CELL AND PLANT RESPONSES TO NACL IN *ZEA MAYS* L. CULTIVARS DIFFERING IN SALT TOLERANCE

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Summary. Two *Zea mays* cultivars, salt sensitive Trihybrid 321 and salt tolerant Giza 2, were studied, namely their adaptation to NaCl imposition at cell and whole plant level. Changes in growth and mineral content of roots and shoots, glycinebetaine (GB) and free proline (Pro) levels of shoots, plasma membrane permeability and solute potential (ψ_s) of leaf sheath subepidermal cells were measured. NaCl decreased fresh mass (FM), dry mass (DM), relative growth rate (RGR) of shoots and roots, and leaf area ratio (LAR) in both cultivars. Greater decrease (except LAR) was obtained in Giza 2 than in Trihybrid 321. NaCl stress resulted in accumulation of GB and free Pro in shoots of both cultivars. The magnitude of increase in both omsolytes was higher in Giza 2 than in Trihybrid 321. Salt stress induced Na^+ and Cl^- accumulation while it decreased K^+ and Ca^{2+} levels in shoots and roots of both cultivars. The increase in Na^+ and the decrease in K^+ and Ca^{2+} was greater in Giza 2 than in Trihybrid 321. Cl^- was increased more in Trihybrid 321 compared to Giza 2. NaCl increased plasma membrane permeability in both cultivars. Salt stress decreased cell ψ_s in both cultivars, especially in Giza 2. It was concluded that Na^+ exclusion from the shoot was not correlated with salt tolerance and that Pro and GB accumulation in the shoot was a possible indicator for salt tolerance in the maize genotypes studied.

Keywords: Cell solute potential, glycinebetaine, maize, plasma membrane permeability, proline.

Abbreviations: DM – dry mass, FM – fresh mass, GB – glycinebetaine, LAR – leaf area ratio, K_s – permeability coefficient, Pro – proline, RGR – relative growth rate, ψ_s - solute potential

INTRODUCTION

Many arid and semi-arid regions in the world contain soils and water resources that are too saline for most of the common economic crops (Pitman and Lauchli, 2002). The majority of crop plants is relatively salt-sensitive and is unable to tolerate high levels of salinity (Levitt, 1980). Salinity affects plants through osmotic effects, ion-specific effects and oxidative stress (Pitman and Lauchli, 2002). Osmotic effects are due to salt-induced decrease in the soil water potential. Salinity results in a reduction of K^+ and Ca^{2+} content and an increased level of Na^+ and Cl^-, which forms its ionic effects. Salt stress induces cellular accumulation of damaging active oxygen species. Active oxygen species can damage membrane lipids, proteins and nucleic acids (Mittler, 2002).

Osmotic adjustment of both halophytes and glycophytes is achieved through the accumulation of organic and inorganic solutes (Yeo, 1998). Therefore, greater decrease in cell solute potential than in the external salt concentration may indicate an osmotic adjustment. Organic solutes are accumulated in the cytosol to balance the solute potential of the vacuole, which is dominated by ions (Flowers et al., 1977; Greenway and Munns, 1980). A large number of plant species accumulate GB and Pro in response to salinity stress and their accumulation may play a role in combating salinity stress (Ashraf, 1994; Hanson and Burnet, 1994; Mansour, 2000; Ashraf and Harris, 2004). GB and Pro functions under stress conditions are presented by Ashraf (1994), Ashraf and Harris (2004), Hanson and Burnet (1994) and Mansour (2000). However, data do not always indicate a positive correlation between the osmolyte accumulation and the adaptation to stress (Wyn Jones et al., 1984; Rains, 1989; McCue and Hanson, 1990; Ashraf, 1994; Lutts et al., 1996; Mansour, 2000; Ashraf and Harris, 2004).

Previous studies suggested that plasma membrane might be the primary site of salt injury (Epstein, 1980; Levitt, 1980; Cramer et al., 1985; Lauchli, 1990; Mansour, 1997). To test this hypothesis, the response of the plasma membrane to salinity in genotypes contrasting in salt tolerance was studied by measuring the plasma membrane permeability. Plasma membrane permeability probes the changes or differences in the membrane structure/composition (Simon, 1974; Carruthers and Melchoir, 1983; Stadelmann and Lee-Stadelmann, 1989; Magin et al., 1990). Plasma membrane permeability is altered markedly in salt sensitive cultivars whereas the effect is always marginal in salt tolerant cultivars upon salt exposure (Leopold and Willing, 1984; Mansour et al., 1993a; Mansour and Stadelmann, 1994; Mansour, 1997; Mansour and Salama, 2004).

