Diallel Analysis of Salt Tolerance at Germination and the Seedling Stage in Barley (*Hordeum vulgare* L.)

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Summary

Diallel cross analysis for eight varieties of barley (*Hordeum vulgare* L.) differing in their salt tolerance at germination and at the seedling stage was performed. Salt tolerance at germination was evaluated from average shoot length after ten days of incubation in 250 mM NaCl solution. Salt tolerance at germination was mainly controlled by recessive genes. Non-allelic gene interaction was not observed. Non additive genetic variance was larger than additive genetic variance, and the mean degree of dominance was 1.47. The broad and narrow sense heritabilities were as high as 0.99 and 0.75, respectively. On the other side, a leaf injury index was used to assess tolerance at the seedling stage after exposure to 500 mM NaCl solution for four weeks. Salt tolerance at the seedling stage was predominantly controlled by additive genes, and the mean degree of dominance was 0.52. Non-allelic gene interaction was absent, and dominance was directed toward tolerance. Heritabilities were 0.85 and 0.75 in a broad and a narrow sense, respectively. No correlation was observed between salt tolerance at germination and the seedling stage in the 8×8 diallel tables. Thus the mode of inheritance for salt tolerance was different between germination and the seedling stage.

Key Words : diallel analysis, germination, *Hordeum vulgare*, salt tolerance, seedling test.

Introduction

Salinization threatens irrigation agriculture in arid and semi-arid regions in the world. In these areas, low rainfall and high evaporation cause the accumulation of salts at the soil surface, and the resulting soil salinity limits crop productivity (Batie and Healy 1983, Boyer 1982, Epstein *et al.* 1980).

In North China, for example, salinization due to lack of water and improper irrigation has deteriorated the cultivated field. In the project of "Improvement of Salinized Soil and Agricultural Development in North China Plain", Takeda *et al.* (1995) selected barley and wheat varieties, which adapted to the semi-arid and highly saline conditions, from over 10,000 accessions in the Heilonggang region of China. In addition, cultivation of these tolerant varieties has been started in this re-

gion. Together with above practical approach, improved cultural practices and plant breeding are necessary to overcome the physiological limitations of crop productivity.

Salt tolerance at germination and the seedling stage are important because the initial stand of plant affects the final production. In these growth stages, salt tolerance and the varietal rankings could be different in rice (Heenan *et al.* 1988, Pearson *et al.* 1966), corn (Kaddah and Ghowail 1964, Maas *et al.* 1983), wheat (Maas and Poss 1989), and barley (Greenway 1965, Mano and Takeda 1995).

Genetical studies of salt tolerance have been reported by several authors. At germination, additive effect was important and heritability values were high in tomato (Fooland and Jones 1991, 1992) and forage species (Ashraf *et al.* 1987). At the seedling stage, both additive and dominance genetic effects were important, and the genotype-environment interactions were large in rice (Akbar *et al.* 1985, Gregorio and Senadhira 1993, Moel-jopawiro and Ikehashi 1981) and sorghum (Azhar and McNeilly 1988).

In barley, only a few studies on the inheritance of salt tolerance have been reported. Maddur (1977), using 6×6 diallel crosses selected from 33 accessions of barley, reported that salt tolerance was controlled by incomplete dominant genes at germination and nearly complete dominant genes at the seedling stages. Non-allelic gene interaction was important at the seedling stage.

We had previously assessed the salt tolerance of barley at germination and the seedling stage using over 6,500 accessions from the world barley collection preserved at the Barley Germplasm Center of Okayama University (Mano and Takeda 1995, Mano *et al.* 1996). The present study was conducted to provide further genetic information about salt tolerance at germination and the seedling stages. Eight barley varieties, representing the most salt tolerant or sensitive varieties at either growth stage were selected for diallel analysis.

