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Mapping QTLs with epistatic effects and QTL × treatment interactions for salt tolerance at seedling stage of wheat

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Abstract Quantitative trait loci (QTLs) with additive (*a*), additive × additive (*aa*) epistatic effects, and their treatmental interactions (*at* and *aat*) were studied under salt stress and normal conditions at seedling stage of wheat (*Triticum aestivum* L.). A set of 182 recombinant inbred lines (RILs) derived from cross Xiaoyan 54 × Jing 411 were used. A total of 29 additive QTLs and 17 epistasis were detected for 12 traits examined, among which eight and seven, respectively, were identified to have QTL × treatment effects. Physiological traits rather than biomass traits were more likely to be involved in QTL × treatment interactions. Ten intervals on chromosomes 1A, 1D, 2A (two), 2D, 3B, 4B, 5A, 5B and 7D showed overlapping QTLs for different traits; some of them represent a single locus affecting different traits and/or the same trait under both treatments. Eleven pairs of QTLs were detected on seemingly homoeologous positions of six chromosome groups of wheat, showing synteny among the A, B and D genomes. Ten pairs were detected in which each pair was contributed by the same parent, indicating a strong genetic plasticity of the QTLs. The results are helpful for understanding the genetic basis of salt tolerance in wheat and provide useful information for genetic improvement of salt tolerance in wheat by marker-assisted selection.

Keywords Epistasis · QTL × treatment · Salt tolerance · Quantitative trait locus (QTL) · Wheat

Abbreviations

CHL	Chlorophyll content (SPAD value)
MAS	Marker-assisted selection
N	Normal water treatment
QTL	Quantitative trait locus
$Q \times E$	QTL × environment
$Q \times T$	QTL × treatment
a	Additive
aa	Additive × additive
at	Additive × treatment
aat	Epistasis × treatment
RDW	Root dry weight
RIL	Recombinant inbred line
RKC	Root K^+ concentration
RKN	Root K^+/Na^+ concentration ratio
RL	Root length
RNC	Root Na^+ concentration
S	Salt stress treatment
SDW	Shoot dry weight
SH	Shoot height
SII	Salt injury index

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SKC Shoot K^+ concentration
SKN Shoot K^+/Na^+ concentration ratio
SNC Shoot Na^+ concentration
TDW Total dry weight

Introduction

Salinity is one of the major problems constraining crop production and food security worldwide (Pitman and Läuchli 2004). Understanding the genetic control of salt tolerance is the basis for breeding new crop plant cultivars with improved productivity in saline environments. Quantitative trait locus (QTL) analysis provides an effective means of dissecting quantitative traits into single components to study their relative impacts on a specific trait (Doerge 2002). Marker-assisted selection (MAS) based on QTL analysis can greatly facilitate crop improvement (Tuberosa and Salvi 2007). Many QTLs for salt tolerance have already been detected in barley (*Hordeum vulgare* L.) (Mano and Takeda 1997), rice (*Oryza sativa* L.) (Gong et al. 1999; Lee et al. 2006; Lin et al. 2004; Prasad et al. 2000; Takehisa et al. 2004), tomato (*Solanum lycopersicum* L.) (Foolad 1999; Foolad and Chen 1999; Foolad et al. 2001; Villalta et al. 2008) and arabidopsis (*Arabidopsis thaliana* L.) (Quesada et al. 2002).

Epistasis and QTL × environment ($Q \times E$) interaction are important genetic components. Most quantitative traits are greatly affected by either one of them or both (Xu and Crouch 2008). Epistasis and $Q \times E$ analyses have been conducted in rice (Cao et al. 2001; Fan et al. 2005; Liao et al. 2001; Liu et al. 2007; Xing et al. 2002), cotton (*Gossypium hirsutum* L.) (Shen et al. 2006; Wang et al. 2007), soybean (*Glycine max* L. Merr.) (Han et al. 2008), maize (*Zea mays* L.) (Ma et al. 2007b), wheat (*Triticum aestivum* L.) (Yang et al. 2007a; Zhang et al. 2008, 2009), and other plant species. Trials at different levels of salt stress also have been conducted to determine whether the expression of a trait is constitutive, and to identify salt stress-specific and non-stress-specific traits (Genc et al. 2010). However, differences in mapping results among various environment/treatment combinations have resulted in unreliable indications of the significance of $Q \times E$ (Jansen et al. 1995).

In saline field, the concentration of salt is nonuniform, which affects phenotyping greatly; and QTLs obtained under saline field conditions may be not exact for salt tolerance. Hydroponic experiments in different salt concentrations can ensure that the QTLs were definitely associated with the salt treatments. This can give us more accurate evidence to understand the genetic control of salt tolerance. Wheat is one of the most important food crops in the world. It is grown on 17% of all crop area worldwide and represents a staple food for 40% of the world's population (Gupta et al. 2008). QTL analysis for salt tolerance have been conducted in wheat at germination (Ma et al. 2007a), seedling stage (Genc et al. 2010; Lindsay et al. 2004; Ma et al. 2007a) and at maturity (Quarrie et al. 2005). There have been no reports on QTL analysis for salt tolerance in relation to the root traits of wheat. In the present study, morphological traits and physiological traits related to the roots and the shoots at seedling stage were investigated in a recombinant inbred line (RIL) population under salt stress and normal conditions to (1) study the relationships between the traits at seedling stage under salt stress, (2) detect QTLs with additive (*a*) and additive × additive (*aa*) epistatic effects, as well as their treatmental interactions (*at* and *aat*), and (3) analyze the differences between the roots and shoots in salt tolerance.

Materials and methods

Plant materials

A population of 182 F_{11} RILs derived from a cross between wheat cultivars Xiaoyan 54 and Jing 411 was used in this study. Xiaoyan 54 was derived from Xiaoyan 6, a cultivar that has been widely cultivated for the past 25 years in China. Xiaoyan 6 was derived from hybridization of wheat and *Thinopyrum ponticum* ($2n = 10x = 70$), and was characterized by high yield potential, wide environmental adaptability, and good bread-making quality (Li et al. 2008). Jing 411 was one of the main cultivars at the Northern Winter Wheat Region of China in the 1990s, and had been widely grown as much as 1.87 million ha.

