

## Varietal differences in agronomic performance of six wheat varieties grown under saline field environment

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### Abstract

Six wheat varieties (SARC-1, SARC-2, SARC-3, SARC-4, LU26S and Punjab-85) were planted in the field to evaluate their comparative performance under saline conditions. LU26S appeared the most salt-tolerant variety and gave the highest grain weight due to its low Na<sup>+</sup> uptake, high K<sup>+</sup>/Na<sup>+</sup> ratio, higher dry weight of shoots and spikes and better grain development. Better exclusion of Na<sup>+</sup> and other ions from the leaves of salt-tolerant variety LU26S could also be a reason for its ability to maintain a higher grain weight in the saline soil. Punjab-85 appeared the most salt-sensitive variety as its dry weight of main shoots and spikes were also found to be the lowest. High Na<sup>+</sup> uptake, lower K<sup>+</sup>/Na<sup>+</sup> ratio, lower dry weight of main shoots and spikes and lower 100 grain weight were the main reasons for salt-sensitivity in Punjab-85. Dry weight of shoots, spikes and grain weight of SARC-3 under saline soil conditions was almost similar to the salt-sensitive variety Punjab-85 and could be classified as salt-sensitive. Flag leaf area decreased drastically due to salt stress in all the varieties and this could be a major cause for low yield. There was however, a very low linear correlation between the flag leaf area and the grain weight in pooled data for all the six wheat varieties.

**Key words:** Soil salinity, wheat, grain yield, Na<sup>+</sup>, K<sup>+</sup>, K/Na ratio

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### Introduction

Saline soils are characterized with pH < 8.5, exchangeable sodium percentage <15 and high soluble salts indicated by high electrical conductivity of the saturation extract >4 dS/m (Qadir, *et al.* 2000). Excessive amounts of soluble salts can result in ionic imbalance in root medium, osmotic effects and water availability to plants proves harmful for the plants due to increased osmotic pressure. Plants differ genetically in their response to salt stress. Different mechanisms of salt tolerance by plants have been suggested by different workers (Flowers and. Hajibagheri, 2001; Gorham, 1994; Kingsbury and Epstein, 1986; Schachtman and Munns, 1992). Accumulation of excessive Na<sup>+</sup> causes premature senescence of leaves, and hence the ability of the plants to accumulate Na<sup>+</sup> in leaves can serve as an important mechanism for salt tolerance (Schachtman and Munns, 1992). Kingsbury and Epstein (1986) found that the salt composition of different isosmotic solutions had little effect on the growth of a salt tolerant wheat line but a sensitive line was affected significantly. The sensitive line tended to accumulate more Na<sup>+</sup> than the tolerant line under high Na<sup>+</sup>

concentration of the growth medium. They suggested that compartmentation of toxic ions, principally Na<sup>+</sup>, may be a mechanism of salt tolerance.

Salt tolerance studies are often carried out in hydroponics in glasshouse in controlled environment. The plant may face more heterogeneous conditions in fields as compared to uniform saline root medium conditions in hydroponics (Ashraf and McNeilly, 1991). In glasshouse the seedlings are often pre-germinated in salt free media (sand or on capillary matting), to obtain a uniform stand in the experiment. Water and nutrient availability, salt content and weather conditions under field situation can be substantially different from solution culture conditions in a growth chamber or glasshouse. Under field conditions the seeds are sown directly into the saline/sodic soil and the seedlings have to undergo salt stress immediately after their germination. There is every possibility that differences in plant growth conditions under the two situations might alter the response of crop cultivars to salt stress. Most crop plants attain increased salt tolerance at later growth stages, which

may also contribute to variable responses between systems. In the field also, the responses of cultivars may be quite different under different types of growing conditions. Therefore, this field trial was conducted on a saline soil to evaluate agronomic performance of different wheat varieties known to have variable degree of salt-tolerance in solution culture studies. Sodium and potassium concentrations in flag leaves of the wheat varieties were also correlated with their yield and yield components.