In the current study, two cultivars of maize contrasting in salt tolerance were used to test their differential response to salinity at cell and whole plant level. Comparative response studies could provide insights on the salt tolerance mechanism in maize. Growth parameters (fresh mass, dry mass, relative growth rate, leaf area ra-

tio), element contents, osmolyte accumulation (GB, Pro), cell solute potential, and plasma membrane permeability were measured to address such a comparative responses of both maize genotypes to NaCl stress.

MATERIALS AND METHODS

Plant materials and growth conditions

The *Zea mays* caryopses of Giza 2 (salt tolerant) and Trihybrid 321 (salt sensitive) were obtained from the National Agriculture Research Center, Giza, Egypt. The caryopses of both cultivars were kept at 4°C.

The *Zea mays* caryopses of the both cultivars were soaked in tap water for two hours and the water was renewed every 15 minutes. The caryopses were then germinated in Petri dishes containing filter paper moistened with 15 mL of ¼-strength modified Hogland solution (MHS, Epstein, 1972). The caryopses were placed in a dark incubator at 28°C for five days. In the sixth day of germination, the caryopses were transferred into 0.8-liter black plastic pots containing aerated ¼-strength MHS. Six plants were fixed in a foam disc supported at the top of each pot. For each cultivar, three treatments were applied: one pot presented the control where no NaCl was added to ¼-strength MHS, the second and third treatments received 75 or 150 mM NaCl, respectively, added to ¼-strength MHS. Each treatment was replicated three times and each replicate consisted of three pots. The seedlings were exposed to salt for 15 days. The solutions were renewed every five days. The plants were grown in a controlled growth chamber under the following growth conditions: 15-h photoperiod; 65-75% relative humidity; day and night temperature of 22°C and 20°C, respectively. The photosynthetic photon flux density (PPFD) at maximum plant height was about 440 μmol m^{-2} s^{-1}.

Growth analysis

After 15 days of salt treatment, the seedlings were harvested, shoots were separated from roots and FM (g $plant^{-1}$) and DM (g $plant^{-1}$) of shoots and roots were determined. For dry mass determination, shoots and roots were left at 80°C for 2 days. RGR (on dry mass basis, d^{-1}) and LAR (cm^{-2} g^{-1}) were determined by the formulas of Hunt (1981).

Elemental analysis

Elements were determined in dry mass according to Ranganna (1977). Ca^{2+}, K^{+} and Na^{+} were determined by the atomic photometer. Cl^{-} was measured by titrimetric method.

Pro and GB determination

Free Pro was determined according to Bates et al. (1973). GB was determined according to Grieve and Maas (1984).

Permeability measurement

The plasmometric method (Mansour, 1997; Stadelmann and Lee-Stadelmann, 1989) as detailed by Mansour et al. (1993a), was used for the measurement of the plasma membrane permeability coefficient (K_s) of individual subepidermal cells of the leaf sheath.

Cell ψ_s measurement

The ψ_s of subepidermal cells of the leaf sheath was measured by the plasmometric method (Lee-Stadelmann and Stadelmann, 1989; Mansour et al., 1993b).

Statistical analysis

The student's t-test was used to compare the differences between the mean values of control and treated plants.

RESULTS AND DISCUSSION

NaCl reduced the FM, DM and RGR of the shoots and roots of both cultivars (Table 1). The reduction was stronger in Giza 2 than in Trihybrid 321. Salinity-induced growth reduction has been previously reported in several plant species: maize (Izzo et al., 1991; Alberico and Cramer, 1993; Cramer, 1993; Cramer et al., 1994), barley (Munns, 1985), wheat (Kingsbury and Epstein, 1986; Sharma et al., 1994; Mansour and Salama, 1996), and tomato (Sanchez-Blanco et al., 1991). A reduction in water absorption may explain the salt induced reduction in FM (Azaizeh et al., 1992). This reduction in water absorption and subsequently FM could be attributed to the decrease in water permeability under salinity, as reported by Mansour (1994), Mansour and Stadelmann (1994), and Zekri and Parsons (1989). The greater reduction of DM and RGR in Giza 2 than in Trihybrid 321 (Table 1) may imply an adaptive response to cope with salinity stress. Under salt stress, growth reduction could help the tolerant plants to save energy for the maintenance of the processes. Similar conclusion has been reached by Mladenova (1990), Kuiper et al. (1988), and Mansour and Salama (1996). They found a greater growth inhibition in different tolerant genotypes relative to sensitive ones under salt stress, which was interpreted by the authors to correlate with salt tolerance.

