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Improving yield and quality traits of durum wheat by introgressing chromosome segments from hexaploid wheat

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ABSTRACT. Durum wheat (*Triticum turgidum durum*; 2n = 4x = 28; genome AABB) has long been an important food resource for human diets. The projected increase of the world's population to 9.1 billion by 2050 has highlighted the importance and urgency for improving the yield and quality performance of durum wheat. A backcrossed population, which was derived from the durum wheat variety 'Bellaroi' (recurrent parent) and the hexaploid genotype 'CSCR6' (donor parent), was used to investigate the feasibility of improving yield- and quality-related traits of durum wheat by introgressing chromosome fragments from hexaploid wheat. The population means for grain protein content, gluten content, spike length, and spikelet number were improved compared with those of the recurrent parent 'Bellaroi'. A small proportion of the backcross population lines showed significant improvements in spike length and spikelet number compared with the recurrent parent

'Bellaroi'. Some loci with significant effects for plant height, spike length, spikelet number, and thousand-grain weight were identified. Several of these loci affected more than one trait. These results showed that the introgression of chromosome fragments from 'CSCR6' into the durum genetic background could be an effective method for improving yield and quality traits of durum wheat. In addition, the loci showing significant effects on desired traits in this study could be fine mapped using an F_2 population obtained by backcrossing the lines that carry the positive allele(s) with the recurrent parent.

Key words: Durum wheat; Gene transfer; Introgression lines; Yield traits; Quality traits

INTRODUCTION

Despite its lower growing area and lower annual production compared to hexaploid wheat (*Triticum aestivum*, 2n = 6x = 42, genome AABBDD), durum wheat (*Triticum turgidum durum*, 2n = 4x = 28, genome AABB) has long remained an important food resource for human diets. Durum wheat is most commonly used for producing pasta, couscous, and flatbreads, due to its unique qualities such as its hardness, high protein content, and gluten strength. Durum wheat production has gradually increased globally since the 1950s. The annual durum wheat production is currently approximately 36 million tons per year. However, as the world population is predicted to rise to 9.1 billion by 2050 (FAO, 2009), which is 34% higher than the current population size, breeding cereals, including durum wheat, with improved yield and quality performance has become urgent and relevant.

Breeding is considered to be an "art", as it involves combining different alleles that are associated with beneficial genes or quantitative trait loci (QTLs) into a single species. The availability of a large number of genetic resources is essential for this procedure. To date, significant progress in identifying QTLs conferring yield components, grain qualities, and disease resistance in durum wheat varieties has been achieved (Zhang et al., 2008; Simons et al., 2011; Roncallo et al., 2012). The wild germplasm of durum wheat, which represents a rich potential source of useful under-exploited genes, has also been used as a resource to provide genes of interest. The genes/QTLs controlling powdery mildew resistance, drought resistance, and grain mineral nutrient concentrations have been identified in wild emmer wheat (*Triticum turgidum dicoccoides*, 2n = 4x = 28, genome AABB) (Rong et al., 2000; Peleg et al., 2009a,b). On the other hand, studies concerning transferring genes from hexaploid wheat to durum wheat remain scarce. The hexaploid wheat, which shares the same A and B chromosomes with durum wheat, is a potential resource for providing useful genes to durum wheat. Hexaploid wheat has been much more widely investigated than durum wheat. If genes can be directly transferred between these two species by conventional crossing with the help of molecular marker assisted selection, the breeding of durum wheat will be accelerated. However, to our knowledge, only one study has been carried out in this area to date. A backcross population, which was developed by crossing durum wheat 'Bellaroi' and hexaploid wheat 'CSCR6', was used to investigate the possibility of improving disease resistance of durum wheat by introgressing the resistant genes from hexaploid into the durum genetic

background (Ma et al., 2012a). The results indicated that 67% of the population lines showed better crown rot resistance than the recurrent durum parent 'Bellaroi'. A small proportion of the population lines even showed similar resistance to the control; a level of resistance that is deemed acceptable by durum growers. Therefore, these results suggested that it might be feasible to improve durum wheat disease resistance by the introgression of hexaploid chromosome segments.

