

SCREENING OF WHEAT (*Triticum aestivum* L.) GENOTYPES AGAINST SALINITY IN SOLUTION CULTURE

Mtab Naseem, R. H. Qureshi, J. Akhtar & M. A. Masood

Saline Agriculture Research Cell, Department of Soil Science, University of Agriculture, Faisalabad

A solution culture experiment was carried out to screen wheat genotypes against salinity. The experiment was conducted in a greenhouse by growing forty wheat genotypes in 200 L capacity tubs containing Hoagland solution. There were three treatments viz. control (non-saline), 100 and 200 mol m⁻³ NaCl arranged according to completely randomized design with five replications. Salinity was imposed gradually and plants were harvested forty days after stress. An increase in salinity reduced the vegetative growth significantly. Genotype BWN-75 proved to be tolerant at both the stress levels due to exclusion of Na⁺ and Cl⁻, and tolerance of PARC-N1, PARC-N2 and Bakhtawar could be attributed to better management of these ions, while that of PARC-N3 due to both the mechanisms.

Key words: salinity, screening wheat genotypes, solution culture

INTRODUCTION

Wheat (*Triticum aestivum* L.) is the most important staple food crop consumed throughout the world and a source of almost 20% of total calories of the world's population (Anonymous, 1991-92). Although wheat is moderately a salt-tolerant crop (Maas and Hoffman, 1977; Qureshi and Barrett-Lennard, 1998), but its growth parameters are greatly suppressed with increasing concentration of salt in growth medium (Rashid, 1986).

Many different approaches can be used to manage salt-affected soils. Though well established techniques such as provision of adequate drainage and use of amendments are available for this purpose yet due to limitations of availability of good quality irrigation water, high cost of amendments and low soil permeability, it is very difficult to tackle this problem. Saline agriculture is another appropriate approach to utilize salt-affected soils, which involves the cultivation of salt-tolerant species/crop cultivars that produce economic yields under adverse soil conditions. Selection for salt tolerance can be made at various stages of plant growth but selection at seedling stage is easier and economical. Due to both spatial and temporal variability in soil salinity, screening under natural saline field is not feasible (Richards, 1983). To avoid this problem crop gene stocks are often screened in nutrient solution to which NaCl is added. Screening of crop varieties against salinity in solution culture is well established (Qureshi et al., 1990). In wheat, differences in varietal response to salt stress and various physiological parameters related to such differences have been studied earlier by many scientists. In line with these studies, a greenhouse experiment was conducted with

the objective to screen salt-tolerant genotypes and identify their characteristics of salt tolerance.

MATERIALS AND METHODS

Seedlings of forty wheat genotypes were germinated in 60cm x 45cm x 5cm trays having two inch gravel layer, sprayed with 250 ml per day 1/2 strength Hoagland solution (Hoagland and Arnon, 1950). At two leaf stage, seedlings were transplanted to 200 L capacity iron tubs lined with polyethylene sheets containing Hoagland nutrient solution, which was continually aerated. There were three treatments i.e. control, 100 and 200 mol m⁻³ NaCl. In salinity treatments salinity was imposed gradually with daily increments of 25 and 50 mol m⁻³ NaCl for 100 and 200 mol m⁻³, respectively. Solution pH was maintained between 6.0-6.5 daily and solutions were changed after every 10 days during the entire experimental period. Ten plants of each genotype were grown in each treatment and were split into five replications, each with two plants. Plants were harvested 40 days after stress and data regarding shoot fresh and oven dry weights were recorded. Leaf samples (third leaf) were collected in 1.5 cm³ polypropylene microcentrifuge tubes and were subjected to freezing. Frozen samples were thawed and leaf sap was extracted by crushing them using a metal rod with tapered end (Gorham et al., 1984). The tissue sap was diluted as required by adding distilled water. The sodium and potassium concentrations in leaf sap were measured using a Jenway PFP 7 Flame Photometer and chloride by Coming 926 Chloride Analyzer. The data thus obtained were statistically analyzed using CRD design with factorial classification (Steel and Torrie, 1980) and means were compared by using Duncan's multiple range test (Duncan, 1955).

