



Comprehensive screening and selection of okra (*Abelmoschus esculentus*) germplasm for salinity tolerance at the seedling stage and during plant ontogeny*

Ikram-ul-HAQ¹, Asif Ali KHAN^{†‡1}, Iqrar Ahmad KHAN², Muhammad Abubakkar AZMAT^{†‡1}

⁽¹⁾Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan)

⁽²⁾Institute of Horticultural Sciences, University of Agriculture, Faisalabad, Pakistan)

[†]E-mail: asifpbg@uaf.edu.pk; knnike@yahoo.com

Received Jan. 25, 2012; Revision accepted Apr. 11, 2012; Crosschecked June 5, 2012

Abstract: The okra germplasm was screened for salinity tolerance at the seedling stage and during plant ontogeny. Substantial variation existed in okra for salinity tolerance at the seedling stage. An 80 mmol/L NaCl concentration was suitable for discriminating tolerant and non-tolerant okra genotypes. The pooled ranking of the genotypes, based on individual rankings for each trait (root and shoot length, germination percentage, and relative Na⁺ and K⁺) in individual NaCl concentrations, was effective for selecting tolerant genotypes. Genotypes selected at the seedling stage maintained their tolerance to NaCl during plant ontogeny, suggesting that screening of the germplasm entries and advanced breeding materials for salt tolerance at the seedling stage is effective. Among 39 okra genotypes, five were identified as the most tolerant genotypes and showed potential for use in breeding programs that focus on the development of salt-tolerant, high-yield okra cultivars.

Key words: Salinity tolerance, Okra, Growth stage, Genetic variation, Mechanism, Potassium to sodium ion ratio (K⁺/Na⁺)
doi:10.1631/jzus.B1200027 **Document code:** A **CLC number:** Q943.2

1 Introduction

Okra (*Abelmoschus esculentus* L.) is a popular vegetable among both the consumers and farmers because it is rich in vitamins and minerals (Oyelade *et al.*, 2003). Although the area under okra has progressively increased during last few years, there is a decreasing trend in its yield per hectare (Anonymous, 2008). Among identified biotic and abiotic stresses, salinity has been the key factor responsible for yield reduction (Khan *et al.*, 2001). Salinity is defined as the amassment of water-soluble salts in the top layer of soil to a level that drastically affects crop production (Rengasamy, 2002). Salinization of soils is one of

the serious problems for irrigated agriculture, and the situation is most severe in tropical regions (Khan *et al.*, 2003).

The ion toxicity has negative impacts on plant growth and development due to low water potential within the local root environment (Munns and Tester, 2008). Ions of sodium (Na⁺) and chlorine (Cl⁻) (>40 mmol/L) can be toxic to plants at levels that result in an imbalance in plant nutrition due to decreased nutrient uptake and transport to new shoots (Cramer, 2003; Tester and Davenport, 2003; Munns and Tester, 2008). High salinity modifies plant metabolisms, which results in altered plant morphology; cultivar type, duration, and intensity of stress determine the extent of morphological modification (Khan *et al.*, 2003; Munns and James, 2003). The excess salt can cause decreased seed germination, seedling growth, and dry matter production (Nautiyal *et al.*, 1989; Singh *et al.*, 1989; Janila *et al.*, 1999). Salinity

[‡] Corresponding authors

* Project supported by the Indigenous 5000 Fellowship Program (Batch II) of the Higher Education Commission, Pakistan

© Zhejiang University and Springer-Verlag Berlin Heidelberg 2012

also induces Fe^{2+} , K^+ , and Ca^{2+} deficiencies (Singh *et al.*, 2004), resulting in yield losses (Hunshal *et al.*, 1991). Okra is cultivated in sub-tropical areas, and its cultivation is hampered in saline and sodic (having more Na^+) soil as it is sensitive to such soils. Physiological mechanisms like ion exclusion, ion accumulation, production of compatible solutes, and osmotic adjustment are considered to be associated with genetic variation in salt tolerance.

Characteristics of a salt-tolerant variety include Na^+ exclusion, potassium to sodium ion ratio (K^+/Na^+) discrimination, retention of ions in the leaf sheath, tissue tolerance, and ion partitioning into different-aged leaves. Osmotic adjustment, transpiration efficiency, early vigor and early flowering leading to a shorter growing season, and the increased water use efficiency are also the features of typical salt-tolerant varieties (Colmer *et al.*, 2005). Salinity affects plant growth most dramatically during developmental stages, and the sensitivity of different crops varies from one growth stage to another (Shannon, 1984). Such developmental effects are observed in rice (Akbar and Yabuno, 1974), sorghum (Maas, 1986), and cowpeas (Maas and Poss, 1989). Thus, plant responses to salinity are influenced by its ontogenic stage at the time of stress (Shannon, 1985). This suggests that the ability of a plant to respond to salt stress depends upon genes that are functioning at a particular stage of development (Foolad and Jones, 1991). For varietal improvement to be effective for salinity tolerance, information about the effect of salinity on all phases of plant growth is essential (Azhar and McNeilly, 1989).

One strategy to address the problem of salt in soil is identification and exploitation of existing or created genetic variability within plants, specifically, that which gives rise to plant phenotypes capable of sustaining a reasonable yield within salt-affected soils (Ashraf *et al.*, 2003). Effective screening protocols depend on an understanding of the response mechanism at different plant growth stages under saline conditions. Knowledge about these mechanisms assists breeders in looking for plants of economic importance with improved salt tolerance (Flowers and Yeo, 1995; Khan *et al.*, 2003). Okra pod yield is a function of physiological and agronomic characters acting singly or in interaction with each other (Adeniji and Peter, 2005). The ultimate yield of a crop depends

upon the interaction between its genetic makeup and environmental factors faced during its entire growing period (Humphreys, 1989; Ashraf and Fatima, 1994).

Keeping in view the nutritional and economic importance of okra and deteriorated soil and water quality, a comprehensive sodium chloride (NaCl) screening study was conducted to gain information on the extent of genetic variation in the okra genotypes for salinity tolerance at all the growth and reproductive stages.