Similar to disease resistance, yield- and quality-related traits are also a major concern for durum wheat breeding. The aims of the present study were to investigate the effects of introgressed hexaploid chromosome segments for yield- and quality-related traits in the durum genetic background and to detect the loci for yield- and quality-related traits for further wheat improvement.

MATERIAL AND METHODS

Plant materials

A developed BC_2F_8 population was used in this study. This population was generated between the durum variety 'Bellaroi' (Australian durum variety, used as the recurrent parent) and the hexaploid genotype 'CSCR6' (belonging to *Triticum spelta*, used as the donor parent). For generating the BC_1F_1 population, a single F_1 hybrid plant was backcrossed to the recurrent parent 'Bellaroi'. To minimize the chance of the transmission of D-genome chromosomes, the F_1 hybrid was used as the male parent. The recurrent parent 'Bellaroi' was then crossed with each of the BC_1F_1 plants individually, and a total of over 170 crosses were made in generating the BC_2F_1 population. The population was then advanced to the BC_2F_8 generation by single seed descent, and 121 of the BC_2F_8 lines were randomly selected and used in the present study.

The parents and 121 BC_2F_8 lines were planted in Zhangbei (114.71°E, 41.16°N, sea level, 1400 m), China in 2008 (spring sown). In 2009 and 2010, the plant materials were grown in Baoding (115.50°E, 38.87°N; sea level, 32 m) and Zhangbei, China, respectively (spring sown). All experiments were performed with a random block design, with three replications, four rows per line, 2.5 m row lengths, 40 grains in each row, and using conventional management strategies that are used in grower fields.

Evaluation of agronomic traits

Five agronomic traits related to yield were evaluated in 2008, 2009, and 2010. Average plant height (PH), spike length (SL), spikelet per spike (SPI), and grain number per spike (GNS) were calculated from the main stems and spikes of ten plants. Thousand-grain weight (TGW) was measured as the average weight of two independent samples of 1000 grains from each plot of three duplications.

Quality trait analysis

Kernels from each BC_2F_8 line at each replication were milled on a Quadrumat Junior Mill (Brabender, Germany) after conditioning to a pre-determined moisture level of approxi-

mately 14%. Flour water content was tested using the Rapid Moisture Tester (Brabender). Grain protein content (GPC) and grain hardness (GH) were determined with a DA7200 near infrared spectroscopy apparatus (Perten Instruments, Sweden). Gluten content (GC) was measured with a Glutomatic System 2200 (Perten Instruments) according to manufacturer instructions. Falling number (FN) was deduced in a Falling Number 1600 with the flour produced by Laboratory Milling 3100 (Perten Instruments) according to criterion No. 107 of the International Association for Cereal Chemistry (ICC). The sedimentation value (SV) was obtained based on ICC standard No. 116. Swelling power (SP) was tested using the method described by Du (2002).

Genotyping and statistical analysis

A total of 778 simple sequence repeats (SSRs) were tested against the two parents of the BC_2F_8 population. SSR markers with known locations on chromosomes belonging to either the A or B genome were then selectively used for genotyping the whole population. A D-genome-specific marker, with sequences of the forward primer: CTTCTGACGGGTCAGGGGCAC and reverse primer: CTGAATGCCCCTGCGGCTTAAG, kindly provided by Dr. Evans Lagudah, was also used for analyzing the BC_2F_8 population. Based on the presence or absence of a given SSR marker allele from the hexaploid parent 'CSCR6', the 121 BC_2F_8 lines were grouped into two classes, one homozygous for the allele from the donor parent (AA) and the other homozygous for the allele from the recurrent parent (aa). The difference in the target traits between the two genotype classes was used for measuring the effect of a chromosome segment tagged by each of the SSR markers. The Student *t*-test was performed to determine whether the observed differences were significant. The size and number of introgressions were determined using the GGT software.