RESULTS

Growth: Shoot fresh weight (SFW) of all the genotypes decreased significantly with an increase in salinity except SARC-3, as its relative shoot fresh weight (RSFW) at 100 mol m⁻² salinity was 118.95% of the control but its shoot fresh weight decreased at salinity of 200 mol m⁻², where its relative shoot fresh weight was 63.03%. At salinity of 100 mol m⁻², the second highest RSFW was observed in Bakhtawar, whereas the minimum RSFW was observed in BWN-138 (Table 1a). But at salinity of 200 mol m⁻², maximum RSFW was found in SARC-3, while minimum in BWN-117 and BWN-93. Data regarding shoot dry weight (SDW) followed similar trend as was observed in case of SFW. Again SARC-3 produced maximum relative shoot dry weight (RSDW) i.e. 136.84% followed by Bakhtawar (95.74%) at 100 mol m⁻² NaCl salinity, while BWN-138 produced minimum RSDW at the same stress level. But at higher salinity level (200 mol m⁻² NaCl), maximum RSDW was found in Bakhtawar and minimum in BWN-68 (Table 1b).

Chemical Composition: Sodium concentration in leaf sap increased significantly with increase in salinity. Among genotypes maximum Na⁺ concentration was found in SARC-3 and minimum in BWN-85 and PARC-N3 at lower salinity level (100 mol m⁻² NaCl), whereas at higher salinity level (200 mol m⁻² NaCl), maximum Na⁺ concentration was found in BWN-126 and minimum in BWN-125 (Table 2 a). Salinity disturbed the K⁺ concentration, but its effect was more pronounced at high salinity. Overall, addition of salts decreased the K⁺ concentration in leaf sap. On an average, higher salinity level i.e. 200 mol m⁻² NaCl, decreased the K⁺ concentration significantly, while there was a non-significant reduction at lower salinity level. Both at 100 and 200 mol m⁻² NaCl salinity, maximum K⁺ concentration was found in BWN-141 while minimum in BWN-142 (Table 2 b). In similarity with Na⁺, mean concentration of Cl⁻ also increased significantly with an increase in salinity. Among genotypes, at 100 mol m⁻² NaCl maximum Cl⁻ concentration was found in BWN-66 and minimum in BWN-123, whereas at 200 mol m⁻², BWN-118 accumulated the maximum, while BWN-74 and BWN-142 had minimum Cl⁻ concentration (Table 2 c).

DISCUSSION

Growth: Shoot fresh and dry weights of all genotypes decreased significantly with an increase in salinity except SARC-3, where SFW and SDW were higher at 100 mol m⁻² NaCl when compared with control but

these parameters showed a decrease at 200 mol m⁻² NaCl stress. Depressed growth with increasing salinity could be attributed to decreased water potential of rooting medium due to high ion concentration (Munns et al., 1995) and accumulation of Na⁺ and Cl⁻ to toxic levels in leaves interfering metabolic processes occurring in cytoplasm (Brugnoli and Lauter, 1991; Munns et al., 1995; Shafqat et al., 1998) due to inefficient compartmentation of the ions in cells (Greenway and Munns, 1980). Presence of high concentrations of Na⁺ and Cl⁻ in the rooting medium can suppress the uptake of K⁺, Ca²⁺, NO₃⁻, etc. and ultimately the growth (Gorham and Wyn Jones, 1993). Under saline rooting environment plant cell turgor pressure decreases and stomatal closure takes place resulting in decreased photosynthesis (Gale and Zeroni, 1984). Salinity disturbs the carbohydrate and protein metabolism and thus inhibits plant growth. Osmotic synthesis to withstand salinity stress utilizes much of carbon and reduces metabolite synthesis, and thus ultimately biomass production is reduced (Cheesman, 1988). Increased SFW and SDW of SARC-3 at 100 mol m⁻² NaCl could be attributed to high K⁺ absorption and better management of Na⁺. Higher K⁺:Na⁺ ratio indicates the presence of K⁺:Na⁺ selectivity character for this genotype. The reduced shoot fresh and dry weights of SARC-3 at salinity of 200 mol m⁻² could be due to build up of Na⁺ and Cl⁻ in tissues above the threshold level of this genotype, because when the salt concentration increases above threshold level, both the rate of growth and vigour of plant species are progressively decreased (Aslam et al., 1991).