2 Materials and methods

2.1 Assessment of genetic variability for NaCl tolerance in germination and seedling stages of okra

The genetically pure selfed seed of 39 okra genotypes (Table 1) were collected from different sources and subjected to screening for salinity tolerance at the seedling stage. Seeds were surface sterilized in a solution of 2% (0.02 g/ml) hypochlorite for 5 min and washed with distilled water. Individual seeds were planted in triplicate in pots filled with sterilized coarse river sand containing one of six NaCl concentrations as per a randomized complete block design (RCBD). Two pots were used per replication of each genotype. NaCl concentrations of 0, 40, 60, 80, 100, and 120 mmol/L were prepared in half strength Hoagland's nutrient solution (Hoagland and Arnon, 1950). Growth was carried out in a growth chamber adjusted at (28 ± 1) °C, with a relative humidity between 75%–80% and a photoperiod of 16 h. Hoagland's Solutions were added at 3-d intervals. Data for different seedling traits were recorded from three-week-old seedlings. Seedling traits included percentage of germination, root length, shoot length, Na^+ and K^+ concentrations, K^+/Na^+ ratio. The means of all observations were calculated and subjected to analysis of variance (ANOVA) and Pearson's correlation using a general linear model of SPSS 12 (SPSS, Chicago, IL) and MVSP 3.1 (Kovach Computing Services, Anglesey, Wales), respectively. Box-whisker analysis was performed to assess the level of dissimilarity among accessions using Microsoft Excel (QI Macros). A phenogram was constructed with Euclidian distances based upon the response of okra genotypes to different NaCl concentrations.

Table 1 Performance-based ranking of okra genotypes for different seedling traits

Genotype	Rank													Cumulative
	Overall	RL	SL	GP	RRL	RSL	RGP	Na ⁺	K ⁺	K ⁺ /Na ⁺	RNa ⁺	RK ⁺	RK ⁺ /Na ⁺	
Acc. No. 019232	1	1	4	5	1	1	2	13	3	8	2	3	2	45
Acc. No. 000010-10237	2	7	3	13	4	8	14	1	13	3	1	5	1	73
Chinese Red	3	3	1	3	5	5	12	8	6	6	13	6	11	79
Ikra III	4	2	11	4	13	10	6	11	2	1	6	8	5	79
Acc. No. 015371	5	4	7	14	9	12	5	7	4	2	12	1	8	85
Punjab Selection	6	8	10	8	6	2	1	5	8	10	8	9	10	85
Parbhani Kranti	7	11	8	2	7	3	7	6	14	13	7	7	7	92
Acc. No. 019231	8	14	6	6	10	14	9	2	12	4	3	10	4	94
Ikra I	9	6	14	7	11	11	11	3	10	11	4	4	3	95
Acc. No. 019223	10	12	5	10	8	6	8	10	5	7	5	13	6	95
Acc. No. 019236	11	13	12	9	3	9	3	14	1	5	14	2	14	99
Acc. No. 019221	12	5	2	11	2	4	13	9	7	12	10	14	13	102
Acc. No. 019217	13	10	13	1	14	13	4	4	11	9	11	12	12	114
IN-1048	14	9	9	12	12	7	10	12	9	14	9	11	9	123
Clemson Spineless	15	19	19	15	20	17	19	24	17	19	21	18	18	226
Acc. No. 019215	16	16	27	22	21	26	28	21	20	20	18	17	16	252
Acc. No. 015373-10811	17	24	20	25	26	16	29	15	22	17	15	26	17	252
University Okra	18	26	18	21	15	31	16	23	25	22	19	22	15	253
Acc. No. 019224	19	20	16	30	17	15	22	19	19	16	34	19	32	259
Acc. No. 019228	20	17	22	19	22	18	17	34	18	26	25	21	21	260
Acc. No. 019216	21	15	17	18	16	21	25	17	28	27	23	32	26	265
Acc. No. 000004	22	25	23	26	25	23	18	25	24	18	26	20	20	273
IN-97	23	23	29	31	18	25	33	20	15	15	30	16	28	283
Green Wonder	24	18	15	17	23	27	20	18	32	30	31	31	34	296
Acc. No. 019211	25	22	24	23	19	19	21	31	27	29	29	24	29	297
Pusa Green	26	21	33	20	30	22	15	26	23	21	35	29	33	308
Ikra IV	27	31	32	32	24	30	24	28	21	24	27	15	23	311
Acc. No. 019218	28	34	21	24	31	29	31	16	31	28	20	27	22	314
Acc. No. 019235	29	29	28	16	32	24	23	27	26	23	33	30	30	321
Sabzpari 2001	30	33	26	34	34	20	26	35	16	25	24	28	24	325
Acc. No. 019234	31	35	35	27	27	34	30	29	30	33	16	25	19	340
Acc. No. 019230	32	32	25	28	28	28	27	33	29	32	22	33	27	344
Acc. No. 000026-10496	33	27	34	35	29	32	34	22	33	31	28	23	31	359
Pusa Sawani	34	30	31	33	33	35	35	30	34	34	17	34	25	371
IN-89	35	28	30	29	35	33	32	32	35	35	32	35	35	391
Acc. No. 019225	36	36	37	36	38	36	36	37	36	36	38	37	38	441
Acc. No. 015380-10934	37	38	39	37	37	39	37	36	37	37	36	36	36	445
Acc. No. 019233	38	39	38	38	39	38	38	38	38	38	37	38	37	456
Acc. No. 015382	39	37	36	39	36	37	39	39	39	39	39	39	39	458

RL: root length; SL: shoot length; GP: germination percentage; RRL: relative root length; RSL: relative shoot length; RGP: relative germination percentage; RNa⁺: relative Na⁺; RK⁺: relative K⁺; RK⁺/Na⁺: relative K⁺/Na⁺. The rankings were based on evaluation of each parameter with number 1 being the most tolerant

2.2 Response of okra genotypes to NaCl salinity during plant ontogeny

Based on the overall pooled ranking of the genotypes for salinity tolerance at the seedling stage, ten genotypes from both extremes of salinity tolerance were selected (Table 2). Selected genotypes were grown to maturity in earthen pots of 30 cm diameter lined with a polyethylene sheet and filled with gravel soil (electrical conductivity of saturation extract (EC_e)=1.6 dS/m, saturation=30.65%). Three NaCl concentrations consisting of 0 (control), 60, and 80 mmol/L were created in the growth medium, keeping in view the EC_e , pH, and saturation percentage of the soil by adding the appropriate amount of salt in half strength Hoagland's solution following US Salinity Laboratory Staff (1954). The experiment was comprised of three replicates for each treatment. Nutrient solutions were applied every 3 d and continued until plant maturation was completed. The experiment was conducted under natural environmental conditions during the summer 2008 and spring 2009. Recommended plant protection practices and cultural practices were adopted until maturity, such as irrigation, weeding, and hoeing. Data were collected at four growth stages viz. seedling stage, bud stage, flowering stage, and maturity for various biochemical/physiological parameters including Na^+ and K^+ concentrations, plant height, number of branches, days to first flower, pods per plant, pod weight, pod length, pod girth, and yield per plant. Data for both absolute and relative values were collected from the ten genotypes for Na^+ and K^+ concentrations and K^+/Na^+ ratio at all the four growth stages, and the remaining parameters were measured only at the maturity stage. The ANOVA, Pearson's correlation, and heredity estimates were calculated using SPSS 12, MVSP 3.1, and Microsoft Excel, respectively.

