Biochemical, Physiological and Morphological Responses of Sugar Beet to Salinization

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Abstract

Biochemical, physiological and morphological responses of sugar beet grown on sandy soil under three levels of NaCl salinity in irrigation water, i.e. control, 3000 & 6000 ppm was studied in pot experiment. Results showed that root fresh weight linearly decreased by increasing NaCl salinity levels up to 6000 ppm, but sucrose percentage in root was significantly increased. On the other hand, increasing NaCl levels resulted in significant increase of Na content in both of shoot and root Meanwhile, K content in shoot was sharply decreased but K content in root didn't significantly differ by increasing NaCl levels. Also, under salinity results indicated a strongly negative correlation between shoot osmotic potential and shoot Na content while it was mainly with sucrose concentration in root. Thus, sugar beet plant has an active mechanism to include higher amount of Na in leaves and utilizes it to regulate leave osmotic potential under saline condition. Despite of this mechanism the transpiration rate and stomatal conductance showed significant decrease by increasing NaCl levels up to 6000 ppm. Moreover, stomatal behavior and stomatal morphology revealed a gradual response to the level of NaCl salinity used. Stomatal density, area and pore area strongly decreased by raising NaCl level from control to 3000 ppm with no effect on stomatal closure. No further response was shown for stomatal area by increasing NaCl from 3000 to 6000 ppm, while stomatal closure recorded 60% in lower & 30% in upper leaf surface at 6000 ppm NaCl level. Generally, it could be pointed out that the decrease of sugar beet root fresh weight at low salinity level (3000 ppm) may be due to osmotical stress while at high level of NaCl (6000 ppm) it was attributed to toxic effect of higher Na accumulation on photosynthesis which led to closed stomata in order to inhibit Na transport into leaves.

Introduction

Salinity is one of the principal abiotic factors affecting crop yield in arid and semi-arid areas**.** Because sugar beet has halophytic ancestors, *Beta vulgaris* ssp. *Maritima*, which is found in salt marshes so, sugar beet is a good target crop for studying in such salt-affected areas.
On the other hand, not enough knowledge of the biochemical and physiological basis of the detrimental effect of salt on growth and root yield of sugar beet is the main reason for the limited success of sugar beet planting under high salt condition. Therefore, intensive investigations have to be carried aimed at the understanding of the biochemical and physiological basis of sugar beet salt tolerance mechanisms in order to improve those mechanisms and consequently achieving salt tolerance not only of sugar beet but also of other conventional field crops.
Until now reduction of sugar beet root yield under salinization is unclear. However, many investigations suggested that this reduction is caused by inhibition of photosynthesis or nutrient deficiency or by mineral toxicity. Brugnoli and Bjorkman (1992) reported that the lowering of conductance to CO_2 diffusion caused by stomatal closure accounts for much of the reduction in photosynthesis under moderate salt stress. Also, Delfine *et al.* (1998) found that salt accumulation caused a drop of the Ca and Mg content in spinach leaves which might have decreased membrane stability and chlorophyll content respectively. Moreover, they concluded that salinity reduced photosynthesis primarily by reducing the diffusion of CO_2 to the chloroplast both by stomatal closure and changes in mesophyll structure, which decreased the conductance to CO_2 diffusion within the leaf. However, Very *et al.* (1998) reported that the halophyte *Aster tripolium* partially closes its stomata in response to high Na concentrations. Despite the fact that *Aster tripolium* possesses no specific morphological adaptation to salinity, this stomatal responses preventing excessive accumulation of Na within the shoot via the control of the transpiration rate, is probably a principal feature of observed salt tolerance within the shoot. On the other hand, Ali *et al.* (2000) summarized some of the salt tolerance mechanisms of sugar beet such as replacing most of the K in leaves by Na and selectivity of K over Na in young leaf as compared with the old leaf. Moreover, Flowers (1988) found that in genotypes with salt inclusion, the predominant strategy of osmotic adjustment is achieved by the accumulation of salts (mainly NaCl) in the leaf tissue, which is also indicated from the work of Warne *et al.* (1990) who reported that *Chenopodium rubrum* osmotical adjustment is achieved by accumulating electrolytes in leaves.

