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Photosynthesis in two wheat cultivars differing in salt susceptibility

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Abstract

Salinised (150 mM NaCl for 15 d) roots excised from salt sensitive wheat cultivar Giza 163 showed about 15-fold increase in the ratio of Na/K while salt tolerant Sakha 92 exhibited only 7.5-fold increase compared to their control ratios. Root ratio of saturated/unsaturated fatty acids was stimulated twice in the sensitive cultivar *versus* 1.7-fold increase in the tolerant ones. Salinity enhanced greatly the accumulation of spermine (Spm) and spermidine (Spd) contents associated with a decrease in putrescine (Put) content in both wheat cultivars. Higher ratios of Spm+Spd/Put associated with lower content of proline and low ethylene evolution were detected in shoots and roots of salt tolerant cultivar. Chlorophyll *a/b* ratio showed an increase from 1.3 in control of both cultivars to 1.6 and 1.4 in stressed Giza 163 and Sakha 92, respectively. A reduced Hill reaction activity (19 %) was observed in stressed chloroplasts isolated from leaves of the tolerant cultivar *versus* 40 % inhibition in the sensitive ones. Moreover, chloroplasts isolated from stressed leaves of the sensitive cultivar showed about 25 % reduction in fluorescence emission at 685 nm as well as shifts in the peaks in the visible region.

Additional key words: cultivar differences; ethylene; fatty acids; fluorescence emission spectra; polyamines; proline; putrescine; salinity; spermine; spermidine.

Introduction

The mechanisms of tolerance of plants exposed to salinity stress have been investigated in numerous plant species. Membranes are the primary site of NaCl injury and alterations in plasma membrane lipid composition can affect ion transport (*e.g.*, Mansour *et al.* 1994, Wu *et al.* 1998). Salinity stress also induces changes in polyamine metabolism (Bouchereau *et al.* 1999). Proline accumulation is a common metabolic response of higher plants to salinity stress (Larher *et al.* 1993). The correlation between proline content and the changes in polyamine metabolism was demonstrated in tomato leaves (Aziz *et al.* 1998). The interaction between ethylene and polyamine biosynthesis was documented in soybean leaves (Turano *et al.* 1997), rice leaves (Lutts *et al.* 1996), and in barley seedlings (Tamai *et al.* 1999). Photosynthesis is one of the most important processes inhibited under NaCl stress and the degree of salt tolerance depends mainly upon plant species and intercellular ionic status. Suppression of photosynthesis under salinity stress could be attributed to the reduction in primary photochemical activities (Kaiser *et al.* 1983) and/or inhibition of CO_2 assimilation (Khavari-Nejad and Mostofi 1998).

The aim of this work was to investigate the response of two different wheat cultivars: Sakha 92, one of the salt tolerant cultivars in Egyptian fields, and the less tolerant Giza 163 (Nesiem and Ghallab 1998). Plants were analysed for fatty acid composition, polyamine and proline contents, ethylene evolution, and photosynthetic activity.

Materials and methods

Plants: Caryopses of two wheat (*Triticum aestivum* L.) cultivars, Giza 163 and Sakha 92, were obtained from National Agricultural Research Center, Egypt. Caryopses of both cultivars were surface sterilised with 1 % sodium hypochlorite for 20 min, then rinsed with distilled water several times. Wheat caryopses were germinated for 3 d in the dark at 25 °C in Petri dishes on filter paper soaked with water. Selected seedlings were placed in plastic boxes for 15 d and fertilised with half-strength Hoagland solution every 2 d. The plants were divided into two groups; one represented control (irrigated with Hoagland solution) and the other represented salinised plants (irri-

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gated with Hoagland solution containing 150 mM NaCl). Plants were grown under day/night temperatures of 25/15 °C and relative humidity of 65-75 %. 18-d-old plants were collected and used for the different measurements. Every measurement was repeated 3 times.

