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Phylogenetic relationship of salt tolerance in early Green Revolution CIMMYT wheats

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Abstract

Twenty-five genotypes of early CIMMYT hexaploid wheat (*Triticum aestivum* L.) were screened for salt tolerance in a glasshouse experiment at 150 mol m^{-3} NaCl in sand culture. The genotypes Na(20)TPP, Penjamo 62, and Inia 66 exceeded all the lines in grain yield per plant under salt stress, whereas Nainari 60 and Norin 10 were the lowest of all genotypes. However, Jaral 66 and Yaqui 54 were the lowest of all the genotypes in all growth and yield attributes. Considerable variation in accumulation of Na$^+$ and Cl$^-$ in different plant parts of 25 genotypes of early CIMMYT wheat under salt stress was observed. The genotype Noreste 66 was the lowest in leaf Na$^+$ and Cl$^-$, and it had highest leaf K/Na ratio and K versus Na selectivity of all the genotypes, but in terms of growth and grain yield, it was moderately tolerant. The other genotype Norin 10 was the highest in leaf Na$^+$ and Cl$^-$ of all genotypes, but its leaf K/Na ratio and K versus Na selectivity were considerably low. However, in shoot biomass it was the highest and in grain yield the lowest of all genotypes. In view of phylogenetic lineage of the genotypes, most of the genotypes have evolved from Norin 10, so the trait of high uptake of Na$^+$ and Cl$^-$ in most genotypes may have been inherited from Norin 10. The ion exclusion trait in the moderately salt tolerant genotype Noreste 66 was possibly inherited from Yaqui 50 as it was the only among all putative parents which showed low uptake of toxic ions. Overall, owing to the complex nature of the salt tolerance trait being controlled by polygenes, it was not easy to draw relationships between degree of salt tolerance and pattern of uptake of toxic ions and maintenance of leaf K/Na ratios. However, from the phylogenetic lineage of the 25 genotypes it was possible to draw relationships between degree of salt tolerance and mechanism of ion uptake between parents and progeny.

Keywords: Genetic interrelationships; Ion uptake; Ion exclusion; Salt tolerance; Wheat

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1. Introduction

The loss of land previously exploited for crop production under irrigation in arid and semi-arid zones of the world is a continuing problem reducing world food production for a growing world population. Given the scale of agricultural land losses increasing annually, and the extent land area already lost from agriculture due to salinization, the possibility of reclamation of such land using good quality water is not an option.

The solution must therefore rely upon the domestication of wild salinity tolerant plants, or the exploitation of the variability in salinity tolerance present in wild relatives of existing crops through

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hybridization, or through exploiting variability within gene pools of the crops themselves. Domestication of wild species is likely to be time consuming, and could suffer consumer preferences, as was the case of the introduction of the CIMMYT wheats Sonora 64 and Lerma Rojo 64-A in India. Both had red grains. Unfortunately, consumers preferred non-red grains. Fortunately two amber grained varieties, Sharbati Sonora and Pusa Lerma, were produced by mutation breeding at I.A.R.I. The use of ‘wild’ tolerance is exemplified in the exploitation of salinity tolerance in the wild halophyte *Agropyron junceum* when it was crossed with the wheat cultivar Chinese Spring (Forster et al., 1987). When both were grown at 250 mol m^{-3} NaCl, the resulting amphiploid grew to maturity and produced seed, whilst Chinese Spring did not survive. The final option would involve exploitation of variability in salinity tolerance such as has been reported within a number of existing crops (Ashraf, 1994) through selection and breeding, at least in the short term.

Wheat gene pools of considerable sizes have been established worldwide, and for some of the accessions within them, variable amounts of information is available about yield, quality, disease/pest resistance/susceptibility. Whereas small amounts of accessions from such large gene pools have been screened for salinity tolerance, very little screening on larger scales has been undertaken. However, Martin et al. (1994) screened 1700 bread wheats for salinity tolerance, and from within them they identified 112 salinity tolerant accessions of diverse origins. A link for example was found between a number of old European varieties used widely in breeding programs in Europe, with the variety Capelle Desprez, and to nine later cultivars with Capelle Desprez in their pedigree.

Salinity tolerance has also been reported in the early CIMMYT ‘Green Revolution’ wheat varieties Tobari 66 and Sonora 64 (Ashraf and McNeilly, 1988). This paper examines patterns of salinity tolerance in a group of CIMMYT wheats, including those related to Tobari 66 and Sonora 64, and patterns of Na^+ and Cl^- accumulation have also been examined in the same group of accessions. Such material may have value in breeding programs for increase in salinity tolerance.

Thus the primary objective of the present study was to draw relationships between parents and progeny in a complete set of early CIMMYT wheat germplasm with respect to mechanism of accumulation and distribution of toxic ions such as Na^+ and Cl^-.

2. Materials and methods

Seeds of 25 genotypes of hexaploid wheat were obtained from Dr. T. McNeilly, School of Biological Sciences, University of Liverpool, UK, who originally obtained them from the International Maize and Wheat Improvement Centre (CIMMYT), Mexico. The experiment was conducted in the Botanic Garden of the University of Agriculture, Faisalabad, in a netting house supplied with natural sunlight during December–April, 2001–2002. The average day and night temperatures were 29 ± 9 and 15 ± 7 °C, respectively. The average relative humidity ranged from 41 to 69% and photoperiod from 10 to 12.5 h. The experiment was laid out in a completely randomized design with four replications, 25 wheat genotypes, and two salt treatments.