Ionic Relations: Exclusion of Na⁺ and Cl⁻ at leaf or cellular level is a character of tolerant plants like wheat (Schachtman and Munns, 1992; Rashid et al., 1999). A positive correlation exists between Na⁺ and Cl⁻ exclusion and relative salt tolerance in many crops like wheat (Torres and Bingham, 1973) and barley (Storey and Wyn Jones, 1978). Tolerant plants compartmentalize the toxic concentrations of salts in their tissues (older leaves) and cells (vacuoles), and osmotic adjustments are accomplished by the synthesis of sugars in the cytoplasm (Gorham and Wyn Jones, 1993).

An increase in salinity level increased the Na⁺ and Cl⁻ uptake but decreased K⁺ uptake. At lower salinity i.e. 100 mol m⁻² NaCl, genotypes BWN-67, BWN-75, BWN-84, BWN-123 and PARC-N3, while at higher salinity level (200 mol m⁻² NaCl), genotypes BWN-125, BWN-138 and BWN-145 exhibited better growth due

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Table 1. Effect of salinity on shoot fresh and dry weights of wheat

Genotypes	Shoot fresh weight (g/plant) (a)			Shoot dry weight (g/plant) (b)		
	To	T ₁	T ₂	To	T ₁	T ₂
BWN-66	12.64 a-f	6.60(52.21)b-i	1.69(13.37)e-h	1.48 b-f	1.07(72.29)a-c	0.36(24.32)c-i
BWN-67	11.38 Cog	6.80(59.75)b-h	2.14(18.38)d-h	1.26 c-k	1.04(82.53)a-e	0.42(33.33)b-i
BWN-68	15.11 ab	5.99(39.64)b-l	1.96(12.97)e-h	1.90 ab	0.86(45.26)b-i	0.30(15.78)e-i
BWN-69	8.58 g-j	4.33(50.64)j-q	2.80(32.63)c-g	0.97 h-n	0.60(61.85)h-l	0.49(50.51)b-g
BWN-70	13.26 a-c	6.07(45.77)b-l	2.67(20.13)c-g	1.45 Cog	0.91(62.75)b-h	0.46(31.72)b-i
BWN-72	9.35 d-j	6.49(69.41)b-j	1.99(21.28)f-h	0.99 g-n	0.88(88.88)b-h	0.37(37.37)c-i
BWN-74	12.65 a-f	5.24(41.42)d-n	2.41(19.05)d-h	1.56 b-d	0.79(50.64)c-j	0.42(26.92)b-i
BWN-75	7.31 i-k	4.74(64.84)h-q	2.65(36.25)c-g	0.82 k-o	0.69(84.14)f-k	0.48(58.53)b-h
BWN-76	11.18 e-h	6.04(54.02)b-l	2.68(23.97)c-g	1.18 dol	0.86(72.88)b-j	0.45(38.13)b-i
BWN-84	11.92 bog	7.11(59.64)a-f	2.96(24.83)b-e	1.33 c-j	0.98(73.68)a-g	0.54(40.60)b-e
BWN-85	9.6 c-j	4.83(50.31)hop	1.88(19.58)e-h	1.25 d-k	0.79(63.20)b-j	0.40(32.00)b-i
BWN-91	9.43 b-j	4.38(46.44)j-q	2.28(24.17)d-h	0.97 ion	0.59(60.82)h-l	0.42(43.29)b-i
BWN-93	11.02 c-i	5.99(54.35)b-l	1.30(11.89)hi	1.07 e-m	0.80(74.76)b-j	0.25(23.36)hi
BWN-94	13.03 a-d	7.33(56.21)a-d	3.77(28.91)a-c	1.42 c-l	1.02(71.83)a-f	0.46(32.39)b-i
BWN-95	16.06 a	7.16(44.58)a-e	3.34(20.79)a-d	2.00 a	0.88(44.00)b-h	0.57(28.50)bc