Materials and Methods

The present study was carried out at the Faculty of Agriculture, Ain Shams University, Cairo, Egypt. Ten seeds of sugar beet (*Beta vulgaris* ssp. *vulgaris*) variety Top were sown on November 15th 1999 in pots (30 cm diameter with a bottom drainage hole) that were filled with 9.5 kg sandy soil (97.0 % sand, 1.6 % silt and 1.4 % clay).
Plants were thinned after 4 weeks to one plant per pot. Complete randomized design with ten replicates was used. Each replicate included three levels of NaCl salinity namely, control (tap water), 3000 and 6000 ppm. Salt treatments were added to irrigation water after 4 weeks from the sowing date and continued till the end of experiment. Modified nutrient solution after Arnon and Hoagland (1940) was used till 13 weeks from sowing. Plants were harvested 23 weeks after sowing, then immediately separated into shoot and storage root (root & crown at

the lowest leaf scar). Fresh weights of shoot and root were determined. Sucrose and glucose concentrations were determined in root and shoot fresh weight according to the method of Shaffer and Hartmann (1921). Sodium and potassium contents in sugar beet shoots and roots were measured using a flame photometer Petracourt PFP1 in the Biophysics Laboratory, Department of Biochemistry, Faculty of Agriculture, Ain Shams University. Osmotic potential of root and shoot material was estimated using the refractometric method described by Slavik (1974). Leaf temperature, transpiration rate and stomatal conductance were measured by a porometer L1-1600 (Licorginc, USA) on the leaf No.10 (from top to bottom of the plant). The morphological changes of stomata for leaf No.10 from different treatments were examined and calculated through a Joel Scanning Electron Microscope (T.33A) linked with the semafour software program in the Central Laboratory of the Faculty of Agriculture, Ain Shams University.

Statistical analysis

Statistical analysis was performed using the Statgraphics plus program, version 7 (1993). Means were compared using the least significant difference after Duncan (1955) at the 5% level of probability.

Results

Data in Table 1 show that the first level of NaCl (3000 ppm) resulted in a significant reduction of sugar beet root fresh weight to about 63 % of that found for the controls, while shoot fresh weight was not significantly affected. Raising the NaCl level to 6000 ppm lead to a significant reduction in both root and shoot fresh weight to 29.5 and 54.5 %, respectively, of that obtained in the control treatments. Consequently, root/shoot ratio was decreased linearly by increasing NaCl levels up to 6000 ppm in the nutrient medium.
Responses of sucrose and glucose content to increased NaCl levels detected for both root and shoot were varied (Table 1 & Fig.3). On the one side increasing NaCl levels up to 6000 ppm significantly increased root sucrose percentage but on the other, sucrose percentage in shoots showed no significant response. On the other hand, interesting results were shown for the glucose percentage in both shoot and root as affected by increasing NaCl levels in nutrient medium. Whereas glucose concentration increased in the roots it was reduced in the shoots by increasing NaCl level. This inverse responses of root and shoot glucose concentration to increased NaCl levels resulted in an obvious increases of root/shoot glucose concentration ratio.

Table 1: Effect of different levels of NaCl on sugar beet root and shoot fresh weight, root/shoot fresh weight ratio and sucrose concentration in roots (fw = fresh weight).

	Root	Shoot	Root/ shoot ratio	Root sucrose	Shoot sucrose	Sucrose root/shoot ratio
	(g plant^{-1} fw)			(g 100 g^{-1} fw).		
NaCl (ppm)						
Control	373a	110a	3.7	16.21c	0.55a	29.4
3000	235b	100a	2.7	18.03b	0.58a	31.1
6000	110c	60b	1.8	19.70a	0.62a	31.8

Means with the same letter in the same column are not significantly different at the 5% probability level.

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The data in Table 2 show that increasing NaCl levels up to 6000 ppm significantly increased Na content for both root and shoot. However, increasing NaCl levels had no significant effect on root K content but shoot K content was significantly reduced. Another aspect of NaCl salinity effects on the distribution of K and Na between root and shoot is shown in Table 2. It's clear that higher amounts of K and Na in shoots than in roots were found even under salinization. However, the replacement of K by Na was more effective in leaves than in roots. Moreover, the selectivity of K in roots is more evident than in leaves, nevertheless K / Na ratio was decreased by increasing NaCl levels for both roots and shoots. In addition, the osmotic potential in either roots or shoots was significantly decreased as associated with increasing NaCl level in nutrient medium. However, in roots a lower osmotic potential (more negative value) was recorded than in shoot as shown in table 2.