Chemical analyses: Wheat roots were ground, oven dried, and wet combusted in a mixture of concentrated perchloric and nitric acids (1 : 2, v/v). Na and K contents were determined spectrophotometrically as described by Yahya (1998). Lipids were extracted from wheat roots and fatty acid contents were determined as their ester derivatives using gas chromatography according to El-Shintinawy and Selim (1995). Polyamines were extracted as their dansyl derivatives from shoots and roots of wheat and quantified using high performance liquid chromatography (HPLC) according to the method described by Smith and Davies (1985). Proline was extracted from wheat plants and determined quantitatively using HPLC according to the method described by Weibull *et al.* (1990).

Ethylene evolution: Ten plants were placed in a test tube sealed with a rubber serum cap and stored under "white light" (40 W m^{-2}) at room temperature for 15 min. Rate of ethylene production was measured using gas chromatography as described by El-Shintinawy (1999).

Chloroplasts were isolated from wheat leaves as described by Osman and El-Shintinawy (1988). Chlorophyll (Chl) concentration was detected spectrophotometrically as described by Mackinney (1941). Absorption and fluorescence emission spectra of chloroplasts at room temperature were measured using the *Perkin-Elmer LS50B* fluorometer. Hill reaction activity was measured using 2,6-dichlorophenol indophenol (DCPIP) according to Biswal and Mohanty (1976). Irradiance of 100 µmol m^{-2} s^{-1} was made for 5 min and the electron transport rate was measured by recording the absorbance at 620 nm against the dark controls.

Results and discussion

Preliminary experiments (based on measuring the fresh mass) showed that Giza 163 plants survived for about 25 d at 150 mM NaCl and they could not survive at higher concentrations while Sakha 92 plants continued their growth maximally at 175 mM for 35 d (values not shown). Therefore, the impact of salinity stress on all the tested criteria was presented for plants treated for 15 d with 150 mM to show the NaCl toxicity just before the more sensitive Giza 163 individuals were completely injured. Na content in roots of Giza 163 treated with 150 mM NaCl for 15 d was 6 times higher than that in control roots coupled with about 2.5 times decrease in K content. Thus, the ratio of Na/K in salinised roots was 15 fold more than that of control roots. On the other hand, Na content determined in salinised roots of Sakha 92 plants increased about 4 fold accompanied with 1.9 fold reduction in K content compared to control roots. Consequently, the ratio of Na/K increased 7.5 times (Table 1). These values are consistent with those reported by Kingsbury *et al.* (1984) using different wheat genotypes.

Table 1. Changes in Na and K contents [mol kg^{-1}(DM)] estimated in salinized (150 mM NaCl for 15 d) and control roots of two wheat cultivars Giza 163 and Sakha 92. Means ± SD of 3 replications.

	Giza 163		Sakha 92	
	Control	NaCl	Control	NaCl
Na	0.34+0.21	2.02+0.11	0.33+0.22	1.30+0.26
K	0.38+0.10	0.15+0.23	0.36+0.11	0.19+0.32
Na/K	0.89+0.23	13.46+0.34	0.91+0.22	6.80+0.23

At the plasma membrane, the combination of lipid barrier and the selective ion transporters allows cells to accumulate essential ions while excluding toxic ions (Wu *et al.* 1998). The exclusion of Na, for example, is an important trait of salt tolerance in some plant species, *e.g.*, barley cultivars (Jeschke 1984). Therefore, changes in Na/K ratio observed in our work pointed out to a possible alternation in the membrane composition of salinised roots of both wheat cultivars.

NaCl-treated roots of both cultivars had the same fatty acids as the controls but with different molar ratios, namely linolenic (C 18:3), linoleic (18:2), oleic (18:1), stearic (18:0), palmitic (16:0), and palmitoleic (16:1). Salinity induced an increased content of total saturated fatty acids in control roots of Giza 163 from 60.9 % to 77.2 % and in control Sakha 92 from 62.5 % to 72.1 %. The highest increase was recorded in stearic acid (18:0) content; it increased about 2.2 and 1.3 times in Giza 163 and Sakha 92, respectively, compared to each control. The modest variation in fatty acid content agrees with the results reported for wheat roots (Mansour *et al.* 1994) and soybean (Surjus and Durand 1996) under salt stress. These changes in fatty acid contents reflected modification in the lipid composition of salinised wheat roots as shown by Zenoff *et al.* (1994) using soybean roots and by Zhao *et al.* (1993) using wheat roots. The high content of saturated fatty acids of lipids extracted from salinised roots implied that an oxidative damage has been initiated (Shalata and Tal 1998). Similar observations were recorded in wheat roots (Mansour *et al.* 1994), in *Dunaliella salina* (Peeler *et al.* 1989), and in *Spartina patens* (Wu *et al.* 1998).