BWN-96	12.14 bog	5.28(43.59)don	2.73(22.41)c-g	1.20 dol	0.73(60.83)d-k	0.45(37.50)b-i
BWN-117	13.36 a-c	4.93(36.90)g-o	1.48(11.07)g-i	1.44 e-h	0.72(50.00)d-k	0.32(22.22)d-i
BWN-118	9.11 e-j	4.21(46.21)k-q	1.78(19.58)e-h	1.00 g-n	0.60(60.00)h-l	0.41(41.00)b-i
B\YN-122	12.85 a-e	4.95(38.52)f-o	2.50(19.45)c-h	1.50 b-e	0.71(47.33)e-k	0.47(31.33)b-i
BWN-123	10.07 c-i	5.34(53.02)con	2.03(20.15)d-h	1.22 dol	0.99(81.11)a-g	0.38(31.14)c-i
BWN-125	7.31 i-k	4.37(59.78)j-q	2.70(36.93)c-g	0.92 j-n	0.60(65.21)h-l	0.51(55.43)b-f
BWN-126	10.38 c-i	5.33(51.34)con	1.77(17.05)e-h	1.02 f-n	0.70(68.62)f-k	0.32(31.37)d-i
BWN-127	9.28 d-j	5.38(57.97)con	2.37(25.53)d-h	0.82 k-o	0.71(86.58)d-k	0.43(52.43)b-i
BWN-135	4.61 k	2.62(56.83)q	1.26(27.33)hi	0.460	0.41(89.00)k-l	0.26(56.52)g-i
BWN-138	8.44 g-j	2.77(32.81)pq	2.65(31.39)c-g	0.90 j-o	0.34(37.77)l	0.48(53.33)b-h
BWN-139	7.54 h-k	3.58(47.48)m-q	1.58(20.95)e-h	1.19 dol	0.55(46.21)i-l	0.31(26.05)e-i
BWN-140	9.28 d-j	3.49(37.60)n-q	2.45(26.40)d-h	1.18 dol	0.55(46.61)i-l	0.50(42.37)b-g
BWN-141	6.24 jk	3.92(62.82)l-q	1.60(25.64)f-h	0.70 m-o	0.53(75.71)j-l	0.30(42.85)f-i
BWN-142	6.07 jk	2.92(48.10)o-q	1.30(21.41)hi	0.77 l-o	0.45(58.44)k-l	0.24(35.08)l
BWN-143	9.63 c-j	5.70(59.19)c-m	1.88(19.52)e-h	1.16 dol	0.91(78.44)b-h	0.35(30.17)c-i
BWN-144	15.14 ab	6.20(40.95)b-k	2.32(15.43)d-h	1.71 a-c	0.89(52.04)b-h	0.42(24.56)b-i
BWN-145	10.41 c-i	4.28(41.11)k-q	2.86(27.47)c-f	1.21 dol	0.63(52.60)h-l	0.51(42.14)b-f
BWN-148	10.00 c-i	4.90(49.00)g-o	2.66(26.60)c-g	1.05 e-m	0.68(64.76)g-k	0.59(46.46)b-g
PARC-N1	15.39 ab	7.45(48.40)a-c	4.11(26.70)ab	1.58 b-d	1.04(65.82)a-d	0.81(51.21)a
PARC-N2	11.73 bog	9.04(77.06)a	4.49(38.27)a	1.36 c-j	1.23(90.44)a	0.79(58.08)a
PARC-N3	7.576 h-k	5.07(66.97)e-o	2.83(37.38)c-f	0.85 k-o	0.80(94.11)b-j	0.55(64.70)b-d
Bakhtawar	8.89 f-j	7.02(78.96)a-d	3.77(42.40)a-c	0.94 j-n	0.90(95.74)b-h	0.63(67.02)ab
SARC-1	7.41 h-k	4.43(59.78)i-q	1.95(26.31)e-h	0.80 k-o	0.59(73.75)h-l	0.37(46.25)c-i
SARC-2	12.88 a-e	7.93(61.56)ab	2.78(21.58)c-g	1.47 g-h	1.12(76.19)ab	0.51(34.69)b-f
SARC-3	4.22 k	5.02(118.95)e-o	2.86(63.04)c-i	0.57 no	0.78(136.84)c-j	0.36(63.15)c-i
Mean	10.32A	5.38B	2.43C	1.17A	0.77B	0.44C

To = control; T₁ = 100 mol m⁻² NaCl; T₂ = 200 mol m⁻² NaCl.

Means with different letters differ significantly according to DMR test (P = 0.05).

Values in parentheses are % of control.