## Materials and Methods

Six wheat varieties, (SARC-1, SARC-2, SARC-3, SARC-4, LU26S and Punjab-85) were included in this study. The seeds for these varieties were obtained from Saline Agriculture Program, Department of Soil Science, University of Agriculture, and Faisalabad, Pakistan. The field study was conducted at the Soil Salinity Research Institute, Pindi Bhattian, Pakistan. The soil at the experimental site was well-drained and water table remained below 3 metres during most part of the year. The experiment was carried out at two adjacent sites which were about 300 metres apart. One site was a non-saline soil and had an  $EC_e = 1.9$  dS/m at the time of sowing. It was previously reclaimed with excessive leaching with good quality water and had been under cropping for the last 7 years. The other site was a saline soil with an  $EC_e = 12.7$  dS/m. The soil texture at both the sites was sandy loam.

The crop rotation followed at the two sites was wheat-rice. Analysis of the soil was conducted to assess the nature and magnitude of the salt problem (Table 1). Soil salinity was monitored at different growth stages of the wheat. Before sowing the experiment, a heavy irrigation was applied with good quality irrigation water to leach down the excessive salts. For laboratory analysis, a composite sample (1 kg.) was made out from sub-samples drawn randomly from fifteen different locations before sowing. The second and third soil sampling was done at booting and harvesting stage of the crop, respectively. The soil samples were analysed for various physico-chemical characteristics.

After first soil sampling, 135 kg. N/ha as urea, 110 kg. P<sub>2</sub>O<sub>5</sub>/ha as single super phosphate and 60 kg K<sub>2</sub>O/ha as potassium sulphate were applied as recommended for wheat in the area. One third of the N and all the phosphorus and potassium were applied before sowing. The remaining N was applied in two equal splits with the first and third irrigation.

The wheat varieties were sown at the two sites (non-saline and saline) in November. Seven, 10 m. long rows at 30 cm. apart were sown to each variety in triplicate at each site according to randomized complete block design. Irrigation was applied according to crop demand with a 1:1 mixture of good quality canal water and tube well water of marginal quality. A total of 5 irrigations were applied up to the maturity of the crop.

Table 1: Physico-chemical soil characteristics (Electrical conductivity ( $EC_e$ ) of saturation paste extract in dS/m, pH of saturation paste, soluble carbonates ( $CO_3^{2-}$ ), bicarbonates ( $HCO_3^-$ ), chlorides ( $Cl^-$ ), calcium plus magnesium ( $Ca^{2+}+Mg^{2+}$ ) sodium ( $Na^+$ ), sodium adsorption ratio (SAR) and exchangeable sodium percentage (ESP)

me/l									
Time of Sampling	$EC_e$ (dS/m)	pH	$CO_3^{2-}$ (me/l)	$HCO_3^-$ (me/l)	$Cl^-$ (me/l)	$Ca^{2+}+Mg^{2+}$	$Na^+$	SAR	ESP *
Non-saline soil (0-15 cm.)									
Sowing	1.9	8.4	-	5.7	8.8	6.1	10	5.7	6.7 (6.1) *
Booting	1.5	8.3	-	2.7	4.7	3.9	7.8	5.6	6.5 (5.9)
Harvest	0.8	8.3	-	3	1.4	4.4	4.4	3	3.0 (3.6)
Saline soil (0-15 cm.)									
Sowing	12.7	8.6	Tracs	9.5	97.7	15.1	110.3	40.1	36.7 (14.7)
Booting	9.7	8.5	-	3.3	77.1	8.2	87.2	43	38.4 (14.5)
Harvest	15.8	8.3	-	5.2	45.6	9.1	119	55.8	44.8 (14.9)

\* ESP values within the parentheses are actual values obtained through laboratory assay of exchangeable  $Na^+$ . ESP values outside the parentheses were calculated from SAR data.

\* Concentration of  $CO_3^{2-}$ ,  $HCO_3^-$ ,  $Cl^-$ ,  $Ca^{2+} + Mg^{2+}$  and  $Na^+$  are in meq. per litre ( me/l).