Twenty seeds of each genotype were sown in each earthen pot (28 cm diameter) containing 8.5 kg river sand. After 14 days of growth, plants were thinned to six per pot. The plants were grown in full strength Hoagland’s nutrient solution in sand culture for 41 days from sowing, after which NaCl treatment was begun. Two liters of Hoagland’s nutrient solution was applied on alternate days to each pot so as to flush all salts previously present in the sand. The NaCl treatments used were 0 (without salt) and 150 mol m^{-3} in full strength Hoagland’s nutrient solution. The NaCl concentration was increased step-wise in aliquots of 50 mol m^{-3} every day until the appropriate concentration was attained. Each time treatment solutions were applied in the evening.

Two plants from each replicate were harvested at the boot stage. Plants were uprooted carefully and washed with distilled water. After recording the fresh weights of both shoots and roots, they were oven-dried at 65 °C for 1 week and dry weights recorded. Remaining four plants were used for attaining seed yield. The dried ground shoot (only third leaf from top) and root material (0.1 g) were digested with sulphuric acid hydrogen peroxide according to the method of Wolf (1982). Cations such as Na^+, K^+, and Ca^{2+} were determined with a flame photometer (Jenway, PFP-7). For the determination of Cl^-, shoot and root samples of 100 mg were ground and extracted in 10 ml of distilled water by heating at 80 °C for 3 h. Cl^- content in the extracts was determined with a chloride meter (Jenway, PCLM-3).

K versus Na selectivity ($S_{K,\ Na}$) was calculated as the ratio of tissue K/Na ratio to the growth medium K/Na ratio.

$$S_{\mathrm{K,Na}} = \frac{\mathrm{K/Na\ ratio\ in\ plant\ or\ root}}{\mathrm{K/Na\ ratio\ in\ growth\ medium}}$$

Analyses of variance of data for all attributes and correlation coefficients among different attributes were computed using COSTAT computer package (Cohort Software, Berkeley, USA). Since the main factors for most of the parameters were significant, the mean values were compared with the least significant difference test (Fisher's LSD) following Snedecor and Cochran (1980).

3. Results

The data for shoot fresh and dry weights recorded at boot stage show that there is considerable variation in salt tolerance among 25 genotypes of wheat (Tables 1 and 2). Genotypes differed significantly on the basis of shoot fresh and dry weights (both $P < 0.001$). Frontana, Norin 10, Noreste 66, and Mayo 54 exceeded all the lines in shoot fresh and dry weights. However, Jaral 66, Inia 66, Yaqui 54, and Lerma 52 were the lowest in shoot fresh and dry weights of all the genotypes. Frontana, Noreste 66, Yaktana, and Kenya 58 had the highest relative shoot fresh and dry weights (more than 70%), whereas Yaqui 54, Jaral 66, Lerma Rojo, Lerma 52, and Nainari 60 were lower in percent shoot fresh and dry weights, having less than 45% of shoot fresh and dry weights under saline conditions. Considerable genotypic variation with respect to root fresh and dry weights, plant leaf area, and plant height was observed (Tables 1–3).

In grain yield, genotypes Na(20)TPP, Penjamo 62, Inia 66, Frontana, Siete Cerros, and Jaral 66 had higher (grain yield greater than 1.12 g per plant), whereas Norin 10, Nainari 60, and Mayo 54 lower mean grain yield (less than 0.50 g per plant) than the other lines (Table 4). On percent of control basis, Norteno 67, Penjamo 62, and Na(20) TPP had higher relative grain yield (more than 40%) than the other genotypes under saline conditions (Table 4). In contrast, Norin 10, Mayo 54, Nainari 60, and Pitic 62 had considerably lower (less than 15%) grain yield as compared to other genotypes. For 1000 grain weight,

Table 1
Mean squares from analyses of variance of data for different growth attributes at the boot stage, and yield and yield components of semi-dwarf CIMMYT wheats when 41 days-old plants were subjected to 0 (control) or $150\ \mathrm{mol\ m^{-3}}$ NaCl in Hoagland's nutrient solution

Source of variation	d.f.	Shoot fresh weight	Shoot dry weight	Plant leaf area
Salt levels (S)	1	7346.8***	244.98***	1718889.8***
Genotypes (G)	24	50.4***	2.58***	93767.9***
S × G	24	27.7***	1.28***	16524.7ns
Error	150	8.67	0.52	11549.1

Source of variation	d.f.	Plant height	Root fresh weight	Root dry weight
Salt levels (S)	1	9650.4***	464.08***	33.45***
Genotypes (G)	24	489.5***	4.23***	0.265***
S × G	24	59.4***	2.53***	0.234***
Error	150	24.3	0.462	0.055

Source of variation	d.f.	Number of spikes per plant	Grain yield per plant	Number of grains per plant	1000-grain weight
Salt levels (S)	1	46.07***	326.04***	108019.5***	14016.4***
Genotypes (G)	24	1.35***	0.839***	1642.5***	126.9***
S × G	24	0.566ns	0.910***	428.8ns	97.7***
Error	150	0.440	0.349	329.8	17.9

*,**,***: significant at 0.05, 0.01, and 0.001 levels, respectively. ns: non-significant.