3 Results and discussion

3.1 Genetic variability for NaCl tolerance at the seedling stage in okra

The box-whisker analysis provided useful information for the comparison of genotypes and showed differential responses of genotypes. Germination percentage, root and shoot length, and accu-

mulation of Na^+ and K^+ , and K^+/Na^+ ratio at the seedling stage under different concentrations of NaCl were considered in the analysis. Increasing salt concentrations significantly affected the germination percentage, root length, and shoot length of genotypes to a varying degree. The ranking of the genotypes was done on the basis of their performance for each trait and under each NaCl concentration, separately. The genotypes were ranked as 1–39 with '1' as the most tolerant and '39' as susceptible based upon their abilities to withstand saline conditions. The ranks under each NaCl concentration were pooled to calculate an overall ranking of the genotypes on the basis of the traits in this study. Ranks depict the performance of genotypes under all salt concentrations.

Salinity increases osmotic potential of the soil solution and causes seeds to use more energy to absorb water from the soil, which reduces germination (Kafi and Goldani, 2001; Jamil and Rha, 2004). Acc. No. 019217 (71.42%), Parbhani Kranti (65.13%), Chinese Red (58.67%) and Acc. No. 015382 (15.50%) were ranked as 1, 2, 3, and 39, respectively, on the basis of germination percentage (Table 1). Acc. No. 019217 consistently showed the highest germination in increasing NaCl concentrations, and maintained 51.67% germination in 120 mmol/L NaCl, with a mean of 68.28% germination across all of the NaCl concentrations. Similarly the genotypes Parbhani Kranti, Ikra III, Chinese Red, Acc. No. 019231, Ikra I, Acc. No. 019221, Acc. No. 019236, Acc. No. 019223, Punjab Selection, Acc. No. 000010-10237, IN-1048, Acc. No. 015371, and Acc. No. 019232 maintained mean germination percentages ranging from 50.20% to 62.67% in NaCl concentrations. The majority of accessions failed to germinate at 100 and 120 mmol/L NaCl. The differences in the behavior of genotypes could be attributed to the differences in gene frequencies and their interaction with the environment (Maas, 1986). A significant negative correlation was observed between percentage of germination and increase in salt concentration (Table 3). Acc. Nos. 019232 (5.41 cm), 019221 (4.46 cm), and 019236 (3.39 cm) were the top three genotypes on the basis of relative root length. With reference to relative shoot length, Acc. No. 019232 (10.26 cm), Punjab Selection (9.50 cm), and Parbhani Kranti (8.16 cm) secured the top three ranks, respectively. The three-week-old seedlings showed

Table 2 Physiological performance of ten selected okra genotypes at different salt concentrations during plant ontogeny

Genotype/stage	NaCl (mmol/L)	Na ⁺ (mmol/L)	K ⁺ (mmol/L)	K ⁺ /Na ⁺	Genotype/stage	NaCl (mmol/L)	Na ⁺ (mmol/L)	K ⁺ (mmol/L)	K ⁺ /Na ⁺
Ikra III					Acc. No. 015371				
Seedling stage	0	3.31	15.73	4.75	Seedling stage	0	4.44	34.49	7.79
	60	5.59	10.47	1.88	60	6.99	26.08	2.40	
	80	8.52	8.19	0.96	80	16.29	17.05	1.05	
Bud stage	0	7.06	40.03	5.67	Bud stage	0	2.13	43.35	20.76
	60	12.60	30.19	2.40	60	10.86	32.73	4.72	
	80	18.68	25.75	1.38	80	10.90	18.84	1.73	
Flowering stage	0	1.95	30.68	16.36	Flowering stage	0	1.17	22.26	19.15
	60	3.57	12.55	3.51	60	3.62	12.43	3.44	
	80	10.53	9.93	0.95	80	4.48	4.18	0.94	
Maturity stage	0	1.31	22.79	17.37	Maturity stage	0	1.49	13.49	9.41
	60	2.99	13.67	4.66	60	3.07	10.75	3.54	
	80	4.26	8.13	1.91	80	8.32	9.50	1.14	
Acc. No. 019221					Acc. No. 019233				
Seedling stage	0	2.89	32.70	11.35	Seedling stage	0	2.86	31.41	10.99
	60	6.46	23.22	3.61	60	18.50	12.20	0.66	
	80	14.34	17.21	1.20	80	31.83	4.88	0.15	
Bud stage	0	6.87	41.73	6.08	Bud stage	0	2.61	27.92	10.83
	60	12.91	32.34	2.51	60	15.03	13.71	0.92	
	80	20.84	22.33	1.07	80	35.45	8.74	0.25	
Flowering stage	0	1.90	17.97	9.52	Flowering stage	0	4.30	36.67	8.54
	60	4.29	12.53	2.92	60	10.45	8.25	0.79	
	80	5.64	11.39	2.02	80	15.80	5.31	0.34	
Maturity stage	0	3.00	14.52	4.88	Maturity stage	0	1.44	18.46	13.01
	60	4.17	11.34	2.72	60	5.08	6.65	1.32	
	80	5.68	8.88	1.57	80	7.99	4.06	0.51	
Acc. No. 019236					Acc. No. 000010-10237				
Seedling stage	0	3.72	34.43	9.29	Seedling stage	0	6.06	30.66	5.07
	60	7.65	23.16	3.03	60	10.12	20.16	1.85	
	80	10.59	12.45	1.18	80	18.98	15.38	0.81	
Bud stage	0	4.61	47.68	10.41	Bud stage	0	5.51	34.74	6.34
	60	10.84	25.26	2.33	60	10.90	27.23	2.70	
	80	15.04	19.65	1.31	80	13.89	20.35	1.46	
Flowering stage	0	2.43	25.22	10.59	Flowering stage	0	1.49	27.46	19.27
	60	3.81	15.43	4.07	60	6.44	16.86	2.62	
	80	6.01	8.85	1.48	80	14.45	6.85	0.47	
Maturity stage	0	2.10	27.67	13.44	Maturity stage	0	1.75	11.23	6.47
	60	4.78	18.74	3.93	60	2.86	13.90	4.91	
	80	8.33	10.90	1.32	80	5.75	9.83	1.72	
Acc. No. 019232					Chinese Red				
Seedling stage	0	2.83	27.25	9.70	Seedling stage	0	7.45	41.21	5.53
	60	6.52	21.45	3.29	60	13.55	34.16	2.53	
	80	12.83	11.92	0.93	80	24.56	26.82	1.09	
Bud stage	0	3.64	52.15	14.45	Bud stage	0	10.61	49.40	4.66
	60	8.13	35.57	4.42	60	15.16	38.94	2.58	
	80	12.98	24.24	1.87	80	31.94	30.58	0.96	
Flowering stage	0	2.48	29.15	11.79	Flowering stage	0	2.60	22.39	8.72
	60	4.11	11.35	2.77	60	3.95	9.37	2.39	
	80	7.22	7.53	1.05	80	6.05	7.06	1.17	
Maturity stage	0	1.51	13.46	9.00	Maturity stage	0	1.87	19.99	10.05
	60	3.64	7.29	2.01	60	2.85	8.68	3.06	
	80	6.78	4.95	0.73	80	3.69	7.60	2.09	
Acc. No. 015380-10934					Ikra I				
Seedling stage	0	1.55	45.73	29.55	Seedling stage	0	7.38	39.64	5.37
	60	15.46	14.56	0.94	60	11.27	32.11	2.85	
	80	29.01	9.03	0.31	80	18.63	21.91	1.18	
Bud stage	0	3.69	37.90	10.36	Bud stage	0	9.21	68.19	7.21
	60	16.50	21.49	1.30	60	16.78	30.01	1.79	
	80	39.50	16.57	0.42	80	20.77	22.76	1.10	
Flowering stage	0	1.02	28.19	28.58	Flowering stage	0	5.06	26.39	5.22
	60	6.41	6.25	0.98	60	7.32	17.11	2.34	
	80	13.94	4.25	0.31	80	9.53	12.47	1.31	
Maturity stage	0	2.82	15.18	5.40	Maturity stage	0	1.90	13.24	7.05
	60	7.31	6.09	0.84	60	4.23	10.78	2.57	
	80	12.47	6.75	0.54	80	5.89	7.78	1.33	