Experimental design

The experiment was conducted in hydroponic culture under greenhouse condition at Center for Agricultural Resources Research, Institute of Genetics and

Developmental Biology, Chinese Academy of Sciences, Shijiazhuang, China, in November and December 2009. The 182 RILs and their parents were evaluated for salt tolerance at two salt concentrations: 0 (nil) and 150 mM NaCl, designated N treatment and S treatment, respectively. Each treatment had three replicates.

The seeds of each line were surface sterilized in 10% H_2O_2 for 5 min, rinsed with deionized water, and then allowed to germinate on filter paper in petri dishes containing distilled water for 7 days. The 18 most uniform seedlings of each genotype were selected, and their endosperms were removed. Then they were transplanted into plastic tanks, and fixed on the cover of the tanks using soft sponge rubber on 4.6 cm centers, with three seedlings for each genotype of each replicate. The tanks were opaque and each tank contained 62 L deionized water. Four days after transplanting, half-strength Hoagland's Nutrient Solution (Hoagland and Arnon 1950) was introduced, and increased to full-strength after 2 days. Three days later, NaCl was added to the solution twice daily over 3 days with an increment of 25 mM each time to a final concentration of 150 mM for the S treatment, while no NaCl was added for the N treatment. The solution was continuously aerated and renewed every 7 days; the pH was maintained at 6.0–6.2, and the air temperature ranged from 15 to 30°C. Tanks were randomly placed and rearranged every week.

Trait measurements

After being treated with 150 mM NaCl for 3 weeks, chlorophyll content (CHL) was measured using a leaf chlorophyll meter (SPAD-502 meter, Minolta, Osaka, Japan). Mean leaf CHL content for each genotype was derived from three readings taken at the base, middle and tip of the youngest fully expanded leaf for every seedling. A salt injury index (SII) was recorded using a scale of 1 for green leaves to 5 for leaf death (Liu et al. 2001). After 4 weeks growth in 150 mM NaCl the roots and the shoots were separately harvested, and rinsed with distilled water. Maximum root length (RL) and shoot height (SH) were recorded. The roots and shoots were then oven-dried at 80°C for 48 h and root (RDW) and shoot (SDW) dry weights were weighed. Total dry weights (TDW) were calculated as RDW + SDW. Harvested roots and shoots were digested in a 5 ml HNO_3 + 0.5 ml H_2SO_4 + 0.5 ml 60% TCA solution at 90°C for 5 min and the Na^+ and K^+ concentrations were determined with atomic absorption flame emission spectrophotometer (AA-6501F, SHIMADZU, Tokyo, Japan). The root K^+ (RKC), root Na^+ (RNC), shoot K^+ (SKC), shoot Na^+ (SNC) concentrations were determined.

Statistical and QTL analysis

Analysis of variance (ANOVA) of the data was performed using SPSS 16.0 software (SPSS Inc, Chicago, USA). Trait measurements were averaged over three replications prior to QTL analysis. The linkage map of the "Xiaoyan 54 × Jing 411" population was used in the QTL analysis. The map included 555 markers distributed on 21 wheat chromosomes, comprising 523 simple sequenced repeats (SSRs), 18 expressed sequence tag-SSRs (EST-SSRs) and 14 *Glu* loci. Mixed linear composite interval mapping was undertaken in the software QTLNetwork 2.1 to map QTLs with *a* and *aa* epistatic effects, as well as their treatmental interactions (*at* and *aat*) (Yang et al. 2007b, 2008). Composite interval analysis was undertaken using forward–backward stepwise, multiple linear regression with 1 cM walking speed, 2D genome scan, a probability into and out of the model of 0.05 and window size set at 10 cM. Significant thresholds for QTL detection were calculated with 1,000 permutations and a genome-wide error rate of 0.10 (suggestive) and 0.05 (significant). Multi-trait composite interval mapping (MCIM) (Jiang and Zeng 1995) was conducted using Windows QTL Cartographer 2.5 to detect the pleiotropic QTLs.

Results

Phenotypic variation and correlations among traits

Phenotypes of the RILs and their parents for traits related to seedling growth in the N and S treatments are summarized in Table 1. Xiaoyan 54 produced significantly higher values (8.98–28.67% greater) than Jing 411 for RKC in the N treatment, SDW and RKN in the S treatment, and RL, SH, RDW, TDW and SNC in both the N and S treatments. Jing 411 was significantly higher (9.12–26.51% greater) than Xiaoyan 54 for SKN in the N treatment, RNC in the S treatment, and CHL in both the N and S treatments.

Table 1 Phenotypic performance for traits related to seedling growth of recombinant inbred lines (RILs) and their parents determined in normal (N) and salt stress (S) treatments