RESULTS

Of the 778 markers screened, 480 (62%) were polymorphic between the two parents. Among the polymorphic SSR markers, 132 that mapped in the wheat SSR consensus linkage map (Somers et al., 2004) were selected for genotyping the 121 BC_2F_8 lines. The number of markers located in each of the chromosomes varied from four (chromosome 6A) to 13 (chromosomes 7A), with an average of nine markers per chromosome. The distances covered by these markers varied from 38 cM (chromosome 3B) to 173 cM (chromosome 5B), with a total of 1034 cM (Table 1). Based on the 132 SSR markers used, each of the 121 lines showed a unique allelic combination, and the chromosome segments of the hexaploid donor 'CSCR6' retained in these lines varied from 2.6 to 31.9%, with an average of 12.7%, which was close to the 12.5% expected from the BC_2 population. Examining the population with the D-genome-specific marker revealed no D-chromosome segments in any of the 121 lines analyzed.

A significant difference was detected between the two parents with respect to PH, SL, SPI, TGW, GC, SV, FN, SP, and GH (Table 2). Compared with Ballaroi, CSCR6 showed a higher value for three agronomic-related traits, PH, SL, and SPI. The largest difference was observed in SL (61%). For the quality-related traits, CSCR6 showed higher means of GPC, GC, SV, and SP than those of Bellaroi. The differences were 10.4% for GPC, 15.1% for GC, 61.4% for SV, and 39.2% for SP.

Table 1. SSR markers used in assessing the BC_2F_8 population derived from a cross between a durum variety 'Bellaroi' and hexaploid genotype 'CSCR6'.

Chromosome	Number of markers	Distance covered (cM)
1A	10	94
1B	7	39
2A	10	129
2B	9	69
3A	12	110
3B	11	141
4A	10	79
4B	7	38
5A	12	94
5B	7	173
6A	4	43
6B	7	44
7A	13	103
7B	12	151

Marker locations and linkage distances were all obtained from Somers et al. (2004).

Table 2. Phenotypic performance of yield and quality traits of the parents and the BC population.

	Parents		BC population	
Traits	Bellaroi	CSCR6	Means	Distribution range
PH	62.14	98.09	62.35	51.22-82.09
SL	5.78	14.94	6.1	4.62-8.15
SPI	14.04	20.31	15.2	12.86-17.74
GNS	42.37	37.09	43.49	29.88-55.71
TGW	40.96	27.2	39.34	30.80-47.86
GPC	17.68	19.74	18.19	16.22-20.73
GC	41.82	49.27	44.3	38.86-50.18
SV	20.2	52.33	17.3	13.79-23.06
FN	278.29	338.59	274.14	108.00-364.83
GH	69.3	54.54	61.16	51.50-69.89
SP	4.42	7.27	4.49	3.05-6.76

PH = plant height; SL = spike length; SPI = spikelet per spike; GNS = grain number per spike; TGW = thousand-grain weight; GPC = grain protein content; GC = gluten content; SV = sedimentation value; FN = falling number; GH = grain hardness; SP = swelling power.

The population means of SL, SPI, GNS, GPC, and GC were all higher compared to those of Bellaroi, but were not significantly different. Large variation was observed in all of the traits measured in the population. Transgressive segregations were observed for some traits. Thirteen lines showed significantly longer SLs compared to the recurrent parent Bellaroi. The mean SL of these lines was 7.38 cm, which is 28% higher than that of Bellaroi (5.78 cm). Two lines showed significantly shorter SLs compared to Bellaroi. Seven lines showed higher SPIs compared to Bellaroi. The mean SPI of these lines was 14.38, whereas the mean SPI of Bellaroi was 14.04. In addition, three lines and one line showed significantly improved performance in SP and GNS compared with the recurrent parent, respectively.

