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The Performance of Single Chromosome Substitution Lines of Bread Wheat Subjected to Salinity Stress

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The parents (the landrace Chinese spring (CS) and a synthetic hexaploids (S6x)) and 17 derived single chromosome substitution lines (SL) were grown in parallel in the field under non-saline (1.0 dSm^{-1}) and saline (12.0 dSm^{-1}) conditions, and evaluated for a set of phenotypic traits. The performance of CS indicated it to have borderline salinity tolerance with respect to all of the traits except for leaf area (for which it behaved in as a salinity sensitive type). The SL 4D was early in booting, ear emergence, flowering and maturity, while 5D and 2B SLs were both late. The 2B SL produce 33% more ears than CS. The 5D SL under-performed with respect to ear weight, grain number per ear, grain weight per ear and 1000-grain weight both under non-saline and saline conditions. Under saline conditions, four SLs (1A>5A>1D>2B) outperformed Cs for ear length, and six SLs (1D>6A>4B>3A>3B>3D) showed an improved grain weight. The grains produce by the 2B SL were smaller than those of CS. Leaf area developed better in four SLs (4D>2B>1A>7D) than in CS.

Keywords: bread wheat, synthetic hexaploids, substitution lines, salinity

Introduction

Soil salinity represents an important constraint on crop productivity, so an important priority in crop improvement programmes is to identify salinity tolerant materials in order to return arable land affected by salinity to production. Several attempts have been made to screen for salinity tolerance in bread wheat germplasm (Ashraf and O'Leary 1996; Díaz De León et al. 2000), as well as among the wild relatives of wheat with a view to obtaining introgression following wide crossing (Mujeeb-Kazi and Díaz De León 2002).

Chromosome substitutions amongst bread wheat, durum wheat and wild relatives of wheat provide an effective mean of analyzing the genetics of quantitative characters as successfully has been proven with *Kna1* gene mapped on 4DL (Dvořák and Gorham 1992; Dvořák et al. 1994). The bread wheat landrace Chinese spring (CS) has been an ideal parental line to use for chromosome substitution or introgression lines (King et al. 1996;

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Pestsova et al. 2006). CS itself has been variously classified as comparatively salinity tolerant (Díaz De León et al. 2010) or having borderline tolerance (Galiba et al. 1993; Díaz De León et al. 1995). Here, we have exploited an established near complete set of single chromosome substitution lines, in which the chromosomes of CS have been replaced by their homologues from a synthetic hexaploid line, in order to explore the inheritance of salinity stress tolerance in CS and the synthetic hexaploid.

Materials and Methods

Plant material

We used a set of 17 substitution lines CS/"Synthetic 6x" (SL) in which single chromosomes of CS were replaced by homologous chromosomes of "Synthetic 6x" (S6x).

The substitution lines were produced by C.N. Law and A.J. Worland at the John Innes Centre, UK (Arraiano et al. 2001). The progenitor S6x had been obtained by McFadden and Sears (1947) from a cross *T. dicoccoides* var. *spontaneovillosum* × *Aegilops squarrosa* ssp. *eusquarrosa,* as described by Pestsova et al. (2006).

Agronomic phenotyping

The set of 17 SLs and parents were evaluated against salinity in sandy-loam soils of the experimental site of the Universidad Autónoma de Baja California Sur (UABCS), at La Paz, Baja California Sur, México, and under the influence of a climate classified as type Bwh (very warm and dry) as described elsewhere (Díaz De León et al. 2000). Fifty seeds of each genotype were sown in 1 m rows within a 5 × 4 m (20 m^2) plots. Seeds were 2 cm apart in rows that were apart 30 cm. Three rows were sown for each genotype. The genotypes were subjected to two electrical conductivity (EC) treatments: 1.0 dSm^{-1} (no salinity) and 12 dSm^{-1} (salt stress). Treatment without salinity was achieved by irrigation with potable water. For the salinity treatment, sea water was diluted with well-water (EC 4.5 dSm^{-1}) up to a EC of 12 dSm^{-1} and then used for irrigating the plots it respective with 400 liters twice a week. After one week of plant growth all plots were fertilized with 15 g of urea per week up to 8 weeks. Soil EC was determined by examining random samples taken from each plot 24 hours after irrigation. Soil EC determinations followed standard extraction procedures of soil sampling/plot at random points, measuring fresh soil weight, drying of samples at room temperature, taking 100 g sample/plot, extraction of soluble salts with 30 ml distilled water and reading the EC levels (Orion brand conductivity meter). If soil salinity was above the desired EC, in the next irrigation these plots were washed with potable water and then five hours later irrigated with the salinity treatment.