Agronomic data were recorded and flag leaf area and soluble ions from flag leaves were determined.

- **Flag Leaf Area:**

Five flag leaves were taken at random at the time of anthesis in March from each plot to measure the leaf area. The leaf area  $\{(0.9 \times \text{Length}) \times (0.5 \times \text{Width})\}$  was determined using the formula of Robson and Sheehy (1980).

- **Soluble ions:**

Thirty flag leaves (10 from each replication) were collected from each treatment and variety. These were stored in labelled paper bags and were dried in an oven at 70 °C for 72 hours and weighed. The soluble ions from the leaves were extracted in Pyrex test tubes (20 ml. capacity), in 10 ml. of 0.1 M. acetic acid at 80 °C in a water bath for 1.5 hours. The whole leaf was kept submerged in the acetic acid to ensure full extraction. The open ends of the test tubes were covered tightly with cling film to avoid any evaporation and changes in concentration of the extracted ions. The concentrations of sodium and potassium in this extract were measured by atomic absorption spectrophotometer (Pye Unicam Model SP-919) at the School of Biological Sciences, University of Sussex, Brighton.

- **Agronomic data:**

Thirty plants (10 from each replication) were harvested at maturity from each treatment and variety. Data for number of tillers and ears plant<sup>-1</sup>, length of main shoots and spikes, total weight of main shoots and spikes, number of grains in spikes from main shoots, weight of grains per main spike and 100 grain weight were recorded. The data for the two sites were combined and statistically analyzed using analysis of variance. Significance levels were calculated at 0.05 level of probability unless otherwise stated.

## Results

### Soil salinity status during the growth of the crop

The  $EC_e$  of the non-saline soil decreased during the period of wheat growth due to leaching of the salts to lower horizons (Table 1). At the time of harvest, it had dropped to 0.8 dS/m. There was also a small decrease in pH and larger decreases in chlorides,  $Ca^{2+} + Mg^{2+}$ ,  $Na^+$ , SAR and ESP of the soil by the time of harvest.

At the start of the experiment, the  $EC_e$  of the saline soil was about 6 times higher than the non-saline soil. A decrease in  $EC_e$  was noted at booting but at the time of final harvest, it was even greater than at sowing. The soil pH remained close to 8.5

throughout the experiment.  $Cl^-$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ ,  $Na^+$ , SAR and ESP were all considerably higher than the normal soil. During the growth period there were considerable decreases in  $HCO_3^{2-}$ ,  $Cl^-$  and  $Ca^{2+}$  and  $Mg^{2+}$ . Soluble  $Na^+$  was lower at booting than at sowing but became higher at the time of final harvest. SAR and ESP increased during the growth period. The data showed that at all the three growth stages, the soil remained a saline soil ( $EC_e > 4.0$ , pH  $< 8.5$  and ESP  $> 15.0$ ) during the growth of the experiment.

### Flag leaf area

Data for flag leaf area (cm<sup>2</sup>) at anthesis stage are presented in Table 2. The effects of salinity were highly significant ( $p < 0.01$ ) while those of variety and the variety x salinity interaction were non-significant. In the saline soil there was a highly significant decrease in flag leaf area which ranged from 50% in salt-sensitive variety Punjab-85 to 63% in SARC-4. Under the same conditions, decrease in leaf area in salt-tolerant variety LU26S was about 56% as compared to the normal soil.

### Length of main shoots and spikes

The effects of salinity and variety on main shoot length and the variety x salinity interaction were significant (Table 2). SARC-2 was the tallest variety in non-saline soil but its stem length was not significantly different from those of all other varieties except SARC-1. Punjab-85 was the shortest variety. There was a significant decrease in the length of main shoots in saline soil which ranged from 24% in SARC-2 to 44% in the salt sensitive variety Punjab-85. The effects of salinity on length of main shoots were the least in SARC-1 (24%) followed by salt tolerant variety LU26S (26%). Spike length in normal soil was highest in SARC-3, which was statistically similar to all other varieties except Punjab-85, which had the shortest spikes (Table 2). There was a considerable decrease in spike length of these varieties due to salt stress which ranged from 8% in SARC-1 to 28% in SARC-3. In the saline soil, spike length was lowest in the salt sensitive variety Punjab-85. The longest spikes were noted in SARC-2 followed by LU26S. The length of spikes of these varieties in saline soil, were almost similar to the non-saline soil.