Table 2: Effect of different levels of NaCl on sodium and potassium content, potassium / sodium ratio and osmotic potential of sugar beet roots and shoots (OP = Osmotic Potential , MPa = mega pascals)

Plant organ	Root				Shoot			
Parameters	K	Na	K/Na	OP	K	Na	K/N	OP
	(mg g^{-1} dry weight)			(MPa)	(mg g^{-1} dry weight)			(MPa)
NaCl levels (ppm)								
Control	8.0_a	0.2_c	40	- 1.2	52_a	2.2_c	24	- 0.32
3000	9.2_a	2.4_b	3.8	- 1.5	40_b	38_b	1.05	- 0.49
6000	10.0_a	3.4_a	2.9	- 1.7	30_c	65_a	0.46	- 0.58

Means with the same letter at the same column are not significant different at 5% probability level.

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The data in table 3 show that the application of NaCl was followed by a reduction of both transpiration rate and stomatal conductance of leaf no.10. On the other hand, leaf temperature did not show any response to increasing salinity. However, the highest reduction of transpiration rate and stomatal conductance occurred at the higher level of NaCl. Whereas the values of transpiration rate and stomatal conductance at 3000 ppm NaCl were 34 and 37% less than in the control treatment, raising NaCl to 6000 ppm caused a reduction of these parameters by 47.5 and 50%.

Table 3: Effect of different levels of NaCl on temperature, transpiration rate and stomatal conductance of sugar beet leaf No.10 (from top to bottom).

	Leaf temperature (^oC)	Transpiration rate (mmol m^{-2} s^{-1})	Stomatal conductance (mmol m^{-2} s^{-1})
NaCl levels (ppm)			
Control	34_a	0.61_a	427_a
3000	34_a	0.40_b	270_b
6000	34_a	0.32_c	212_c

Means with the same letter at the same column are not significantly different at the 5% probability level

Concerning the morphological changes of stomatal criteria to salinity (Table 4), it is quite evident that each parameter observed exhibits its individual response to increased NaCl levels. Whereas stomatal density linearly decreased by increasing NaCl levels up to 6000 ppm, significant reduction of stomatal area was detected up to 3000 ppm and no further response was shown even at 6000 ppm. Stomatal closure showed another different response along with increased NaCl levels. This parameter showed no effective response concomitant with increasing NaCl up to 3000 ppm but stomata were closed at the highest NaCl level (6000 ppm). More focusing to the effect of salinity on stomatal closure for the upper (adaxial) and the lower (abaxial) leaf surface are shown in table 4. The distribution of stomatal density between the abaxial and adaxial leaf surface was decreased in a much more pronounced way for the abaxial than for the adaxial leaf surface as the NaCl level increased. Accordingly, the adaxial / abaxial distribution ratio of stomatal density was obviously decreased from 71.7 to 63.7 % by increasing NaCl level up to 6000 ppm. The opposite trend was true for stomatal pore area. Consequently, the closing of stomatal pores was more evident for abaxial than for the adaxial leaf surface. Results of stomatal closure (Table 4) supported the previous conclusion. The stomatal closure was firstly detected for the abaxial leaf surface at the lower level of NaCl (3000 ppm) while at 6000 ppm, stomatal closure was detected for both abaxial and adaxial leaf surfaces. However, stomatal closure was two times higher at the abaxial than at the adaxial leaf surface at the high NaCl level (6000 ppm).

Table 4: Effect of different levels of NaCl on stomatal density, stomatal area, stomatal pore area and stomatal closure for upper and lower surfaces of sugar beet leaf No.10 (from top to bottom). Stomatal closure (%) = No. of Stomata closed : No. of total stomata x 100. ND: Not detectable.