Table 2
Shoot fresh and dry weights and leaf area per plant of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	Shoot fresh weight (g)		Shoot dry weight (g)		Plant leaf area (cm^2)	
	Control	Salt	Control	Salt	Control	Salt
Chris sib	27.0	10.9 (40.3)	6.11	2.81 (45.7)	699.3	435.2 (62.2)
Ciano 67	20.6	10.6 (51.5)	4.82	1.94 (42.7)	459.8	175.6 (38.2)
Frontana	26.2	17.13 (65.3)	5.37	3.90 (73.6)	678.3	442.5 (65.2)
Gabo 55	20.5	9.52 (46.5)	4.01	2.19 (53.7)	435.2	239.7 (55.1)
Inia 66	19.6	8.22 (41.8)	3.89	1.84 (47.5)	346.1	271.2 (78.4)
Jaral 66	24.7	8.53 (34.4)	5.35	1.77 (32.6)	449.1	89.5 (19.9)
Kenya 58	22.0	13.7 (62.4)	4.04	2.85 (70.6)	506.2	396.7 (78.4)
Lerma 52	23.9	9.27 (38.7)	4.29	1.87 (43.4)	670.0	381.3 (56.9)
Lerma Rojo	26.3	11.4 (43.5)	5.32	2.36 (44.1)	606.6	285.9 (47.1)
Lerma Rojo 64	13.2	9.82 (74.4)	4.50	2.81 (62.9)	347.8	268.7 (77.3)
Mayo 54	30.6	15.7 (51.3)	5.79	3.40 (59.2)	590.7	423.5 (71.7)
Mayo 64	29.0	11.6 (40.0)	5.07	2.70 (54.5)	524.3	442.9 (84.5)
Na(20)TPP	25.4	10.7 (42.3)	4.79	2.21(46.0)	466.8	277.7 (59.5)
Nainari 60	29.4	11.78 (40.1)	6.32	2.89 (44.7)	728.6	425.9 (58.5)
Noreste 66	22.9	15.57 (67.9)	4.25	3.11 (73.4)	463.3	403.5 (87.0)
Norin 10	22.1	15.4 (69.6)	5.01	3.49 (69.6)	821.5	593.8 (72.3)
Norteno 67	18.8	9.61 (50.9)	3.52	2.01 (57.2)	394.7	302.9 (76.7)
Penjamo 62	24.2	13.9 (57.5)	4.96	3.02 (60.9)	549.1	418.2 (76.2)
Pitic 62	27.0	13.9 (51.6)	5.86	3.04 (51.0)	522.7	509.9 (97.5)
Siete Cerros	24.2	13.8 (57.2)	4.61	2.99 (64.3)	606.9	393.7 (64.8)
Sonora 64	22.5	10.7 (47.8)	4.97	2.66 (53.8)	536.0	293.5 (54.7)
Tobari 66	19.3	12.2 (63.4)	3.70	2.35 (61.8)	444.1	27.3 (62.5)
Yaktana 54	27.1	13.1 (48.5)	4.99	3.37 (71.4)	472.8	324.6 (68.6)
Yaqui 50	21.6	10.74 (49.7)	3.79	2.26 (59.3)	466.6	296.9 (63.6)
Yaqui 54	27.7	8.21 (29.6)	5.85	1.85 (31.4)	403.5	184.8 (45.8)
LSD 5% (S × G)	4.11		1.01		150.2	

Figures in parentheses are percent of control.

Na(20)TPP, Penjamo 62, and Frontana excelled the other genotypes under salt stress, although they were moderate in number of grains per plant or number of spikes per plant (Table 4).

Ranking of all the 25 CIMMYT wheat genotypes on the basis of their cumulative performance under salt stress with respect to each of the four different attributes (shoot dry weight, grain yield, leaf Na^+, and Leaf K/Na) (Table 5) showed that the response of the genotypes was different in the salt treatment. In shoot biomass, Frontana, Yaktana 54, Mayo 54, and Norin 10 were tolerant, whereas Yaqui 54, Norteno 67, Lerma 52, Jaral 66, Ciano 67, and Inia 66 were sensitive as compared to the other genotypes. In grain yield under salt stress, the tolerant genotypes categorized were Penjamo 62, Na(20)TPP, and Inia 66, whereas the sensitive were Nainari 60 and Norin 10. The genotype which accumulated low amount of Na^+ in its leaves was Noreste 66. The high Na^+ accumulating genotypes were Nainari 60, Penjamo 62, Yaktana 54, and Norin 10. Genotypes which maintained high K/Na in their leaves under salt stress were Noreste 66, Lerma Rojo 64, Chris sib, Na(20)TPP, and Kenya 56, whereas those which maintained low leaf K/Na were Nainari 60, Lerma 52, Jaral 66, Lerma Rojo, Penjamo 62, Pitic 62, Ciano 67, Mayo 54, and Norin 10.

Considerable variation was observed in the set of 25 genotypes with respect to accumulation of different ions in shoots or roots (Table 6). In leaf Cl^-, Norin 10 and Lerma Rojo were the highest of all genotypes (Table 7). Genotypes Noreste 66 followed by Tobari 66 were the lowest in leaf Cl^- accumulation of all the cultivars examined (Table 7). Five genotypes Nainari 60, Lerma 52, Pitic 62, Ciano 67, and Na(20)TPP

Table 3
Plant height, and root fresh and dry weights of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	Plant height (cm)		Root fresh weight (g)		Root dry weight (g)	
	Control	Salt	Control	Salt	Control	Salt
Chris sib	83.9	58.0	2.92	0.54	1.25	0.17
Ciano 67	53.3	37.6	1.70	0.41	0.58	0.06
Frontana	67.6	53.4	2.67	1.25	1.19	0.39
Gabo 55	52.9	43.2	2.06	0.55	0.82	0.21
Inia 66	54.1	43.1	1.77	0.45	0.59	0.10
Jaral 66	46.3	35.8	3.18	0.61	1.12	0.21
Kenya 58	54.4	45.9	2.35	1.62	0.66	0.46
Lerma 52	70.3	46.3	2.70	0.75	1.04	0.17
Lerma Rojo	71.2	55.7	4.66	0.82	1.41	0.17
Lerma Rojo 64	53.5	41.4	1.60	0.76	0.62	0.02
Mayo 54	76.1	49.1	3.30	0.74	1.31	0.21
Mayo 64	59.9	47.7	4.01	0.56	1.17	0.15
Na(20)TPP	70.1	50.4	2.19	0.62	0.66	0.17
Nainari 60	61.9	41.0	4.67	0.81	1.57	0.17
Noreste 66	51.7	42.8	4.77	1.52	1.39	0.40
Norin 10	37.9	30.7	4.93	2.61	1.05	0.49
Norteno 67	52.6	46.2	2.37	1.42	0.72	0.39
Penjamo 62	61.7	49.4	4.97	1.40	1.46	0.39
Pitic 62	63.8	46.7	4.19	0.60	1.17	0.22
Siete Cerros	59.2	51.9	4.79	0.80	1.56	0.22
Sonora 64	55.2	42.8	4.05	0.90	1.55	0.32
Tobari 66	55.2	41.6	2.07	0.95	0.91	0.26
Yaktana 54	65.4	54.5	1.77	0.78	0.64	0.27
Yaqui 50	66.5	49.3	2.13	0.71	0.89	0.21
Yaqui 54	67.1	48.3	4.33	0.56	1.26	0.12
LSD 5% (S × G)	6.89		0.95		0.33	