The LAR decreased significantly only in Trihybrid 321 (Fig. 1). Similar finding is reported in other maize cultivars by Alberico and Cramer (1993) and Cramer et al

Table 1. Effect of different concentrations of NaCl added to the growth medium during growth for 15 days on fresh mass (FM, g plant $^{-1}$), dry mass (DM, g plant $^{-1}$) and relative growth rate (RGR on dry mass basis, d $^{-1}$) of maize cultivars differring in salt tolerance. Each value is the mean ± S.D. of three replications.

	Shoot			Root		
Cultivar/conc.	**FM**	**DM**	**RGR**	**FM**	**DM**	**RGR**
Giza 2 (tolerant)						
0 mM	1.92 ± 0.063	0.15 ± 0.015	0.07 ± 0.006	1.30 ± 0.039	0.12 ± 0.009	0.04 ± 0.002
75 mM	1.52 ± 0.097	0.10 ± 0.014	0.05 ± 0.009	0.91 ± 0.180	0.08 ± 0.010	0.02 ± 0.006
150 mM	1.04 ± 0.120	0.08 ± 0.016	0.03 ± 0.015	0.40 ± 0.067	0.05 ± 0.009	0.01 ± 0.0005
Trihybrid 321 (sensitive)						
0 mM	2.07±0.026	0.14 ± 0.006	0.08± 0.003	0.90 ± 0.024	0.03 ± 0.007	0.05 ± 0.005
75 mM	1.52 ± 0.167	0.12 ± 0.001	0.07 ± 0.006	0.70 ± 0.097	0.02 ± 0.004	0.03 ± 0.008
150 mM	1.22 ± 0.042	0.11 ± 0.009	0.07 ± 0.005	0.67 ± 0.019	0.01 ± 0.002	0.02 ± 0.008

(1994). A rapid and potentially lasting reduction in the number of elongating cells and/or a reduction in the rate of cell elongation may be induced by NaCl to cause the decreased LAR (Munns, 1993). The reduction in LAR was found only in Trihybrid 321, although its FM, DM, and RGR were greater than those of Giza 2. These results suggest that the difference in salt tolerance between the two cultivars may not be associated with the differences in LAR. A similar conclusion has been reached by Cramer et al. (1990) and Mansour and Salama (1996) in barley and wheat under saline conditions.

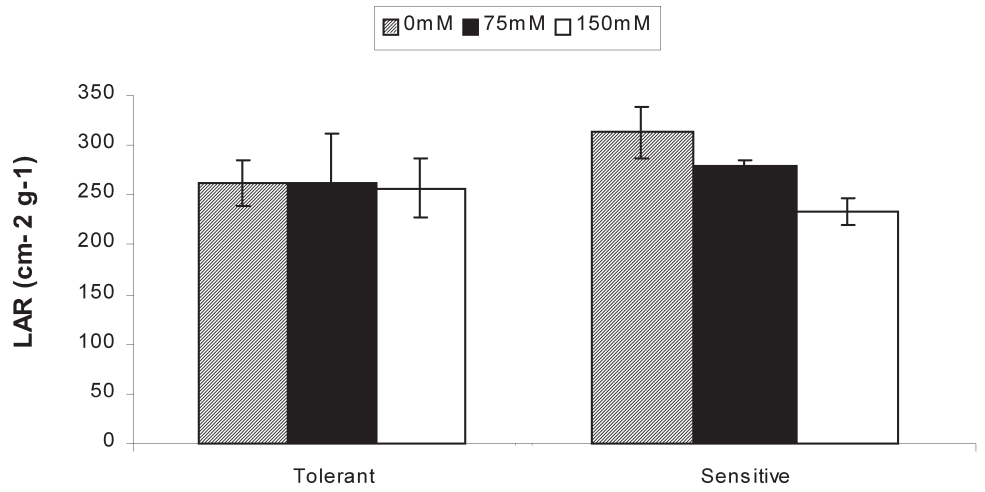

Fig. 1. Leaf area ratio (LAR) of Giza 2 (tolerant) and Trihybrid 321 (sensitive) in response to different concentrations of NaCl added to the growth medium for 15 days. Vertical bars are the S.D. of three replications. NaCl decreased only the LAR of Trihybrid 321.

