Heritability and gene effects for salinity tolerance in cucumber (*Cucumis sativus* L.) estimated by generation mean analysis

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ABSTRACT

Cucumber production is greatly reduced by high salinity. Our recent identification of cucumber geno-types with relative tolerance to salinity provides the potential for development of salt tolerant cultivars if the mode of inheritance for this trait is known. In this study, two cucumber parental lines, 11411S (P_1, salt tolerant), 11439S (P_2, salt sensitive) were crossed to study gene actions responsible for inheritance of salinity tolerance (TOL), relative leaf number (RLN14), area of second largest fully expanded leaf (LA) and vine length (VL) under saline growing conditions. The six populations denoted as P_1, P_2, F_1, B_1 ($F_1 \times P_1$), B_2 ($F_1 \times P_2$) and F_2 ($F_1 \times F_1$) were subjected to 80 mM NaCl stress in greenhouse pot experiments and data subjected to generation mean analysis. Epistatic gene effects on all the traits were not detected by A, B, C scaling test while joint scaling test showed the presence of non-allelic interactions for all the traits. TOL and RLN14 were predominantly under additive gene effect while inheritance LA was largely influenced by dominance and additive gene effects. Dominant gene effect significantly controlled the inheritance of VL. The narrow sense heritability for TOL, RLN14, VL and LA was 0.57, 0.26, 0.74 and 0.66, respectively. VL and LA registered significant positive heterobeltiosis. The presence of dominance gene effect and low heritability of photosynthesis enhancing trait, RLN14 makes it impractical to improve salinity through simple selection or pedigree breeding. Simultaneous selection for RLN14 and TOL in segregating population at advanced filial generations in this cross may be useful in developing cucumber varieties with increased salinity tolerance. Alternatively, intermating of superior segregants may be explored to concentrate the favorable genes for salt tolerance.

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1. Introduction

Salinity is one of the most important abiotic factors limiting growth and productivity of crops worldwide. About 7% (830 million ha) of the total global land is salt affected (FAO, 2009). It is estimated that 1/3 of world food production is obtained from irrigated agriculture unfortunately 20% (45 million ha) of the irrigated area is salt affected resulting in reduced yields (Negrão et al., 2011). The ever increasing world population and decreasing arable land due to factors such as land degradation poses a serious threat to food security (Davies et al., 2009).

Efforts to grow crops in salt affected soils as well as irrigating with saline waters have been employed through expensive technical reclamation methods (Davies et al., 2009). Other researches have shown that cucumber grafted on salt tolerant rootstocks had improved growth and yield (El-Shraiy et al., 2011). However,

the main limitation of this approach is high labor requirement and bulkiness. The most feasible alternative to growing crops under salinity prone environments is through genetic improvement (Tiwari et al., 2011). Unfortunately, salt tolerant cucumber is yet to be developed. Recently, Munns et al. (2012) developed tolerant wheat through conventional breeding. This provides hope for genetic improvement provides hope of salt tolerant cucumber if accurate selection and screening method is identified. Moreover, seeds of salt tolerant crop cultivars could be produced through conventional breeding can be readily availed to farmers unlike the transgenic materials, which suffer stringent legal restrictions.

Cucumber is a popular fruit vegetable consumed worldwide and it has moderate sensitivity to salinity meaning that growth and productivity is restricted by high saline conditions (Mather and Jink, 1982). Genotypic variation salt tolerance in cucumber has already been confirmed (Malik et al., 2010; Tiwari et al., 2011). However, the genetics of salt tolerance in cucumber is poorly understood (Tiwari et al., 2011) due to the complexity of salt tolerance (Maas and Poss, 1989; Munns and Tester, 2008). Therefore it is necessary to investigate viable selection traits that can predict salinity tolerance of cucumber at the seedling stage. The

potential for genetic improvement of salt tolerance in cucumber is feasible if the gene action of superior parents is fully understood and a suitable breeding program selected (Dashti et al., 2012).

Several screening criterion for salt tolerance have been proposed for glycophytes. Na^+ exclusion is widely accepted as an efficient salt selection criterion for cereals (Munns et al., 2012; Munns and Tester, 2008). However, the utilization of this trait in routine breeding is limited. Munns and Tester (2008) pointed out that the Na^+ exclusion by the roots is only feasible under mild salinity for a short time. Malik et al. (2010) reported lower leaf Na^+ content in salt tolerant cucumber. In the contrary, the results of our previous study showed that both salt-tolerant cucumber genotypes, 11411S (salt tolerant) and salt-sensitive, 11439S did not have significant differences in shoot Na^+ under salinity (Supplementary Table S1). The conflicting results might be explained by differences in stress period and screening system and method of inducing stress. A parallel study comparing salt stress and salt induced osmotic shock showed differential gene expression profile (Shavrukov, 2012). This underscores the importance of inducing salinity stress to assess salt tolerance in plants. In the present study, we applied NaCl gradually to simulate natural osmotic stress experienced under soil conditions.

