Responses of some newly developed salt-tolerant genotypes of spring wheat to salt stress: II. Water relations and photosynthetic capacity

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SUMMARY

Photosynthetic capacity and water relations of two newly developed salt-tolerant genotypes of spring wheat, S24 and S36, were assessed with respect to their parents, LU26S (from Pakistan) and Kharchia (from India). These four lines, together with a salt-tolerant genotype SARC-1 and two salt-sensitive cvs Potohar and Yecora Rojo, were grown until the booting stage in salinized sand culture containing 0, 125 or 250 mol m⁻³ NaCl in full strength Hoagland's nutrient solution.

S24 and S36 produced significantly greater fresh and dry plant biomass than their parents and the two salt-sensitive lines under saline conditions. There was no consistent relationship between growth and assimilation rate of all cultivars differing in degree of salt tolerance. Stomatal conductance was reduced due to salt stress in all cultivars except Yecora Rojo. The newly evolved genotypes showed relatively higher stomatal conductance than the other cultivars at the highest salt treatment, but there was no consistent relationship between assimilation rate and stomatal conductance. Transpiration in all cultivars reduced consistently with increase in salt concentration of the growth medium, but S36 and S24 had higher transpiration than that of the other lines. The higher transpiration rate in S24 and S36 resulted in lowering their water use efficiency compared with the other cultivars. Water potential and turgor potential of only the two salt-sensitive cultivars, Potohar and Yecora Rojo, were significantly lower than those of the other lines, which themselves did not differ.

The physiological traits, such as assimilation rate and water-use efficiency, did not prove conducive to discriminate high salt-tolerant and low salt-tolerant lines examined in this study.

Key-words: photosynthetic capacity, salt tolerance, stomatal conductance, transpiration, water-use efficiency, wheat.

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INTRODUCTION

It is now well evident that soil salinity can reduce plant growth by perturbing matter allocation, ion relation, water relations and other biochemical/physiological processes, or by a combination of such factors (Greenway 1973; Greenway & Munns 1980; Maas 1987; Ashraf 1994). The reduction in growth in many crops is often attributable to gas exchange (Seemann & Critchley 1985; Yeo et al. 1985; Rawson et al. 1988; Myers et al. 1990). Salinity stress influences photosynthesis in two major ways: first, by reducing stomatal conductance, and secondly by inhibiting the rate of appropriate biochemical processes. The reduction in stomatal conductance leads to changes in water status of plant cells. Thus, the principal aim of the present study was to draw relationships between growth, gas exchange and water relation parameters in two newly developed genotypes of spring wheat (S36 and S24) with respect to their salt-tolerant parents (LU26S and Kharchia) and two salt-sensitive cvs (Potohar and Yecora Rojo). In a previous study using the same lines it was found that the high tolerance of S24 and S36 was related to their partial exclusion of Na from leaves and maintenance of higher leaf K/Na and K versus Na selectivity than those of their parents as well as from the salt-sensitive lines (Ashraf & O'Leary 1996). In the present study an attempt was made to investigate whether the improvement in degree of salt tolerance contributed to enhanced photosynthesis. It is generally expected that photosynthesis in salt-tolerant cultivars may also be relatively insensitive to salinity. There are many studies in which a close association of growth and gas exchange under salt stress has been found, e.g. Phaseolus vulgaris (Seemann & Critchley 1985), grape-vines (Downton 1977; Walker et al. 1981), onion, bean and cotton (Gale et al. 1967), rice (Yeo et al. 1985), and spinach (Robinson et al. 1983). Conversely, there are contrasting reports in the literature regarding the relationship of growth and photosynthesis in different crops. For instance, in Trifolium repens L. no significant differences in the photosynthetic rates were found between lines differing in leaf Cl content (Rogers & Noble 1992). Similarly, the effect of NaCl salinity was investigated with respect to the growth response, ionic content, and gas exchange characteristics of spring wheat plants raised on nitrate or ammonium nutrition or different Ca concentrations in the nutrient medium and no clear relationship between growth and photosynthetic response was found under salinity stress (Hawkins & Lewis 1993). A similar lack of relationship of gas exchange leaf characteristics and growth occurred in barley (Rawson et al. 1988), Hibiscus cannabinus (Curtis & Läuchli 1986), and Diplachne fusca (Myers et al. 1990).

