could be overcome by studying RSA under control conditions at earlier stages of growth (e.g. 10 days age). For this reason, it was only possible for us to study the RSA of cvs. 'Giza 45' and 'Giza 90' only under salinity stress.

Identifying potential root traits in Egyptian cotton desirable for salinity tolerance

sum cotton, i.e. root length, root fresh weight, root dry weight, lateral root number, lateral root dry weight, total root dry weight, root volume, and root-to-shoot ratio was reported in previous studies (Basal et al. 2003; AbouKheir et al. 2008). This variability, however, seems to be much lower in genotypes adapted to humid and high-rainfall-conditions (Quisenberry et al. 1981). In the case of our experiments, substantial variation in root traits was detected between cvs. 'Giza 90' and 'Giza 45'. The analyzed data of mini-rhizotron root system image shows that cv. 'Giza 90' root system architecture

various parameters including total root size, main root length, cumulative lateral root length, average lateral root length, number of lateral roots, length of basal and branched zones, and depth. This was also concentrated in deeper layers. This high density of lateral roots per cm of main root. This trait present in salt tolerant cv. 'Giza 90' cotton suggests its advantage as a donor genotype for this particular desirable root trait to other elite cotton cultivars in any of the ongoing breeding programs for salinity and drought tolerance. This trait is normally translated as a higher root biomass as shown earlier (Table 1). The body of literature published on the effect of salinity on root traits of cotton in general, and RSA in particular, is very limited (Gorham et al. 2010). However, a number of different root morpho-physiological traits have been proposed and be implicated as important mechanisms that impact salinity tolerance as well. These include RSA parameters. The possibility of phenotyping cotton RSA at early stages of plant development, later developmental stages, using a mini-rhizotron system which was demonstrated being more accurate using solid MS media than peat moss/sand as substrate (Pace et al. 1999). Our results show that cv. 'Giza 90' possesses several of the aforementioned traits and root traits for salinity tolerance, such as a longer main root and lateral roots in the basal zone, a

CONCLUSIONS

Salt tolerant 'Giza 90' cotton cultivar showed superior shoot/root biomass, higher K⁺/Na⁺ ratio and proline content. This superiority also holds true regarding the ratio of root system architecture (RSA) parameters. The possibility of phenotyping cotton RSA at early stages of plant development, later developmental stages, using a mini-rhizotron system which was demonstrated being more accurate using solid MS media than peat moss/sand as substrate (Pace et al. 1999). Our results show that cv. 'Giza 90' possesses several of the aforementioned traits and root traits for salinity tolerance, such as a longer main root and lateral roots in the basal zone, a

T a b l e 2

56\$ SDUDPHWHUV RI FYV μ*L]D ¶ DQG μ*L]D software under 150 mM NaCl salinity stress (Experiment 2)

Root system architecture (RSA) parameter	'Giza 45'	'Giza 90'
Main root "MR" length [cm]	14.47 ± 0.12	19.01 ± 0.72
Lateral roots "LR" cumulative length [cm]	19.64 ± 4.66	97.56 ± 3.98
Total root size "cumulative length of LR and MR" [cm]	35.38 ± 6.05	120.43 ± 8.56
Number of lateral roots per main root (#)	19 ± 0	43 ± 4
Average length of lateral roots [cm]	0.93 ± 0.18	1.94 ± 0.17
Average lateral root length as ratio of main root length [%]	6 ± 0	9 ± 0
Main root length as ratio of total root size [%]	45 ± 4	19 ± 2
Length of basal zone [cm]	1.04 ± 0.92	0.74 ± 0.54
Length of branched zone [cm]	8.42 ± 0.22	18.63 ± 1.87
Length of apical zone [cm]	6.29 ± 2.10	7.30 ± 0.55

Each value represents the mean ± standard error of 3 replicates. Means with asterisk (*) (P < 0.05) according to t-test.