### Total number of tillers and spikes per plant

The decrease in the total number of tillers in saline soil ranged from 21% in LU26S to 53% in SARC-4 (Table 2). The effect of salinity was highly significant while the effect of variety and variety x salinity

interaction was non-significant. Salinity resulted in a significant decrease in the total number of spikes per plant (Table 2). This ranged from 25% in the salt tolerant variety LU26S to 57% in the salt sensitive Punjab-85. The effect of salinity was highly significant while the effects of variety and salinity x variety was non-significant in number of spikes per plant also.

#### Weight of main shoots and spikes

Very large reduction in the weight of main shoots was noted in all the varieties under saline conditions. It ranged from 21% in SARC-2 to 56% in Punjab-85 (Table 2). The variety x salinity interaction was non-significant, which indicated that the varieties performed similarly at the two sites. Averaged over the two sites, main shoot weight was highest in SARC-2 and LU26S but these varieties were similar to SARC-3 and SARC-4. Lowest main shoot weight was noted in Punjab-85 which is a salt sensitive variety in solution culture studies. Decrease in the weight of spikes was also significant in saline soil as compared to the non-saline soil. The decrease ranged from 13% in SARC-2 to 52% in SARC-3 (Table 3), although the variety x salinity interaction was not significant. Averaged over the two sites, weight of spikes was significantly higher in the salt tolerant variety LU26S and lowest in the salt sensitive variety Punjab-85.

#### Grain weight per spike and yield component

Data showing the grain weight and number of grains per spike on the non-saline and saline sites is presented in Table 3. The interaction of variety and salinity was significant for number of grains per spike and weight of grains per spike. This interaction was non-significant for 100 grain weight (Table 3), indicating that the differences between varieties were similar on the two sites. There was a significant decrease in the number and weight of grains per spike in the saline soil as compared to the non-saline soil. The decrease in number of grains per spike ranged from 8% in SARC-2 to 53% in SARC-3 (Table 3). The decrease in this parameter due to salt stress was quite low in the salt tolerant variety LU26S (17%). The decrease in weight of grains ranged from 13% in SARC-2 to 52% in SARC-3. There was also a comparatively smaller decrease in grain weight in the salt tolerant variety LU26S (14%).

#### K<sup>+</sup>, Na<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> ratios in flag leaves

There was a very large and significant increase in Na<sup>+</sup> contents of flag leaves accompanied by in

significant decrease in K<sup>+</sup> contents in all the varieties due to salinity (Figure 1). Differences between varieties in Na<sup>+</sup> contents were significant on the normal as well as saline soil. Under saline conditions, significantly lowest Na<sup>+</sup> was recorded in the salt tolerant variety LU26S and highest values were noted in the salt sensitive variety Punjab-85. The decrease in K<sup>+</sup> concentration in all the varieties except SARC-2 was significant ( $p < 0.05$ ) in the saline soil as compared to non-saline soil (Figure 1). K<sup>+</sup>/Na<sup>+</sup> ratios in the non-saline soil were very high (Figure 2). A large decrease in these ratios was noted under the saline conditions and higher values were noted in SARC-3, SARC-2 and the salt tolerant variety LU26S. In the saline soil, K<sup>+</sup>/Na<sup>+</sup> ratio was statistically similar in all the varieties except SARC-3 which was similar to LU26S and SARC-2 but greater than the other varieties. In the non-saline soil, K<sup>+</sup>/Na<sup>+</sup> ratio was highest in SARC-2 and significantly lowest in the salt-tolerant variety LU26S.