	Stomatal density (No. mm^{-2})			Stomatal area (μm^2)			Stomatal pore area (μm^2)			Stomatal closure (%)		
	Upper	Lower	Upper /lower	Upper	Lower	Upper /lower	Upper	Lower	Upper /lower	Upper	Lower	Upper /lower
NaCl (ppm)												
Control	81b	113a	71.7	530a	510a	104	40.0a	41.9a	0.95	ND	ND	ND
3000	60c	90.6b	66.8	364b	322b	113	29.8b	18.0c	1.7	1.0	11.0	0.1
6000	41.7d	65.5c	63.7	350b	360b	97	28.0b	11.0d	2.5	30	60	0.5

Means with the same letter for the same parameter are not significantly different at the 5% probability level.

Discussion

Starting with the responses of sugar beet yield to increased NaCl salinity levels up to 6000 ppm, it is clear that, despite of the linear decrease of root fresh weight nevertheless, root sucrose percentage was increased. At the same time, it was obvious that the reduction of root / shoot ratio along with increasing NaCl levels might be a modificative adaptation to reduce root mass. Consequently, root sucrose percentage was concentrated and thus root osmotic potential adjusted against high NaCl concentration around root system. However, the detrimental effects of salt on sugar beet yield have already been indicated by many investigators (Nassar, 1989; El-Hawary, 1990; Eisa, 1999). They reported that reduction of shoot as well as root fresh and dry weight were associated with increasing salinity levels. On the other hand, the ability of sugar beet to change its osmotic potential as a response to salt stress was discussed by Lindhauer *et al.* (1990) who reported that inorganic salts such as potassium, sodium and magnesium played the main role in osmotic potential adjustment in sugar beet leaves whereas sucrose dominated root osmotic potential. Also, results obtained in the present work revealed a more pronounced accumulation of both sucrose and glucose in the roots than in the shoots at increasing NaCl levels. Besides, a higher concentration of inorganic solutes (Na and K) were observed in shoots than in roots. However, correlation analysis (Figure 1) identified Na as the main solute for osmotic potential adjustment in sugar beet leaves under salinity conditions. Moreover, both sucrose and K are the main solutes for osmotic potential adjustment in roots followed by glucose and Na. Accordingly, it may be concluded that high Na concentration plays an important role in leaf metabolic function such as turgor maintenance. This ability to adjust shoot osmotic potential by using Na under saline condition is in agreement with characterizing sugar beet as a salt inclusion species.