Table 2. Effect of salinity on Na⁺, K⁺ and Cl⁻ concentration in leaf sap of wheat

Genotypes	Na ⁺ concentration mol m ⁻³ (a)			K ⁺ concentration mol m ⁻³ (b)			Cl ⁻ concentration mol m ⁻³ (c)		
	T ₀	T ₁	T ₂	T ₀	T ₁	T ₂	T ₀	T ₁	T ₂
BWN-66	11.0 f-l	90.0 c	168.3 c	172.7 c-m	186.0 dog	119.3 j-l	32.2 h-o	125.5 a	171.6 h
BWN-67	10.5 h-m	65.7 g-i	182.7 be	193.3 a-e	156.0 k-n	120.0 j-l	34.8 g-m	91.2 i-k	185.9 fg
BWN-68	12.0 e-i	70.6 fg	155.5 ef	189.0 a-f	157.7k-m	114.0lm	28.1 moo	83.6kl	201.8 ef
BWN-69	5.80	66.0 g-i	132.7 g-i	159.0 j-n	202.1 ab	214.0 b	28.31-0	91.2 i-k	203.0 ef
BWN-70	9.6 h-n	77.6 e'	164.3 cd	186.0 a-h	163.7 jk	160.7 f-h	30.9 i-o	110.4 d-f	200.9 ef
BWN-72	12.2 e-h	101.7 b	182.7 be	157.3 k-n	114.0 q	101.01-n	31.0 i-o	115.6 b-d	156.1j
BWN-74	8.8j-n	54.4 kl	106.7 k-n	155.3 k-n	166.0 i-k	137.3 h-k	25.70	70.9 m	109.80p
BWN-75	10.1 h-m	43.8 m	115.3 i-l	173.3 c-l	190.0 c-f	154.7f-i	35.8 f-l	98.0 g-i	179.4 gh
BWN-76	14.6 c-e	60.4 i-j	140.0 f-i	209.3 a	171.0 h-j	167.7 f-h	42.4 d-f	69.8 m	184.0 fg
BWN-84	11.3 f-k	44.2 m	114.0 i-l	161.3 g-n	159.0 kl	154.0 f-i	36.0 f-k	92.4 h-k	213.0 de
BWN-85	8.8j-n	30.9 n	111.0j-m	172.0 c-m	141.0 p	122.0 j-l	37.5 e-j	77.11m	133.3 l
BWN-91	9.3 ion	56.6 j-l	200.0 b	195.3 a-d	187.3 d-f	170.0 eg	31.1 i-o	77.11m	255.3 b
BWN-93	8.11-0	54.0 kl	168.3 c	160.0 ion	200.0 a-c	214.3 b	27.0 no	124.4 a	252.5 b
BWN-94	11.5 f-j	68.8 g	165.0 b-d	171.0 d-rn	202.3 ab	205.7 c	31.5 i-o	92.9 h-k	185.9 fg
BWN-95	7.8m-o	58.2j-k	165.0 b-d	168.0 a-m	196.7 a-d	197.4 cd	31.1 i-o	97.9 g-i	212.0 de
BWN-96	9.2 i-n	60.2 i-k	157.3 de	206.7 a	167.0 i-k	150.0 g-j	30.3 j-o	73.7m	184.0 fg
BWN-117	10.4 h-m	40.9 m	113.7 j-l	185.3 a-i	152.71-0	104.01-n	30.4 i-o	75.71m	136.5 k-n
BWN-118	10.4 h-m	60.0 i-k	201.0 b	190.7 a-f	146.3 n-p	102.01-n	47.8 b-d	78.51m	282.5 a
BWN-122	10.2 h-m	38.3 m	92.6 moo	168.7 e-m	198.0 a-d	120.0 j-l	54.0 b	77.4 lm	213.0 de
BWN-123	8.5 k-o	44.4 m	82.0 n-p	189.3 a-f	197.0 a-d	170.0 e-g	26.2 no	53.1 n	1.12.60
BWN-125	7.8 moo	54.5 kl	76.60-q	177.3 c-l	175.7 g-i	155.0 f-l	29.6 k-o	93.4 h-j	115.4 no
BWN-126	8.21-0	87.2 cd	212.0 a	191.0 a-f	172.7 h-j	145.0 j-k	42.4 d-f	91.1 i-k	250.0 be
BWN-127	10.2 h-m	96.4 b	202.0 b	187.0 a-g	179.0 f-h	167.7f-h	28.1 moo	107.4 d-f	227.0 b-e
BWN-135	8.8j-n	50.9 l	102.01-0	173.3 c-l	176.0 g-i	118.3 kl	34.5 g-m	105.3 e-g	126.7 mn
BWN-138	11.0 f-l	75.9 ef	102.01-0	204.0 ab	189.0 c-f	172.0 e-g	33.4 g-n	110.4 d-f	117.3 n-p
BWN-139	8.5 k-o	64.8 g-i	102.71-0	147.3 mu	206.7 a	214.3 b	42.4 d-f	112.3 c-e	169.0 h-l
BWN-140	8.4 k-o	67.7 g-h	85.6 n-p	184.7 a-j	191.3 b-e	188.0 d-f	36.2 f-k	109.8 d-f	168.0 h-l
BWN-141	13.4 dog	40.8 m	126.0 h-k	152.01-n	207.0 a	220.0 a	51.0bc	91.7 i-k	135.1 kl
BWN-142	10.8 g-m	55.7 j-l	85.6 n-p	197.3 abc	109.0 q	85.0 no	39.2 e-h	73.7m	109.80p
BWN-143	15.7 cd	78.7 e	92.0 mop	180.0 b-k	184.3 e-g	137.3 h-k	40.0 cd	114.3 c-e	126.D mu
BWN-144	19.4 a	77.3 e	97.61-0	177.3 c-l	181.0 gh	191.0 de	32.6 h-o	101.4 f-h	169.0 hi
BWN-145	15.0 cd	56.1 j-l	102.01-n	180.0 b-k	188.0 d-f	188.7 d-f	37.5 e-j	110.2 d-f	139.9 kl
BWN-148	16.6 be	100.1 b	166.0 be	191.3 a-f	206.3 a	207.3 c	36.7 f-k	109.2 d-f	179.4 gh
PARC-N1	18.2 ab	81.9 de	155.7 ef	159.3j-n	190.0 c-f	196.0 cd	40.1 e-g	91.1 i-k	170.0 h
PARC-N2	13.6 dog	61.4 h-j	166.3 b-e	173.7 c-l	180.0 e-h	188.0 d-f	37.1 e-k	72.0 m	184.0 fg
PARC-N3	6.8 no	30.3 n	147.8 e-g	177.3 c-l	148.0 mop	120.0 j-l	67.3 a	69.9 m	151.1 j
Bakhtawar	11.8 e-i	90.4 c	185.0 be	160.7 h-n	167.0 i-k	170.0 e-g	32.2 h-o	92.9 h-k	200.0 ef
SARC-1	10.1 h-m	102.3 b	140.0 f-l	180.0 b-k	142.70p	117.0 kl	37.9 e-i	119.9 a-c	161.5 ij
SARC-2	13.7 d-f	80.0 e	126.0 h-k	165.3 f-m	160.0j-m	115.0lm	33.3 g-n	84.4 j-l	135.0 kl
SARC-3	15.4 cd	109.1 a	155.0 ef	140.0 n	143.30p	100.0 mu	44.1 de	123.9 ab	169.0 hi
Mean	11.1 C	66.2B	138.6 A	176.5 A	173.7 A	154.8 B	36.2C	94.0B	174.4 A