MATERIALS AND METHODS

Seeds of the spring wheat (*Triticum aestivum* L.) cultivars, Kharchia (an Indian salt-tolerant variety), salt-tolerant cv. LU26S, and a newly developed salt-tolerant genotype SARC-1 and salt-sensitive cv. Potohar were obtained from the University of Agriculture Faisalabad, Pakistan. Two salt-tolerant genotypes S24 and S36 were selected from the F_3 seed material derived from a cross, LU26S × Kharchia, using 24·0 and 36·0 dS m⁻¹ of NaCl+CaCl₂ (1:1 ratio equivalent wt. basis). The selection procedure has been described elsewhere (Ashraf & O'Leary 1996). The seed of cv. Yecora Rojo was obtained from Dr M. Ottman, University of Arizona, Tucson. All seed samples were surface sterilized in 5% sodium hypochlorite solution for 8 min before experimentation. In October 1993, 300 seeds of each line were sown randomly

about 5 mm deep in thoroughly washed sand contained in plastic containers $(32 \times 32 \times 7 \text{ cm})$. These containers had drainage holes in the bottom. The sand was irrigated on alternate days with 31 of full strength Hoagland's nutrient solution (Epstein 1972) prepared in tap water (chemical composition of tap water in mol m⁻³ K=0.036, Na=1.08, Ca=0.78, Mg=0.08, Cl=0.83, pH=6.91). The experiment was conducted in a naturally lit glasshouse in which PAR measured at noon ranged from 450 to 1350 µmol m⁻² s⁻¹, relative humidity day/night 60/80% and temperature 21/2°C. After 5 days, seven seedlings were transplanted into a plastic pot (21.5 cm diameter and 21.0 cm deep) which contained 6.35 kg of well-washed dry sand. All the pots were irrigated for 14 days with full strength Hoagland's nutrient solution. Salt treatments in this solution were begun 19 days after the start of the experiment. The NaCl treatments used were 0, 125 or 250 mol m⁻³ in full strength Hoagland's nutrient solution.

The experiment was arranged in a completely randomized design with four replicates, three salt treatments. Salt treatment was increased stepwise in aliquots of 50 mol m⁻³ in Hoagland's nutrient solution every time daily until the appropriate salt treatments were reached. Treatments continued with the addition of 2 l of the appropriate solution to each pot twice a week. This volume was sufficient to wash through solution already present in the sand, as determined from the electrical conductivity of the effluent solution from the pots. Every day 200 ml of distilled water was added to each pot to compensate for evapotranspiration loss.

Just before the onset of the booting stage the following physiological parameters were measured.

All measurements of water relations and gas exchange were nade on the third leaf from top. The leaf was excised from each plant at 08.00 a.m. and the leaf water potential measurements were made with a Scholander pressure chamber. A part of the lamina of the same leaf was frozen in 2 cm^3 polypropylene microfuge tubes for 2 weeks, thawed, and frozen sap was extracted by crushing the material with a metal rod. The sap was used directly for osmotic potential determination in an osmometer (Wescor 5500). Leaf turgor potential was estimated as the difference between water potential and osmotic potential.

Gas exchange and stomatal conductance. Instantaneous measurements of net CO₂ assimilation rate (A) were made on intact third leaf of each plant using an LCA-3 ADC portable infrared gas exchange system (Analytical Development Company, Hoddesdon, UK). Measurements were performed from 09.00 to 11.00 a.m. with the following specifications/adjustments: volume of chamber 16.0 cm³, flow rate 3.25 ml s⁻¹, and ambient temperature range from 22.6 to 33.3°C, ambient CO₂ concentration 650 μ l 1⁻¹ and RH of the chamber 57%.

Stomatal conductance (g) and transpiration (E) of the same leaf were measured with an LI-1600 Steady State Porometer (Li-Cor Inc., USA).