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Salinity can be simply be assessed by simple measurements of growth parameters under stressed condition especially when using large number of germplasm (Tavakkoli et al., 2012). Stunting, reduced emergence and expansion of new leaves are generally accepted as adaptive mechanisms of plants exposed to osmotic stress due to salinity (Vaario et al., 2011). However, development of simple, replicable and reliable criteria for screening cucumber under salinity has remained elusive. Leaf and other growth parameters may serve as useful selection criterion for salt tolerance in cucumber at seedling stage if the inheritance pattern is known.

Generation mean analysis is a powerful tool that has been used to study various quantitative traits in crops such as yield (Rashwan, 2010), sucrose content (Tchiagam et al., 2011), sugar content (Audilakshmi et al., 2010), drought tolerance (Golparvar, 2011; Naveed et al., 2009) and aluminum tolerance (Spehar and Galway, 1995), salt tolerance (Dashti et al., 2012; Samineni et al., 2011) and waterlogging (Yeboah et al., 2008) in various crops. However, there are no reports on studies on inheritance of salt tolerance in cucumber using generation mean analysis.

The findings of the current study would improve our understanding of inheritance of salt tolerance in cucumber as well as facilitate planning possible breeding programmes. In this study we measured gene action using genetic components of variance approach. The objectives of the current study were to determine gene action and inheritance pattern of salt tolerance in cucumber using generation mean analysis.

2. Materials and methods

The experimental materials consisted of parental lines of six basic population (P_1 and P_2, F_1, F_2, B_1 and B_2) developed from the cross of 11411S (P_1, salt tolerant female parent) and 11439S (P_2, salt sensitive male parent). P_1 and P_2 were developed as inbred lines after several selfing of single plants derived from Hazerd and L8 cucumbers, respectively. Hazerd is a greenhouse cucumber type originating from America while L8 is a parthenocarpic Chinese type. The salinity response of the parental lines was evaluated at 80 mM NaCl under both in vitro and greenhouse pot conditions, respectively (Malik et al., 2010; Kere et al., unpublished). Based

on survival rate, electrolyte leakage, leaf relative water content, relative leaf number and Na^+/K^+ ratio, we established that 11411S was more tolerant than 11439S at 80 mM NaCl (Supplementary Table S1). Although, Na^+ exclusion is key to salt tolerance in cucumber, it could not explain the why 1411S was salt tolerant. Huang et al. (2012) reported that grafting improves salt tolerance of cucumber through exclusion and retention of Na^+ by pumpkin roots. The salt tolerance of 11411S may be attributed to increased antioxidant activity (Malik et al., 2010), sustained photosynthetic activities and K^+ retention (Kere et al., unpublished data). 11411S and 11439S were crossed to produce F_1 (11411S × 11439S). F_1 progeny was either self pollinated or backcrossed to obtain F_2 and respective backcrosses, B_1 (F_1 × 11411S) and B_2 (F1 × 11439S) in a greenhouse at the Jiangpu Experimental Station, Nanjing Agricultural University.

The salt tolerance evaluation was conducted in a plastic tunnel at Nanjing Agricultural University during autumn of 2011. Seeds of the parents, F_1, B_1, B_2 and F_2 were soaked overnight in warm water at 28 °C for 24 h in an incubator. The sprouting seeds were transferred into germination medium and raised until the two-leaf stage. Uniform seedlings were transplanted into 1.5 L plastic pots filled with vermiculite and peat mixed in the ratio 1:1 (v/v). All the seedlings were watered with full strength Hoagland solution every other day to pot 'field capacity' (irrigation varied from 100 to 150 mL) according to weather conditions and growth stage. All the six populations were grown in a complete randomized design replicated twice. The cucumber generations were subjected to salt treatment at the two leaf stage. The treatment was applied every 2 days at incremental rates of 20 mM NaCl up to the maximum 80 mM NaCl for 21 days. The mean temperature and relative humidity during the study period was 20.65 °C and 60%, respectively. Non-segregating (parental lines and F_1) and segregating (backcrosses and F_2) generations represent homogenous and heterogenous populations, respectively. Thus we collected data from 10 plants for non-segregating populations (parental lines and F_1) while backcrosses and F_2 consisted of 30 and 70 individuals, respectively.