Traits	Treatment	Parents		RILs				
		Xiaoyan 54	Jing 411	Mean	Min.	Max.	SD	CV (%)
Salt injury index, SII	S	2.2 ± 0.3	2.1 ± 0.3	2.2	1.0	3.3	0.4	16.5
Maximal root length, RL (cm)	N	19.3 ± 0.6	15.0 ± 0.5*	17.2	10.0	28.5	3.9	22.8
	S	17.8 ± 0.6	13.9 ± 0.5*	15.6	8.1	22.8	2.7	17.5
Shoot height, SH (cm)	N	30.0 ± 1.5	27.5 ± 1.1*	29.2	21.4	38.5	3.2	10.8
	S	23.4 ± 1.2	19.8 ± 1.1*	22.1	15.0	28.0	2.7	12.3
Root dry weight, RDW (g plant^{-1})	N	11.5 ± 0.9	9.4 ± 1.1*	9.6	6.1	14.7	1.6	16.9
	S	10.8 ± 1.0	8.7 ± 0.9*	10.1	5.3	15.4	1.7	17.2
Shoot dry weight, SDW (g plant^{-1})	N	45.5 ± 3.5	43.0 ± 2.8	42.4	21.4	66.6	8.2	19.4
	S	29.7 ± 2.0	26.9 ± 2.1*	30.1	16.7	45.3	5.2	17.4
Total dry weight, TDW (g plant^{-1})	N	57.0 ± 4.2	52.3 ± 3.6*	51.9	28.0	78.7	9.5	18.3
	S	40.5 ± 2.9	35.5 ± 2.9*	40.2	23.5	58.9	6.6	16.5
Chlorophyll content (SPAD value), CHL	N	28.1 ± 0.7	30.7 ± 0.8*	28.5	23.7	33.9	1.6	5.6
	S	29.5 ± 0.6	34.0 ± 0.4*	31.6	27.4	36.5	1.7	5.4
Root K^+ concentration, RKC (m mol g^{-1} DW)	N	1.136 ± 0.011	1.042 ± 0.017*	1.050	0.774	1.354	0.133	12.7
	S	0.401 ± 0.009	0.380 ± 0.005	0.375	0.255	0.553	0.064	17.1
Root Na^+ concentration, RNC (m mol g^{-1} DW)	N	0.076 ± 0.006	0.075 ± 0.004	0.065	0.041	0.104	0.011	17.1
	S	1.305 ± 0.096	1.424 ± 0.103*	1.393	0.929	1.744	0.144	10.4
Root K^+/Na^+ concentration ratio, RKN	N	14.23 ± 0.95	13.26 ± 0.54	15.33	9.51	23.47	3.11	20.3
	S	0.31 ± 0.02	0.28 ± 0.03*	0.27	0.17	0.49	0.06	21.9
Shoot K^+ concentration, SKC (m mol g^{-1} DW)	N	1.941 ± 0.029	1.966 ± 0.021	1.966	1.676	2.295	0.133	6.7
	S	1.161 ± 0.022	1.082 ± 0.031	1.159	0.879	1.464	0.122	10.5
Shoot Na^+ concentration, SNC (m mol g^{-1} DW)	N	0.072 ± 0.003	0.059 ± 0.003*	0.065	0.030	0.106	0.014	21.9
	S	1.486 ± 0.091	1.335 ± 0.092*	1.494	0.877	2.824	0.382	25.6
Shoot K^+/Na^+ concentration ratio, SKN	N	27.50 ± 1.10	34.79 ± 2.96*	31.27	15.46	51.66	7.64	24.4
	S	0.79 ± 0.03	0.82 ± 0.03	0.85	0.28	1.59	0.27	31.5

* The parents were significantly different at the 0.05 probability level

The two parents showed little difference for SDW, RNC and RKN in the N treatment, for SII, RKC and SKN in the S treatment, and for SKC in both the N and S treatments.

The phenotypic values for the traits exhibited wide ranges among the 182 RILs, with the coefficient of variation (CV) higher than 10% for all traits except for CHL in both the N and S treatments and SKC in the N treatment (Table 1). Treatment effects were observed for all the traits, the RILs mean values in the N treatment were higher than that in the S treatment for RL, SH, SDW, TDW, RKC, RKN, SKC and SKN, but lower for RDW, CHL, RNC and SNC (Table 1). The frequency distributions of all the traits showed continuous variation and significant transgressive segregation in both directions (Table 1), which might be attributed to the polygenic inheritance of the traits.

The SII showed significantly positive correlation with SNC ($r = 0.44$, $P \leq 0.01$), but negative correlations with SKC ($r = -0.44$, $P \leq 0.01$), SKN ($r = -0.43$, $P \leq 0.01$), CHL ($r = -0.28$, $P \leq 0.01$) and the biomass traits ($-0.41 \leq r \geq -0.30$, $P \leq 0.01$) in the S treatment (Table 2). SNC was negatively correlated with the biomass traits in both the N and S treatments, while SKC and SKN were positively correlated with the biomass traits (Table 2). These

Table 2 Correlation coefficients among traits related to seedling growth in N (below diagonal) and S (above diagonal) treatments

	RL	SH	RDW	SDW	TDW	CHL	RKC	RNC	RKN	SKC	SNC	SKN
SII	−0.32**	−0.30**	−0.38**	−0.39**	−0.41**	−0.28**	−0.12	0.11	−0.11	−0.44**	0.44**	−0.43**
RL		0.21**	0.65**	0.35**	0.45**	0.26**	−0.06	0.07	−0.10	0.33**	−0.17*	0.26**
SH	0.03		0.44**	0.66**	0.64**	0.14	0.35**	−0.07	0.32**	0.53**	−0.53**	0.55**
RDW	0.52**	0.32**		0.74**	0.85**	0.34**	−0.06	0.06	−0.09	0.45**	−0.36**	0.42**
SDW	0.22**	0.70**	0.72**		0.98**	0.29**	0.29**	0.05	0.19*	0.59**	−0.39**	0.47**
TDW	0.28**	0.67**	0.80**	0.99**		0.32**	0.21**	0.06	0.13	0.58**	−0.40**	0.49**
CHL	0.13	−0.06	0.22**	0.12	0.14		−0.14	−0.02	−0.11	0.14	−0.19*	0.23**
RKC	0.05	0.40**	0.20**	0.39**	0.37**	−0.08		−0.10	0.86**	0.43**	−0.30**	0.35**
RNC	−0.21**	−0.03	−0.22**	−0.05	−0.08	−0.06	0.18*		−0.54**	−0.04	0.38**	−0.26**
RKN	0.21**	0.31**	0.32**	0.32**	0.33**	0.02	0.50**	−0.73**		0.33**	−0.41**	0.38**
SKC	0.20**	0.45**	0.43**	0.62**	0.61**	−0.21**	0.36**	0.04	0.19*		−0.58**	0.79**
SNC	−0.18*	−0.30**	−0.46**	−0.48**	−0.50**	−0.10	−0.20**	0.24**	−0.36**	−0.37**		−0.90**
SKN	0.29**	0.36**	0.56**	0.55**	0.57**	0.00	0.23**	−0.22**	0.38**	0.55**	−0.90**	

* Significant at the 0.05 probability level

** Significant at the 0.01 probability level

results indicated that SNC is a major factor constraining salt tolerance and biomass production, while improved SKC and SKN facilitated salt tolerance of the seedlings. In the S treatment, SKC showed a strong negative correlation ($r = -0.58$, $P \leq 0.01$) with SNC, indicating a competition relationship between K^+ and Na^+. Finally, SNC, SKC and SKN of the shoots were significantly correlated with SII and the biomass traits; while the corresponding traits of roots, RNC, RKC, and RKN had no significant or rather weak correlations with SII and the biomass traits (Table 2). This indicated the mechanisms controlling salt stress in the shoots and roots are different.