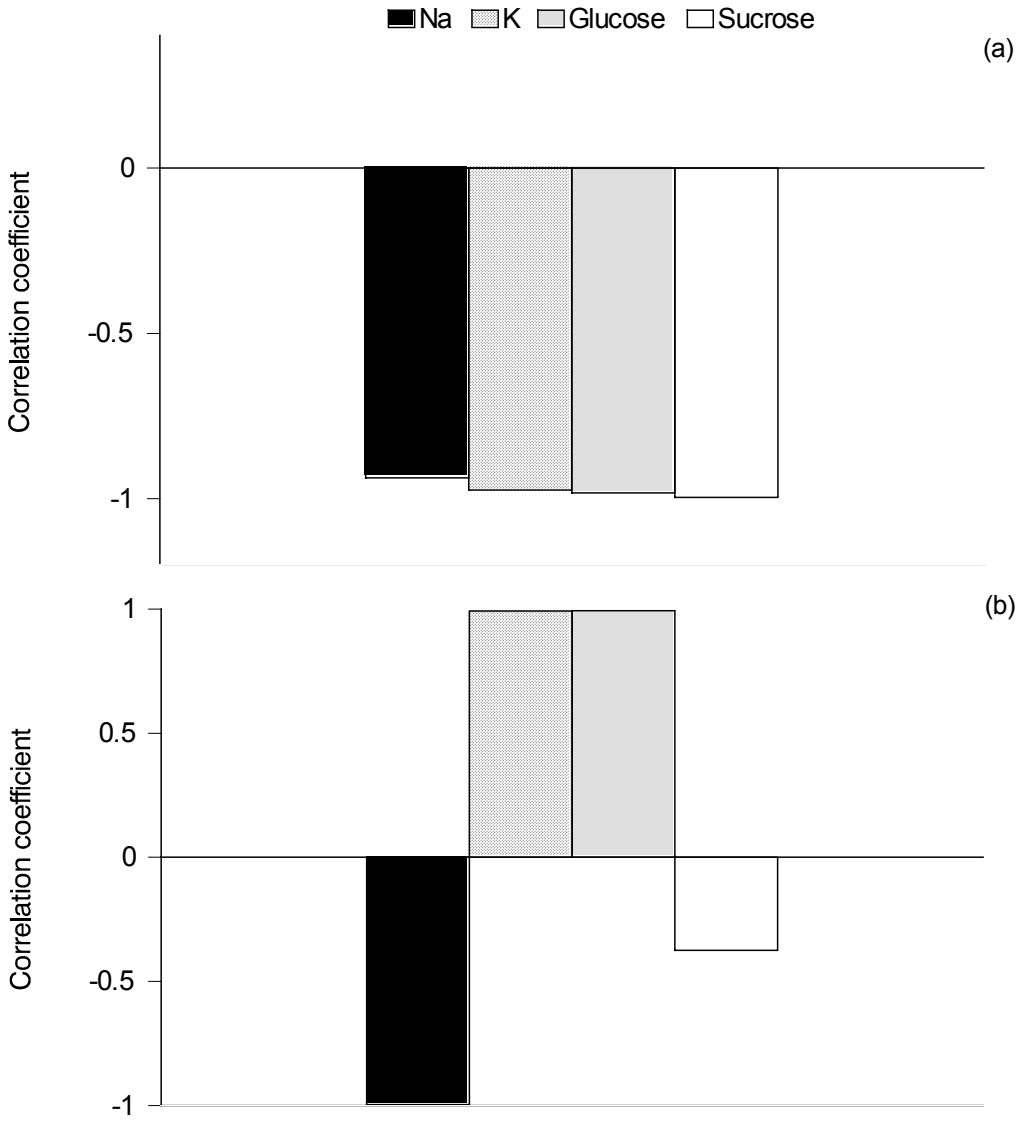

Fig.(1): Correlation coefficient between root (a) and shoot (b) osmotic potential and sodium, potassium, glucose and sucrose of sugar beet root and shoot under different concentrations of NaCl levels.

On the other hand, correlations presented in figure 2 illustrate that both K/Na ratio and osmotic potential in root and shoot were inversely correlated with stomatal closure whereas Na and sucrose content correlated proportionally with stomatal closure. It is clear that Na and sucrose content in both root and shoot led to a decrease of the osmotic potential which resulted in elevation of stomatal closure under saline condition. However stomatal closure correlated better with root osmotic potential (r = -0.9) than with that of the shoot (r = -0.8) and that may accentuate that stomatal closure was more a response to root osmotic potential than to that of the shoot under saline condition.