To assess the salt tolerance of the six basic populations the following parameters were assessed: Relative leaf number (RLN14) calculated by dividing the number of leaves on day 14 after start of salt treatment by number of leaves before salt treatment; salt tolerance score (TOL) estimated using a scale of 1–5 (0 = no green part, 5 = green, no sign of salt injury); vine length (VL) of individual plants measured from the apex to the base of growth medium at the end of the experiment. The area of the second fully expanded leaf from the apex of each plant estimated by the formula, $(LW \times 0.82) - 0.427$ (Blanco and Folegatti, 2005), where L, length; W, largest width.

Analysis of variance was conducted for all the six generations. Estimates of genetic parameters were obtained with variances of parents, F_1, B_1, B_2 and F_2 generations. The adequacy of the simple additive-model was tested using the Kearsey and Pooni (1998) equation:

$$A = \text{Mean } (2B_1 - F_1 - P_1)$$

$$B = \text{Mean } (2B_2 - F_1 - P_2)$$

$$C = \text{Mean } (4F_2 - 2F_1 - P_1 - P_2)$$

We used t-test to detect if A, B, C were significantly different from zero. We tested the presence of non-allelic interactions using the joint scaling test as described by Cavalli (1952). The observed means of the 6 generations were used to estimate m, $[d]$, $[h]$, $[i]$ and $[j]$ (mean, pooled additive, dominance, additive × additive, and additive × dominance effects, respectively) as per the joint scaling test of Cavalli (1952). A model was declared adequate when the t-test and chi-square test was significant and non-significant, respectively. Since the sample sizes were different, the parameters

Table 1
Generation mean for various traits in six populations of a cucumber cross, 11411S and 11439S at 80 mM NaCl salinity.

Generation	Traits			
	TOL	RLN14	LA (cm^2)	VL (cm)
P$_1$	3.60 ± 0.22 a	1.93 ± 0.07 a	38.91 ± 4.28 c	42.72 ± 2.61 d
P$_2$	2.50 ± 0.17 c	1.53 ± 0.07 d	43.12 ± 4.54 c	45.05 ± 2.31 cd
F$_1$	3.20 ± 0.20 abc	1.80 ± 0.06 ab	81.87 ± 3.65 a	61.99 ± 2.28 a
F$_2$	2.87 ± 0.20 c	1.72 ± 0.06 bc	32.46 ± 3.34 c	52.44 ± 4.94 bc
B$_1$	3.40 ± 0.19 ab	1.90 ± 0.03 a	66.55 ± 3.77 b	46.80 ± 3.27 cd
B$_2$	3.07 ± 0.12 abc	1.68 ± 0.06Bcd	37.38 ± 217 c	56.86 ± 4.48 ab

TOL, RLN14, LA, and VL denote the salinity tolerance score, relative leaf number at 14 days after start of salinity, area of second fully expanded leaf and vine length, respectively. Values followed with same letters within a column are not significantly different at $P < 0.05$.

were estimated by weighted least square method using reciprocals of the variance of respective mean weight (Kearsey and Pooni, 1998). The estimates of dominance ratio, narrow sense heritability, heterosis (mid-parent), heterosis (better parent) and potence ratio were calculated using the following equation (Kearsey and Pooni, 1998):

Environmental variance, $V_E = \frac{1}{4}[s^2P_1 + s^2P_2 + 2s^2F_1]$;

Additive variance, $V_A = [s^2F_2 - (s^2B_1 + s^2B_2)]$;

Variance of dominance in F$_2$, $V_D = [(s^2B_1 + s^2B_2) - s^2F_2 - V_E]$;

Mid-parent heterosis $(H\%) = \left[\frac{F_1 - MP}{MP}\right] \times 100$

Heterobeltiosis $(HB\%) = \left[\frac{F_1 - BP}{BP}\right] \times 100$.

where s^2, MP and BP represent the variance, mid-parent and better parent means, respectively.

Dominance ratio $= \left(\frac{4V_D}{2V_A}\right)^{1/2}$

Narrow sense heritability, $h_n^2 = \frac{2s^2F_2 - (s^2BC_1 + s^2BC_2)}{s^2F_2}$

Phenotypic correlations were estimated in F$_2$ individuals using MINITAB statistical software. Genotypic correlation (r_g) between two traits (X, Y) was estimated using the formula (Ehdaie et al., 1993).