QTL with additive and additive × treatment interaction effects

A total of 29 QTLs for 11 traits were detected on 14 chromosomes (Table 3; Fig. 1). Twenty-one of the QTL had only *a* effects, while eight had both *a* and *at* effects. The QTL explained 0.21–14.75% of the phenotypic variation (Table 3).

Four and three QTLs were detected for RL and SH, respectively; and three, one and two QTLs in four chromosomal intervals were detected for RDW, SDW and TDW, respectively. The QTLs *QRl-7B* and *QSh-4B* were detected with significant *at* effects. Both Xiaoyan 54 and Jing 411 alleles contributed to the *a* and/or *at* effects of biomass traits, suggesting that the alleles for increased biomass production were dispersed in the two parents, which may have resulted in the observed transgressive segregations (Table 1). The locus *QRl-5A* was co-located with *QRdw-5A*, which also had a negative *a* effect. Two pairs of QTLs, *QRdw-2D* and *QTdw-2D*, contributed by Xiaoyan 54, and *QSdw-2A* and *QTdw-2A*, contributed by Jing 411 were co-located. The QTL *QRdw-3B2* was co-located with *QSkc-3B*, both contributed by Jing 411 (Table 3; Fig. 1).

Only one QTL was identified for CHL, which was contributed by Xiaoyan 54 allele on chromosome 5B. The QTL accounted for 5.11% of the phenotypic variation.

Four, two and three QTLs were detected for RKC, RNC and RKN, respectively. The QTLs *QRkc-5A1* and *QRkc-5B* for RKC, and *QRkn-5B* and *QRkn-7D* for RKN were with significant *at* effects. Both the Xiaoyan 54- and Jing 411-derived alleles contributed

Table 3 QTLs with additive effects (*a*) and additive × treatment interaction effects (*at*) detected at seedling stage in the N (t_1) and S (t_2) treatments

Traits	QTLs	Marker intervals[a]	Site[b] (cM)	*a*[c]	h^2 (*a*)	at_1	at_2	h^2 (*at*)
RL	*QRl-1B*	*Xgwm153-Xgwm274.1*	0	0.88***	6.76			
	QRl-5A	*Xag24.1-Xgwm443.1*	5	−1.11***	9.53			
	QRl-6A	*Xgwm570-Xgwm169.2*	16	1.21***	1.39			
	QRl-7B	*Xgwm297-NP43*	0	1.34***	14.75	0.41*	−0.41*	1.50
SH	*QSh-4A*	*Xbarc190-Xbarc237*	0	−0.67***	7.13			
	QSh-4B	*Xgwm192.1-Xbarc20*	3	−0.71***	6.79	−0.40*	0.40*	1.97
	QSh-5A	*Xgwm156.1-Xgwm328*	15	1.63***	14.63			
RDW	*QRdw-2D*	*Xcfd53-Xwmc112*	0	0.51***	8.05			
	QRdw-3B2	*Xbarc251-Xbarc164*	0	−0.44***	7.58			
	QRdw-5A	*Xag24.1-Xgwm443.1*	2	−0.22**	4.22			
SDW	*QSdw-2A*	*Xgwm294-Xwmc181*	11	−1.38***	5.50			
TDW	*QTdw-2A*	*Xgwm294-Xwmc181*	11	−1.71***	4.51			
	QTdw-2D	*Xcfd53-Xwmc112*	0	1.61***	5.23			
CHL	*QChl-5B*	*Xgwm639.1-Xwmc388.4*	0	−0.23**	5.11			
RKC	*QRkc-1D*	*Xbarc169-Xbarc162*	0	−0.013**	1.08			
	QRkc-5A1	*Xbarc151-Xgwm666.1*	0	−0.013**	0.21	−0.015*	0.014*	0.87
	QRkc-5A3	*Xswes157-Xswes182*	0	0.017***	6.73			
	QRkc-5B	*Xgwm133.2-Xgwm274.2*	2	0.048***	14.33	0.028***	−0.027***	3.94
RNC	*QRnc-2B*	*Xcfd73.1-TC311989*	1	−0.017**	3.60			
	QRnc-3B	*Xbarc147-Xgwm493*	9	−0.018**	2.92			
RKN	*QRkn-4B*	*Xbarc193-TC246843*	0	−0.34**	4.64			
	QRkn-5B	*Xgwm133.2-Xgwm274.2*	3	0.42***	4.05	0.39**	−0.38**	4.09
	QRkn-7D	*Xgwm44-Xbarc245*	10	−0.50***	3.95	−0.46**	0.47**	4.16
SKC	*QSkc-2B*	*Xbarc1155-Xag24.2*	9	−0.039***	7.98			
	QSkc-3B	*Xbarc251-Xbarc164*	0	−0.023***	2.86			
	QSkc-4B	*Xbarc193-TC246843*	2	−0.037***	5.99			
	QSkc-6A	*Xbarc1055-Xbarc146.1*	0	0.037***	6.24			
SNC	*QSnc-5A*	*Xgwm443.1-Xcfa21041*	1	−0.042**	2.38	0.037*	−0.037*	2.50
	QSnc-7A	*Xbarc257.1-Xbarc121*	5	0.044**	2.97	−0.040*	0.040*	3.91

*, **, *** Significant at 0.05, 0.01, 0.001 probability levels, respectively

[a] Marker interval means the interval of the *F value* peak for QTLs

[b] Site means the distance of *F value* peak for QTL after the first marker in the marker interval

[c] Positive effect, increased effect contributed by Xiaoyan 54; negative effect was contributed by Jing 411

to the QTLs for RKC and RKN, while the Jing 411-derived alleles contributed to the QTLs for RNC. The QTLs *QRkc-5B* and *QRkn-5B* were co-located and had similar *a* and *at* effects; while *QRkn-4B* co-located with *QSkc-4B*, both contributed by Jing 411 allele.