After all these measurements, the plants were harvested. Plant roots were removed carefully from the sand and then were washed for 2–3 min in cold LiNO₃ solution isotonic (125 or 250 mol m⁻³) with the corresponding treatment in which the plants were growing. The LiNO₃ was made isotonic with the treatment to avoid osmotic shock during washing; 1 mol m⁻³ Ca(NO₃)₂.4H₂O was added in LiNO₃ to maintain membrane integrity. Plants were separated into shoots and roots. Fresh weights of (120, 100) Round Retaried Section of The Netherlands. Acts Ret. Next 45, 20-20

		S	Salt treatments	$(mol m^{-3})$			
	0	125	250	0	125	250)
Cultivar/line	Sh	oot fresh weig	;ht	Ro	oot fresh wei	ght	
S36	41·41 a	10·95 a (26·4)	5·35 a (13·0)	6·49 a	0.90 a	0.67	a
S24	47·49 b	12·87 b (27·1)	6·42 a (13·5)	6.88 a	l·72 b	0.73	a
SARC-1	41·33 a	11·37 ab (27·5)	3.75 bc (9.1)	4.15 bc	2.06 c		bc
LU26S	44·75 ab	10·14 a (22·7)	3·79 bc (8·5)	7·75 a	0·86 a	0.46	
Kharchia	42·27 a	11·51 a (27·2)	3·90 b (9·2)	4·30 bc	1.22 ab	0.34	
Potohar	43·23 a	8·82 c (20·4)	2·92 c (6·8)	6.68 a	1.08 ab	0.20	
Yecora Rojo	42·33 a	10·84 a (25·6)	2·74 c (6·5)	5·19 c	0·94 ab	0.10	С
	SI	noot dry weig	ht	R	oot dry weig	ht	-
S36	7·14 a	2·83 a (39·7)	1.59 a (22.3)	1.11 ac	0·21 a	1.13	a
S24	6∙38 b	2.86́a (44.8)	1.49 ac (23.4)	1.19 ac	0·24 a	0.087	b
SARC-1	4·52 c	2·13 bd (47·1)	0.79 bc (17.5)	0·83 b	0·36 b	0.04	c
LU26S	6·79 ab	2·63 ab (38·9)	0.88 bc (13.0)	1·44 a	0·14 c	0.07	
Kharchia	4·57 c	2·19 bd (47·9)	0·95 c (20·8)	0·86 b	0·13 c	0.07	
Potohar	5.65 d	1.60 cd (28.4)	0·67 bc (11·9)	1.04 ac	0·10 c	0.03	
Yecora Rojo	5·97 d	2·03 cd (34·0)	0.61 bc (10.2)	0.91 bc	0·15 c	0.03	c

Table 1. Fresh and dry weights (g plant⁻¹) of shoots and roots of seven cultivars/lines of spring wheat at the onset of booting stage, when grown in sand culture salinized with 0, 125, or 250 mol m⁻³ NaCl in full strength Hoagland's nutrient solution

Means with the same letters in each column (within each treatment) do not differ significantly at the 5% level. Figures in parentheses are percentages of control.

shoots and roots of all the plant samples were recorded. Samples were then dried at 65°C for 1 week and dry weights recorded.

Statistical analysis of data. Analysis of variance of data for all the parameters was computed using the COSTAT computer package (CoHort Software, Berkeley, CA, USA). The least significant differences between the mean values were calculated following Snedecor & Cochran (1980).

	Salt treatment (mol m^{-3})				
Cultivar/line	0	125	250		
S36	6·45 a	13·49 ad	12·24 a		
S24	5·34 a	11·92 a	17·14 b		
SARC-1	5·45 a	5∙93 b	19∙74 b		
LU26S	4·73 a	18·80 c	12.58 a		
Kharchia	5·31 a	16.83 cd	13·56 a		
Potohar	5·45 a	16.10 cd	22·35 c		
Yecora Rojo	6·54 a	13.54 ad	20·34 bc		

Table 2. Shoot/root ratios (dry weight basis) of seven cultivars/lines of spring wheat at the onset of booting stage, when grown in sand culture salinized with 0, 125, or 250 mol m⁻³ NaCl in full strength Hoagland's nutrient solution

Means with the same letters in each column do not differ significantly at the 5% level.

RESULTS

The newly developed lines of spring wheat, S36 and S24, had significantly greater $(P \le 0.05)$ mean fresh and dry weights of shoots and roots than their parents (LU26S and Kharchia) and the two salt-sensitive cultivars, Potohar and Yecora Rojo, at 250 mol m⁻³ NaCl (Table 1). Both the lines and SARC-1 had greater relative shoot fresh and dry weights than the two sensitive lines at both salt treatments, although such patterns of root fresh biomass production were not found at 125 mol m⁻³ NaCl. However, at the same treatment S36, S24 and SARC-1 had significantly greater root dry matter than the remaining salt-tolerant and salt-sensitive cultivars/lines. Data for shoot/root ratios (Table 2) show that the root growth was more inhibited in the two salt-sensitive lines than in the other cultivars, particularly at the highest salt level.