Growth and developmental stages were recorder as: % of survival *(Sp)* at 30 days (in relation to germinated seeds), days to booting *(B),* leaf area (determined by measuring base wide and length of flag leaf) *(La),* days to flowering *(F),* days to ear emergence *(Ee),* days to physiological maturity *(M),* ear per plant *(Enu),* height *(Ht);* and yield components as: ear weight *(Ew),* ear length *(El)* number of grains per ear *(Gnu),* weight of grain per ear *(Gw)* and 1000-grain weight *(Tgw)*.

Statistical analysis

The data were analyzed by one-way ANOVA, two-way ANOVA and paired *t*-test using the SigmaPlot statistics software (SigmaPlot for Windows Version 11.0).

Results

The performance of CS showed that it was only marginally salinity tolerant. All the plant traits assessed were reduced by about 25%, except for leaf area which was reduced by 50% (Table 1). S6x did not reach flowering under these conditions, as it requires vernal-

Table 1. The performance of CS under salinity stress. Values represent the mean of three replicates. T1 = 1.0 dSm^{-1} and T3 = 12.0 dSm^{-1}. A trait ratio between T1 and T3 was 0.75–1.0 reflects salinity tolerance; 0.60–0.74 medium tolerance; 0.00–0.59 sensitive

Traits	Treatment					
	T1	T3	T3/T1	T1	T3	T3/T1
	2003			2004		
Flowering (days)	90	88	0.98	92	89	0.96
Height (cm)	123	92.2	0.75	114.80	86.20	0.75
Leaf area (cm^2)	23.01	13.21	0.57	18.52	8.29	0.44
Ear number (#)	60	44	0.73	n.d.	n.d.	–
Ear length (cm)	8.38	7.5	0.89	7.87	7.5	0.95
Ear weight (g)	2.23	1.67	0.75	1.79	1.40	0.78
Spikelet number (#)	26.4	24.4	0.92	n.d.	n.d.	–
Grain weight/ear (g)	1.75	1.27	0.73	1.35	1.03	0.76
Grain number (#)	65.6	61.4	0.94	50.53	48.6	0.96
1000-grain weight (g)	26.74	20.72	0.77	27.67	19.69	0.71

n.d. = not determined

ization to make the switch from the vegetative to the reproductive stage. The ANOVA output showed that the traits *Ps, B, Ee, F* and *M* were affected significantly ($P < 0.05$) between treatments or between lines. However, no significance, between the lines/treatment interactions was found. The analysis between treatments indicated that salinity induced a slight inhibition for *B, Ee, F* and *M,* however, *Enu* trait was severely affected and reached an inhibition of 37.8%. In the absence of salinity stress, 5D and 2B SLs were late for *Ps, B, Ee, F* and *M* while 4D, 2D and 5A SLs were early (Table 2). There was a significant genotypic effect in the non-saline and the saline treatments for both *Ht* and *La,* and the yield components *Ew, El, Gnu, Gw* and *Tgw* (Table 3) as well as significant genotype/treatment (Table 4). In the absence of salinity, after ANOVA of calculated ratios CS/SLs, the performance of over half of the SLs differed that of CS with respect to the majority of the traits (but not *Ht* or *La*). The 5A SL showed an improvement in *Ew, El, Gnu* and *Gw,* while the 5D SL under-performed for *Ew, Gnu, Gw* and *Tgw*. For *El,* six SLs out-performed CS, in the order 5A>1A>5D> (1D, 2D) >4B. Similarly, for *Gnu* five SLs were superior to CS (5A>1D>3A>5B>7D), while the 5D SL performed very poorly. *Gw* was higher than in CS for three SLs (7D>5A>5B) (Table 3). However, after paired *t*-test of calculated ratios

Table 2. Effects on agronomic performance of the substitution of CS chromosomes by S6x ones. Data obtained from triplicated experiments. ANOVA and *t*-tests for each trait show significant genotypic effects ($p < 0.001$)

Traits	Effect between treatments Inhibition (%)	Chinese spring (days)	Effect between substitutions Chromosome (days)	
			Earliness	Lateness
Ps	not significant	92	6D (76)**	5D (96)**
B	2.0**	85	4D, 5A (70)**	5D, 2B (97)**
Ee	0.7*	91	4D (77)**	5D, 2B (101)**
F	not significant	94	4D, 5A, 5B (80)**	5D, 2B (106)**
M	2.0**	119	4D (106)**	5D, 2B (125)
		(#)	Stimulatory	Inhibitory
Enu	38***	456	2B (607)**	3A, 5B, 1D, 5A (351)**

* $p < 0.01$; ** $p < 0.001$; *** $p < 0.0001$

CS/SLs, 74.5% of substitutions were associated with significant effects on traits. Again, it was notorious that substitution 5A boosted *El, Gnu* and *Gw* traits performance as compared with CS, while 5D chromosome inhibited substantially *Ht, Ew, Gnu, Gw* and *Tgw*. The *El* trait, under paired *t*-test, was improved with substitutions 5A>1A>5D> (1D, 2D, 6A) >6D but inhibited by 7B substitution. All other significant differences found in other traits were inhibitory except 7D and 5A substitutions (Table 3).