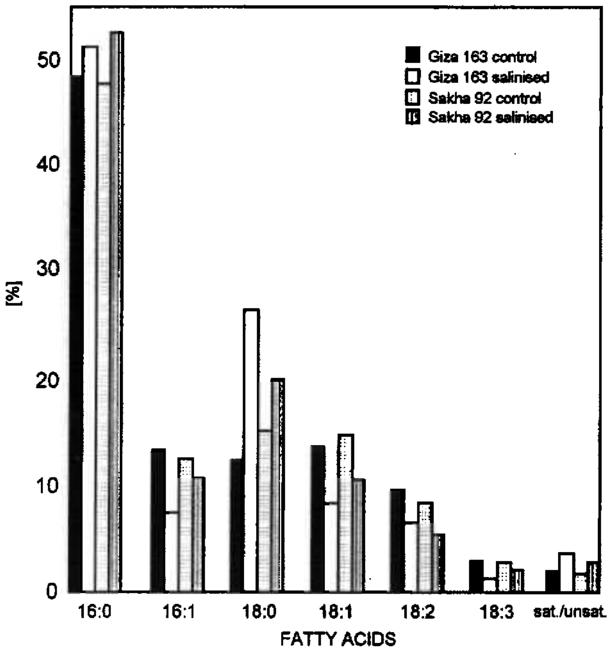

Fig. 1. Changes in fatty acid composition of root lipids extracted from salinised (150 mM NaCl for 15 d) and control wheat cultivars Giza 163 and Sakha 92. Means of 3 replications.

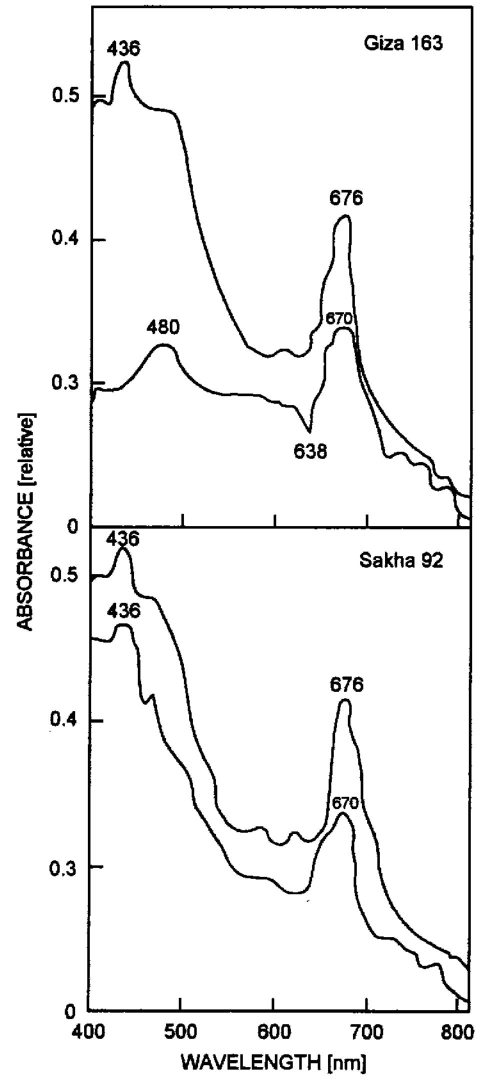

Fig. 2. Differences in absorption spectra of chloroplasts isolated from leaves of wheat cultivars Giza 163 and Sakha 92. *Upper curve* represents control and *lower curve* represents salinised chloroplasts for each cultivar.