Salt tolerance is not negatively correlated with Na^+ accumulation in different plant species (Lauchli, 1984; He and Cramer, 1992; Alberico and Cramer, 1993; Cramer, 1993; Cramer, 1994; Essah et al., 2003; Flowers, 2004). Previous reports support our finding that shoots of Giza 2 have greater levels of Na^+ than those of Trihybrid 321 under NaCl treatments (Table 2), although Trihybrid 321 is severely affected by NaCl. Visible symptoms of Na^+ toxicity (e.g. chlorosis, data not shown) appeared only in Trihybrid 321 despite its lower Na^+ accumulation relative to Giza 2. From these results, we concluded that the difference in growth between the two cultivars might not be due to their tissue Na^+ concentrations. It seems, therefore, that Giza 2 had the ability to sequester Na^+ into the vacuole more efficiently than Trihybrid 321, and thus Giza 2 avoids Na^+ toxicity of the cytoplasm. Various reports indicate that the absence of ion compartmentation may contribute to toxic effects of ions in shoot of sensitive plants (Flowers et al., 1977; Greenway and Munns, 1980; Flowers and Yeo, 1997). Our results are in accordance with Hajibagheri et al. (1987, 1988), and Hajibagheri and Flowers (1989) who report that salt tolerant maize cultivars had lower Na^+ concentrations in the cytoplasm than salt sensitive ones. Flowers and Hajibagheri (2001) found that salt tolerant barley had lower cytoplasmic Na^+ than sensitive cultivar.

NaCl decreased K^+ and Ca^{2+} concentrations in Giza 2 roots stronger than in Trihybrid 321 (Table 2). This result is in accordance with Cramer et al. (1994). The lack of correlation between accumulation of Na^+, decreasing of K^+, Ca^{2+} and salt sensitivity in the maize cultivars led Cramer et al. (1994) to the conclusion that mineral nutrition of maize is not correlated with salt tolerance and that the growth response of maize to salinity may be primarily affected by osmotic factors.

The level of Cl^- was higher in Trihybrid 321 shoots and roots than in Giza 2 ones (Table 2). Higher cytoplasmic Cl^- concentrations were found in maize and barley salt sensitive cultivars than in salt tolerant ones (Hajibagheri et al., 1988, 1989; Flowers and Hajibagheri, 2001). Marschner (1995) reports that high tissue Cl^- found in salt treated bean is the principle cause for salt-induced growth reduction. It is likely that Cl^- toxicity may account for salt sensitivity in maize. Zidan et al. (1992) and Cramer et al. (1994) have reached similar conclusion.

Salinity increased markedly the Pro content in different salt sensitive and tolerant species/genotypes: with more Pro accumulation in salt tolerant ones, which is supposed to correlate with the adaptation to salinity (Wyn Jones et al., 1984; Rains, 1989; Ashraf, 1994; Lutts et al., 1996; Hare and Cress, 1997; Mansour, 2000; Hien et al., 2003; Ashraf and Harris, 2004). Our results implicate that NaCl stress increases Pro accumulation in the shoots of the two maize cultivars, strongly in Giza 2 (Table 3). We infer that Pro accumulation in Giza 2 might have a role in its salt tolerance.

NaCl increased GB accumulation more in Giza 2 than in Trihybride 321 (Table 3), which is in accordance with previous data (Wyn Jones and Storey, 1981; Hanson and Grumet, 1985; Rhodes *et al*., 1987; Hanson and Burnet, 1994; Mansour, 2000; Ashraf

Table 2. Effect of different concentrations of NaCl added to the growth medium during growth for 15 days on different ions concentrations (mg of ion/gm dry mass) of maize cultivars differring in salt tolerance. Each value is the mean ± S.D. of three replications.

	Shoot				**Root**			
	Na^+	K^+	Ca^{2+}	Cl^-	Na^+	K^+	Ca^{2+}	Cl^-
Giza 2 (tolerant)								
0 mM	0.09 ± 0.01	0.32 ± 0.02	0.009 ± 0.002	0.64 ± 0.02	7.64 ± 0.69	1.48 ± 0.51	0.30 ± 0.010	0.56 ± 0.08
75 mM	2.44 ± 0.44	0.25 ± 0.42	0.006 ± 0.001	1.07 ± 0.18	35.95 ± 6.47	0.67 ± 0.23	0.13 ± 0.007	1.65 ± 0.26
150 mM	3.32 ± 0.90	0.20 ± 0.01	0.008 ± 0.002	5.25 ± 0.57	36.29 ± 0.95	0.70 ± 0.09	0.23 ± 0.008	3.35± 0.20
Trihybrid 321 (sensitive)								
0 mM	0.09 ± 0.007	0.34 ± 0.006	0.013 ± 0.001	0.39 ± 0.03	6.52 ± 0.84	1.32 ± 0.07	0.36 ± 0.05	0.52 ± 0.13
75 mM	1.67 ± 0.071	0.26 ± 0.001	0.009 ± 0.001	0.95 ± 0.15	35.84 ± 1.01	1.13 ± 0.07	0.18 ± 0.01	1.95 ± 0.21
150 mM	2.94 ± 0.082	0.22 ± 0.003	0.008 ± 0.001	7.75 ± 0.21	50.50 ± 0.87	0.84 ± 0.01	0.19 ± 0.02	6.15 ± 0.21

Table 3. Effect of different concentrations of NaCl added to the growth medium during growth for 15 days on proline concentration (м Moles proline/g fresh mass) and glycinebetaine concentration (м Moles glycinebetaine/g dry mass) of maize cultivars differring in salt tolerance. Each value is the mean ± S.D. of three replications.