contained K^+ in their leaves over 1000 mmol kg^{-1} dry weight under saline conditions. In contrast, Siete Cerros, Lerma Rojo, Gabo 55, and Norin 10 had leaf K^+ almost equal to 800 mmol kg^{-1} dry weight (Table 8). The genotypes showed a marked difference with respect to leaf Ca^{2+} (Tables 6 and 7). Of all the genotypes, the highest accumulation of Ca^{2+} in the leaves was observed in Mayo 54, Pitic 62, and Nainari 60 under salt stress, whereas the lowest in Lerma Rojo 64 and Chris sib (Table 7).

Accumulation of Na^+ in the roots was the highest in Nainari 60, Lerma Rojo 64, and Yaktana, and the lowest in Na(20)TPP and Norteno 67 under salt stress (Table 8). However, root Cl^- was the highest in Pitic 62 and Lerma Rojo 64, and the lowest in Noreste 66 and Inia 66 (Table 8). Gabo 55 was the highest in root K^+, whereas Tobari 66, Lerma Rojo, and Norin 10 the lowest of all the cultivars under salt stress (Table 8). Yaktana and Na(20)TPP maintained higher Ca^{2+} in the roots, whereas Lerma Rojo and Tobari 66 lower under salt stress as compared to the other cultivars (Table 8).

Genotypes also exhibited considerable variation with respect to K versus Na selectivity of both shoots and roots under salt stress (Tables 6 and 9). Root K/Na ratios were higher in Lerma 52, Chris sib, and Na(20)TPP and lower in Nainari 60, Lerma Rojo 64, Lerma Rojo, Yaktana, and Norin 10 as compared to the other cultivars under saline conditions. Shoot K versus Na selectivity was the highest in Noreste 66, Lerma Rojo 64, Chris sib, Na(20)TPP, and Kenya 58, whereas the lowest in Nainari 60, Jaral 66, and Mayo 54 of all the lines under saline substrate. Root K versus Na selectivity was higher in Lerma 52 and Na(20)TPP and lower in Nainari 60, Yaqui 50, Lerma Rojo 64, Lerma Rojo, Yaktana, and Norin

Table 4
Number of spikes per plant, grain yield/plant, number of grains per plant, and 1000-grain weight of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	Number of spikes per plant		Grain yield per plant (g)		Number of grains per plant		1000-grain weight (g)	
	Control	Salt	Control	Salt	Control	Salt	Control	Salt
Chris sib	3.88	2.69	3.65	1.08 (28.8)	114	52	32.0	24.0
Ciano 67	3.56	2.69	3.41	1.04 (29.9)	100	77	33.5	17.0
Frontana	2.94	2.14	3.15	1.11 (25.6)	88	44	36.2	24.7
Gabo 55	3.38	2.62	3.36	0.52 (15.8)	90	62	37.5	14.0
Inia 66	3.00	1.56	2.92	1.13 (38.7)	86	56	33.7	20.7
Jaral 66	3.58	2.12	3.86	1.10 (28.9)	133	77	29.2	15.0
Kenya 58	2.62	2.12	3.21	0.76 (24.6)	98	47	32.7	16.5
Lerma 52	2.75	1.75	3.31	0.79 (25.0)	93	40	35.2	18.5
Lerma Rojo	2.81	1.62	2.78	0.63 (25.5)	86	48	29.7	15.5
Lerma Rojo 64	3.33	2.69	3.47	0.64 (18.0)	113	65	28.7	10.2
Mayo 54	3.81	3.29	4.74	0.50 (7.98)	122	70	38.5	9.67
Mayo 64	3.75	3.25	4.69	0.77 (16.4)	134	87	33.2	9.00
Na(20)TPP	3.56	2.25	3.20	1.29 (40.0)	99	57	32.2	28.6
Nainari 60	3.44	2.19	3.47	0.31 (8.72)	110	50	34.7	6.00
Noreste 66	3.00	2.69	3.17	0.64 (23.9)	98	61	26.7	11.6
Norin 10	4.56	1.92	2.59	0.06 (2.35)	86	12	27.7	5.33
Norteno 67	2.19	1.81	2.51	0.93 (50.3)	76	47	31.7	16.2
Penjamo 62	3.19	2.25	2.97	1.18 (45.3)	98	54	30.5	26.3
Pitic 62	3.12	2.25	3.82	0.52 (13.4)	110	71	34.7	7.00
Siete Cerros	3.58	1.75	3.31	1.11 (27.2)	111	46	30.2	23.2
Sonora 64	3.31	3.00	3.45	0.75 (22.0)	132	79	20.2	9.50
Tobari 66	3.44	2.44	3.57	1.05 (28.1)	110	54	32.0	18.7
Yaktana 54	2.69	2.50	2.84	1.11 (29.0)	74	62	37.7	17.6
Yaqui 50	3.62	2.12	2.45	0.53 (25.5)	100	48	24.5	7.33
Yaqui 54	3.38	1.88	4.17	0.69 (16.9)	111	43	30.3	15.7
LSD 5% (S × G)	0.931		0.825		25.4		5.91	

Figures in parentheses are percent of control.