Differences of contents of polyamines, spermine (Spm), spermidine (Spd), and putrescine (Put) in response to salinity stress have been reported. Salinity induced the accumulation of Spm and Spd content associated with an increase in total polyamine content and a decrease in Put content. Spm content increased about 1.3 and 1.2 fold in shoots of Giza 163 and Sakha 92 *versus* 4.2 and 6.6 fold in their roots as compared to control values. In addition, Put decreased about 1.5 and 2.6 fold in shoots of Giza 163 and Sakha 92 *versus* 2.6 and 2.0 fold in their roots compared to control values. Consequently, the ratio of Spm+Spd/Put in salinised shoots of Giza 163 and Sakha 92 was 2 and 3 times higher compared to control ratios. Salinity also induced about 10.6 and 13.2 fold stimulation in this ratio in roots of Giza 163 and Sakha 92 compared to control ratios (Table 2). The increased ratio detected in our work was observed also in tomato cultivars differently tolerant to salt stress (Santa-Cruz *et al.* 1997). In rice plants, Prakash and Parthapsenan (1988) showed decreased contents of polyamines under NaCl stress whereas Basu *et al.* (1988) reported the accumulation of these compounds. In sorghum, Spm and Spd accumula-tion during salt stress was considered as an adaptive response (Erdei *et al.* 1996). In support to our work, Krishnamurthy and Bhagwat (1989) and Lin and Kao (1995) reported that salt tolerant rice cultivars accumu-lated high contents of Spd and Spm associated with a decreased content of Put. Also, changes in polyamine metabolism under salt stress were recorded in different wheat cultivars (Reggiani *et al.* 1994). One of the main functions of Spm and Spd is to reduce ethylene synthesis which is a factor in promoting leaf senescence, probably by increasing Chl breakdown (Kushad and Dumbroff 1991). This reduction may be due to the inhibition of ACC (1-aminocyclopropane-1-carboxylic acid) synthase and conversion of ACC to ethylene (Davies *et al.* 1991). About 3.6 fold increase in ethylene evolution was detected in salinised Giza 163 *versus* a 2 fold increase in Sakha 92 compared to control values (Table 3). Proline is the most widely distributed compatible osmolytic amino acid and the negative correlation between its cellular content and endogenous Put content has been found (Aziz *et al.* 1998). Thus the low Put content coupled with proline accumulation observed in our work under salt stress may regulate osmotic balance in plant cells as mentioned by Aziz *et al.* (1998) and play a role in mechanism of tolerance in both wheat cultivars. Poly-amines, particularly Put, could have a role in free radical scavenging because Put could bind to the antioxidative enzyme superoxide dismutase (Bouchereau *et al.* 1999). In our work, the high Spm+Spd/Put ratio coupled with the increased total polyamine content under salinity could be taken as a criterion of measuring salt tolerance as suggested by Santa-Cruz *et al.* (1997). In addition, the alterations in proline and ethylene contents implied that Sakha 92 is a salt tolerant wheat cultivar while Giza 163 is less tolerant.

Table 2. Changes in polyamine (spermine - Spm, spermidine - Spd, putrescine - Put) contents [mg kg^{-1}(f.m.)] estimated in salinised (150 mM NaCl for 15 d) and control of two wheat cultivars, Giza 163 and Sakha 92. Values represent means ± SD of 3 replications.

Polyamine	Giza 163 Shoot Control	 Salinised	 Root Control	 Salinised	Sakha 92 Shoot Control	 Salinised	 Root Control	 Salinised
Spermine	259.3±0.1	348.2± 0.1	34.8±0.3	145.9±0.3	268.7±0.5	322.4±0.6	33.5±0.5	222.5±0.3
Spermidine	4.4±0.5	5.8±0.1	1.7±0.1	4.1±0.2	2.4±0.9	3.4±0.3	1.5±0.4	6.5±0.2
Putrescine	17.6±0.2	11.7±0.0	103.5±0.2	40.0±0.2	18.3±1.8	7.1±0.2	102.0±0.4	51.0±0.3

Table 3. Changes in ethylene evolution [mol kg^{-1}(f.m.) s^{-1}] and proline content [g kg^{-1}(f.m.)] estimated in salinised (150 mM NaCl for 15 d) and control plants of wheat cultivars Giza 163 and Sakha 92. Means ± SD of 3 replications.