Table 3 Correlation coefficients for different seedling traits

Parameter	NaCl (mmol/L)	Correlation coefficient					
		GP	RL	SL	Na ⁺	K ⁺	K ⁺ /Na ⁺
GP	0	1	0.160	0.327*	0.327*	-0.067	-0.486**
	40	1	0.641**	0.688**	-0.756**	0.643**	0.704**
	60	1	0.788**	0.875**	-0.829**	0.736**	0.820**
	80	1	0.793**	0.845**	-0.843**	0.739**	0.836**
	100	1	0.924**	0.932**	0.453**	0.885**	0.918**
	120	1	0.941**	0.930**	0.676**	0.907**	0.926**
	Mean	1	0.792**	0.857**	-0.312	0.714**	-0.647**
RL	0		1	-0.210	0.268	0.234	-0.023
	40		1	0.560**	-0.742**	0.727**	0.808**
	60		1	0.776**	-0.725**	0.803**	0.798**
	80		1	0.857**	-0.738**	0.818**	0.814**
	100		1	0.937**	0.418**	0.906**	0.926**
	120		1	0.950**	0.725**	0.951**	0.950**
	Mean		1	0.792**	-0.106	0.825**	-0.410**
SL	0			1	-0.201	-0.089	0.063
	40			1	-0.766**	0.646**	0.741**
	60			1	-0.866**	0.786**	0.842**
	80			1	-0.807**	0.790**	0.827**
	100			1	0.558**	0.933**	0.923**
	120			1	0.798**	0.955**	0.958**
	Mean			1	-0.189	0.792**	-0.564**
Na ⁺	0				1	0.067	-0.642**
	40				1	-0.751**	-0.894**
	60				1	-0.720**	-0.895**
	80				1	-0.765**	-0.872**
	100				1	0.614**	0.318*
	120				1	0.801**	0.677**
	Mean				1	0.153	0.312
K ⁺	0					1	0.254
	40					1	0.897**
	60					1	0.867**
	80					1	0.856**
	100					1	0.919**
	120					1	0.967**
	Mean					1	-0.414**

GP: germination percentage; RL: root length; SL: shoot length. ‘-’ shows negative correlation. * Significant correlation ($P < 0.05$); ** Highly significant correlation ($P < 0.01$)

no consistent relationships between root and shoot length in saline or non-saline conditions. The genotypes, five NaCl concentrations and their interactions were significantly different ($P \leq 0.01$) from each other for germination percentage and root and shoot length (Table 4). Thus, the different genotypes responded differently under increasing NaCl concentrations. The depressed growth of genotypes may be ascribed to the toxic effect of NaCl and low water potential in the rooting medium (Ayers, 1953).

Leaf Na⁺ ion uptake increased with an increase in external NaCl concentrations in all genotypes, but the difference among the genotypes was not significant ($P > 0.05$) for Na⁺ accumulation (Table 4). The interaction between the genotypes and NaCl concentrations was significant, indicating that the genotypes responded differently to increasing NaCl concentrations. A minimum Na⁺ accumulation was observed in Acc. No. 000010-10237 (47.44 mmol/L) and a maximum in Acc. No. 015382 (231.81 mmol/L). On

the basis of relative accumulation of Na^+ , Acc. No. 000010-10237, 019232, and 019231 were classified as tolerant genotypes. The K^+ concentration was observed to be inversely proportional to the increase in external NaCl concentration. The interaction between the genotypes and NaCl concentrations was significant ($P \leq 0.01$) (Table 4), indicating that the accumulation of K^+ affects genotypes variably in the increasing NaCl concentrations. Acc. No. 019236, Ikra III, and Acc. No. 019232 maintained relatively maximum K^+ in descending order. The values for K^+ accumulation ranged from 10.40 to 85.95 mmol/L; Acc. No. 015382 accumulated minimum K^+ . Under salt stress, plants maintain high concentrations of K^+ and low concentrations of Na^+ in the cytosol. Plants regulate the expressions and activities of K^+ and Na^+ transporters and H^+ pumps that generate the driving force for ion transport (Zhu, 2003). A greater degree of salt tolerance in plants was found to be associated with a more efficient system for selective uptake of K^+ over Na^+ (Neill *et al.*, 2002). The selective uptake of K^+ in contrast to Na^+ is considered to be one of the most important physiological mechanisms contributing to salt tolerance in many plant species (Poustini and Siosemardeh, 2004).

An increase in external NaCl concentration significantly affected the leaf K^+/Na^+ uptake ratio within all genotypes, but the difference among the genotypes and replicates was not significant ($P > 0.05$) (Table 4). The interaction between the five genotypes and NaCl concentrations differed significantly ($P \leq 0.01$) from each other. Increasing salinity adversely affected K^+/Na^+ ratio to a different extent in different genotypes. The K^+/Na^+ uptake ratio varied from 0.05 to 46.07, indicating an inverse proportion with increasing NaCl concentration. On the basis of K^+/Na^+ ratio, Ikra III, Acc. No. 015371, and Acc. No. 000010-10237 were ranked as 1, 2, and 3, respectively (Table 1).