Four and two QTLs were detected for SKC and SNC, respectively. Positive alleles for the QTLs were derived from both the Xiaoyan 54 and Jing 411 alleles. The two QTLs for SNC were detected to have significant *at* effects.

QTLs with epistasis and epistasis × treatment interaction effects

Seventeen pairs of QTLs with digenic effects were detected for ten traits on 19 chromosomes (Table 4; Fig. 1). Among them, seven were with significant *aat*

effects. These epistatic effects explained 1.78–8.51% of the phenotypic variation (Table 4).

Two epistasis were detected for RL. The *QRl-1B/QRl-5A* epistasis increased RL by 0.56 (cm) in the recombination type $Q_1Q_1q_2q_2$. The *QRl-1D/QRl-6B* epistasis was detected to have *aat* effect, with parental type $Q_1Q_1Q_2Q_2$ increased RL by 1.25 cm in the N treatment, but only by 0.21 cm in the S treatment. The recombinant type $q_1q_1Q_2Q_2$ decreased RL at both the two loci.

Five epistasis were identified for RDW, SDW, and TDW. The parental type $Q_1Q_1Q_2Q_2$ increased RDW (*QRdw-2A/QRdw-3B1* epistasis), SDW (*QSdw-5B/QSdw-5D* epistasis), and TDW (*QTdw-1A/QTdw-3A* and *QTdw-1D/QTdw-4B* epistasis), but decreased SDW with the *QSdw-2D/QSdw-5A* epistasis (Table 4). The recombinant type $q_1q_1Q_2Q_2$ had the reverse effects of $Q_1Q_1Q_2Q_2$.

For CHL, three epistasis (*QChl-1D/QChl-4A*, *QChl-2A/QChl-4D* and *QChl-6B/QChl-6D*) were detected. The CHL values were increased by 0.46–0.48 in the parental type $Q_1Q_1Q_2Q_2$, but decreased in the recombination type $q_1q_1Q_2Q_2$.

Seven epistasis were identified for traits related to K^+ and Na^+ concentrations, with six had significant *aat* effects. The parental type $Q_1Q_1Q_2Q_2$ resulted in increased RKC in the *QRkc-5A1/QRkc-5B* epistasis, while the recombination type $Q_1Q_1q_2q_2$ had the negative effect. Significant *aat* effects were detected in the *QRkc-5A2/QRkc-7B*, *QRnc-2A/QRnc-7D*, *QRkn-2B/QRkn-2D*, *QSnc-2D/QSnc-3D*, *QSkn-1A/QSkn-3A* and *QSkn-3B/QSkn-3D* epistasis (Table 4). The parental type $Q_1Q_1Q_2Q_2$ increased RKC, SNC and SKN, but decreased RNC and RKN due to *aat* effects.

MCIM analysis for QTL clusters

Among the QTLs, 21 out of the 29 additive QTLs and 10 out of the 17 epistasis were detected to have no $Q \times T$ effects (Tables 3, 4); indicating that the QTLs can affect the traits in both the N and the S treatments. Furthermore, ten intervals on chromosomes 1A, 1D, 2A (two), 2D, 3B, 4B, 5A, 5B and 7D showed overlapping QTL regions for at least two traits (Fig. 1). MCIM analysis using individual treatment data indicated 14 intervals that associated with more than one QTL on chromosomes 1B, 2D, 4B, 5A, 5B, 7A, 7B and 7D (Table 5). Eleven intervals on chromosomes 1B, 2D, 4B, 5A, 5B, and 7B can affect at least one trait in both the N and S treatments, while eleven intervals on chromosomes 2D, 4B, 5A, 5B, 7A, 7B and 7D were associated with more than one trait.