$r_g = \frac{COVg(X, Y)}{[(Vg(X) \cdot Vg(Y)]^{1/2}}$

where

$COVg = (X, Y)F2 - (1/4)[COV(X, Y)P1 + COV(X, Y)P2$
$\qquad + 2COV(X, Y)F1]$

COVg, (X, Y)F2, COV(X, Y)P1, COV(X, Y)P2, COV(X, Y)F1 are covariances of traits X and Y with genetic and non-allelic effects and Vg(X) and Vg(Y) are genetic variances of X and Y, respectively.

3. Results

The mean values for TOL and RLN14 in F$_1$ was close to the average of the two parental lines while the means for VL and LA in F$_1$ was greater than in the mean values of the two parents (Table 1). The mean values for all the traits in F$_2$ were lower than P$_1$ but similar to P$_2$ except for RLN14 (Table 1). Although P$_1$ and B$_1$ had significantly higher TOL than P$_2$ and F$_2$, the TOL values were not significantly different among P$_1$, F$_1$ and B$_1$ at 80 mM NaCl (Table 1). At 80 mM NaCl,

the RLN14 for P$_1$ and P$_2$ were highest and lowest ($P < 0.05$, respectively (Table 1)). Although, there were no significant differences between the parental lines with respect to LA and VL, F$_1$ individuals exhibited the highest values for the two traits (Table 1). For LA, B$_1$ had higher mean values than the salt tolerant parent, whereas no differences were observed between P$_1$, P$_2$ and B$_1$ with regards to VL (Table 1). The B$_1$ mean performance was significantly higher than B$_2$ for all the traits except TOL (Table 1). Mean performance of F$_2$ individuals was lower than F$_1$ progeny for all traits except TOL indicating inbreeding depression. The F$_2$ individuals showed wide transgressive segregation in all traits studied (Fig. 1).

The A, B, C scaling test was non-significant for all the traits (data not presented). However, all the traits had significant X^2 estimates for 3-parameter model under saline conditions indicating that the inadequacy of additive-dominance model (Table 2). Component 'm' was significant for all the traits (Table 2) indicating that they are inherited quantitatively. Additive gene effect was predominant for TOL and RLN14, whereas LA and VL were predominantly influenced by dominance [h] and additive × additive [i] epistatic gene effects (Table 2). For TOL and RLN14 and VL, the best model was m, [d], [h] and [i], whereas the best model fit for LA was m, [d], [h], [i] and [j] (Table 2).

Estimates of additive, dominance, environmental components of variance, dominance ratio, mid-parent heterosis, better parent heterosis, potence ratio and narrow sense heritability are shown in Table 3. Dominance ratio for all the traits was lower than 1 except for RLN14. TOL and RLN14 had very low mid-parent heterosis, whereas LA and VL showed higher mid-parent heterosis (Table 3). The better parent heterosis was negative for both RLN14 and TOL, whereas the values for VL and LA were high and positive (Table 3). For TOL and RLN14, narrow sense heritability was moderate (0.57) and low (0.25), respectively, while LA and VL had high narrow sense heritability (0.66 and 0.74 for LA and VL, respectively).

Relationships of TOL, RLN14, LA and VL were estimated in the F$_2$ population under salinity stress. A moderately significant positive phenotypic correlation (0.58, $R^2 = 0.31$, $P = 0.001$) was observed between RLN14 and TOL while a weak significant negative phenotypic correlation (-0.39, $R^2 = 0.12$, $P = 0.03$) was observed between TOL and VL (Table 4). Similarly a highly significant negative phenotypic correlation (-0.54, $R^2 = 0.28$, $P = 0.002$) was recorded between RLN14 and VL. There was no correlation between LA and other traits in cucumber subjected to salinity stress. Genotypic correlation between TOL and RLN14 was positive while it was negative for TOL versus LA or VL (Table 4). Genotypic correlation of RLN14 with other traits also followed a similar trend while VL and LA had positive genotypic relationship (Table 4).