10 as compared to the other genotypes under salt treatment.

4. Discussion

On the basis of data for shoot dry weight and grain yield the 25 wheat genotypes were possible to rank for salt tolerance. Although there was a positive correlation between data for shoot dry weight and that of grain yield ($r = 0.854^{***}$), the responses of individual genotypes to salt stress in the two attributes was different. Frontana, Yaktana 54, and Mayo 54 were ranked as tolerant on shoot dry weight basis, but in grain yield they were moderately tolerant. Moreover, Norin 10 was the highest in shoot dry matter, but it was the lowest in grain yield of all genotypes. In grain yield, Penjamo 62, Na(20)TPP, and Inia 66 were ranked as tolerant. Genotypes Jaral 66 and Yaqui 54 were the lowest of all the genotypes in terms of their cumulative performance in all growth and yield attributes on mean and relative basis. No positive relationship between shoot dry weight and grain yield was found in most of individual genotypes. This is parallel to what recently has been observed in two genetically diverse cultivars of wheat (Ashraf and Bashir, 2003). In view of many earlier studies grain yield is the net outcome of the synthesis of assimilates by leaves and translocation of these assimilates to the developing seed where they are utilized to synthesize other organic compounds such as starch, proteins, oil, etc. (Wardlaw, 1990; Pettigrew and Meredith, 1994; Lawlor, 1995; Egli, 1999). Thus these processes differ to a varying extent in different genotypes of wheat (Ashraf and Bashir, 2003).

Table 5
Scoring of 25 wheat genotypes on the basis of their performance in shoot dry weight, grain yield, and leaf Na^+ concentration under salt stress

Genotypes	Shoot dry weight	Grain yield	Leaf Na^+	Leaf K/Na
Chris sib	2	2	2	1
Ciano 67	3	2	2	3
Frontana	1	2	2	2
Gabo 55	2	2	2	2
Inia 66	3	1	2	2
Jaral 66	3	2	2	3
Kenya 58	2	2	2	1
Lerma 52	3	2	2	3
Lerma Rojo	2	2	2	3
Lerma Rojo 64	2	2	2	1
Mayo 54	1	2	2	3
Mayo 64	2	2	2	2
Na(20)TPP	2	1	2	1
Nainari 60	2	3	3	3
Noreste 66	2	2	1	1
Norin 10	1	3	3	3
Norteno 67	3	2	2	2
Penjamo 62	2	1	3	3
Pitic 62	2	2	2	3
Siete Cerros	2	2	2	2
Sonora 64	2	2	2	2
Tobari 66	2	2	2	2
Yaktana 54	1	2	3	2
Yaqui 50	2	2	2	2
Yaqui 54	3	2	2	2

For shoot dry weight, grain yield, and leaf K/Na: 1 = tolerant > overall mean of 25 genotypes + S.D.; 2 = moderately tolerant = overall mean of 25 genotypes ± S.D.; 3 = sensitive < overall mean of 25 genotypes − S.D. For leaf Na^+: 1 = low in leaf Na^+, i.e., greater than overall mean of 25 genotypes + S.D.; 2 = moderate in leaf Na^+, i.e., overall mean of 25 genotypes ± S.D.; 3 = high in leaf Na^+, i.e., overall mean of 25 genotypes − S.D.

Considerable variation in accumulation of Na^+ and Cl^-, and maintenance of K/Na ratios in different plant parts of 25 genotypes of early CIMMYT wheat under salt stress was observed. The genotype Noreste 66 was the lowest in leaf Na^+ and Cl^-, and it had highest leaf K/Na ratio of all the genotypes, but in terms of growth and grain yield it was moderately tolerant. The other genotype Norin 10 was the highest in leaf Na^+ and Cl^- of all genotypes and its leaf K/Na ratio and K versus Na selectivity were considerably low. However, in shoot biomass it was the highest and in grain yield the lowest of all genotypes. Although Lerma Rojo 64, Chris sib, and Kenya 56 were in the category of those genotypes which maintained their leaf K/Na ratio very high, the relationships of this trait of these three genotypes cannot be drawn with leaf Na^+ content, shoot biomass, or grain yield.

Grain yield of a grain crop is one of the most important characters in farmers' viewpoint. Keeping this in view the 25 genotypes were ranked on the basis of grain yield per plant produced under saline conditions. Genotypes Na(20)TPP, Penjamo 62, and Inia 66 had higher, whereas Norin 10 and Nainari 60 lower mean grain yield than the other genotypes under salt level. However, no clear-cut relationships can be drawn between grain yield and pattern of uptake of toxic ions in all these genotypes differing in grain production under salt stress, because some of the high yielding genotypes accumulated high shoot Na^+ while the others low, and the same was true for K/Na ratios. Only the high yielding Na(20)TPP had a positive relationship with its leaf K/Na ratio.