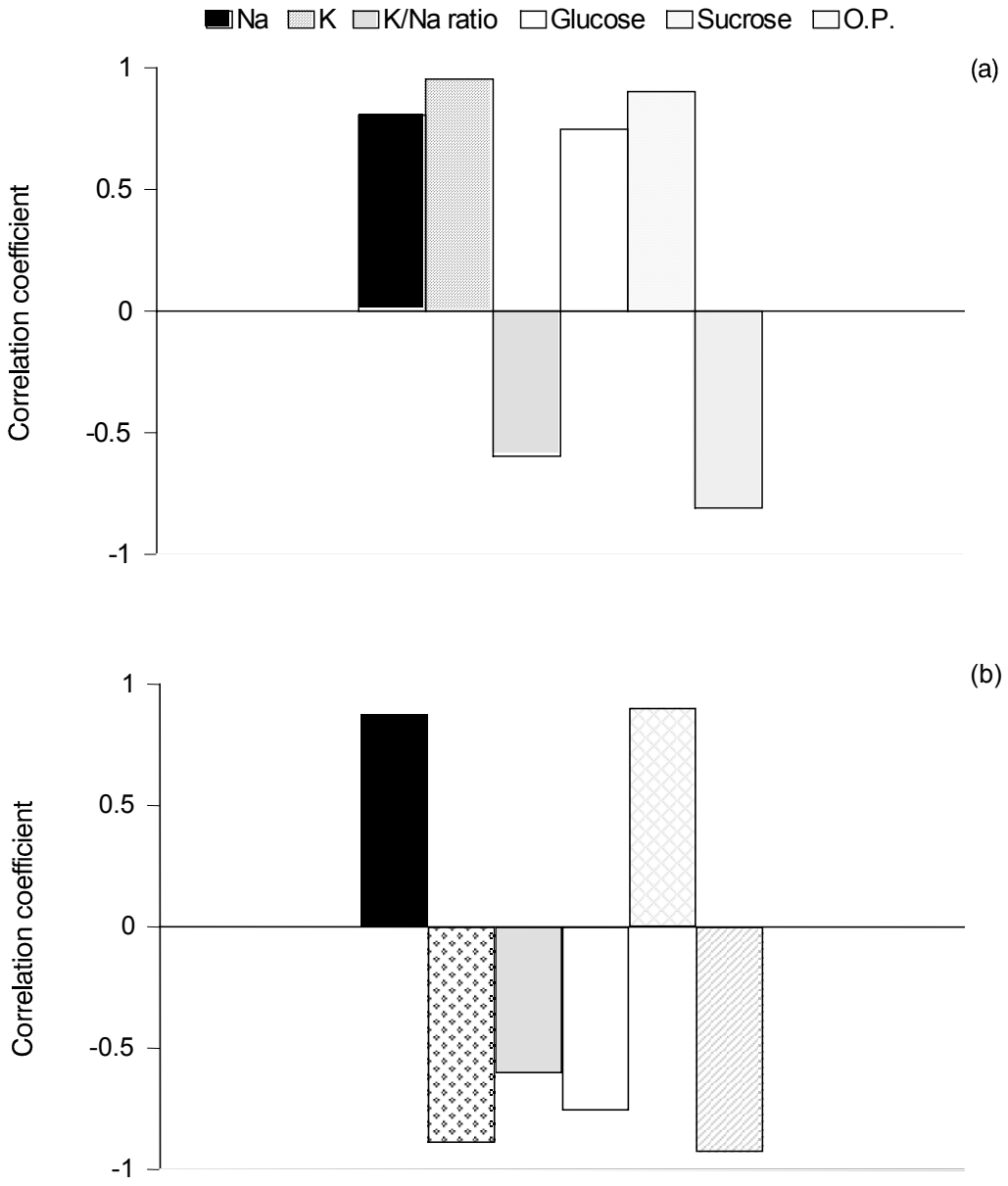

Fig.(2):Correlation coefficient between stomatal closure and sodium, potassium, K/Na ratio,glucose and sucrose of sugar beet root (a) and shoot (b) under different concentrations of NaCl levels.

Concerning the effect of increasing NaCl levels on sodium and potassium content, the present results show that increasing NaCl levels up to 6000 ppm greatly increased Na content in both shoots and roots, but sharply decreased K content in shoots (Table 2). On the other hand, root potassium content was not significantly affected by increasing NaCl levels. Accordingly, K / Na ratio, particularly for the shoot was obviously decreased. This pointed out a mechanism for replacing most of the potassium by sodium. As indicated by the higher amounts of Na accumulating in the shoots, an elimination of Na from the root by transportating it to the shoot where it replaces most of the K in leaves must be assumed. This mechanism (salt inclusion) has been detected by several investigators in some natrophylic plants to achieve salt tolerance (Greenway and Munns,1980; Gorham et al.,1985; Marschner, 1995); Haneklaus et al.,1998; Eisa, 1999; Ali et al. (2000).