	Giza 163 Control	 Salinised	Sakha 92 Control	 Salinised
Ethylene	1230.3±1.2	4552.1±3.0	1245.2±1.5	2490.4±2.5
Proline	54.9±0.5	247.1±0.2	53.5±0.4	107.5±0.9

Table 4. Changes in chlorophyll (Chl) content [g kg^{-1}(d.m.)], Hill activity [mol(DCPIP red.) kg^{-1}(Chl) s^{-1}], and fluorescence spectra [relative] in chloroplasts isolated from salinized (150 mM NaCl for 15 d) and control wheat cultivars Giza 163 and Sakha 92. Values represent means ± SD of 3 replications.

	Giza 163 Control	 Salinised	Sakha 92 Control	 Salinised
Chl *a*	7.7±0.5	4.1±1.2	7.6±0.9	6.1±0.5
Chl *b*	5.8±1.2	2.5±0.8	6.0±0.2	4.3±0.9
Chl *a/b*	1.3	1.6	1.3	1.4
Hill activity	30.4±0.7	18.2±0.8	29.9±1.2	24.2±0.5
F_{685}	100.0±2.5	75.0±2.1	100.0±1.2	88.0±1.5

Treatment with 150 mM NaCl for 15 d caused a significant decrease of Chl contents in leaves of both wheat cultivars (Table 4). Salinity induced 47 and 20 % decrease in Chl *a* content in Giza 163 and Sakha 92. Similarly, Chl *b* content decreased with 57 and 30 % of Giza 163 and Sakha 92, respectively. Chl *a/b* ratio increased from 1.3 in control of both cultivars to 1.6 and 1.4 in salinised Giza 163 and Sakha 92, respectively. Our results agree with those for wheat plants with different degree of tolerance (Reddy and Vora 1986). Similar results were found in sensitive and tolerant rice (Singh and Dubey 1995). The increased ratio of Chl *a/b* reflected that photosystem 2 (PS2) was more affected by salinity stress. The alternations in pigment contents reflect the changes in composition and structure of the light-harvesting complex leading to a disturbance in the chloroplast architecture (Ghoshroy and Nadakavukaren 1990). Chloroplasts isolated from salinised Giza 163 and Sakha 92 leaves showed about 1.7 and 1.2 decrease in Hill reaction activity in comparison to their control activity. The decrease in photochemical efficiency could be due to either the declined transfer of energy from the light-harvesting complex to the reaction centre or the inability of the reaction centre to accept photons as a result of the altered architecture of the PS2 complex (Cao and Govindjee 1990). To examine the above possibilities, the characteristics of absorption spectra of chloroplasts isolated from both cultivars under salinity were studied (Fig. 2). Salinity induced a major decrease in the absorption spectra with shifts in peaks observed more drastically in chloroplasts isolated from salt stressed leaves of Giza 163 than Sakha 92. In stressed chloroplasts of the sensitive cultivar, the marked differences were a disappearance of a peak at 436 nm, presence of a sharp peak at 480 nm (both originated from carotenoids), appearance of a peak at 670 nm (originated from Chl), and a depression at 638 nm. Chloroplasts isolated from leaves of Sakha 92 showed fewer differences in the absorption spectrum characters reflecting that Giza 163 is more sensitive to salinity than Sakha 92. The characters of absorption spectra of the non-salinised chloroplasts isolated from both cultivars were similar. Furthermore, fluorescence at 685 nm (F_{685}) emitted from PS2 Chl molecules of salinised Giza 163 was diminished by 13 % compared of that of Sakha 92 cultivar (Table 4). Thus, the lower Hill activity and the quenching of fluorescence emission spectra reflected the impairment of photochemical efficiency of PS2 protein complex of salinised chloroplasts of both cultivars; Giza 163 is more drastically affected. More tolerant cultivars show fewer disturbances in the photosynthesis under salinity stress as shown in barley (Belkhodja *et al.* 1999).

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