Materials and Methods

Salt tolerance at germination

A set of diallel crosses was made using eight barley varieties (Table 1), which were selected from over 6,500 accession (Mano *et al.* 1996). Fifty seeds of reciprocal F₁ plants (F₂ generation) and their parents were germinated on two layers of filter paper moistened with

Table 1. Morphological type and salt tolerance at germination (T_1) and the seedling stage (T_2) of the parental varieties used in the diallel analysis

Code	OU No. ¹⁾	Variety	Origin	Hull type	Row type	K.W. ²⁾	T_1 ³⁾	T_2 ⁴⁾
P1	OUJ417	Kumoi	Japan	Covered	Six-rowed	33.6	45.2	1.7
P2	OUC346	Shanghai 1	China	Naked	Six-rowed	40.3	42.2	1.7
P3	OUA019	Beldi Giant	U.S.A.	Covered	Six-rowed	54.4	38.8	3.5
P4	OUK666	Jeomchon Naked 2	Korea	Naked	Six-rowed	38.4	35.9	1.9
P5	OUI385	Partek 1	India	Naked	Six-rowed	41.9	18.1	3.3
P6	OUJ220	Fuji Nijo	Japan	Covered	Two-rowed	53.8	14.6	3.0
P7	OUE211	Ethiopia 633	Ethiopia	Covered	Six-rowed	54.5	0.0	1.3
P8	OUE812	Ethiopia 638	Ethiopia	Covered	Six-rowed	61.2	0.0	4.4

¹⁾ : Accession number at the Barley Germplasm Center of Okayama University.

²⁾ : 1,000-kernel weight (g). The kernel weight of the naked parents were adjusted to covered type by multiplying their kernel weight by 1.1.

³⁾ : Salt tolerance at germination was evaluated by the average shoot length (mm) after ten days of incubation in 250 mM NaCl solution at 20 °C.

⁴⁾ : Salt tolerance at the seedling stage was classified into five tolerance classes, 1 (sensitive) to 5 (tolerant), by visually rating of leaf injury.

250 mM NaCl solution in 135×20 mm Petri dishes. In our previous study, obvious varietal variation for salt tolerance at germination was observed in 250 mM NaCl solution (Mano *et al.* 1996). The germination test was carried out at 20 °C under a 12 hour light/12 hour dark photoperiod in the growth chamber with three replications. After ten days of incubation, shoot length averaged over all shoots including non-germinating seeds, was recorded. Preliminary studies detected no obvious differences in shoot length of the parents in non-saline solution, thus salt tolerance at germination could be precisely evaluated by shoot length in salt solution.

Salt tolerance at the seedling stage

Eight varieties, which were used in the diallel analysis of salt tolerance at germination, and their reciprocal F_1 plants were tested for salt tolerance at the seedling stage. Five plants of each parental varieties and their 56 F_1 progeny were seeded in a seedling box (50×35×10 cm) filled with a standard soil at a plant density of 3.0×2.5 cm, and were grown in a phytotron with natural light at 20 °C. The seedlings were raised to the third leaf stage, then were irrigated at every third or fourth day with 500 mM NaCl solution for four weeks. The NaCl concentration was decided on the basis of previous study (Mano and Takeda 1995). A volume of 6 liters of NaCl solution per seedling box was added in total. After the four weeks from initiation of NaCl treatment, plants of each parental variety and their F_1 progeny were scored in five tolerance classes for leaf injury i. e. score 1; death, 2; delayed death, 3; severe, 4; trace, 5; clear. The experiment was conducted with three replications.

The diallel analysis was performed according to Hayman (1954a, b) and Griffing (1956), and was calculated using the computer program DIALL (Ukai 1989).

Results

Diallel analysis of salt tolerance at germination

As shown in Table 2, salt tolerance at germination, evaluated by the average shoot length, shows wide variation among both the eight parents (0 to 45.2 mm; average 24.4 mm) and their 56 F_1 progeny (0 to 50.7 mm; average 23.7 mm).

Both additive (a) and dominance effects (b) were significant for salt tolerance at germination (Table 3). The dominance effect was attributable to differences in the distribution of dominant alleles among the parents (b_2) and to specific combining ability effect (b_3). Although the specific reciprocal difference (d) was significant, reciprocal effect (c) was not significant, indicating the absence of maternal effect as a whole.

The significance of the specific reciprocal difference (d) was mainly due to differences of reciprocal crosses in P4 (OUK666)×P6 (OUJ220) and P2 (OUC346)×P3 (OUA019), which were contributed to 21.6 % and 17.3 % of sum of square, respectively. In detail, the F_1 of P3 × P2 (30.5 mm) was weaker than the weaker parent P3 (38.8 mm); this must be due to experimental error. The difference between P4×P6 and its reciprocal might be due to maternal effect.