As for biochemical aspects, it was evident that leaf glucose concentration sharply decreased by increasing NaCl up to 6000 ppm while the opposite response was observed for root glucose concentration (Figure 3). However, decreasing glucose concentration in the shoot and increasing concentration in the root as affected by salinity may favor sucrose transport and accumulation in the root. This might be reflected by a lower activity of acid invertase associated with high activity of sucrose–P synthase in leaves but the reverse was true in roots. Thus, it seems that under salinity stress sugar beet leaves are mainly a source while roots seem to be a main or the single sink as the formation of of new leaves was strongly reduced or even inhibited. On the other hand, control plants have two sinks, namely, young growing leaves and the root. This might be the second reason for increasing sucrose concentration in the root at increased salinity levels. Salt stress could be considered a factor helping plant leaves to shift from functioning as a sink to become a source by the aforementioned mechanism. Consequently, sucrose concentration increases in sugar beet roots. In this regard, Eschrich (1984) and Marschner (1995) reported that in sugar beet leaves the shift from sink to source is closely correlated with changes in enzyme activities associated with carbohydrate metabolism, namely a decrease in acid invertase activity (sucrose hydrolysis) and a sharp increase in sucrose–P synthase activity (sucrose synthesis). They added that sinks like young leaves and roots are characterized by high activities of acid invertase in the apoplasm. This enzyme hydrolyzes sucrose to form hexoses and thereby maintains a low sucrose concentration in the apoplasm. Consequently, sucrose transporting is enhanced by phloem unloading into the sink. Moreover, inhibitatited invertase activity in response to salinity was reported in sugar beet leaves (Rathert, 1982a), in cotton (Rathert, 1982b), and soybean (Rathert and Doring, 1983).

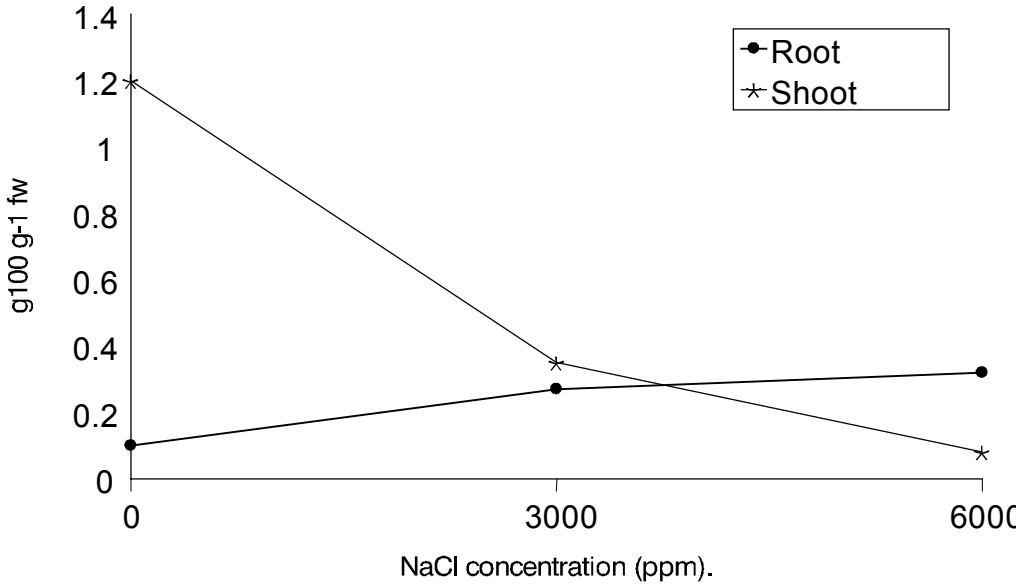

Fig. (3): Glucose concentration in root and shoot of sugar beet plant under two levels of (3000 and 6000 ppm NaCl)

Here again, concerning the effect of increasing NaCl levels on the K content in the root, the present data show slight accumulation of K content in the roots due to increased NaCl levels whereas K in the shoots decreased linearly at increasing NaCl levels. However, the accumulation of a suitable amount of K in root despite the increasing NaCl levels in the nutrient medium may have occurred due to a restricted transport of K from the root (sink) to the shoot (source).

This result was found to be in agreement with Wolf et al. (1991) who assumed that the high K and low Na concentration in young barley leaves and productive organs (sinks) were achieved by low xylem import of both K and Na but high phloem import of K from the mature leaves (source). However, the restriction of K transport into the shoot at increasing NaCl levels may be the second reason for K accumulation in the roots.

Accordingly, maintaining K at a suitable level in roots may be important for some essential metabolic functions in root such as enzyme activities. In this regard, Saftner and Wysc (1980) and Willenbrink *et al.* (1984) reported that in storage cells of sugar beet roots accumulation of sucrose is stimulated by potassium. Also, they added that sodium has an even greater stimulatory effect on sucrose accumulation.