T₀ = control; T₁ = 100 mol m⁻³ NaCl; T₂ = 200 mol m⁻³ NaCl.

Means with different letters differ significantly according to DMR test (P = 0.05).

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to exclusion of Na⁺ and Cl⁻ because concentration of Na⁺ and Cl⁻ ions in these genotypes was lesser than those which showed poor growth. But BWN-93, PARC-N2 and PARC-N3 at lower, and BWN-75 and BWN-140 at higher salinity level, excluded either Na⁺ or Cl⁻. Tolerance of genotypes BWN-72, BWN-94, BWN-143, PARC-N1 and Bakhtawar at lower while that of BWN-69, BWN-76, BWN-95, BWN-148, PARC-N1, PARC-N2 and Bakhtawar at higher salinity level could be attributed to better management of Na⁺ and Cl⁻ ions, because these genotypes exhibited better growth even maintaining high Na⁺ and Cl⁻ concentrations in their leaf tissues (Rashid et al., 1999).

Conclusions: Genotypes BWN-75, PARC-N1, PARC-N2, Bakhtawar and PARC-N3 showed better growth at both the stress levels, however, their mechanisms of salt tolerance were different because these genotypes maintained different Na⁺, Cl⁻ and K⁺ concentrations in their leaf tissues. Genotype BWN-75 showed better growth due to exclusion of Na⁺ and Cl⁻ and genotypes PARC-N1, PARC-N2 and Bakhtawar due to better management of Na⁺ and Cl⁻ in cells possibly by compartmentation in vacuoles. Growth of PARC-N3 was better partly due to exclusion and partly due to better management of high Na⁺ and Cl⁻ in the cells.

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