The salt exclusion mechanism observed in Noreste 66 is quite similar to the general argument of Munns (2002) that salt exclusion is one of the most important adaptive mechanisms in both glycophytes and halophytes. In view of phylogenetic lineage of the genotypes (Fig. 1), most of the genotypes have been evolved from Norin 10 so the trait of high uptake of Na^+ and Cl^- in most of the descendents may have been inherited from Norin 10. The most efficient genotype Noreste 66 in terms of exclusion of Na^+ and Cl^- from the leaves was developed from the cross of Lerma Rojo 64 × Sonora 64. Lerma Rojo 64 was developed from the cross [(Yaqui 50 × Norin 10-Brevor) Lerma 52] Lerma Rojo. If we look at the leaf Na^+ and Cl^- concentrations of all the four genotypes of the cross, the lower accumulation of the two ions was found in Yaqui 50. Thus it is possible that genes for low uptake of toxic ions in Noreste 66 and its sister genotypes Inia 66 and Norteno 67 might have transmitted from Yaqui 50. The possibility of contribution of the other parent Sonora 64 of the three genotypes (Inia 66, Noreste 66, and Norteno 67) in transmitting genes for low uptake of toxic ions cannot be ruled out because the parents of Sonora 64, i.e., Yaktana 54 and Yaqui 54, had lower concentrations of both Na^+ and Cl^- in the leaves as compared to most of the genetically related genotypes.

Of all the genotypes, Jaral 66 and Yaqui 54 were ranked as the lowest in terms of their growth and yield performance under saline substrate, but they had

Table 6

Mean squares from analyses of variance of data for concentrations of different nutrients, K/Na ratios, and K vs. Na selectivities in shoots and roots of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Source of variation	d.f.	Shoot Na	Shoot K	Shoot Ca	Shoot Cl
Salt levels(S)	1	10271255.9**	111442.8*	34351.3***	8527217.6***
Genotypes (G)	24	149641.6***	23799.4ns	5770.2***	113181.7***
S × G	24	150659.2***	25741.1ns	10497.4***	96434.8***
Error	150	15237.8	17096.9	283.7	12286.8
Source of variation	d.f.	Root Na	Root K	Root Ca	Root Cl
Salt levels(S)	1	18856241.4***	313.1ns	1280272.0***	9364433.1***
Genotypes (G)	24	35432.1**	7876.6***	11509.6***	11993.6***
S × G	24	31848.7*	3362.4ns	12113.9***	10144.9**
Error	150	17091.5	2798.2	1267.8	4892.3
Source of variation	d.f.	Shoot K/Na	Root K/Na	Shoot selectivity ($S_{K,Na}$)	Root selectivity ($S_{K,Na}$)
Salt levels(S)	1	286.9***	31.9***	126328.0***	3031.2***
Genotypes (G)	24	12.1***	0.204***	896.5***	2.77***
S × G	24	10.6***	0.175***	890.2***	2.65***
Error	150	1.32	0.020	43.9	0.320

*,**,***: significant at 0.05, 0.01, and 0.001 levels, respectively. ns: non-significant.

moderate levels of both Na^{+} and Cl^{-} in their leaves. Jaral 66 was developed from the cross (Sonora 64 × TPP) Nainari 60. Of these three parents, Nainari 60 is among the Na^{+} and Cl^{-} includers, whereas Sonora 64 and TPP are moderate in accumulation of these two toxic ions in the leaves. Thus it is likely that genes for moderate uptake of toxic ions in Jaral 66 were transmitted from Sonora 64 or TPP.

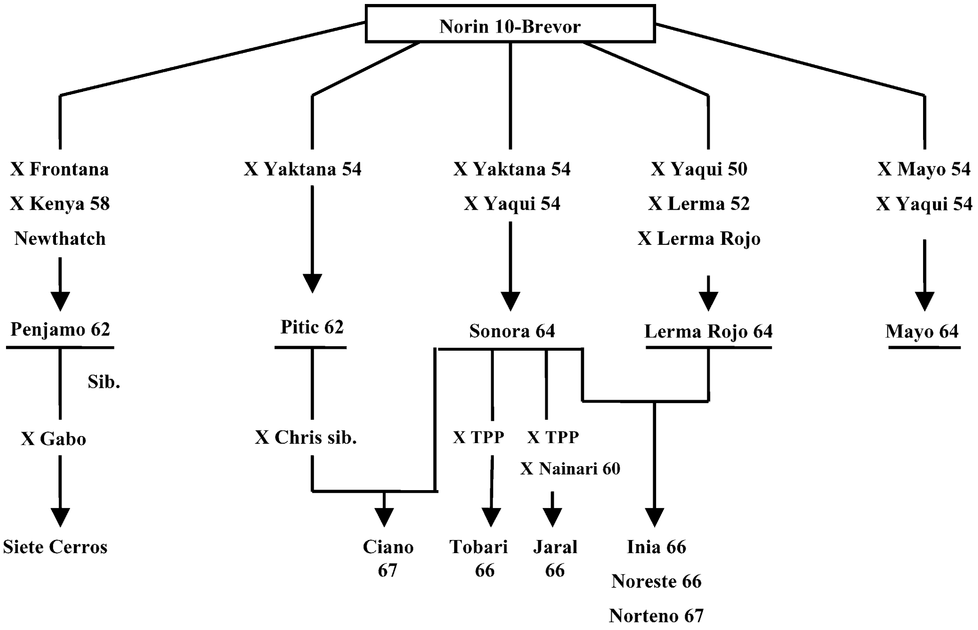

Fig. 1. Genetic interrelationships of early CIMMYT wheats (Source: CIMMYT Annual Report, 1972).