Correlation coefficients among the traits indicated that germination percentage has significant positive correlation with root length, shoot length, K^+ concentration, and K^+/Na^+ at all concentrations while it has a negative correlation with Na^+ concentration at 40, 60, and 80 mmol/L and positive correlation at 100 and 120 mmol/L. A similar correlation was observed for root and shoot length. Na^+ accumulation showed a significant negative correlation with K^+ concentration and K^+/Na^+ at all NaCl concentrations except at 100 and 120 mmol/L. A significant positive correlation was also found for K^+ concentration and K^+/Na^+ (Table 3).

A Euclidian distance-based phenogram assigned 39 okra genotypes into two main clusters. All the salt-tolerant genotypes clustered separately from the more susceptible genotypes. Each cluster showed particular morphological characteristics (Fig. 1 and Table 5).

Based on the overall pooled ranking of the genotypes for salinity tolerance at the seedling stage, Acc. No. 019232, Acc. No. 000010-10237, Chinese Red, Ikra III, and Acc. No. 015371 were selected as the most tolerant. Ikra I, Acc. No. 019236, and Acc. No. 019221 were selected as relatively tolerant, and the two genotypes Acc. No. 015380-10934 and Acc. No. 019233 as non-tolerant (Table 2).

3.2 Performance of okra genotypes under saline conditions during plant ontogeny

Salinity affects plant growth during all developmental stages. Therefore the crop responses to salinity may vary during the plant ontogeny (Maas and Hoffman, 1977; Shannon, 1985; Azhar and McNeilly, 1989; Maas and Poss, 1989). For the selection of salt-tolerant breeding plants, information about the degree of salt tolerance at all plant growth stages in a crop species is important. Without this

Table 4 Mean squares for different physiological and morphological traits of 39 okra genotypes

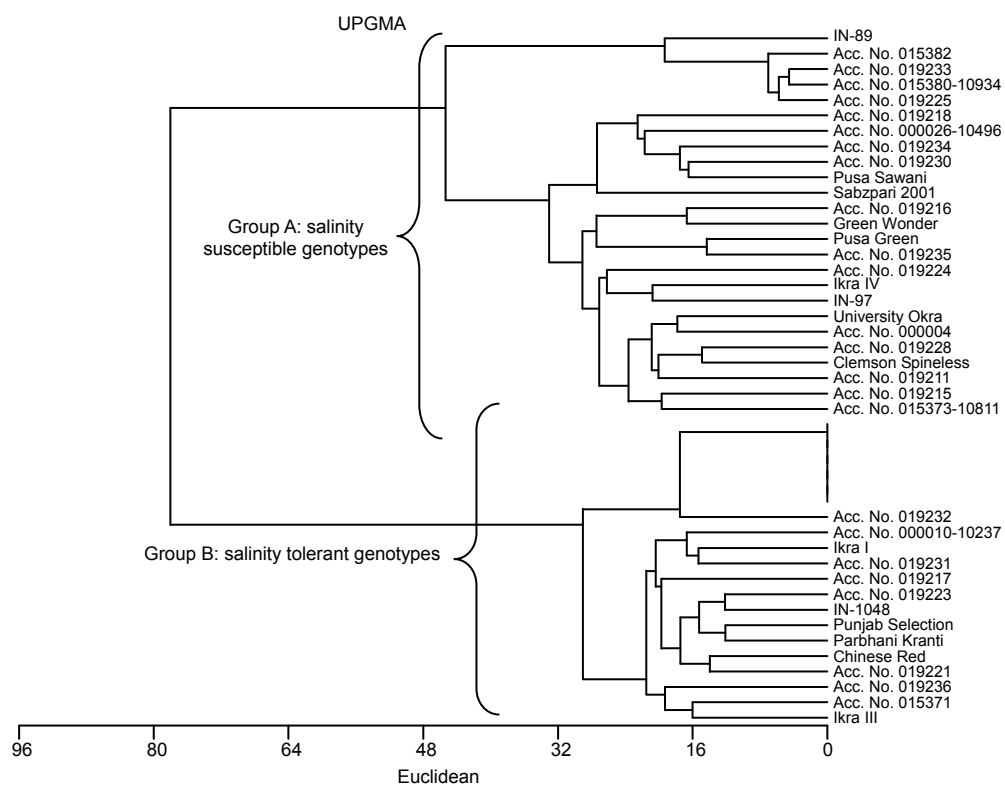
Source of variation	df	Mean square for physio-morphological traits					
		GP	RL	SL	Na^+	K^+	K^+/Na^+
Genotypes (<i>G</i>)	38	14508.436**	87.023**	145.417**	4767.340 ^{NS}	2058.786**	40.192 ^{NS}
NaCl concentration (<i>c</i>)	5	188320.735**	1302.305**	10132.259**	167423.024**	40750.180**	3840.209**
Replications	2	890.363**	0.162 ^{NS}	0.416 ^{NS}	22.544**	25.075**	0.272 ^{NS}
<i>G</i> × <i>c</i>	190	892.907**	3.807**	20.749**	5581.485**	165.076**	48.983**
Within+residual	1870	18.232	0.167	0.676	1.815	0.915	0.466

df: degree of freedom; GP: percentage of germination percentage; RL: root length; SL: shoot length. * Significant at $P \leq 0.05$; ** Significant at $P \leq 0.01$; ^{NS} Non-significant ($P > 0.05$)

Table 5 Heredity estimates for different morphological traits at maturity during spring and summer under control and saline conditions

Trait	Season	GV		PV		GCV		PCV		H	
		Control	80 mmol/L NaCl	Control	80 mmol/L NaCl	Control	80 mmol/L NaCl	Control	80 mmol/L NaCl	Control	80 mmol/L NaCl
PH	Spring	123.47	69.10	123.53	69.21	23.88	31.96	23.88	31.99	0.99	0.99
	Summer	205.30	195.04	214.67	195.81	15.11	29.78	15.45	29.84	0.95	0.99
NB	Spring	0.69	0.41	0.73	0.43	22.12	36.72	22.75	37.64	0.94	0.95
	Summer	0.42	0.19	0.54	0.21	17.32	31.29	19.60	32.89	0.78	0.90
DF	Spring	16.40	9.63	16.84	9.77	7.92	4.97	8.02	5.00	0.97	0.98
	Summer	41.82	49.50	43.85	50.68	14.56	11.50	14.91	11.64	0.95	0.97
P/Pl	Spring	9.87	3.95	10.12	3.98	21.92	37.92	22.20	38.06	0.97	0.99
	Summer	8.52	11.49	8.95	12.10	14.07	32.80	14.42	33.66	0.95	0.94
PW	Spring	0.39	1.16	0.46	1.26	8.12	22.60	8.83	23.54	0.84	0.92
	Summer	1.25	1.01	1.46	1.15	20.11	33.15	21.69	35.38	0.86	0.87
PL	Spring	0.43	1.58	0.51	1.61	6.99	26.26	7.57	26.45	0.85	0.98
	Summer	0.27	0.54	0.66	0.68	6.67	14.30	10.40	16.05	0.41	0.79
PG	Spring	0.005	0.01	0.012	0.01	5.37	10.00	8.30	10.29	0.41	0.94
	Summer	0.006	0.0019	0.0092	0.017	6.55	3.82	7.60	11.53	0.74	0.10
Y	Spring	522.39	164.16	523.04	165.32	21.40	49.82	21.41	50.00	0.99	0.99
	Summer	393.84	44.81	395.21	181.05	18.31	21.10	18.34	42.41	0.99	0.24