The relationship between array variance (V_r) and array parent-offspring covariance (W_r) for salt tolerance at germination is shown in Fig. 1. The regression coefficient of W_r on V_r was close to unity, indicating that the simple additive-dominance genetic model was adequate and that non-allelic interaction was absent.

Salt sensitive parents, such as P8 (OUE812) and P7 (OUE211), were located near the origin, suggesting that P8 and P7 possessed more dominant genes. On the other hand, salt tolerant parents, such as P2 (OUC346) and P3 (OUA019), were located near the upper end of the regression line, indicating that P2 and P3 harbored more recessive genes. There was a significant and positive correlation between salt tolerance at germination in

Table 2. Salt tolerance at germination in F_1 progeny and their parental varieties of barley

♀ ♂		P1	P2	P3	P4	P5	P6	P7	P8	Mean
P1	OUJ417	45.2	44.4	45.3	50.7	45.6	26.3	27.5	17.2	37.8
P2	OUC346	49.9	42.2	41.6	47.0	25.8	20.4	2.4	14.1	30.4
P3	OUA019	38.9	30.5	38.8	33.9	42.6	23.9	5.7	3.3	27.2
P4	OUK666	50.6	39.9	41.4	35.9	34.5	36.3	18.9	9.8	33.4
P5	OUI385	44.3	26.1	42.1	32.6	18.1	24.1	16.3	20.3	28.0
P6	OUJ220	32.9	16.1	15.0	24.2	27.0	14.6	1.0	2.4	16.7
P7	OUE211	23.6	12.0	4.2	19.0	12.6	1.1	0.0	0.0	9.1
P8	OUE812	23.8	7.7	4.1	5.8	17.6	1.3	0.0	0.0	7.5
Mean		38.7	27.4	29.1	31.2	28.0	18.5	9.0	8.4	23.8

Boldface : parents.

Salt tolerance was evaluated by the average shoot length (mm) after ten days of incubation in 250 mM NaCl solution at 20 °C.

Table 3. Analysis of variance for salt tolerance at germination and the seedling stage of barley in the diallel tables

Item	df	MS	
		Germination	Seedling stage
a	7	1942.01**	4.09**
b	28	66.41**	0.24**
b ₁	1	3.33	1.39**
b ₂	7	92.58**	0.13
b ₃	20	60.40**	0.22**
c	7	13.11	0.11
d	21	15.50**	0.09
Error	126	7.68	0.10

** : Significant at the 1 % level.

Error MS was estimated from replication × genotype interaction.

a : additive effects, b : dominance effects, b₁ : mean dominance effects, b₂ : additional dominance effects, b₃ : residual dominance effects, c : reciprocal effects, d : specific reciprocal effects.

Fig. 1. W_r/V_r graph for salt tolerance at germination in barley. The numbers correspond to parental varieties in Table 1. **Fig. 2.** Correlation between (W_r+V_r) and salt tolerance at germination in the parental varieties (Pr). The numbers correspond to parental varieties in Table 1. * : Significant at the 5 % level.

the parental varieties (Pr) and W_r+V_r , indicating that salt tolerance at germination was mainly controlled by recessive genes (Fig. 2).

The dominance effect (H_1) was larger than the additive effect (D), and the mean degree of dominance ($\sqrt{H_1/D}$) was estimated at 1.47. This suggests that salt tolerance at germination was controlled by the over-dominant genes (Table 4). The sum of product of the additive and dominance effects (F) was negative, suggesting that recessive alleles for salt tolerance were more frequent than dominant ones. Average direction of dominance (h) was negative, indicating that recessive genes for salt tolerance generally acted toward increasing salt tolerance. The broad (h^2_B) and narrow (h^2_N) sense heritabilities were estimated at 0.99 and 0.75, respectively.