Table 7
Na^+, K^+, Ca^{2+}, and Cl^- concentrations in shoots of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	Na^+ (mmol kg^{-1} dry weight)		K^+ (mmol kg^{-1} dry weight)		Ca^{2+} (mmol kg^{-1} dry weight)		Cl^- (mmol kg^{-1} dry weight)	
	Control	Salt	Control	Salt	Control	Salt	Control	Salt
Chris sib	72.5	315.2	766.0	939.1	102.5	16.6	344.3	762.6
Ciano 67	74.0	695.6	735.0	1028.8	43.7	25.0	393.6	785.2
Frontana	84.4	384.0	951.9	935.8	20.1	29.1	402.1	635.2
Gabo 55	105.9	372.2	884.6	826.9	108.3	25.0	318.3	636.6
Inia 66	112.2	548.9	923.0	967.9	67.5	33.3	375.3	872.5
Jaral 66	95.2	652.1	875.0	858.9	117.5	20.8	416.2	765.5
Kenya 58	79.6	336.9	923.0	935.9	102.5	20.8	400.7	677.4
Lerma 52	81.5	652.1	884.6	1089.7	20.6	54.1	428.8	814.7
Lerma Rojo	122.2	1072.5	814.1	820.5	20.6	54.1	367.6	1215.0
Lerma Rojo 64	97.8	307.9	903.8	942.3	112.5	16.6	380.2	659.1
Mayo 54	86.9	684.7	814.1	887.8	66.6	169.1	395.0	888.7
Mayo 64	78.8	453.8	951.9	996.8	25.0	34.3	478.7	677.4
Na(20)TPP	84.2	351.4	919.8	1105.7	25.0	25.0	375.3	748.5
Nainari 60	81.6	833.6	891.0	1057.6	20.8	125.0	397.1	988.7
Noreste 66	76.1	244.5	948.7	939.1	141.8	29.1	357.0	452.8
Norin 10	97.8	1380.4	980.0	822.0	21.8	40.2	452.1	1530.9
Norteno 67	90.5	342.4	1057.6	897.4	20.6	91.6	379.5	767.9
Penjamo 62	108.7	717.3	932.6	942.3	29.3	25.0	386.6	932.3
Pitic 62	65.2	891.3	817.3	1012.8	45.8	129.1	377.4	1153.5
Siete Cerros	68.8	293.4	804.4	817.3	130.8	25.0	398.5	679.1
Sonora 64	141.3	572.2	862.1	908.7	123.3	20.8	433.8	700.0
Tobari 66	119.5	457.9	990.3	971.1	16.8	25.0	415.9	602.8
Yaktana 54	157.4	494.5	929.4	977.5	135.8	25.0	502.8	831.6
Yaqui 50	168.4	385.8	961.5	862.1	145.6	21.8	364.0	649.2
Yaqui 54	148.5	489.1	820.5	978.6	141.2	78.1	330.9	728.8
LSD 5% (S × G)	172.5		182.7		23.5		154.9	

Plants can use three strategies for the maintenance of low cellular/tissue Na^+ concentration: sodium exclusion, sodium compartmentation, and sodium secretion (Zhang et al., 2001). Sodium transport out of the cell can take place by the operation of plasma membrane-bound Na^+/H^+ antiports. Transport mechanisms can also actively move ions across the tonoplast into the vacuole, removing the potentially harmful ions from the cytosol. These ions, in turn, act as an osmoticum within the vacuole, which then maintain water flow into the cell. The presence of large, acidic-inside, tonoplast-bound vacuoles in plant cells allows the efficient compartmentation of sodium into the vacuole, through the operation of vacuolar Na^+/H^+ antiports (Shi et al., 2000; Mansour et al., 2003). Most plants, when exposed to saline medium, accumulate some Na^+ and Cl^- in their roots and exclude them from the shoots (Wyn Jones, 1981; Ashraf, 1994). Low rate of Na^+ and Cl^- transport to plant tissues seems to be one of the important adaptive components of plants to salt stress (Munns, 2002). In wheat, Gorham et al. (1991) showed a positive relationship between salt tolerance and partial exclusion of Na^+ and Cl^- from the shoots. On the basis of their repeated experimentation with wheat they were able to suggest the partial exclusion of toxic ions as the primary selection criterion in this crop. This is true in some genotypes like Noreste 66 but not for most of the genotypes examined in this study.

High K^+/Na^+ selectivity in plants under saline conditions has been suggested as an important selection criterion for salt tolerance (Greenway and Munns, 1980; Wyn Jones, 1981; Ashraf, 1994; Gorham et al., 1997). In *Agropyron* spp., the high salt tolerance of

Table 8
Na^+, K^+, Ca^{2+}, and Cl^- concentrations in roots of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	Na^+ (mmol kg^{-1} d.wt)		K^+ (mmol kg^{-1} d.wt)		Ca^{2+} (mmol kg^{-1} d.wt)		Cl^- (mmol kg^{-1} d.wt)	
	Control	Salt	Control	Salt	Control	Salt	Control	Salt
Chris sib	236.4	902.1	262.8	278.8	350.0	21.8	142.6	661.2
Ciano 67	144.8	929.3	256.4	323.7	179.1	40.6	190.8	638.7
Frontana	364.1	818.8	358.9	299.1	79.3	31.8	154.2	623.4
Gabo 55	192.9	980.9	333.3	397.4	83.1	43.7	180.9	656.2
Inia 66	205.3	830.4	310.8	273.5	54.1	25.0	195.0	472.5
Jaral 66	252.7	798.9	278.8	275.6	144.4	37.5	223.2	645.7
Kenya 58	210.1	934.7	269.2	285.2	150.0	28.1	175.3	680.7
Lerma 52	255.4	760.8	291.6	314.1	212.5	45.6	169.5	596.1
Lerma Rojo	288.0	923.9	275.6	243.5	275.0	18.7	154.9	634.8
Lerma Rojo 64	282.6	1038.0	285.2	264.9	123.5	29.3	280.2	702.8
Mayo 54	358.6	847.8	246.7	272.4	218.7	34.3	178.8	664.7
Mayo 64	331.5	786.9	278.8	278.8	187.5	46.8	173.9	583.8
Na(20)TPP	309.7	684.7	272.4	301.2	133.3	50.0	211.2	523.1
Nainari 60	326.0	1201.0	278.8	310.9	221.8	28.1	207.0	634.5
Noreste 66	304.3	891.2	362.1	301.2	129.1	28.1	177.4	469.0
Norin 10	285.0	898.5	282.0	243.5	125.0	34.3	153.5	621.7
Norteno 67	253.5	682.0	407.0	311.3	83.3	25.0	197.8	582.3
Penjamo 62	289.8	836.9	304.4	256.4	255.7	31.2	183.1	614.0
Pitic 62	250.0	876.8	237.1	256.4	253.1	33.3	147.1	721.8
Siete Cerros	312.5	934.7	317.3	311.9	251.4	29.1	201.4	697.6
Sonora 64	206.5	945.6	277.7	330.1	134.7	25.0	191.5	684.5
Tobari 66	228.2	739.1	275.6	235.0	200.0	20.6	188.7	536.6
Yaktana 54	307.0	1032.6	256.4	262.8	279.1	50.0	209.1	672.3
Yaqui 50	358.6	994.5	262.8	275.6	304.3	28.1	135.9	552.8
Yaqui 54	298.9	934.7	253.2	269.2	191.6	33.1	162.6	625.3
LSD 5% (S × G)	182.7		–		49.8		97.7	