#### Discussion and Conclusion

Highly significant reduction in the grain weight per spike, yield components and different growth parameters was noted as a result of salt stress. Better performance of LU26S under saline conditions might be due to its significantly higher dry weight of main shoots, better grain development and increased seed weight (expressed as the weight of 100 grains), higher spike length and spike weight as compared to all the other varieties. These results corroborate Francois, *et al.* (1986), and Srivastava, *et al.* (1988). Punjab-85 proved to be the most salt-sensitive variety and its dry weight of main shoots and spikes were also found to be the lowest. Dry weight of shoots, spikes and grain weight of SARC-3 under saline soil conditions was almost similar to the salt-sensitive variety Punjab-85 and could be classified as salt-sensitive. Low dry weight of shoots and spikes was also considered a major reason for low yield in some wheat varieties grown under salt stress by Srivastava, *et al.* (1988). Another major cause for low grain weight per spike in this variety was comparatively lower number of seeds per spike. Soil salinity at the booting/reproductive stage was considerably lower than the other two sampling times, which might have proved beneficial for all the varieties during the reproductive process (Maas and Poss, 1989). Other varieties included in this study were intermediate in their grain weight per spike and could be classed as having medium salt tolerance under saline field conditions.



Table 2: Performance of six wheat varieties under non-saline and saline soil conditions

Non-saline soil		Saline soil					
Parameters		Wheat varieties					
		SARC-1	SARC-2	SARC-3	SARC-4	LU 26S	Punjab 85
Flag leaf area (cm <sup>2</sup> )	19.4±2.0	21.0±1.4	20.1±1.5	21.8±2.4	18.8±1.0	19.2±1.0	
Main shoot length (cm.)	84±2	104±3	101±6	98±2	100±2	92±1	
Main shoot weight (g.)	1.5±0.1	1.6±0.2	1.8±0.2	1.7±0.2	1.8±0.1	1.4±0.1	
Spike length (cm.)	9.2±0.2	10.4±0.4	10.7±0.2	9.6±0.3	10.2±0.3	9.0±0.1	
Spike Weight (g.)	2.8±0.1	3.0±0.2	3.1±0.1	3.2±0.2	3.3±0.1	2.8±0.1	
Number of tillers per plant	8.0±0.3	7.9±0.6	6.7±0.5	8.3±0.6	7.6±0.4	8.1±0.3	
		8.9±1.3	10.4±1.5	8.7±0.4	8.2±1.5	8.3±0.6	9.6±1.4
		64±1	79±1	58±6	69±6	74±1	51±4
		0.9±0.1	1.3±0.1	0.8±0.1	0.9±0.1	1.2±0.1	0.6±0.1
		8.5±0.7	9.6±0.2	7.7±0.6	8.5±0.7	9.4±0.3	7.2±0.2
		2.1±0.2	2.6±0.1	1.5±0.5	2.3±0.4	2.7±0.1	1.5±0.4
		4.8±0.7	5.1±0.4	4.2±0.6	3.9±0.3	6.0±0.6	1.5±0.4

All values are mean of 30 observations except flag leaf area where means are of 15 observations

Table 3: Performance of six wheat varieties under normal and saline soil conditions

Non-saline soil										Saline soil			
Parameters		Wheat varieties											
		SARC-1	SARC-2	SARC-3	SARC-4	LU 26S	Punjab 85	SARC-1	SARC-2	SARC-3	SARC-4	LU 26S	Punjab 85
Number of spikes per plant	7.9± 0.3	7.9± 0.6	6.7± 0.5	8.3± 0.6	7.6± 0.4	8.1± 0.3	4.5± 0.6	5.1± 0.4	3.6± 0.4	3.6± 0.3	5.7± 0.7	4.1± 0.2	
Weight per spilke (g.)	2.8± 0.1	3.0± 0.2	3.1± 0.1	3.2± 0.2	3.3± 0.1	2.8± 0.1	2.1± 0.2	2.6± 0.1	1.5± 0.4	2.3± 0.3	2.7± 0.1	3.4± 0.3	
Weight of grains per spike (g.)	2.2± 0.1	2.3± 0.1	2.4± 0.1	2.5± 0.1	2.5± 0.1	2.2± 0.1	1.7± 0.1	1.9± 0.1	1.2± 0.3	1.9± 0.3	2.2± 0.1	1.5± 0.3	
Number of grains per spike	43.7±1.36	46.1±3.48	49.4±0.46	46.8±4.20	47.4±2.07	48.1±1.05	34.0±2.20	42.5±2.49	23.3±2.41	36.3±1.98	39.5±1.71	26.6±2.22	
100 grain weight (g.)	4.99±0.09	4.93±0.06	4.93±0.09	5.30±0.14	5.34±0.03	4.53±0.09	4.93±0.03	4.63±0.15	5.54±0.28	5.09±0.13	5.55±0.14	4.05±0.40	