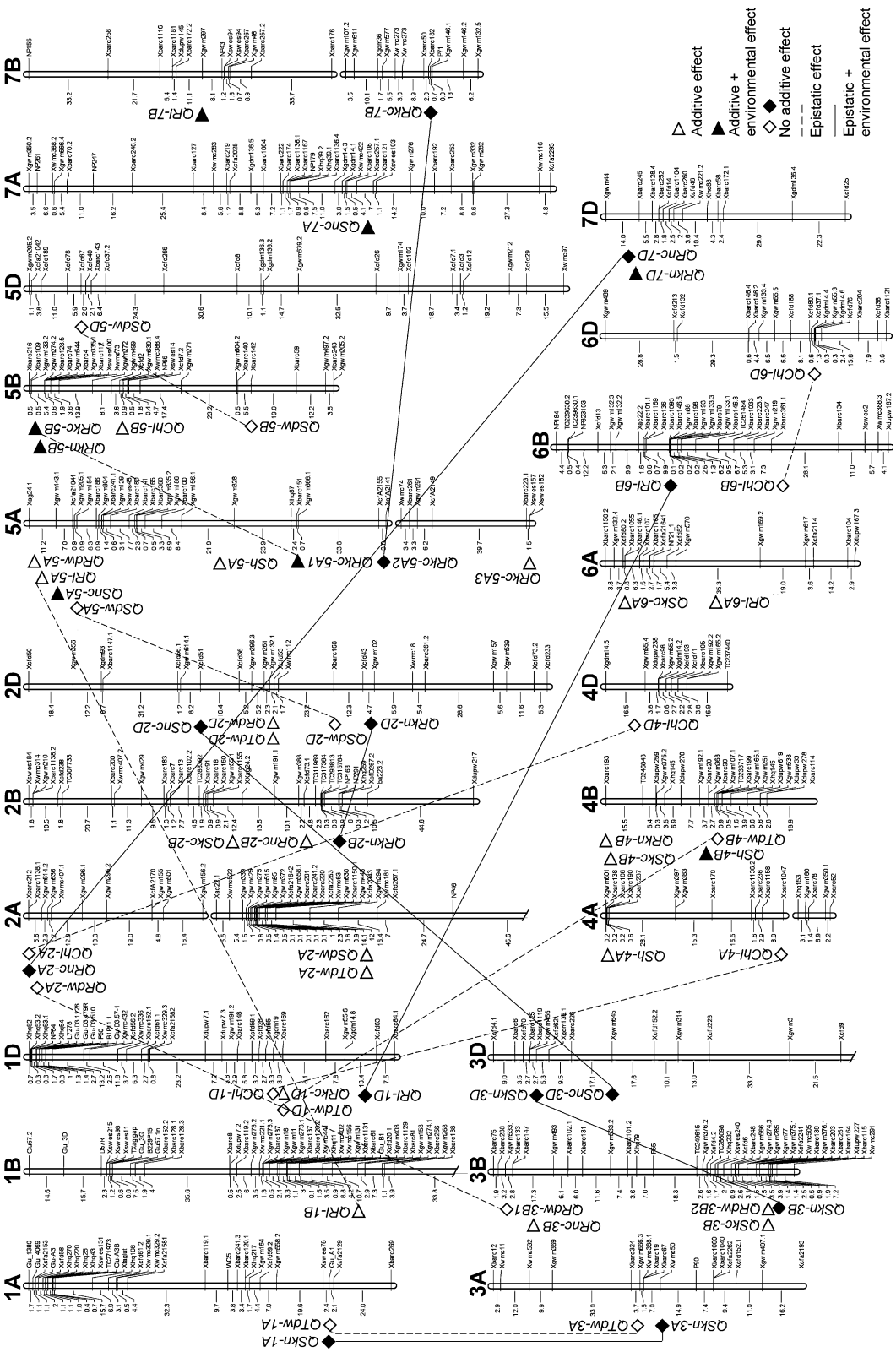
The interval *Xcfd53-Xwmc112* on chromosome 2D for biomass production was the most significant of overlapping QTLs. It can affect RDW, TDW and RL with LOD scores more than 2.5; while affect SDW and SKC with lower LOD scores (Table 5; Fig. 2). Furthermore, it was also associated with plant height, spike length and kernel weight per spike at various environments in field experiments (Wang et al. unpublished). The RILs were divided into Xiaoyan 54 and Jing 411 genotype classes according to the presence of the co-segregation marker *Xcfd53*. The two genotype classes were significantly different for RDW, SDW and TDW in both the N and S treatments (Fig. 3).

Discussion

Relationships between the traits and salt tolerance

Appropriate traits and efficient techniques are necessary for identifying salt tolerance. Both morphological traits and physiological traits can be used as indicators for salt tolerance. A detailed list of traits and techniques used to evaluate salt tolerance was summarized (Munns and James 2003). The Na^+ concentration and K^+/Na^+ ratio were critical measures of salt tolerance in plants (Munns and Tester 2008; Tester and Davenport 2003). The K^+/Na^+ ratio was regarded as the most important determinant of salt tolerance (Chhipa and Lal 1995; Pardo 2010; Shavrukov et al. 2009).

In our study, all the biomass traits and some of the physiological traits (CHL, SNC, SKC and SKN) were significantly correlated with SII, indicating the traits can be used for evaluating salt tolerance. The Na^+ exclusion from the shoots, K^+ accumulation in the shoots, and increased K^+/Na^+ ratio can improve salt tolerance of wheat. The element Na^+ inhibits K^+ uptake and competes with K^+ for binding sites in enzymes due to their physicochemical similarity, and may result in cytotoxicity (Pardo 2010; Qi and Spalding 2004; Rodriguez-Navarro and Rubio 2006; Serrano 1996). In our study, SKC and SNC were negatively correlated ($r = -0.58$, $P \leq 0.01$) in the S


Additive effect
Additive + environmental effect
No additive effect
Epistatic effect
Epistatic + environmental effect
1A
1B
1D
2A
2B
2D
3A
3B
3D
4A
4B
4D
5A
5B
5D
6A
6B
6D
7A
7B
7D
QSkn-1A
QTdw-1A
QSkn-3A
QTdw-3A
QRkn-2D
QSdw-2D
QTdw-2D
QOrnc-2D
QSsc-2D
QRkn-2B
QTdw-2B
QOrnc-2B
QSsc-2B
QRkn-2A
QSdw-2A
QTdw-2A
QOrnc-2A
QChl-2A
QRkn-1D
QTdw-1D
QOrnc-1D
QChl-1D
QRkn-1B
QOrnc-3B
QRdw-3B1
QSkn-3B
QSkc-3B
QRdw-3B2
QSkn-3D
QSnc-3D
QRkn-4A
QSkn-4A
QTdw-4A
QChl-4A
QRkn-4B
QTdw-4B
QSkc-4B
QSh-4B
QChl-4B
QRkn-4D
QChl-4D
QRkn-5A
QRdw-5A
QRl-5A
QSdw-5A
QSnc-5A
QRkc-5A1
QRkc-5A2
QRkc-5A3
QSh-5A
QRkn-5B
QRkc-5B
QChl-5B
QSdw-5B
QRkn-5D
QSdw-5D
QRkn-7D
QRnc-7D
QChl-6D
QRl-6B
QChl-6B
QSkc-6A
QRl-6A
QRkn-7A
QSnc-7A
QRkc-7B
QRl-7B

◀**Fig. 1** Locations of QTLs for traits related to seedling growth in N and S treatments based on RILs derived from Xiaoyan 54 × Jing 411. QTLs are indicated on the *left side* of each chromosome; markers are shown on the *right*

treatment, indicating that the uptake of K^+ may restrain the uptake of Na^+. A similar competition relationship between shoot K^+ and Na^+ under salt stress was found in rice (Lin et al. 2004).