4. Discussion

The findings of this study reveal that the salt tolerant parent as well tolerant segregants had higher relative leaf number than the sensitive parent at 80 mM NaCl. Our findings agree with the report
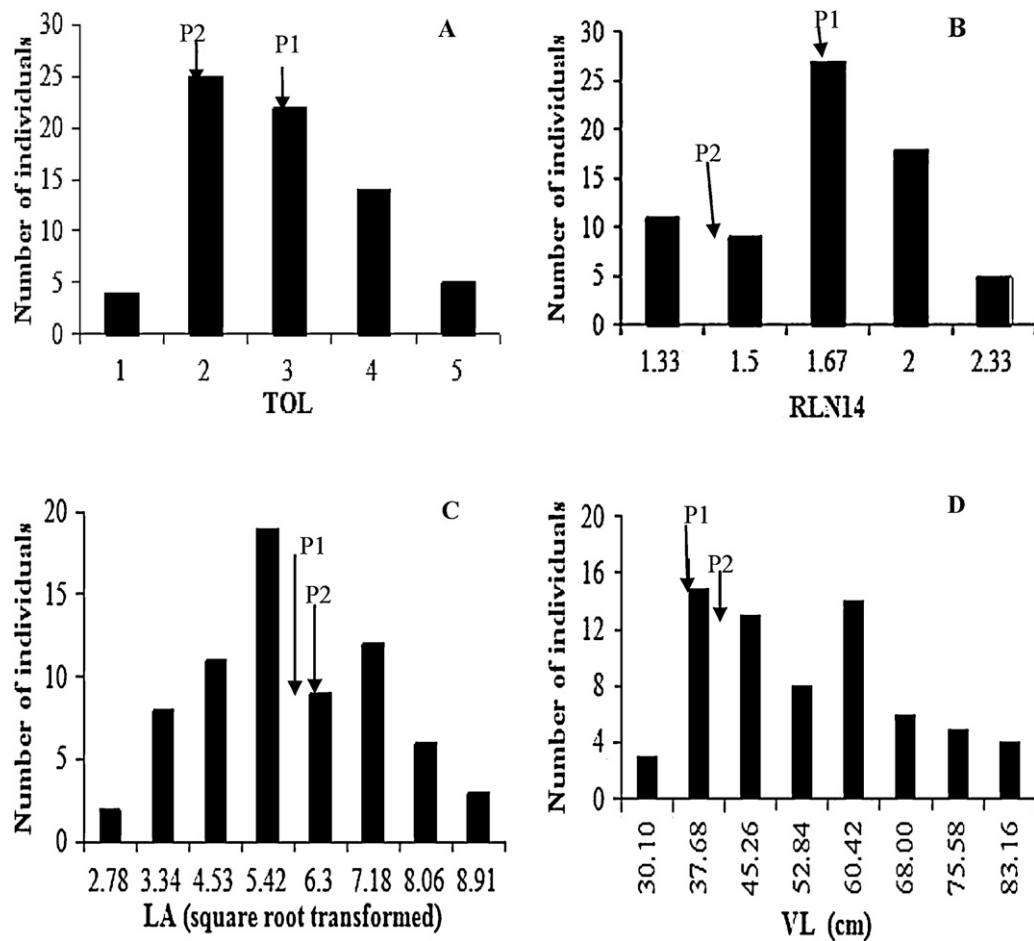
Fig. 1. Frequency distribution of TOL (A), RLN14, LA (C) and VL of F2 individuals from a salt tolerant, 11411S (P1) crossed with salt sensitive, 11439S (P2) cucumber genotypes under 80 mM NaCl at seedling stage. The arrows indicate relative positions parental means.

Table 2
Estimates of genetic components based on generation means in a cucumber cross, 11411S × 11439S.

Traits	Parameters						
	m	$[d]$	$[h]$	$[i]$	$[j]$	$[l]$	X^2(df)
TOL	$2.78 \pm 0.39^{**}$	$0.56 \pm 0.14^{*}$	0.52 ± 0.54	0.32 ± 0.43	0.64 ± 0.51	–	2.20 (1)
RLN14	$1.57 \pm 0.20^{**}$	$0.29 \pm 0.05^{*}$	0.29 ± 0.36	0.17 ± 0.21	-0.17 ± 0.21	–	0.23 (1)
LA	$2.53 \pm 0.53^{*}$	-0.17 ± 0.24	$6.58 \pm 069^{*}$	$3.1 \pm 0.61^{*}$	-4.43 ± 0.83	–	3.57 (1)
VL	$41.14 \pm 5.36^{**}$	-1.66 ± 1.51	$20.65 \pm 6.89^{*}$	3.11 ± 5.80	17.29 ± 7.17	–	0.13 (1)

m, $[d]$, $[h]$, $[i]$, $[j]$, $[l]$ and X^2 denote mean, additive, dominance, additive × additive, additive × dominance, chi square test, respectively. Values in brackets represent level of degree of freedom.