F DVH RI μ * L J D ¶ FXOWLYDU ZD V 6 1 G B C Q W (6 6 H 2 G B 5 4 2 L V 3 0 6 R Z , & , 7 < B \$ 1 ' (; 3 5 (6 6 , 2 1 B 2) B , 2 1 B 7 5 \$ 1 6 3 2 5 7 (5 B * (1 (6 B , 1 B 7 2 0 \$ 7 2 B 3 / \$ 1 7 6 O L Q N V G D D H E H EFFECT-OF-SALT-STRESS-ON-ROOT-PLASTICITY- \$ 1 ' (; 3 5 (6 6 , 2 1 2) , 2 1 7 5 \$ 1 6 3 2 5 7 (5 * (1 (6 IN-TOMATO-PLANTS.pdf \$ 9 (1 3 2 5 7 5 - ± 0 8 1 2 = 0 \$ < 2 5 \$ ± - + \$ ' ± (SAH, P.A. – RUS, A. – TESTER, M. 2007. The Na⁺ transporter AtHKT1;1 controls retrieval of Na⁺ from the xylem in Arabidopsis. *In* Plant, Cell and Environment, vol. 30, pp. 497–507. DOI: 10.1111/j.1365-3040.2007.01637.x BIAVIENNE-BARRET, F. – RICHARD-MOLARD, C. – CHELLE, M. – MAURY, O. – NEY, B. 2006. Ara-rhizotron: An effective culture system to study simultaneously root and shoot development of Arabidopsis. *In* Plant and, Soil vol. 280, pp. 253–266. DOI: 10.1007/s11104-005-3224-1 EL-KADI, D.A. – AFIAH, S.A. – ALY, M.A. – BADRAN, A.E. 2006. Bulked segregant analysis to develop molecular markers for salt tolerance in Egyptian cotton *Arab Jour nal of Biotechnology* vol. 9, pp. 129–142. Available from: K W W S V Z Z Z U H V H D U F K J D W H Q H W S U R I S X E O L F D W L R Q B % X O N H G B V H J U H J G H Y H O R S B P R O H F X O D U B P D U N H U V B I R U B V D W E N O R Z O W S G J H G T K H ¿ Q D Q E I F I F = \$ + \$ % \$ \$ \$ 6 D O W W R O H U D Q F H R I H I ton varieties. Part II. At the seedling stage *Zeitschrift für \$ F N H U X Q G 3 Å D Q J H Q E D X*, vol. 133, pp. 308–314. GARCIADEBLAS, B. – SENN, M.E. – BANUELOS, M.A. – 5 2 ' 5 È * 8 (= 1 \$ 9 \$ 5 5 2 \$ 6 R G L X P W U D Q V S H K T transporters: the rice model. *In* Plant Journal, vol. 34, S S ± ' 2 , M ; [GORHAM, J. – LAUCHLI, A. – LEIDI, E.O. 2010. Plant re- V S R Q V H V W R V D O L Q L W \ , Q 6 7 (: \$ 5 7 - 0 Å ' 0 Å + (, 7 + 2 / 7 - - Å 0 \$ 8 1 (< Phys-5 (G V iology of Cotton. London : Springer, pp. 129–141. DOI: B HE, G. – SHEN, G. – PASAPULA, V. – LUO, J. – VEN . 7 \$ 5 \$ 0 \$ 1 , 6 ± 4 , 8 ; ± . 8 3 3 8 6 ± . 2 5 1 < YEY, D. – HOLADAY, A.S. – AULD, D. – BLUMWALD, (± = + \$ 1 * + (F W R S I A N H X I S U H V V L R Q F cotton (*Gossypium hirsutum* L.) increases proline content and enhances photosynthesis under salt stress conditions. *In* Journal of Cotton Science vol. 11, pp. 266–274. Available from: <http://www.cotton.org/journal/2007-11/4/upload/jcs11-266.pdf> JULKOWSKA, M.M. – TESTERINK, C. 2015. Tuning plant signaling and growth to survive salt. *Trends in Plant Sci ence* vol. 20, pp. 586–594. DOI: [http://dx.doi.org/10.1016/j. tplants.2015.06.008](http://dx.doi.org/10.1016/j.tplants.2015.06.008) KARLEY, A.J. – LEIGH, R.A. – SANDERS, D. 2000. Dif- I H U H Q W L D O L R Q D F F X P X O D W L R Q D Q G L R G and epidermis of barley. *In* Plant Physiology vol. 122, pp. 835–844. DOI: 10.1104/pp.122.3.835. MUNNS, R. – TESTER, M. 2008. Mechanisms of salinity tolerance. *In* Annual Review of Plant Biology vol. 59, pp. 651–681. DOI: 10.1146/annurev.arplant.59.032607.092911 MURASHIGE, T. – SKOOG, F. 1962. A revised medium for rapid growth and bio assays with tobacco tissue cultures. *In* Physiologiae Plantarum vol. 15, pp. 473–497. DOI: 10.1111/j.1399-3054.1962.tb08052.x OOSTERHUIS, D.M. – WULLSCHLEGER, S.D. 1988. Drought tolerance and osmotic adjustment of various crops in response to water stress. *Arkansas Farm Research* vol. 37, pp. 12. PACE, P.F. – CRALLE, H.T. – EL-HALAWANY, S.H. – CO- THREN, J.T. – SENSEMAN, S.A. 1999. Drought-induced changes in shoot and root growth of young cotton plants. *In* B () (& 7 B

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