The relationship between salt tolerance at germination and the 1,000-kernel weight was examined among the parental varieties and their 56 F_1 progeny. In this analysis, the kernel weight of the naked parents and their F_1 progeny were adjusted to covered type by multiplying their kernel weight by 1.1. The correlation coefficients between salt tolerance at germination and 1,000-kernel weight were -0.743 in the parental varieties, and -0.704 in their F_1 progeny, respectively, indicating that salt tolerant varieties and F_1 progeny generally had smaller seeds.

Since the kernel weight correlated with salt tolerance at germination, two sets of 4×4 subdiallel analyses were performed in the smaller (P1, 2, 4, 5; average 1,000-kernel weight 40.9 g) and larger (P3, 6, 7, 8; average 60.8 g) seed size groups. Comparing among the full-diallel and two sets of subdiallel sets, many of the genetic components were similar to each other, but the components of gene distribution (F) and direction of dominance (h) were different (Table 4).

Following to the above mentioned diallel analysis, detailed analysis on segregation in the F_2 generation was performed (Fig. 3). In this analysis, each reciprocal

Table 4. Estimates of the genetic components of salt tolerance at germination and the seedling stage of barley obtained from the diallel and subdiallel analysis

Component	Estimated value			
	Germination			Seedling
	8 × 8 Diallel	4 × 4 Subdiallel (P1,2,4,5) ¹⁾	(P3,6,7,8) ²⁾	
D ³⁾	337.47	144.63	330.44	1.09
F ⁴⁾	-164.88	-26.23	268.58	0.11
H ₁ ⁵⁾	724.52	482.75	616.22	0.29
H ₂ ⁶⁾	470.79	392.86	553.00	0.27
E ⁷⁾	7.68	2.88	4.26	0.10
$\sqrt{H_1/D}$ ⁸⁾	1.47	1.83	1.37	0.52
h ⁹⁾	-1.21	8.37	-12.28	0.78
$\overline{uv}$ ¹⁰⁾	0.16	0.20	0.22	0.23
h ² _B ¹¹⁾	0.99	0.99	0.98	0.85
h ² _N ¹²⁾	0.75	0.56	0.31	0.75

1) : Parental varieties in the smaller seed size group.

2) : Parental varieties in the larger seed size group.

3) : Additive effects. 4) : Gene distribution. 5), 6) : Dominance effects.

7) : Environmental effects. 8) : Mean degree of dominance.

9) : Direction of dominance. 10) : Balance of positive and negative alleles.

11) : Broad sense heritability. 12) : Narrow sense heritability.

cross was pooled. Salt tolerance at germination, evaluated by shoot length, showed continuous and transgressive segregation in the F_2 populations of the crosses among the salt tolerant parents, P1 (OUJ417), P2 (OUC346), P3 (OUA019), and P4 (OUK666) (Fig. 3). Conversely, no segregation was observed in the F_2 population of a cross between sensitive parents, P7 (OUE211) and P8 (OUE812). As well as the F_2 populations of the crosses among the salt tolerant parents, many highly tolerant F_2 plants were segregated in the F_2 population of a cross between moderately tolerant parents, P5 (OUI385) and P6 (OUJ220). This may indicate recombination of the different salt tolerant genes from P5 and P6.

Diallel analysis of salt tolerance at the seedling stage

Salt tolerance at the seedling stage showed wide variation among the parents (1.3 to 4.4; average 2.6) and their 56 F_1 progeny (1.4 to 4.5; average 3.0) (Table 5).

Additive effect (a) was large and the mean dominance effect among parents (b_1) and specific combining ability effect (b_3) were significant (Table 3). Maternal effects (c, d) were not statistically significant.

From the W_r/V_r graphical analysis, the regression coefficient was close to unity suggesting the absence of epistatic interaction (Fig. 4). Salt tolerant parent, such

Fig. 3. Segregation for salt tolerance at germination in 8×8 diallel F_2 populations. Notes: Number of plants of each F_2 population was 300. For cross combination, cf. Table 2. The arrows indicate the parental values. The ordinate indicates the number of plants. The abscissa indicates salt tolerance, evaluated by shoot length (mm) after ten days of incubation in 250 mM NaCl solution at 20 °C.