  [*] Significant t-test at 5% level.
  [**] Significant t-test at 1% level.

by Frary et al. (2010) who demonstrated that salt stress reduces formation of new leaves and further supports us our hypothesis that a high relative number of leaves in cucumber growing under salinity stress indicates salt tolerance. The importance of high rate of

formation of new leaves is linked to sustained photosynthetic activity under salinity (Asgari et al., 2012; Prudent et al., 2009; Vaario et al., 2011). The high rate of development and maintenance of a higher number of leaves under salinity stress may dilute deleterious

Table 3
Variance components, dominance ratio, heterosis, heterobeltiosis, potence ratio and narrow-sense heritability estimates of some traits studied under 80 mM NaCl stress in cucumber under salt stress.

Trait	V_A	V_D	V_{AD}	V_E	Dominance ratio	H%	HB%	Pot	h_n^2
TOL	0.62	0.08	−0.30	0.39	0.29	4.92	−11.11	0.27	0.57
RLN14	0.02	0.02	0.03	0.04	1.41	3.85	−7.41	0.33	0.25
LA	1.66	0.15	−0.07	0.7	0.43	42.90	39.24	16.32	0.66
VL	181.06	19.85	47.23	64.96	0.14	39.73	34.73	5.36	0.74

V_A, additive variance; V_D, dominance variance; V_{AD}, additive dominance variance; V_E, environmental variance; H, heterosis of mid-parent; HB, heterosis better parent; pot, potence ratio; h_n^2, narrow-sense heritability.

Table 4
Pearson correlations of some traits of cucumber F_2 individuals from 11411S × 11439S cross under salinity.

	TOL	RLN14	LA
Phenotypic correlation			
RLN14	0.575		
	0.001 ($R^2 = 0.31$)		
LA	−0.096	−0.800	
	0.606	0.670	
VL	−0.385	−0.544	0.255
	0.03 ($R^2 = 0.12$)	0.002 ($R^2 = 0.28$)	0.166
Genotypic correlation			
RLN14	0.68		
LA	−0.01	−0.05	
VL	−0.38	−0.47	0.27

The upper and lower numbers represent Pearson correlation and *P*-values, respectively. RLN14: relative leaf number at 14 days post salinity treatment; TOL: salt tolerance score; LA: area of second fully expanded leaf; VL: vine length.

effect of Na^+ and Cl^- while sustaining higher photosynthetic capacity (Vaario et al., 2011). In the current study, VL was inversely proportional to TOL or RLN14. This agrees previous reports that attributed stunted growth of plants under stress to an adaptive response (Queirós et al., 2007).

The mean values for salinity score (TOL) and RLN14 of F_1s in this cross were between mid-parent and tolerant parent values indicating that dominant genes controlled these traits. This dominance effect is further supported by the higher values for the two traits in B_1 than B_2. However, based on potence ratio this dominance was partial for the two traits. Since the phenotypic variation for RLN14 and TOL observed in F_2 was larger than those of the parental lines, we suggest that salt tolerance in this cross is polygenic with alleles from either parents contributing to increases and decreases of salinity tolerance (DeRose-Wilson and Gaut, 2011). The higher mean trait values observed in B_1 compared to B_2 may be attributed to differential contribution of increasing and decreasing alleles from either parents. Although the two parents did not differ in terms of VL and LA, the hybrid means were higher than both the parental and better parent means indicating heterotic response for these traits. The positive significant dominant gene action for these traits confirms our current finding.

Although A, B, C scaling test failed to detect non-allelic interactions for all the traits, the inadequacy of additive-dominance model suggests the presence non-allelic interactions. This is in agreement with observation made by Ray and Islam (2008). Mather and Jinks (1971) attributed this observation to canceling effects of the dispersed gene pair in the gene interactions as well as interaction involving two or more genes. Additive gene actions are important for selection of particular trait in breeding since they are stable fixable components of polygenic variation (Kearsey and Pooni, 1998). Significant positive additive gene and non-significant effects for RLN14 and TOL suggest the possibility of improving salinity tolerance of this cucumber cross by recurrent selfing and selection of advanced filial generations owing to low heritability of the traits. Improvement of LA and VL traits under salinity may be feasible at advanced filial generations owing to the presence of significant positive dominance and positive additive × additive epistatic gene components (Hussain et al., 2008). Although, non-significant, the negative additive × dominance gene effect observed in LA indicates that these effects are not fixable by selfing and selection (Farshadfar et al., 2001). Lack of correlation between LA and TOL in the current study suggests that the two traits are independently inherited at least for this cross.