The cultivars/lines did not differ in leaf water potential at 125 mol m⁻³ NaCl but by contrast at 250 mol m⁻³ NaCl cvs Potohar and Yecora Rojo had significantly lower leaf water potential than the other cultivars/lines (Table 3). Although leaf osmotic potential decreased consistently in all cultivars/lines with increase in salt concentration of the growth medium, the cultivars did not differ at 0 or 125 mol m⁻³ NaCl. However, at 250 mol m⁻³ NaCl only Yecora Rojo had significantly lower value of osmotic potential compared with the other cultivars/lines. Leaf turgor potential was significantly lower in Potohar compared with the other cultivars/lines at 250 mol m⁻³ NaCl, whereas at 125 mol m⁻³ NaCl only cv. Kharchia had significantly greater leaf turgor potential than the other lines.

Assimilation rate data did not show any consistent pattern of increase or decrease in lines under varying salt treatments (Table 4). For instance, at 125 mol m⁻³ NaCl net assimilation rate remained unchanged in S36, S24, SARC-1, Potohar, and Yecora Rojo, whereas at 250 mol m⁻³ it remained unchanged in SARC-1 and Potohar. S24 was the lowest and SARC-1 the highest of all cultivars in assimilation rate at 250 mol m⁻³ NaCl. Leaf stomatal conductance was significantly higher in S36, S24, SARC-1 and Yecora Rojo as compared with the other lines at the highest salt treatment. By contrast, at 125 mol m⁻³ Kharchia was the lowest of all cultivars in stomatal conductance (Table 4).

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				Salt	Salt treatments (mol m ⁻³)	(mol m ^{- 3})			
Cultivare/	0	125	250	0	125	250	0	125	250
currans lines	Osmotic	tic potential (- bar)	(– bar)	Wate	Water potential (- bar)	– bar)	Calculat	Calculated turgor potential (bar)	ential (bar)
536	11·71 a	19-07 a	26·27 ab	7·23 a	16-11 a	24·13 ab	4·48 a	2·96 a	2·14 abc
S24	9-74 a	18·86 a	23·19 a	6-05 a	15·24 a	20-08 a	3·69 a	3·62 a	3.11 ac
SARC-1	9-57 a	18-91 a	26·28 ab	6·29 a	14·97 a	22·52 a	3·28 a	3-94 a	3-76 c
LU26S	9-59 a	20-59 a	24·83 a	6-32 a	17-38 a	22-83 a	3·27 a	3·21 a	2·00 ab
Kharchia	9-70 a	20-43 a	26·70 ab	6-69 a	14·56 a	23-91 a	3-01 a	5-87 b	2·79 ac
Potohar	11-94 a	20-62 a	28·51 bc	7-98 a	17·39 a	27·82 bc	3-96 a	3·23 a	0-69 b
Yecora Rojo	10-56 a	18·66 a	32·49 c	7-52 a	15-81 a	30-61 c	3·04 a	2.85 a	1-88 ab