A. elongatum relative to *A. intermedium*, is associated with its higher uptake of K^+ under saline conditions (Elzam and Epstein, 1969). Experimentation with wheat indicates that salt tolerance is associated with an enhanced K^+/Na^+ discrimination trait (Dvorak et al., 1994; Gorham et al., 1997), although Munns et al. (2000) found large and repeatable genetic variation for low Na^+ accumulation and high K^+/Na^+ discrimination in the durum subspecies (*T. durum*, *T. carthlicum*, *T. turgidum*, *T. turanicum*, and *T. polonicum*) similar in magnitude to bread wheat. The applicability of this criterion in discriminating the 25 wheat genotypes can be observed in very few genotypes but not in most of them. This could be due to some multiple adaptations to toxic ions operating concurrently within a specific plant. These mechanisms can occur in all cells within the plant, or can occur in specific cell types, showing adaptations at cellular or whole plant level (Tester and Davenport, 2003).

Overall, it is now known that salt tolerance trait is very complex because it is controlled by polygenes (Zhu, 2001; Ashraf, 2002; Quesada et al., 2002). Expression of these genes may have cumulative or subtractive effects. Owing to this reason, complexity of the K/Na trait might have occurred during the evolution of different genotypes from their respective parents and thus it was not easy to draw relationships between degree of salt tolerance and pattern of uptake of toxic ions and maintenance of leaf K/Na ratios in the genotypes examined in the present study. However, from the phylogenetic lineage of the 25 genotypes it was possible to draw relationships between degree of salt tolerance and mechanism of ion uptake between parents and progeny.

Table 9
K/Na ratio and selectivity ($S_{\mathrm{K,Na}}$) in shoots and roots of semi-dwarf CIMMYT wheats at the boot stage when 41-day-old plants were subjected to 0 (control) or 150 mol m^{-3} NaCl in Hoagland's nutrient solution

Genotypes	K/Na ratio in shoot		K/Na ratio in root		Selectivity ($S_{\mathrm{K,Na}}$) shoot		Selectivity ($S_{\mathrm{K,Na}}$) root	
	Control	Salt	Control	Salt	Control	Salt	Control	Salt
Chris sib	11.04	3.03	1.12	0.31	1.83	75.2	0.19	7.77
Ciano 67	9.85	1.53	1.79	0.30	1.63	38.1	0.30	7.55
Frontana	11.39	2.17	0.98	0.37	1.89	54.0	0.16	9.08
Gabo 55	11.51	2.39	1.79	0.36	1.91	59.4	0.30	9.13
Inia 66	10.24	1.86	1.54	0.33	1.70	46.4	0.25	8.21
Jaral 66	9.22	1.32	1.02	0.32	1.53	32.4	0.17	7.97
Kenya 58	11.53	2.90	1.38	0.31	1.91	72.3	0.23	7.67
Lerma 52	11.12	1.70	1.16	0.41	1.84	42.4	0.19	10.24
Lerma Rojo	8.43	0.86	1.02	0.26	1.40	21.4	0.17	6.51
Lerma Rojo 64	11.40	3.11	1.03	0.26	1.89	77.4	0.17	6.40
Mayo 54	12.29	1.35	0.70	0.31	2.02	33.6	0.12	8.15
Mayo 64	12.02	2.21	0.84	0.39	1.99	55.2	0.14	9.70
Na(20)TPP	11.54	3.20	0.90	0.41	1.91	79.7	0.15	10.11
Nainari 60	11.79	1.31	0.84	0.26	1.96	32.7	0.14	6.38
Noreste 66	11.99	4.43	1.22	0.34	1.99	110.2	0.20	8.60
Norin 10	10.24	0.62	0.97	0.27	1.70	15.4	0.16	6.74
Norteno 67	11.24	2.36	1.58	0.37	1.86	58.8	0.26	9.32
Penjamo 62	11.22	1.31	1.06	0.30	1.86	32.6	0.18	7.58
Pitic 62	12.71	1.14	1.04	0.29	2.11	28.2	0.17	7.31
Siete Cerros	12.11	2.37	1.02	0.33	2.01	59.0	0.17	8.31
Sonora 64	6.52	1.85	1.26	0.35	1.08	51.3	0.21	8.79
Tobari 66	8.54	2.16	1.28	0.29	1.42	59.4	0.21	7.28
Yaktana 54	5.89	2.25	0.82	0.26	0.98	56.0	0.14	6.43
Yaqui 50	6.05	2.23	0.72	0.28	1.00	55.6	0.12	6.93
Yaqui 54	4.94	2.07	0.84	0.29	0.82	51.6	0.14	7.15
LSD 5% (S × G)	1.61		0.198		9.26		0.790	

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