The positive phenotypic and genotypic correlations between RLN14 and TOL in this study suggest that indirect selection of

photosynthetic enhancing traits such as relative leaf number may be employed to improve salt tolerance in cucumber. However, the feasibility of this approach should be surveyed a cross several crosses and generations of cucumber. Significant additive component coupled with low heritability observed in RLN14 necessitates advanced selection in order to minimize environmental effects and while enhancing additive gene effects. The unfavorable genotypic correlation between TOL and VL implies that selecting for one trait reduces the other. Thus segregants with higher, TOL, VL and RLN14 should be selected simultaneously for maximum salt tolerance performance. Selection of transgressive segregants via sib-mating of F_1 is feasible for improving salt tolerance of cucumber from this cross.

In conclusion, the gene action estimated through generation mean analysis shows the importance of additive and dominance effects for the traits studied under salinity stress. The relative leaf number and salt tolerance are predominantly controlled by additive gene effect while leaf area and vine are mainly controlled by dominance and epistatic gene action. Our findings show that it is complicated to improve salinity tolerance of cucumber through simple selection procedures or pedigree breeding due to presence of dominance gene action. This coupled with low heritability of relative leaf numbers warrants delayed selection at an advanced stages followed by reciprocal recurrent selection in order to yield desirable segregants. To concentrate desirable alleles, inter-mating of superior segregants could also be pursued.

References

Asgari, H.R., Cornelis, W., Van Damme, P., 2012. Salt stress effect on wheat (*Triticum aestivum* L.) growth and leaf ion concentrations. Int. J. Plant Prod. 6, 195–208.
Audilakshmi, S., Mall, A., Swarnalatha, M., Seetharama, N., 2010. Inheritance of sugar concentration in stalk (brix), sucrose content, stalk and juice yield in sorghum. Biomass Bioenergy 34, 813–820.
Blanco, F.F., Folegatti, M.V., 2005. Estimation of leaf area for greenhouse cucumber by linear measurements under salinity and grafting. Sci. Agric. 62, 305–309.
Cavalli, L., 1952. An analysis of linkage in quantitative inheritance, quantitative inheritance. In: Papers Read at a Colloquium held at the Institute of Animal Genetics Edinburgh University under the Auspices of the Agricultural Research Council April 4th to 6th, 1950, HM Stationery Office, pp. 135–144.
Dashti, H., Bihamta, M.R., Shirani, H., Majidi, M.M., 2012. Genetic analysis of salt tolerance in vegetative stage in wheat (*Triticum aestivum*). Plant Omics 5, 19–23.
Davies, B., Baulcombe, D., Crute, I., Dunwell, J., Gale, M., Jones, J., Pretty, J., Sutherland, W., Toulmin, C., 2009. Reaping the benefits: science and the sustainable intensification of global agriculture.
DeRose-Wilson, L., Gaut, B.S., 2011. Mapping salinity tolerance during *Arabidopsis thaliana* germination and seedling growth. PLoS ONE 6, e22832.
Ehdaie, B., Barnhart, D., Waines, J., 1993. Genetic Analysis of Transpiration Effciency, Carbon Isotope Discrmination and Growth Characters in Bread Wheat and Plant Carbon-Water Relations. Academic Press, San Diego, pp. 419–434.
El-Shraiy, A.M., Mostafa, M., Zaghlool, S.A., Shehata, S., 2011. Alleviation of salt injury of cucumber plant by grafting onto salt tolerance rootstock. Aust. J. Basic Appl. Sci. 5, 1414–1423.
FAO, 2009. Land and Plant Nutrition Management Service. http://www.fao.org/ag/agl/agll/spush/ (accessed December 2011).
Farshadfar, E., Ghanadha, Sutka, J., Zahravi, M., 2001. Generation mean analysis of drought tolerance in wheat (*Triticum aestivum* L.). Acta Agron. Hung. 49, 59–66.
Frary, A., Gol, D., Keles, D., Okmen, B., Pinar, H., Sigva, H.O., Yemenicioglu, A., Doganlar, S., 2010. Salt tolerance in *Solanum pennellii*: antioxidant response and related QTL. BMC Plant Biol. 10, 58.
Golparvar, A.R., 2011. Estimation of the genetic parameters and heritability for grain filling rate and relative water content in hexaploid wheat. Int. J. Life Sci. Med. Res. 1, 13–15.
Huang, Y., Bie, Z., Liu, P., Niu, M., Zhen, A., Liu, Z., Lei, B., Gu, D., Lu, C., Wang, B., 2012. Reciprocal grafting between cucumber and pumpkin demonstrates the roles of the rootstock in the determination of cucumber salt tolerance and sodium accumulation. Sci. Hortic. 149, 47–54.