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			Salt trea	Salt treatments (mol m ⁻³)		
	0	125	250	0	125	250
Cultivars/lines	Assimilatic	Assimilation rate (μ mol CO ₂ m ⁻² s ⁻¹)	m ⁻² s ⁻¹)	Stor	Stomatal conductance (cm s ⁻¹)	(₁ _ s ı
S36	13-38 ± 1-17	12.34 ± 1.12	9 .24 ± 0.67	1·27 ± 0·15 a	1.040 ± 0.165 a	0-599 ± 0-175 a
S24	10.32 ± 2.18	11.17 ± 1.55	5·33 ± 1·74	1·41 ± 0·26 a	0.742 ± 0.130 b	0·663 ± 0·130 a
SARC-1	10.45 ± 0.50	12.24 ± 1.78	10.98 ± 1.98	1.15 ± 0.18 a	0.934 ± 0.191 ab	0·536 ± 0·042 a
LU26S	13.36 ± 2.30	8.60 ± 2.34	8.26 ± 1.53	$1.21 \pm 0.05 a$	$0.661 \pm 0.093 $ b	0.370 ± 0.043 b
Kharchia	12.53 ± 1.25	8·34 ± 1·44	6.69 ± 2.69	1·03 ± 0·26 ab	$0.442 \pm 0.059 c$	0·295 ± 0·067 b
Potohar	9.21 ± 0.32	$11 \cdot 14 \pm 1 \cdot 34$	7.41 ± 0.84	0.75 ± 0.07 bc	$0.630 \pm 0.104 \text{ b}$	0·283 ± 0·049 b
Yecora Rojo	9.51 ± 0.85	10.37 ± 1.60	6.33 ± 2.76	$0.58 \pm 0.16 c$	0.521 ± 0.153 bc	0·539 ± 0·139 a
•	TSD	LSD (Lines × Treatment)=NS)=NS			

Table 4. Net as in sand culture

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Transpiration of water from the leaf surface was significantly higher in S36, S24 and SARC-1 compared with the other cultivars at both salt treatments. Cvs Kharchia and Yecora Rojo were the lowest in transpiration of all cultivars at both salt treatments (Table 5). Water-use efficiency (expressed as assimilation rate/transpiration) was significantly higher in Kharchia and Yecora Rojo compared with the other lines at both treatments (Table 5). Cv. Potohar was intermediate in water-use efficiency of all cultivars.

DISCUSSION

The better performance of the two newly developed genotypes, S36 and S24, particularly at the highest salt treatment in biomass production in both mean and relative terms compared with their parents, LU26S and Kharchia, in this experiment can be related to their relatively higher seed yield than their parents as well as the two salt-sensitive cultivars, Potohar and Yecora Rojo, assessed in a previous study (Ashraf & O'Leary 1996).

It is now well accepted that an important factor controlling growth and dry matter production is the photosynthetic activity (Danks et al. 1983; Lawlor 1987). In addition to the synthesis of structural and storage materials in plants, photosynthesis leads to the production of organic osmotica which actively take part in osmoregulation. It is thus expected that the rate of photosynthesis in salt-tolerant plants is less inhibited than that in the salt-sensitive ones. The assimilation rate data clearly show that there was no consistent relationship between photosynthetic activity and growth of strains of spring wheat differing in degree of salt tolerance. For instance, the most tolerant genotype S24 was the lowest in assimilation rate at the highest salt treatment. By contrast, the assimilation rate of salt-sensitive Potohar was not affected by either salt treatment. Since the rate of respiration was not measured in this study, it is not easy to explain the results of assimilation rate of the leaves examined. These data can be related to the earlier findings of Hawkins & Lewis (1993) who did not find any clear trend in the photosynthetic activity of spring wheat plants subjected to moderate salinity. A lack of association between gas exchange and growth was also found in Diplachne fusca (Myers et al. 1990) and Trifolium repens (Rogers & Noble 1992). These results also support the argument of Nieman (1962) that photosynthetic rate may not be a growth-limiting factor under salt stress.

The decline in photosynthetic activity in most glycophytes is found to be partially attributable to stomatal closure (Downton 1977; Seemann & Critchley 1985) and stomatal closure is generally associated with salinization of salt-sensitive species (Gale *et al.* 1967; Longstreth & Noble 1979; Walker *et al.* 1983). The data presented here indicate that stomatal conductance was reduced in all cultivars except Yecora Rojo under salt stress, but it is not easy to draw any parallel between stomatal conductance and assimilation rate in all the cultivars examined, although the newly evolved genotypes showed higher stomatal conductance than the other cultivars at the highest salt treatment. This is in agreement to other findings on cotton (Constable & Rawson 1980), sunflower (Rawson & Constable 1980), barley (Miskin *et al.* 1972), beans (Peet *et al.* 1977), and faba beans (Melesse & Caesar 1992) that stomatal conductance is not always coupled with assimilation. It is also not easy to assess the relationship between stomatal conductance and photosynthetic activity of all cultivars unless the