Under salinity stress, after ANOVA of calculated ratios CS/SLs, 29.4% of chromosome substitutions affected significantly tested traits. Besides, the negative effect of 6Sx chromosome 5D, for *El* four chromosomes out-performed CS (1A>5A>1D>2D) (Table 3). In the other hand, the paired T-test output showed that 76.5% of substitutions associated with significant effects on traits. The great majority of them boosted the trait performance where they were associated. It was shown that substitution 5D was deleterious for *Ew, Gnu, Gw* and *Tgw*. In this case, *El* was favored by substitutions 1A>5A>1D> 2B>6A>6D. For *Gw,* six SLs were better than CS (1D>6A>4B>3A>3B>3D) and two under-performed (5D>2B) (Table 3). SLs 3A, 5A and 5B were affected by salinity stress for every trait.

A one-way ANOVA of calculated ratios T2/T1 proved a significant difference between mean values ($p<0.001$), however, after a paired *t*-test analysis, it was found that very few chromosome substitutions improved significantly very few CS traits. The *La* trait was significantly improved by 4D>2B>1A>7D substitutions, while for *Gw* trait only 1B substitution improved its performance under salt stress (Table 4).

Discussion

CS has provided the genetic background for a spectrum of cytogenetic stocks (Martin et al. 1993; Kato et al. 2000; Pestsova et al. 2001). Its salinity tolerance has been variously considered as being above average for bread wheat (Díaz De León et al. 2010) or borderline (Galiba et al. 1993; Díaz De León et al. 1995), and its field performance here puts it more in the former category. As synthetic hexaploids have been proposed as a potential source of genetic variation relevant for salinity tolerance (Mujeeb-Kazi and Díaz De León 2002),

Table 3. Effects on agronomic performance of the substitution of CS chromosomes by S6x ones under both non-saline and saline conditions. Data obtained from triplicated experiments. Trait ratios (CS/SL): >1.0 indicate inhibition, =1.0 neutrality, <1.0 stimulation. EC: electrical conductivity of the irrigation water. Underlined values indicate statistical significance derived from ANOVA; **bold** values indicate statistical significance from *t*-tests; * superscripts indicate statistical significance (ANOVA) between control and salinity treatments

Traits	Effect of substitution on traits																
	Chromosome																
	1A	1B	1D	2B	2D	3A	3B	3D	4B	4D	5A	5B	5D	6A	6D	7B	7D
EC = 1.2 dSm^{-1}																	
Ht	1.00	1.00	1.06	**1.13**	**1.08**	0.98	1.06	1.03	1.01	1.09	0.97	0.99	**1.13**	1.00	1.03	1.00	1.01
La	**1.46**	1.00	1.31	1.19	**1.46**	1.00	**1.19**	1.17	0.95	1.24	1.27	1.02	1.15	0.73	1.15	1.10	1.06
Ew	0.83	1.02	0.71	1.08	0.84	**0.80**	0.89	1.05	0.87	0.93	0.68	0.71	**2.75**	0.81	0.94	0.94	0.73
El	**0.65**	0.92	**0.84**	0.86	**0.84**	0.89	0.93	0.94	0.99	0.95	**0.56**	1.04	**0.81**	**0.84**	**0.87**	**1.15**	1.03
Gnu	0.88	0.98	0.74	1.00	0.87	0.77	0.83	0.86	0.82	0.87	**0.69**	0.76	**null**	0.87	0.93	0.90	0.78
Gw	0.82	0.99	0.71	1.15	0.84	0.78	0.90	1.02	0.89	0.91	**0.69**	0.70	**null**	0.84	0.90	0.91	**0.67**
Tgw	0.95	1.05	0.99	1.18	1.00	1.05	1.06	**1.23**	1.13	1.11	1.02	0.95	**null**	0.99	1.00	1.05	0.88
EC = 12 dSm^{-1}																	
Ht	0.90*	0.97*	1.00*	1.06*	1.06*	0.98*	1.02*	0.99*	0.98*	1.06*	1.05*	1.08*	1.03*	1.01*	0.94*	1.03*	0.95*
La	0.71	0.82*	0.73	**0.57**	0.93	0.76*	0.94*	0.72	0.68*	**0.56**	1.20*	0.96*	0.94*	0.76*	0.80*	0.93*	**0.61**
Ew	0.83*	0.96	0.73*	1.23	0.82	0.85*	0.88	0.91	0.80	0.75	0.97*	0.90*	**2.86**	0.78	0.80*	0.98	0.76*
El	**0.65**	0.96	**0.82**	**0.83**	0.90*	0.95*	0.95	0.94	1.02	0.99	**0.71***	1.11	0.92*	**0.87**	**0.88**	1.03	1.04
Gnu	0.96	0.96	0.80	1.24	0.94	0.90*	0.87	0.88	0.79	0.84	0.99*	1.05*	**null**	0.89	0.91	0.94	0.84
Gw	0.84	0.96*	**0.77**	**1.63***	0.83*	**0.82***	**0.88**	**0.90**	**0.81**	0.76*	1.00*	0.90*	**null**	**0.80**	0.74	0.96*	0.73*
Tgw	0.82*	0.93*	0.89*	1.25*	0.82*	0.85*	0.94*	0.94	0.95*	0.84	0.96*	0.79*	**null**	0.84*	0.74	0.95*	0.79*