All values are mean of 30 observations

As compared to the other growth parameters, salinity proved more injurious to the flag leaf area of all the wheat varieties and a decrease of about more than 50% was noted in saline soil than the non-saline soil. Decrease in leaf area by salinity has been reported by Srivastava, *et al.* (1988). Singh, *et al.* (1994) also reported that increase in salinity and RSC (sodicity) of the irrigation water increased pH of the soil but decreased flag leaf area. Although flag leaf area was highest in SARC-2 in the saline soil but it did not give the highest grain weight; possibly due to inhibition in translocation of photosynthates (Ahmad, 1999). Punjab-85 had comparatively medium flag leaf area in the saline soil, but this was not reflected towards its grain weight under the saline soil conditions. Thorne (1982) reported that the flag leaves in wheat contribute about 82% of assimilates to the grains and hence the yield of the varieties having larger flag leaf area should be higher but the results obtained in this experiment do not support these findings. Length and number of tillers and spikes in SARC-2 was significantly reduced in the saline soil and its salt tolerance was next to LU26S. Singh, *et al.* (1994) found a similar effect of high salinity on length of tillers and spikes in wheat.

$\text{Na}^+$  content in the flag leave drastically increased and showed significant increase in all the varieties tested. Highest  $\text{Na}^+$  content was found in the salt-sensitive variety Punjab-85 and it was lowest in the salt-tolerant variety LU26S.  $\text{Na}^+$  is a toxic ion and its diminished accumulation in LU26S and increased build up in Punjab-85 could explain their tolerance and sensitivity to salinity respectively.

Schachtman and Munns (1992) reported that salt-tolerant *Triticum* species had lower rate of  $\text{Na}^+$  accumulation than the salt-sensitive ones. The mechanism of  $\text{Na}^+$  uptake was argued to be regulated by root processes and the processes of ion compartmentation within the leaves which enhances the ability to tolerate high concentrations of  $\text{Na}^+$  in the leaves. It has been established that different cultivars may adopt different mechanisms for tolerating high external salinity (Ali, *et al.* 2004; Gorham *et al.* 1994 and Isla, *et al.*, 1998). The exclusion of  $\text{Na}^+$  and  $\text{Cl}^-$ , high RGR for compensating for high  $\text{Na}^+$  uptake or selective uptake of  $\text{Na}^+$  and  $\text{K}^+$  and their compartmentation away from the growing tissues can be important mechanisms for salt tolerance in different wheat genotypes.