Table 5. Salt tolerance at the seedling stage in F_1 progeny and their parental varieties of barley

♀ ♂		P1	P2	P3	P4	P5	P6	P7	P8	Mean
P1	OUI417	1.7	2.2	3.0	2.0	3.0	3.3	2.6	4.0	2.8
P2	OUC346	2.4	1.7	3.3	1.4	2.7	2.7	2.8	3.3	2.6
P3	OUA019	3.1	3.3	3.5	3.4	4.5	4.0	3.1	4.2	3.6
P4	OUK666	2.0	2.0	3.3	1.9	2.8	2.1	2.2	3.2	2.4
P5	OUI385	2.1	2.4	4.0	3.4	3.3	4.0	2.7	3.3	3.1
P6	OUI220	3.0	2.5	3.7	2.4	3.4	3.0	3.2	4.0	3.1
P7	OUE211	2.2	1.8	3.0	2.3	2.3	3.2	1.3	3.9	2.6
P8	OUE812	3.7	3.1	3.7	3.3	3.9	3.7	4.1	4.4	3.8
Mean		2.5	2.3	3.4	2.5	3.2	3.3	2.7	3.8	3.0

Boldface : parents.

Salt tolerance was classified into five tolerance classes, 1 (sensitive) to 5 (tolerant), by visually rating leaf injury.

Fig. 4. W_r/V_r graph for salt tolerance at the seedling stage in barley. The numbers correspond to parental varieties in Table 1.

as P8 (OUE812), located near the lower end of the regression lines, indicating that P8 possessed more dominant genes. Conversely, salt sensitive parent, such as P7 (OUE211), located at the upper end of the regression lines, indicating that P7 harbored more recessive genes. The correlation coefficient between salt tolerance at the seedling stage (Pr) and W_r+V_r was -0.879 , suggesting that the genes controlling salt tolerance at the seedling stage tended to be dominant (Fig. 5).

Genetic components for salt tolerance at the seedling stage are shown in Table 4. The mean degree of dominance ($\sqrt{H_1/D}$) was estimated to be 0.52, exhibiting incomplete dominance. The sum of product of the additive effect and dominance effect (F) was close to zero (0.11). This suggests that the frequencies of dominant and recessive alleles for salt tolerance are equal. Average direction of dominance (h) was positive, indicating that the dominance was directed toward tolerance. The broad ($h^2_B = 0.85$) and narrow ($h^2_N = 0.75$) sense heritabilities

were high.

From computer simulation of diallel crosses, high broad sense heritability with a value of, at least 0.8 is prerequisite for diallel analysis (Ukai 1991). In the present study, this request is cleared both at germination and the seedling stage (Table 4).

The comparison of mode of inheritance for salt tolerance between germination and seedling stages is shown in Table 6. The following similarities were observed between these stages: (1) absence of maternal effect, (2) absence of epistasis, and (3) high heritability. On the other hand, the mode of inheritance for salt tolerance at germination and the seedling stage showed the following differences: (1) overdominance vs. incomplete dominance, (2) greater frequency of recessive alleles vs. equal frequencies of dominant and recessive alleles, and (3) negative vs. positive action of dominant genes. These facts, including the independence between salt tolerance at germination and the seedling stage in the 8×8 diallel tables ($r = -0.363$), indicated that the genetic systems for salt tolerance at these two stages were different.

In addition, characteristic parents, such as P7 (OUE211) and P8 (OUE812), were found. The highly

Fig. 5. Correlation between $(W_r + V_r)$ and salt tolerance at the seedling stage in the parental varieties (Pr). The numbers correspond to parental varieties in Table 1. **: Significant at the 1 % level.

Table 6. Comparison of the mode of inheritance between salt tolerance at germination and the seedling stage in barley

Item	Germination	Seedling
Maternal effect	Absent	Absent
Epistasis	Absent	Absent
Heritability	High	High
Dominance	Over	Incomplete
Gene distribution of recessive alleles	More frequent	Equal
Direction of dominance	Sensitive	Tolerant

salt sensitive parents, P7 and P8, may harbor a large number of common, dominant genes which control salt sensitivity at germination. This is inferred from the data in Fig. 1, where P7 and P8 were located near the origin on the Wr/Vr graph, and Fig. 3, where no segregation was observed in the F₂ population of a cross between them. In contrast, the genetic compositions of salt tolerance at the seedling stage in P7 and P8 showed obvious differences, i. e. the sensitive P7 possessed more recessive genes, whereas the tolerant P8 possessed more dominant genes (Fig. 4).