GV: genotypic variance; PV: phenotypic variance; GCV: genotypic coefficient of variance; PCV: phenotypic coefficient of variance; H: heterosis; PH: plant height; NB: number of branches; DF: days to 50% flowering; P/Pl: pods per plant; PW: pod width; PL: pod length; PG: pod girth; Y: pod yield

**Fig. 1** Phenogram showing variability based on response to salinity, Euclidean distances, and unweighted pair group method with arithmetic mean (UPGMA) clustering

information, selection at a particular stage may produce individuals that exhibit less tolerance to salinity at the next growth stage. Response to salinity is thought to be controlled by a number of genes that may be stage-specific (Foolad and Jones, 1991).

The genotypes in this study responded differently in salt concentrations at different growth stages for the accumulation of Na^+ and K^+ and K^+/Na^+ ratio in leaves. The concentration of Na^+ was increased while the K^+ accumulation and K^+/Na^+ ratio decreased in all the genotypes with increased salinity at all growth stages. However, in the non-tolerant genotypes, Acc. Nos. 019233 and 015380-10934, the Na^+ concentration was greater than that in the tolerant genotypes at all the growth stages under stress. The tolerant genotypes accumulated low Na^+ and maintained higher K^+ and K^+/Na^+ ratio in their leaves. Maximum Na^+ accumulation was observed at the bud stage in all genotypes at all salt concentrations (Table 2). The increased uptake may be due to increased diffusion through damaged membranes and restricted outward active exclusion of Na^+ . This suggests that the okra genotypes used a partial exclusion mechanism for tolerating the toxic ions present in the growth medium (Maas and Nieman, 1978; Greenway and Munns, 1980; Salisbury and Ross, 1992; Shaaban *et al.*, 2004; Ahmadi *et al.*, 2009). It was observed that the accumulation of Na^+ in the cell sap was lower in magnitude than the accumulation by the same genotypes in the screening experiment in sand culture.

The high K^+ concentration at higher salinity level is a good criterion for selecting salt-tolerant genotypes (Flowers *et al.*, 1977). Maintenance of higher K^+/Na^+ ratio in salt-tolerant genotypes may be one of the reasons for their superior growth under saline conditions (Ashraf and Ahmad, 2000). High levels of K^+ in young leaves are associated with salt tolerance in many plant species (Gorham, 1993; Storey *et al.*, 1993; Khatun and Flowers, 1995). Maintenance of higher K^+/Na^+ ratio in salt-tolerant lines may be attributed to K^+/Na^+ exchange across the plasmalemma of root cortex cells and selective uptake of K^+ (Jeschke and Wolf, 1988; Dashti *et al.*, 2009). The sensitive genotypes had K^+/Na^+ ratio less than 1 at higher salinity levels, and the tolerant had K^+/Na^+ ratio more than 1, showing their tolerance at different stages of growth consistently.

Plant height and a number of branch lengths were reduced in the okra genotypes with increased NaCl concentration in growth medium. However, the

reduction level was low in the tolerant genotypes (Acc. No. 019232, Acc. No. 000010-10237, and Chinese Red) and more in the two sensitive genotypes (Acc. No. 019233 and Ikra I) in both summer and spring plantings (Table 5). Due to delayed germination, delayed flowering was observed in non-tolerant okra genotypes under saline conditions. The tolerant genotypes started flowering earlier than the sensitive genotypes. Salinity at lower levels is known to delay germination, and at high levels can even reduce germination percentages (Kuhad and Sheoran, 1987; Jamil and Rha, 2004). The number of pods per plant, pod weight, pod length, and pod girth were significantly reduced by salinity but there was consistency in the tolerance level of the selected genotypes (Table 5). The effects of salinity and genotypic differences were most apparent for the marketable yield of okra genotypes. There was a significant decrease in tender green pod yield of non-tolerant genotypes, but the tolerant genotypes had relatively less reduction in pod yield (Table 5). The heritability estimates indicated a high degree of inheritance for all the morphological traits especially during spring (Table 5); moreover, correlation estimates indicated that fresh green pod yield had significant positive correlation with plant height, pods per plant, pod length, pod width, and pod girth at 80 mmol/L NaCl during both spring and summer (Table 6). These results suggest that for the improvement of yield-related traits, selections would be more effective at 80 mmol/L NaCl during spring.

The assessments of the tolerant and non-tolerant genotypes for physiological parameters at four growth stages and eight morphological traits at maturity suggest that there was consistency in the salinity tolerance of the selected genotypes until maturity. The salt-tolerant plants could be selected at any stage, if they have a consistent pattern of salt tolerance at all growth stages. However, it becomes more difficult for otherwise situation in which the selection is made only at some particular growth stage (Blum, 1985). The selected okra genotypes in this study showed consistency in their tolerance, but no single accession/genotype was found to be consistently superior across the four growth stages. However, the tolerant and non-tolerant genotypes at seedling stage did not change their status during the ontogeny of the whole plant, suggesting that the screening at seedling stage would provide a suitable basis for initial selection of a large number of germplasm entries or breeding populations for salt tolerance.