Regarding the physiological and morphological responses to increasing NaCl levels, greatly reduced transpiration rate and stomatal conductance were observed by applying lower salinity level (3000 ppm NaCl) while a slighty further decrease for both parameters was recorded at the higher NaCl level (6000 ppm).

In the same regard, stomatal conductance was found to be sensitive even under mild salt stress either in salt sensitive beans (Gale et al., 1967) or resistant spinach (Robinson et al., 1983) or sugar beet plants (Heuer and Plaut, 1981). However, concerning the reduction of transpiration rate and stomatal conductance in the present work at the lower NaCl level (3000 ppm) it was attributed to a decrease in stomatal density, size and pore area but stomatal closure didn't play an important role at this level. On the other hand, higher NaCl level (6000 ppm) accounted for a sudden increase of stomatal closure. This sensitivity of stomatal closure at high NaCl (6000 ppm) may be the last mechanism for sugar beet plants to avoid the injuriuos effect of salt. In this regard, it could be suggested that photosynthesis seems to be strongly affected at high NaCl (6000 ppm) due to excessive accumulation of Na in leaves excerting toxic influences on this process. In other words, high transpiration rates lead to more accumulation of Na in leaves via xylem import which reaches the toxic level for active photosynthetic tissues and at this point stomata will be closed as the last way to avoid toxic effects of salt stress. Therefore, it may be concluded that the plant has been finishing off its aforementioned biochemical mechanisms such as replacement of K by Na in leaves.

Additional support that validates this suggestion can be obtained from an earlier report by Eisa (1999) who studied distribution and redistribution of Na in single cells of sugar beet leaves under various salinity levels, i. e. control (distilled water), 3000 and 6000 ppm NaCl. The author also reported that at the lower salt level (3000 ppm), Na accumulates in higher amounts in both upper and lower epidermis cells than in mesophyll cells. Thus, this partitioning mechanism within the leaf tissue eliminates the deleterious effect of Na from photosynthetically active tissue and this, in turn, reflects the insignificant effect of salt stress on the activity or concentration of CO_2 fixation enzymes. He added that, raising NaCl level up to 6000 ppm Na accumulates greatly in mesophyll cells because the epidermal cells were saturated which lead to a significant decrease in Rubisco concentration and increased PEPCase activity. From results presented it could be concluded that increasing PEPCase enzyme activity may an additional clue at limited CO_2 due to closed stomata at high NaCl (6000 ppm).

Conclusion

The present work has pointed out some salt tolerance mechanisms for sugar beet plant which could be summarized as following: Firstly, sugar beet plants have an effective inclusion mechanism through which sodium was readily translocated into the shoot where it replaced most potassium. Secondly, sugar beet plants have an ability to change the osmotic potential of shoot and root under saline condition. While sodium was mainly used for adjustment of shoot osmotic potential under saline condition, sucrose played a main role in the regulation of root osmotic potential followed by potassium, glucose and sodium against low osmotic potential in the nutrient medium. Therefore, increasing sucrose concentration in the root under saline condition may be attributed to the following: A) Decreasing glucose concentration in the shoot increased it in the root in order to orient sucrose translocation into the root. B) Preventing the induction of new leaves will keep the root to be the main sink. C) as a consquence of reduced root mass formation sucrose was concentrated in the root. Thirdly, the ability to regulate leaf transpiration rate and stomatal conductance by gradual control of stomatal behavior according to the salinity level innutrient medium: Primarily at lower NaCl (3000 ppm) the reduction of the transpiration rate was caused by reducing stomatal density, size and pore area but not attributed to stomatal closure while at a higher NaCl (6000 ppm), it was predominantly attributed to stomatal closure. Accordingly, it can be pointed out that the reduction of root fresh weight yield at low NaCl (3000 ppm) may be due to osmotical stress but at high level of NaCl (6000 ppm) to the toxic effect of the higher Na content on photosynthesis. Moreover, another ability to regulate leaf transpiration rate was detected as stomata started to close firstly at lower leaf surface at low level of NaCl (3000 ppm) and then in both leaf surfaces at the higher NaCl level (6000 ppm). However, at high salinity stomatal closure at the lower surface was two times more than at the upper leaf surface.

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