	Proline		Glycinebetaine	
Treatment	**Giza 2 (tolerant)**	**Trihybrid 321 (sensitive)**	**Giza 2 (tolerant)**	**Trihybrid 321 (sensitive)**
0 mM	1.50 ± 0.150	1.87 ± 0.030	106 ± 10	119 ± 1
75 mM	2.00 ± 0.097	2.34 ± 0.122	162 ± 23	150 ± 6
150 mM	4.85 ± 0.490	3.30 ± 0.440	296 ± 72	279 ± 10

and Harris, 2004). These studies report that Salt tolerant species/cultivars have greater capacity for GB accumulation than sensitive ones, which is suggested to be associated with salt tolerance. The greater GB accumulation in Giza 2 may point to its involvement in maize salt tolerance.

High GB and Pro levels are suggestive of their involvement in the osmotic adjustment, since it has proven that high concentrations of GB or Pro are not required for their protective effects under salinity (Mansour, 1998).

NaCl increased plasma membrane permeability, which was similar in both cultivars (Table 4). Results suggest that NaCl leads to specific alterations in the plasma membranes, which reflects in an increased K_s in both cultivars (Kuiper, 1984; Chen et al., 1991; Mansour et al., 1993a; Mnasour and Stadelmann, 1994; Mansour, 1995; Mansour, 1997). Recent studies indicate that salinity stress induces alterations in the structure and composition of the plasma membrane lipids (Hosono, 1992; Mansour et al*.,* 1994; Wu et al., 1998; Kerkeb et al*.,* 2001; Mansour et al*.,* 2002).

Salt sensitive cultivars always show greater increase in the cell permeability compared to salt tolerant cultivars in saline environment (Dwivedi et al., 1981; Leopold

Table 4. Changes in cell membrane permeability coefficient (K_s, cm s^{-1}) x 10^{-6} for urea and osmotic potential ($ш_s$) of leaf sheath subepidermal cells of two maize cultivars differring in salt tolerance in response to NaCl added to the growth medium during growth for 15 days. Each value is the mean ± S.D. of cell number indicated in brackets.

	Permeability coefficient		Osmotic potential	
Treatment	**Giza 2 (tolerant)**	**Trihybrid 321 (sensitive)**	**Giza 2 (tolerant)**	**Trihybrid 321 (sensitive)**
0 mM	1.36 ± 0.21 (27)	1.41 ± 0.27 (20)	- 0.76 MPa (35)	- 0.86 MPa (37)
75 mM	2.82 ± 0.48 (24)	2.22 ± 0.27 (31)	- 0.98 MPa (37)	- 1.13 MPa (31)
150 mM	3.67 ± 0.54 (33)	3.83 ± 0.53 (31)	- 1.28 MPa (32)	- 1.23 MPa (34)

and Willing, 1984; Mansour et al., 1993a; Mansour and Stadelmann, 1994; Mansour and Salama, 1996; Mansour, 1997), which contrasts with the results of the present study. It appears that cell permeability may not be a relevant parameter for differentiating maize cultivars responses to salt stress.

The reduction in cell ψ_s of both cultivars in response to NaCl stress found in this study (Table 4) is in agreement with previous reports (Kingsbury et al., 1984; Kingsbury and Epstein, 1986; Mansour et al., 1993b; Mansour and Salama, 1996). At 150 mM NaCl, the excess ψ_s beyond the NaCl caused depression was 0.27 MPa and 0.12 MPa in Giza 2 and Trihybrid 321, respectively. Greater accumulation of Na^+, Pro and GB in Giza 2 suggests their role in excess ψ_s and hence in increasing osmotic adjustment. Carceller et al. (1990) have reached the same conclusion in other maize cultivars.

Reports indicate that drought tolerance is associated with high osmotic adjustment in various plant species (Morgan, 1983; Blum, 1985; Trivedi et al., 1991; Mansour and Al-Mutawa, 2000). Our results suggest a relation between high osmotic adjustment and salt tolerance in maize.

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