Discussion

The genetic investigation for salt tolerance based on the diallel cross analysis revealed that the mode of inheritance at germination differed from that of the seedling stage. Mano *et al.* (1996) reported that salt tolerance at germination was independent of salt tolerance at the seedling stage in 6,646 barley varieties ($r = -0.061$). We conclude from our results that salt tolerance at germination and the seedling stage are controlled by different genetic mechanisms.

Maddur (1977) found that salt tolerance in barley appeared to be controlled by incomplete dominant genes at germination and nearly complete dominant genes at the seedling stages, and non-allelic gene interaction was important at the seedling stage. In contrast, the present study revealed that salt tolerance at germination and the seedling stage were mainly controlled by overdominant and incomplete dominant genes, respectively, and non-allelic gene interaction was not observed in either growth stage. Thus genetic systems for salt tolerance may be changed even in the same species and the same growth stage, and it may be due to the difference in the genotypes of the parents used.

Maternal effects of quantitative traits in barley have been reported for grain yield, heading date, and plant height (Choo *et al.* 1988), shoot differentiation ability (Komatsuda *et al.* 1989), callus growth (Mano *et al.* 1994), coleoptile length (Takahashi *et al.* 1996), and resistance to fusarium head blight (Takeda and Wu 1996). For salt tolerance at germination, specific reciprocal effect (d) was significant (Table 3) and maternal effect of this trait may be present in some crosses.

A negative correlation was observed between salt tolerance at germination and 1,000-kernel weight. Using a composite cross population of barley, Jana *et al.* (1980) reported that many six-rowed lines were tolerant to salt stress in comparison with two-rowed lines, and sensitive lines generally had larger seeds. Also, Mano *et al.* (1996) found that the salt sensitive barley lines generally had larger seeds. In the subdiallel analyses of salt tolerance at germination, the direction of dominance (h) differed between plants with larger and smaller seed size (Table 4), suggesting that genetic systems for salt tolerance may be changed by the different genetic backgrounds concerning seed size. As the parental range of

salt tolerance at germination was large in both subdiallels (P1 vs. P5 and P3 vs. P7, P8), these difference may not be due to sampling error.

Heritability of salt tolerance at germination was high in tomato (Fooland and Jones 1991, 1992), alfalfa (Allen *et al.* 1985), and forage species (Ashraf *et al.* 1987). As well as these species, salt tolerance at germination in barley was a highly heritable trait (Table 4). At the seedling stage, however, several authors have reported that the genotype-environment interactions were large and the heritabilities were low in rice (Gregorio and Senadhira 1993, Moeljopawiro and Ikehashi 1981) and barley (Mano and Takeda 1995). In the present study, the heritability of salt tolerance at the seedling stage was high (Table 4). Thus, a reliable selection for salt tolerance may be possible under the controlled environmental conditions.

The selection method for salt tolerant lines at each stage was different due to different genetic systems at germination and the seedling stage. Selection for highly tolerant lines at germination could be performed in early generations, because salt tolerance was controlled by recessive genes. In addition, transgressive segregation was observed in the F₂ populations of the crosses among the salt tolerant parents (Fig. 3), thus salt tolerant lines could be selected by pyramiding the different salt tolerant genes. On the other hand, at the seedling stage, dominance was directed toward tolerance, thus selection for tolerance should be delayed to later generations when the most of the dominant genes were fixed.

No correlations were observed between salt tolerance at germination and the seedling stage in the 8×8 diallel tables (Tables 2 and 5) and 6,646 barley varieties (Mano *et al.* 1996). Furthermore, Mano and Takeda (1997) reported that the position of quantitative trait loci for salt tolerance was different between germination and the seedling stage. Judging from these results, selection for highly salt tolerant lines at either growth stage could be conducted without concomitant reduction of tolerance at another growth stage. Because our results were derived from barley parents exhibiting extremes in salt tolerance at the two growth stages, the genetic informations provided by this study should be of value in a practical breeding strategy to develop salt tolerant barley varieties.

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