Relationships between additive, epistatic and $Q \times T$ QTLs

Previous studies have demonstrated that the epistatic and $Q \times E$ interactions were prevalent in quantitative trait inheritance (Doebley et al. 1995; Yu et al. 1997). QTLs with epistatic and $Q \times E$ effects have been detected for plant height (Zhang et al. 2008), heading

Table 4 QTLs with epistatic effects (*aa*) and epistatic × treatment interaction effects (*aat*) detected at seedling stage in the N (t_1) and S (t_2) treatments

Traits	QTL i	Marker intervals[a]	Site[b] (cM)	QTL j	Marker intervals	Site (cM)	*aa*[c]	h^2 *(aa)*	aat_1	aat_2	h^2 *(aat)*
RL	*QRl-1B*	*Xgwm153-Xgwm274.1*	0	*QRl-5A*	*Xag24.1-Xgwm443.1*	5	0.56**	1.87			
	QRl-1D	*Xgdm14.8-Xcfd63*	8	*QRl-6B*	*Xgwm88-Xbarc198*	0	0.73***	3.71	0.52*	−0.51*	1.84
RDW	*QRdw-2A*	*Xbarc1138.1-Xgwm614.2*	3	*QRdw-3B1*	*Xgwm533.1-Xbarc133*	0	0.44***	3.84			
SDW	*QSdw-2D*	*Xbarc168-Xcfd43*	0	*QSdw-5A*	*Xgwm154-Xbarc186*	0	−1.99***	6.01			
	QSdw-5B	*Xbarc142-Xbarc59*	0	*QSdw-5D*	*Xcfd67-Xcfd40*	0	2.51***	8.00			
TDW	*QTdw-1A*	*Glu A1-Xcfa2129*	0	*QTdw-3A*	*Xbarc324-Xgwm666.3*	3	2.40***	7.52			
	QTdw-1D	*Xbarc169-Xbarc162*	0	*QTdw-4B*	*TC233717-Xbarc199*	0	2.27***	6.37			
CHL	*QChl-1D*	*Xgdm19-Xbarc169*	0	*QChl-4A*	*Xbarc1158-Xbarc1047*	8	0.46***	6.59			
	QChl-2A	*Xbarc1138.1-Xgwm614.2*	0	*QChl-4D*	*Xgdm14.5-Xgwm55.4*	12	0.47***	6.00			
	QChl-6B	*Xbarc361.1-Xbarc134*	4	*QChl-6D*	*Xgdm14.4-Xgwm55.3*	0	0.48***	8.51			
RKC	*QRkc-5A1*	*Xbarc151-Xgwm666.1*	0	*QRkc-5B*	*Xgwm133.2-Xgwm274.2*	2	0.018***	1.95			
	QRkc-5A2	*Xcfa2155-Xcfa2141*	2	*QRkc-7B*	*P71-Xgwm146.1*	0	0.022***	3.23	0.016**	−0.016**	1.78
RNC	*QRnc-2A*	*Xbarc1138.1-Xgwm614.2*	0	*QRnc-7D*	*Xgwm44-Xbarc245*	8	−0.028***	2.61	0.025*	−0.024*	3.23
RKN	*QRkn-2B*	*NP291-Xlhq259*	0	*QRkn-2D*	*Xcfd43-Xgwm102*	3	−0.723***	5.82	−0.66***	0.70***	5.43
SNC	*QSnc-2D*	*Xcfd51-Xcfd36*	0	*QSnc-3D*	*Xbarc226-Xgwm645*	17	0.063***	3.97	−0.059**	0.061**	3.36
SKN	*QSkn-1A*	*Xswes78-Glu A1*	2	*QSkn-3A*	*Xwmc50-P90*	1	1.05***	4.45	0.93*	−0.93*	4.23
	QSkn-3B	*Xbarc115-Xwmc291*	0	*QSkn-3D*	*Xcfd62-Xgdm136.1*	0	1.18***	6.02	1.06**	−1.11**	5.14

*, **, ***, [a] and [b] can refer to Table 3

[c] Positive effect, increased effect contributed by the parental type; negative effect was contributed by the recombination type

Table 5 Chromosomal intervals associated with seedling traits in the N and S treatments, detected by multi-trait composite interval mapping (MCIM)

Chromosomes	Marker intervals	Traits (Treatments)
1B	*Xbarc81-Xgwm153*	RL (N), RL (S)
2D	*Xcfd53-Xwmc112*	RDW (N), RDW (S), TDW(N), TDW (S), RL(S)
2D	*Xgwm539-Xcfd73.2*	RNC (S), RKN (S)
4B	*Xbarc193-TC246843*	SH (N), RKC (N), RKC (S), SKC (S), RKN (N)
4B	*Xgwm375.2-Xlhq145*	SH (N), RKC (N), RKC (S), RKN (N), RKN (S)
4B	*Xbarc20-Xgwm107.1*	SH (N), RKC (N), RKC (S), RKN (S),
5A	*Xag24.1-Xgwm443.1*	RL (N), RL (S)
5A	*Xgwm156.1-Xgwm328*	SH (N), SH (S)
5A	*Xswes157-Xswes182*	RKC (N), RKC (S), RKN (S),
5B	*Xgwm133.2-Xgwm274.2*	SH (N), SH (S), RKC (N), RKN (N)
5B	*Xswes14-Xcfd7.2*	RKC (N), RKC (S), RKN (S)
7A	*Xswes103-Xgwm276*	SH (S), SNC (S)
7B	*Xbarc172.2-Xgwm197*	RL (N), RL (S), RDW (N)
7D	*Xgwm44-Xbarc245*	RNC (N), RKN (N)

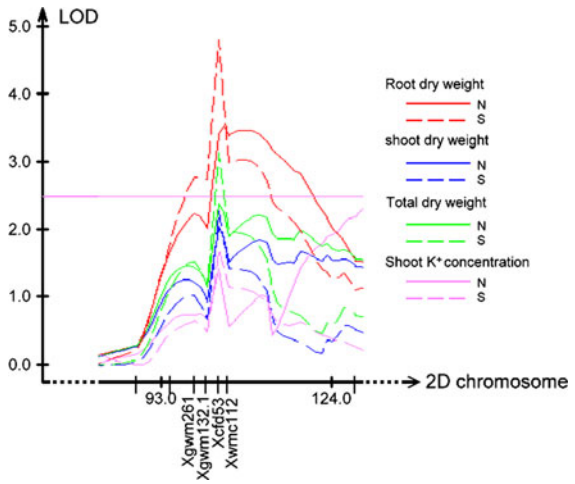


Fig. 2 The QTL cluster on chromosome 2D for biomass production. QTLs are indicated as LOD curves. N and S represent normal condition and salt stress treatments, respectively