Table 4. Neutral, inhibitory or stimulatory effects under salinity stress flowing from the substitution of CS chromosomes by S6x ones. Trait ratios as in *Table 1*. Data were obtained from triplicated experiments. **Bold** values are significant ($p<0.001$) according to a paired *t*-test

Traits	Effect of substitution on traits (% of inhibition)																	
	Chromosome																	
	CS	1A	1B	1D	2B	2D	3A	3B	3D	4B	4D	5A	5B	5D	6A	6D	7B	7D
Ht	0.75	0.83	0.77	0.79	0.80	0.76	0.75	0.77	0.78	0.77	0.77	0.69	0.69	0.82	0.74	0.83	0.73	0.80
La	0.45	**0.91**	0.55	0.80	**0.94**	0.70	0.59	0.56	0.72	0.62	**0.99**	0.47	0.47	0.55	0.43	0.64	0.53	**0.78**
Ew	0.75	0.78	0.83	0.76	0.69	0.81	0.73	0.79	0.91	0.85	0.97	0.55	0.62	0.75	0.82	0.92	0.75	0.75
El	0.95	0.96	0.91	0.98	0.99	0.89	0.89	0.93	0.96	0.92	0.91	0.76	0.90	0.84	0.92	0.94	0.93	0.95
Gnu	1.03	0.89	0.99	0.89	0.77	0.89	0.82	0.93	0.94	1.00	0.99	0.67	0.69	**null**	0.94	0.99	0.92	0.89
Gw	0.76	0.75	0.79	0.70	**0.54**	0.77	0.72	0.78	0.86	0.84	0.92	**0.53**	**0.60**	**null**	0.80	0.93	0.72	**0.69**
Tgw	0.71	0.83	0.80	0.79	0.67	0.87	0.88	0.80	0.93	0.84	0.94	0.76	0.85	**null**	0.84	0.96	0.79	0.79

it was reasonable to focus on the capacity of the S6x chromosomes to increase the level of salinity tolerance present in CS. The two SLs involving chromosomes 5D and 2B flowered very late in the test environment. Similarly, lines derived from the 5D SL carrying S6x alleles for a gene or gene(s) on 5D were thought to be responsible for delayed flowering (Pestsova et al. 2006). The reason for this phenotype was probably due to the presence in CS of the insensitive (spring type) allele at Vrn-D1, while the S6x allele imposes a vernalization requirement. The 4D and 5A SLs were, in contrast, early flowering. The genes responsible for this effect are unclear, although earliness has been associated with the groups 1 and 4 chromosomes (among others) by Griffit et al. (2009).

The comparisons made possible by parallel experiments under two levels of salinity led to the identification of chromosomes 1A, 1D, 5A and 6A carrying allelic variation affecting the traits *El* and *Ew*. Positive effect on *Ew* could be correlated with better grain filling. On chromosome 1D in particular, Börner et al. (2002) were able to locate the QTL Q*Gwe.ipk-1D,* which also acts on this trait. On the other hand, the 5D SL performed poorly for *Ew, Gnu, Gw* and *Tgw* in both the presence and absence of salinity; similarly the introgression lines derived from this SL also under-performed under non-stressed conditions (Pestsova et al. 2006).

A deal of salinity research has focused on the K^+/Na^+ discrimination trait (Colmer et al. 2006) and a QTL for this trait on chromosomes 4DL has recently been mapped (Genc et al. 2010). The same chromosome has also been associated with QTL for shoot and root growth and starch consumption under salinity stress, with the positive alleles being derived from a synthetic hexaploid (Ma et al. 2007; García-Suárez et al. 2010). Compared to CS, the 4D SL was better able to develop its flag leaf area under salinity stress. Leaf area development is important both for maximizing photosynthetic activity as well as for the earlier shading that it provides, which reduces evaporative water loss from the soil (ter Steege et al. 2005). Reductions in leaf area tend to diminish the growth potential of the plant, with direct effects on grain filling, ear weight, yield per plant and ultimately crop yield.

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