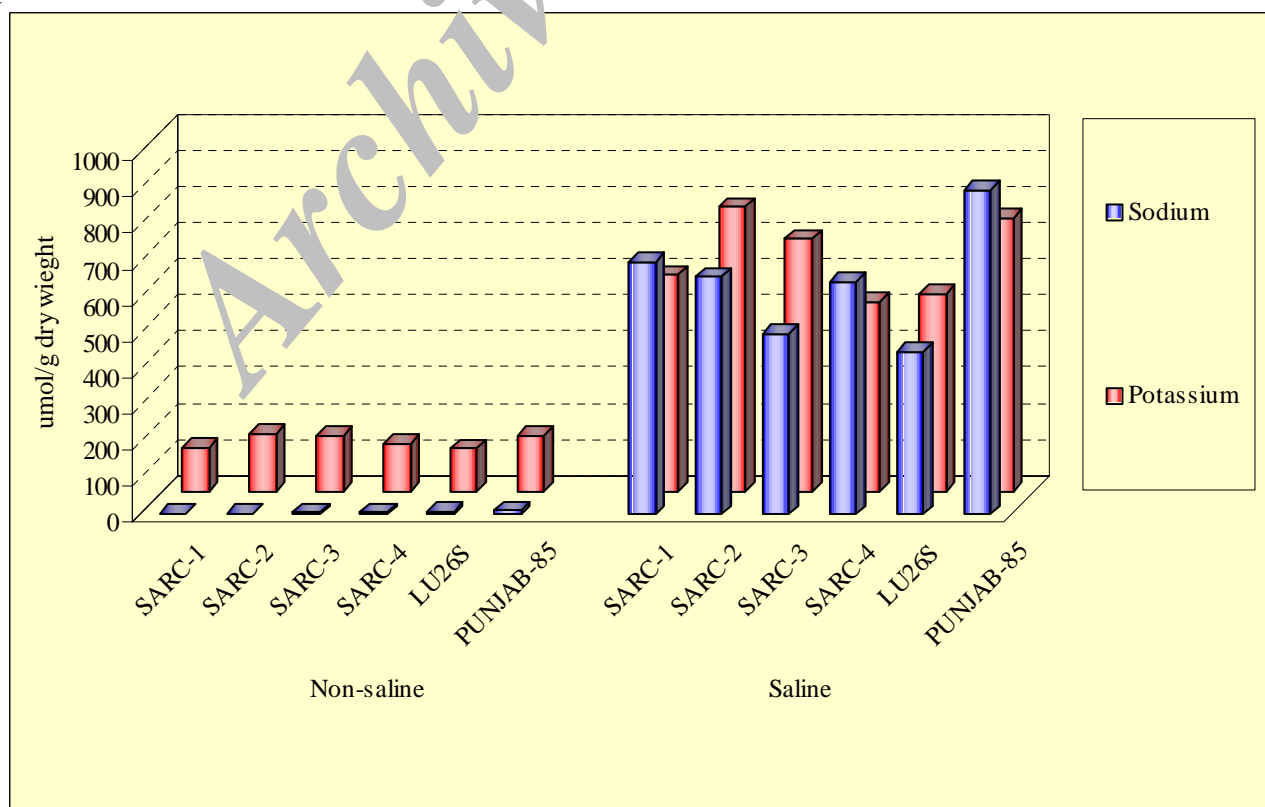


Figure 1: Effect of salinity on sodium and potassium contents of flag leaves in wheat