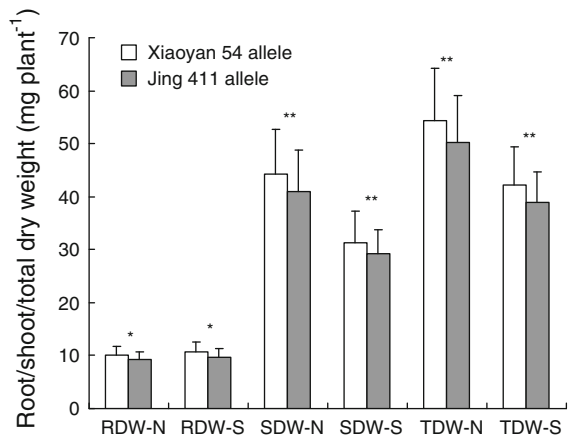


Fig. 3 Mean root dry weight (RDW), shoot dry weight (SDW) and total dry weight (TDW) for genotype classes of Xiaoyan 54 allele and Jing 411 allele at *Xcfd53* on chromosome 2D. N and S represent normal condition and salt stress treatments, respectively. *Error bars* are the standard error of the means. * and ** represent the two genotype classes were significantly different at 0.05 and 0.01 probability levels, respectively

data (Zhang et al. 2009) and water-soluble carbohydrates (Yang et al. 2007a) in wheat. Trials at different levels of salt stress have also been conducted in wheat to compare QTL expression under different salinity levels (Genc et al. 2010). But there have been no reports on epistatic and $Q \times E$ or $Q \times T$ interactions for salt tolerance in wheat.

Among the 29 additive QTLs detected in our study, four were involved in digenic effects. Eight out of the 29 additive QTLs and seven out of the 17 epistasis were identified to have significant $Q \times T$ interactions. For traits related to Na^+, K^+ concentrations and K^+/Na^+ ratio, six out of the 15 additive QTLs and six out of the seven epistatic QTLs were involved in significant $Q \times T$ interactions. But none of the QTLs for biomass production were involved in $Q \times T$ interaction. These results showed that additive and epistatic effects were common, but the physiological traits rather than biomass traits are more likely to be involved in $Q \times T$ interactions at seedling stage of wheat. This could be due to traits related to Na^+, K^+, especially Na^+ concentration had greater differences

between the N and S treatments than biomass traits (Table 1).

QTL co-location and trait correlation

QTL clusters and/or co-located QTLs for different traits were reported in many previous studies (Groos et al. 2003; Li et al. 2007; Marza et al. 2006; Quarrie et al. 2005; Sun et al. 2009). Ma et al. (2007a) found four clusters on chromosomes 4D, 3A, 3B and 6D for traits related to salt tolerance. Genc et al. (2010) detected eight loci on chromosomes 1A, 4B, 5A, 5B, 5D, 6A, 6D and 7A that related to at least two QTLs for different traits.

In the present study, ten loci on chromosomes 1A, 1D, 2A (two), 2D, 3B, 4B, 5A, 5B and 7D were detected to affect more than one trait. For each of the ten loci, the correlations between the traits related were consistent with the additive effects of the corresponding QTLs. Among them, seven loci had similar additive effect for the two traits related, and the correlation coefficients between the two traits were significant and positive. As has been previously noted, each cluster may represent a single locus or tightly linked loci (Ma et al. 2007a; Paterson 1995; Veldboom et al. 1994). MCIM analysis indicated 14 chromosome intervals that affect more than one trait or at least one trait in both the N and S treatments. The QTL clusters on chromosomes 2D, 4B, 5B and 7D were detected to be single loci that affect more than one trait. The closely linked marker *Xcfd53* for the QTL that affect both seedling and maturity biomass/yield traits on chromosome 2D was effective in MAS.

Homoeologous QTLs

Traits may be controlled by homoeologous genes from different chromosomes due to the allopolyploid nature of the wheat genome. Homoeologous QTLs were reported in both hexaploid (Kumar et al. 2007; Quarrie et al. 2005, 2006) and tetraploid wheat (Peleg et al. 2009). For salt tolerance, homoeologous regions have been reported for SII at germination and seedling stage (Ma et al. 2007a) and yield at adult stage under salt stress (Quarrie et al. 2005) on group 5 of wheat. In the present study, 11 pairs of such QTLs were detected on six chromosome groups of wheat, i.e., group 1 for TDW and RL, group 2 for TDW, SDW and RKN, group 3 for SKN, group 4 for SH and CHL, group 5 for RKC, and group 6 for RL and CHL (Fig. 1). The high ratio of homoeologous QTLs is a great reflection of the synteny among the A, B and D genomes of wheat. Among the homoeologous QTLs, each of ten pairs was contributed by a same parent, indicating a strong genetic plasticity of the QTLs.

Salt tolerance differences between the shoots and the roots

Previous QTL analysis for salt tolerance at seedling stage focused on shoots traits; there was only one study in rice that referred to root traits, which suggested that there was a different genetic basis for salt tolerance of Na^+ and K^+ transportation between the shoots and roots (Lin et al. 2004). In our study, three intervals on chromosomes 3B, 4B and 5A were effective for both shoot traits and root traits, among which the interval on chromosome 5A affected the corresponding trait (dry weight) of the shoots and the roots.

The QTLs identified in this study, especially those with epistatic effects and $Q \times T$ interactions, facilitate better understanding of the genetic basis of salt tolerance at seedling stage, and may facilitate further functional analysis of salt tolerance genes in wheat. The molecular markers closely linked to the QTLs provide useful information for the MAS in wheat breeding.

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