Table 6 Correlation coefficients for different morphological traits at maturity during spring and summer

Trait	Season	NaCl (mmol/L)	Correlation coefficient							
			PH	NB	DF	P/Pl	PW	PL	PG	Y
PH	Spring	0	1	-0.240	-0.601	-0.264	0.562	-0.132	0.136	-0.062
		60	1	0.278	-0.743**	-0.043	0.891**	0.447	0.220	0.484
		80	1	0.616*	-0.695*	0.480	0.883**	0.823**	0.761**	0.662*
	Summer	0	1	-0.009	0.505	-0.377	0.079	0.263	0.449	-0.228
		60	1	0.288	-0.632*	0.375	0.521	0.773**	0.833**	0.649*
		80	1	0.414	-0.394	0.457	0.511	0.899**	0.921**	0.630*
NB	Spring	0		1	-0.219	0.284	-0.458	0.088	0.238	0.104
		60		1	-0.360	0.252	0.330	0.669*	0.785**	0.369
		80		1	-0.284	0.481	0.571	0.525	0.733*	0.478
	Summer	0		1	0.220	0.724*	-0.230	0.554	0.496	0.261
		60		1	-0.322	0.769**	-0.156	0.289	0.034	0.236
		80		1	-0.309	0.774**	-0.045	0.578	0.403	0.468
DF	Spring	0			1	0.097	-0.370	-0.049	-0.093	-0.034
		60			1	0.447	-0.526	-0.224	-0.085	0.012
		80			1	-0.184	-0.704*	-0.823**	-0.605*	-0.377
	Summer	0			1	-0.145	0.021	-0.089	0.134	-0.059
		60			1	-0.412	-0.432	-0.323	-0.411	-0.551
		80			1	-0.673*	-0.428	-0.547	-0.682*	-0.728*
P/Pl	Spring	0				1	-0.284	-0.104	-0.397	0.932**
		60				1	0.195	0.501	0.507	0.823**
		80				1	0.663*	0.219	0.723*	0.947**
	Summer	0				1	-0.581	0.567	0.174	0.097
		60				1	-0.147	0.307	0.049	0.388
		80				1	0.047	0.665*	0.566	0.716*
PW	Spring	0					1	0.089	-0.357	0.079
		60					1	0.613*	0.449	0.714*
		80					1	0.850**	0.841**	0.843**
	Summer	0					1	-0.325	0.385	0.747**
		60					1	0.289	0.841**	0.838**
		80					1	0.383	0.614*	0.712*
PL	Spring	0						1	0.283	-0.042
		60						1	0.915**	0.714*
		80						1	0.654*	0.469
	Summer	0						1	0.639*	0.026
		60						1	0.606*	0.394
		80						1	0.891**	0.665*
PG	Spring	0							1	-0.529
		60							1	0.615*
		80							1	0.755**
	Summer	0							1	0.556
		60							1	0.773**
		80							1	0.766**

PH: plant height; NB: number of branches; DF: days to 50% flowering; P/Pl: pods per plant; PW: pod width; PL: pod length; PG: pod girth; Y: pod yield. '-' sign shows negative correlation. * Significant correlation ($P < 0.05$); ** Highly significant correlation ($P < 0.01$)

References

- Adeniji, O.T., Peter, J.M., 2005. Stepwise Regression Analysis of Pod and Seed Yield Characters in Segregating F2 Population of West African Okra (*Abelmoschus caillei*). Proc. 30th Ann. Conf. Gen. Soc., Nig., p.250-258.
- Ahmadi, A., Emam, Y., Pessarikli, M., 2009. Response of various cultivars of wheat and maize to salinity stress. *J. Food Agric. Environ.*, **7**(1):123-128.
- Akbar, M., Yabuno, T., 1974. Breeding for saline resistant varieties of rice. I. Comparative performance of some rice varieties to salinity during early development stages. *Jpn. J. Breed.*, **24**:176-181.
- Anonymous, 2008. Fruits, Vegetable and Condiments Statistics 2006-07. MINFAL, Islamabad, Pakistan.
- Ashraf, M., Fatima, H., 1994. Intraspecific variation for salt tolerance in linseed (*Linum usitatissimum* L.). *J. Agron. Crop Sci.*, **173**(3-4):193-203. [doi:10.1111/j.1439-037X.1994.tb00554.x]
- Ashraf, M., Ahmad, S., 2000. Influence of sodium chloride on ion accumulation, yield components and fibre characteristics in salt-tolerant and salt-sensitive lines of cotton (*Gossypium hirsutum* L.). *Field Crops Res.*, **66**(2):115-127. [doi:10.1016/S0378-4290(00)00064-2]
- Ashraf, M., Arfan, M., Ahmad, A., 2003. Salt tolerance in okra: ion relations and gas exchange characteristics. *J. Plant Nutr.*, **26**(1):63-79. [doi:10.1081/PLN-120016497]
- Ayers, A.D., 1953. Germination and emergence of several varieties of barley in salinized soil cultures. *Agron. J.*, **45**(2): 68-71. [doi:10.2134/agronj1953.00021962004500020008x]
- Azhar, F.M., McNeilly, T., 1989. The response of four sorghum accessions/cultivars to salinity during whole plant development. *J. Agron. Crop Sci.*, **163**(1):33-43. [doi:10.1111/j.1439-037X.1989.tb00734.x]
- Blum, A., 1985. Breeding crop varieties for stress environments. *Crit. Rev. Plant Sci.*, **2**(3):199-238. [doi:10.1080/07352688509382196]
- Colmer, T.D., Munns, R., Flowers, T.J., 2005. Improving salt tolerance of wheat and barley: future prospects. *Aust. J. Exp. Agric.*, **45**(11):1425-1443. [doi:10.1071/EA04162]
- Cramer, G.R., 2003. Differential effects of salinity on leaf elongation kinetics of three grass species. *Plant Soil*, **253**(1):233-244. [doi:10.1023/A:1024527401033]
- Dashti, A., Khan, A.A., Collins, J.C., 2009. Effects of salinity on growth, ionic relations and solute content of *Sorghum bicolor* (L.) Monench. *J. Plant Nutr.*, **32**(7):1219-1236. [doi:10.1080/01904160902945333]
- Flowers, T.J., Yeo, A.R., 1995. Breeding for salinity resistance in crop plants: where next. *Aust. J. Plant Physiol.*, **22**(6): 875-884. [doi:10.1071/PP9950875]
- Flowers, T.J., Troke, P.F., Yeo, A.R., 1977. The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.*, **28**(1):89-121. [doi:10.1146/annurev.pp.28.060177.000513]
- Foolad, M.R., Jones, R.A., 1991. Genetic analysis of salt tolerance during germination in *Lycopersicon*. *Theor. Appl. Genet.*, **81**:321-326.
- Gorham, J., 1993. Genetics and Physiology of Enhanced K/Na Discrimination. In: Randall, P.J., Delhaize, E., Richards, R.A., Munns, R. (Eds.), Genetic Aspects of Plant Mineral Nutrition. Kluwer Acad. Publ., Dordrecht, the Netherlands, p.151-158. [doi:10.1007/978-94-011-1650-3_19]
- Greenway, H., Munns, R., 1980. Mechanisms of salt tolerance in non-halophytes. *Annu. Rev. Plant Physiol.*, **31**(1): 149-190. [doi:10.1146/annurev.pp.31.060180.001053]
- Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil. *Calif. Agric. Exp. Stat. Circ.*, **347**:1-32.
- Humphreys, M.O., 1989. Assessment of perennial ryegrass (*Lolium perenne* L.) for breeding. II. Components of winter hardiness. *Euphytica*, **41**(1-2):99-106. [doi:10.1007/BF00022418]
- Hunshal, C.S., Viswanath, D.P., Chimmad, V.P., Gali, S.K., 1991. Performance of groundnut genotypes under saline water irrigation. *J. Maharashtra Agric. Univ.*, **16**:116-117.
- Jamil, M., Rha, E.S., 2004. The effect of salinity (NaCl) on the germination and seedling of sugar beet (*Beta vulgaris* L.) and cabbage (*Brassica oleracea* L.). *Korean J. Plant Res.*, **7**:226-232.
- Janila, P., Rao, T.N., Kumar, A.A., 1999. Germination and early seedling growth of groundnut (*Arachis hypogaea* L.) varieties under salt stress. *Annals Agric. Res.*, **20**:180-182.
- Jeschke, W.D., Wolf, O., 1988. External potassium supply is not required for root growth in saline conditions: experiments with *Ricinus communis* L. grown in a reciprocal split-room system. *J. Expt. Bot.*, **39**(9):1149-1167. [doi:10.1093/jxb/39.9.1149]
- Kafi, M., Goldani, M., 2001. Effect of water potential and type of osmoticum on seed germination of three crop species of wheat, sugarbeet, and chickpea. *Agric. Sci. Tech.*, **15**:121-133.
- Khan, A.A., McNeilly, T., Azhar, F.M., 2001. Stress tolerance in crop plants. *Int. J. Agric. Biol.*, **3**(2):250-255.
- Khan, A.A., Rao, S.A., McNeilly, T., 2003. Assessment of salinity tolerance based upon seedling root growth response functions in maize (*Zea mays* L.). *Euphytica*, **131**(1):81-89. [doi:10.1023/A:1023054706489]
- Khatun, S., Flowers, T.J., 1995. Effect of salinity on seed set in rice. *Plant Cell Environ.*, **18**(1):61-87. [doi:10.1111/j.1365-3040.1995.tb00544.x]
- Kuhad, M.S., Sheoran, I.S., 1987. Influence of simulated drought and salt stress at iso-osmotic levels on seedling growth of pigeonpea genotypes. *Int. Pigeonpea Newsl.*, **6**:48-50.
- Maas, E.V., 1986. Salt tolerance of plants. *Appl. Agric. Res.*, **1**:12-26.
- Maas, E.V., Hoffman, G.J., 1977. Crop salt tolerance-current assessment. *J. Irrig. Drain. Div. Civ. Eng.*, **103**(2): 115-134.
- Maas, E.V., Nieman, R.H., 1978. Physiology of Plant Tolerance to Salinity. In: Jung, G.A. (Ed.), Crop Tolerance to Suboptimal Land Conditions. Amer. Soc. Agron. Spec. Publ., Madison, WI, Chapter, 13, p.277-299.
- Maas, E.V., Poss, J.A., 1989. Salt sensitivity of cowpea at various growth stages. *Irrig. Sci.*, **10**(4):313-320. [doi:10.1007/BF00257496]