Hussain, M., Azhar, F.M., Khan, A., 2008. Genetic basis of variation in leaf area, petiole length and seed cotton yield in some cotton (*Gossypium hirsutum*) genotypes. Int. J. Agric. Biol. 10, 705–708.

Kearsey, M.J., Pooni, H.S., 1998. The Genetical Analysis of Quantitative Traits. Stanley Thornes (Publishers) Ltd., Cheltenham.

Maas, E., Poss, J., 1989. Salt sensitivity of cowpea at various growth stages. Irrig. Sci. 10, 313–320.

Malik, A.A., Li, W.-G., Lou, L.-N., Weng, J.-H., Chen, J.-F., 2010. Biochemical/physiological characterization and evaluation of in vitro salt tolerance in cucumber. Afr. J. Biotechnol. 9, 3298–3302.

Mather, K., Jink, J., 1982. Biometrical Genetics: The Study of Continuous Variation, 3rd ed. Chapman and Hall, London.

Mather, K., Jinks, J.L., 1971. Biometrical Genetics. Chapman and Hall, London.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681.

Munns, R., James, R.A., Xu, B., Athman, A., Conn, S.J., Jordans, C., Byrt, C.S., Hare, R.A., Tyerman, S.D., Tester, M., 2012. Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. Nat. Biotechnol. 30, 360–364.

Naveed, A., Khan, A., Khan, I.A., 2009. Generation mean analysis of water stress tolerance in okra (*Abelmoschous esculentus* L.). Pakistan J. Bot. 41, 195–205.

Negrão, S., Courtois, B., Ahmadi, N., Abreu, I., Saibo, N., Oliveira, M., 2011. Recent updates on salinity stress in rice: from physiological to molecular responses. Crit. Rev. Plant Sci. 30, 329–377.

Prudent, M., Causse, M., Génard, M., Tripodi, P., Grandillo, S., Bertin, N., 2009. Genetic and physiological analysis of tomato fruit weight and composition: influence of carbon availability on QTL detection. J. Exp. Bot. 60, 923–937.

Queirós, F., Fidalgo, F., Santos, I., Salema, R., 2007. In vitro selection of salt tolerant cell lines in *Solanum tuberosum* L. Biol. Plant. 51, 728–734.

Rashwan, A., 2010. Estimation of some genetic parameters using six populations of two cowpea hybrids. Asian J. Crop Sci. 2, 261–267.

Ray, P.S., Islam, M.A., 2008. Genetic analysis of salinity tolerance in rice. Bangladesh J. Agric. Res. 33, 519–529.

Samineni, S., Gaur, P.M., Colmer, T.D., Krishnamurthy, L., Vadez, V., Siddique, K.H., 2011. Estimation of genetic components of variation for salt tolerance in chickpea using the generation mean analysis. Euphytica 182, 73–86.

Shavrukov, Y., 2012. Salt stress or salt shock: which genes are we studying? J. Exp. Bot. 64, 119–127.

Spehar, C.R., Galway, N., 1995. Generation mean analysis of root growth under aluminium-stress hydroponics in the soybeans (*Glycine max* (L.) Merrill). Pesquisa Agropecuár. Bras. 30, 963.

Tavakkoli, E., Fatehi, F., Rengasamy, P., McDonald, G.K., 2012. A comparison of hydroponic and soil-based screening methods to identify salt tolerance in the field in barley. J. Exp. Bot. 63, 3853–3867.

Tchiagam, J.N., Youmbi, E., Njintang, N., Bell, J., Maina, A.N., 2011. Generation means analysis of seed sucrose content in cowpea (*Vigna unguiculata* L. Walp). Asian J. Agric. Sci. 3, 475–480.

Tiwari, J.K., Munshi, A.D., Kumar, R., Sharma, R.K., Sureja, A.K., 2011. Inheritance of salt tolerance in cucumber (*Cucumis sativus*). Indian J. Agric. Sci. 81, 398–401.

Vaario, L.-M., Yrjälä, K., Rousi, M., Sipilä, T., Pulkkinen, P., 2011. Leaf number indicates salt tolerance of young seedling families of European aspen (*Populus tremula* L.) growing in different soils. Silva Fenn. 45, 19–33.

Yeboah, M.A., Xuehao, C., Guohua, L., Minghong, G., Chenwu, X., 2008. Inheritance of waterlogging tolerance in cucumber (*Cucumis sativus* L.). Euphytica 162, 145–154.