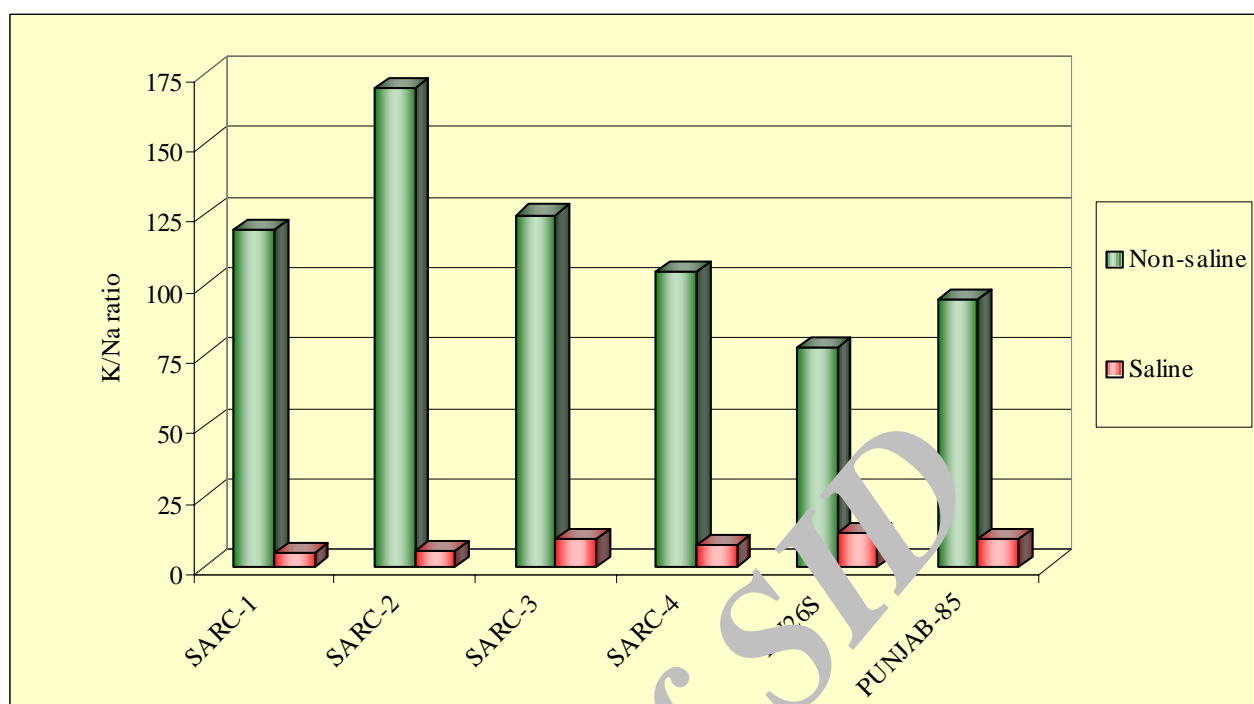


Figure 2: Effect of soil salinity on  $K^+/Na^+$  ratio in flag leaves of wheat

Excessive  $Na^+$  and  $Cl^-$  uptake by the plants may disturb the uptake of  $K^+$  and other nutrient elements (Munns and Termaat, 1986), especially  $NO_3^-$  which in turn may depress the growth and adversely affect the yield and different yield components.

A significant decrease occurred in all the varieties in  $K^+$  contents of flag leaves under saline soil conditions. Flowers and. Hajibagheri (2001) also reported that NaCl salinity decreases  $K^+$  concentration in many species e.g. barley.  $K^+$  concentration in xylem sap was reported to decline when the external NaCl concentrations reached 100 mol/m (Munns and Termaat, 1986). In spite of a significant decrease in  $K^+$  in the saline soil in different varieties,  $K^+$  concentration was 4-6 times more than the  $Na^+$  contents. This high selectivity of  $K^+$  is an important physiological mechanism for plant survival in saline environments (Flowers and. Hajibagheri (2001). This mechanism was more evident in salt-tolerant variety LU26S and least in the salt-sensitive variety Punjab-85. This decrease in  $K^+$  contents ranged from 1-19% in different varieties, highest decrease being noted in SARC-4. Flowers and. Hajibagheri (2001) concluded that greater dry matter accumulation,  $K^+$  and nitrogen contents and reduced uptake of  $Na^+$  and  $Cl^-$  are characters responsible for salt resistance and suggested that these characters could be used as a criterion for rapid screening programmes for different crops. In this study, there was a reduced uptake of  $Na^+$  in the saline soil in

LU26S which is a salt-tolerant variety.  $K^+$  uptake also decreased under saline conditions but there was not a clear trend in this case.

$K^+/Na^+$  ratio was very high in the salt-tolerant variety LU26S in the saline soil which might also be another reason for its better salt tolerance. In the salt-sensitive variety Punjab-85,  $K^+/Na^+$  ratio in saline soil was among the lowest of all the varieties. On the basis of these results, it may be suggested that this ratio may serve as another criteria for salt tolerance in wheat genotypes. It could be concluded that salt tolerance in crops such as wheat and barley is largely determined by their ability to exclude  $Na^+$  and  $Cl^-$  from their shoots and their ability to maintain high shoot  $K^+$  concentrations.

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