			Salt treatments (mol m ⁻³)	s (mol m ^{- 3})		
	0	125	250	0	125	250
Cultivars/lines	Trans	Transpiration (mmol m ⁻² s ⁻¹)	(₁ -1)	Water use er	Water use efficiency (µmol CO ₂ /mmol H ₂ O)	/mmol H ₂ O)
S36 S24 SARC-1 LU26S Kharchia Potohar Yecora Rojo	7.56±0.64 a 8.00±1.56 a 7.46±1.10 a 6.67±0.38 a 5.78±1.81 ab 4.17±1.22 bc 2.66±0.58 c	7.25 ± 0.68 a 4.76 ± 0.98 bd 6.46 ± 1.01 ab 4.89 ± 0.62 bd 1.98 ± 0.36 cd 3.07 ± 0.58 d	4.02 ± 1.63 ab 5.12 ± 0.82 a 3.71 ± 0.44 ab 2.80 ± 0.43 bc 1.42 ± 0.14 c 2.57 ± 0.94 bc 1.81 ± 0.69 bc	1.77 ± 0.09 a 1.29 ± 0.05 a 1.40 ± 0.06 a 2.00 ± 0.13 a 2.17 ± 0.11 a 2.21 ± 0.19 a 3.58 ± 0.24 b	1.70 ± 0.08 a 2.35 ± 0.16 a 1.89 ± 0.18 a 1.76 ± 0.17 a 4.21 ± 0.36 b 3.63 ± 0.29 b 6.06 ± 0.82 c	2:30 ± 0:21 a 1:04 ± 0:09 b 2:96 ± 0:26 a 2:95 ± 0:32 a 4:71 ± 0:36 c 2:88 ± 0:32 a 3:50 ± 0:24 ac

Table 5. Transpiration (E) and water-use efficiency of seven cultivars/lines of spring wheat at the onset of booting stage, when grown in sand culture salinized with 0, 125, or 250 mol m⁻³ NaCl in full strength Hoagland's nutrient solution

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concentration of intercellular CO_2 is determined, since it is known that photosynthetic capacity is affected by both stomatal and substomatal factors.

Leaf transpiration rate was consistently reduced in all cultivars with increased salt concentration of the growth medium, although transpiration was considerably higher in the two newly developed genotypes than that of the other cultivars at the highest salt level. The relatively higher transpiration rate in S36 and S24 resulted in a lowering of their water-use efficiency. It is surprising to note that the most salt-sensitive cv. had the highest water-use efficiency of all the cultivars. These results thus do not agree with the earlier findings of Kalaji & Nalborczyk (1991) who found higher water-use efficiency in salt-tolerant cultivars of barley compared with salt-sensitive lines under salinity stress.

Although leaf water potential and stomatal conductance declined consistently in all cultivars with increase in salt level of the rooting medium, the salt-tolerant and salt-sensitive lines did not show any consistent pattern in relation to these two variables. The leaf stomatal conductance regulates water evaporation and CO₂ diffusion (Jordan et al. 1975; Bates & Hall 1981). It is also generally known that severe plant water deficits are correlated with a decline in leaf stomatal conductance. But there are contrasting reports regarding the correlation between decrease in stomatal conductance due to osmotic stress and leaf water potential. For example, in cowpea it was found that decline in leaf stomatal conductance was independent of leaf water potential (Bates & Hall 1981; Osonubi 1985). Similarly, no consistent relationship between stomatal conductance and water potential or turgor potential was found in maize (Blackman & Davies 1985). In peanut (Arachis hypogaea L.) it was found that neither leaf water potential nor turgor potential was initially changed when stomatal conductance began decreasing in response to water deficit conditions (Black et al. 1985). However, maintenance of relatively lower leaf turgor potential by the two salt-sensitive lines, Potohar and Yecora Rojo under the highest salt concentration is expected in view of the suggestion of Greenway & Munns (1980) and Wyn Jones (1981) that salinity stress causes more reduction in turgor in the salt-sensitive plants than in the salt-tolerant plants.

Overall, the high salt tolerance of the two newly developed genotypes is likely to be a consequence of a number of differing effects of salt on plant metabolic processes, including low accumulation of toxic ions, as assessed in a previous study, and high stomatal conductance and transpiration compared with their parents and salt-sensitive lines, as assessed in this study. The physiological traits, such as assimilation rate and WUE, did not prove helpful in discriminating high salt-tolerant and low salt-tolerant cultivars.

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