- Munns, R., James, R.A., 2003. Screening methods for salinity tolerance: a case study of with tetraploid wheat. *Plant Soil*, **253**(1):201-218. [doi:10.1023/A:1024553303144]
- Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, **59**(1):651-681. [doi:10.1146/annurev.arplant.59.032607.092911]
- Nautiyal, P.C., Ravindra, V., Joshi, Y.C., 1989. Germination and early seedling growth of some groundnut (*Arachis hypogaea* L.) cultivars under salt stress. *Indian J. Plant Physiol.*, **32**:251-253.
- Neill, S., Desikan, R., Hancock, J., 2002. Hydrogen peroxide signalling. *Curr. Opin. Plant Biol.*, **5**(5):388-395. [doi:10.1016/S1369-5266(02)00282-0]
- Oyelade, O.J., Ade-Omowaye, B.I.O., Adeomi, V.F., 2003. Influence of variety on protein, fat contents and some physical characteristics of okra seeds. *J. Food Eng.*, **57**(2): 111-114. [doi:10.1016/S0260-8774(02)00279-0]
- Poustini, K., Siosemardeh, A., 2004. Ion distribution in wheat cultivars in response to salinity stress. *Field Crops Res.*, **85**(2-3):125-133. [doi:10.1016/S0378-4290(03)00157-6]
- Rengasamy, P., 2002. Transient salinity and subsoil constraints to dryland farming in Australian sodic soils: an overview. *Aust. J. Exp. Agric.*, **42**(3):351-361. [doi:10.1071/EA01111]
- Salisbury, F.B., Ross, C.W., 1992. *Plant Physiology*, 4th Ed. Wadsworth Publishing Co., Belmont, CA.
- Shaaban, M.M., El-Fouly, M.M., El-Zanaty, El-Nour, A.A.A., Abdel-Maguid, A.A., 2004. Halophytes and foliar fertilization as a useful technique for growing processing tomatoes in the saline affected soils. *Pak. J. Biol. Sci.*, **7**(4):503-507. [doi:10.3923/pjbs.2004.503.507]
- Shannon, M.C., 1984. Breeding, Selection and Genetics of Salt Tolerance. *In: Staples, R.C., Toenniessen, G.A. (Eds.), Salinity Tolerance in Plants-Strategies for Crop Improvement*. John Wiley & Sons, New York, USA, p.231-254.
- Shannon, M.C., 1985. Principles and strategies in breeding for salt tolerance. *Plant Soil*, **89**(1-3):227-281. [doi:10.1007/BF02182244]
- Singh, A.L., Basu, M.S., Singh, N.B., 2004. *Mineral Disorders of Groundnut*. National Research Center for Groundnut (ICAR), Junagadh, India, p.85.
- Singh, B.G., Rao, P.V., Hiremath, S.M., 1989. Effect of salinity on germination and seedling growth in three varieties of groundnut (*Arachis hypogaea* L.). *J. Res. APAU*, **17**: 432-433.
- Storey, R., Gorham, J., Pitman, M.C., Hanson, M.G., Gage, D., 1993. Response of *Melanthera biflora* to salinity and water stress. *J. Expt. Bot.*, **44**(10):1551-1561. [doi:10.1093/jxb/44.10.1551]
- Tester, M., Davenport, R.J., 2003. Na⁺ transport and Na⁺ tolerance in higher plants. *Ann. Bot. (Lond)*, **91**(5): 503-527. [doi:10.1093/aob/mcg058]
- US Salinity Laboratory Staff, 1954. *Methods for Soil Characterization*. *In: Diagnosis and Improvement of Saline and Alkali Soils*. Agriculture Handbook 60. US Dept. of Agriculture, Washington, DC, p.83-147.
- Zhu, J.K., 2003. Regulation of ion homeostasis under salt stress. *Curr. Opin. Plant Biol.*, **6**(5):441-445. [doi:10.1016/S1369-5266(03)00085-2]