The chromosome segments of the hexaploid donor CSCR6 tagged by 116 of the 132 SSR markers failed to show significant effects in the BC_2F_8 population. Chromosome segments tagged by the remaining 16 markers (loci), which were mostly located on chromosomes 6B and 5A, showed significant effects for a total of 10 traits under at least two environments ($P < 0.01$). Two of these markers, wmc110 and barc24, showed significant effects on multiple traits. The positive allele detected by cfa2163 on chromosome 5A increased SL by 12.71 and

24.66% in two environments, with an average increase of 18.69%. Four positive loci detected by markers on 1A, 3A, and 5A increased the SPI from 3.02 to 16.71%, with an average increase of 8.72%. For the negative loci, one locus on 6B decreased the PH by 7.93 and 8.12% in two environments, with an average of 8.03%, four loci on 2A, 5A, and 6B decreased SL from 5.61 to 10.53%, with an average decrease of 8.38%, one locus on 2A reduced SPI by 4.29 to 6.66%, with an average of 5.53%, and the four loci on 2A, 2B, and 3A reduced TGW from 7.9 to 17.64%, with an average of 11.18% (Table 3).

Table 3. Loci showing significantly positive and negative effects on PH, SL, SPI and TGW detected in the BC_2F_8 population ($P < 0.01$).

Trait	Marker	Chromosome	aa	AA	Difference (%)	P
PH	Barc24	6B	70.575	65.391	-7.93	<0.01
			54.161	50.092	-8.12	<0.01
SL	Wmc110	5A	5.816	5.489	-5.96	<0.01
			6.345	5.799	-9.42	<0.01
	Barc24	6B	6.624	5.993	-10.53	<0.01
			5.725	5.211	-9.86	<0.01
	Cfa2163	5A	6.49	7.435	12.71	<0.01
			5.977	7.933	24.66	<0.01
	Barc178	6B	6.634	6.002	-10.53	<0.01
			5.731	5.312	-7.89	<0.01
	Wmc177	2A	6.701	6.345	-5.61	<0.01
			6.272	5.809	-7.97	<0.01
SPI	Wmc177	2A	16.107	15.429	-4.39	<0.01
			15.863	14.873	-6.66	<0.01
	Barc141	5A	15.733	17.751	11.37	<0.01
			14.292	15.891	10.06	<0.01
			15.304	18.375	16.71	<0.01
	Gwm186	5A	15.734	17.751	11.33	<0.01
			14.291	15.891	10.07	<0.01
			15.306	18.375	16.7	<0.01
	Gwm357	1A	14.203	14.645	3.02	<0.01
			15.158	16.094	5.82	<0.01
	Gwm156	5A	15.591	16.459	5.27	<0.01
			14.193	14.863	4.51	<0.01
	Cfa2262	3A	15.69	16.559	5.25	<0.01
			14.272	14.941	4.48	<0.01
TGW	Wmc181	2A	36.484	32.702	-11.57	<0.01
			43.774	40.556	-7.93	<0.01
	Barc101	2B	36.549	32.272	-13.25	<0.01
			43.651	39.908	-9.37	<0.01
	Wmc332	2B	36.592	33.277	-9.96	<0.01
			43.844	40.634	-7.9	<0.01
	Cfa2234	3A	36.398	32.563	-11.78	<0.01
			38.844	33.018	-17.64	<0.01

'AA' represents homozygous loci from the hexaploid donor 'CSCR6' and 'aa' represents homozygous loci from the recurrent parent 'Bellaroi'. The difference was calculated using the formula (AA - aa) / AA. For abbreviations, see legend to Table 2

The genotyping of the 13 lines showing significantly longer SLs than Bellaroi revealed that only four lines carried the one positive donor allele detected by the SSR marker cfa2163 on chromosome 5A (Table 4). The number of negative loci contained in these 13 lines varied from one to two. Line 73, which showed the longest SL value, had all five positive loci, whereas it did not possess any negative loci from CSCR6 (Table 5). In the seven lines showing higher SPI numbers than Bellaroi, the number of positive CSCR6 loci varied from zero to five. Line 81, which showed the highest SPI, had all five positive loci, whereas it did not possess any negative loci from CSCR6 (Table 5).

Table 4. Alleles with significant effects on spike length (SL) in the thirteen BC_2F_8 lines showing longer SL than 'Bellaroi'.

Line	SL	CSCR6 (%)	Wmc110	Barc24	Cfa2163	Barc178	Wmc177
17	7.27	20.5	AA	aa	AA	aa	AA
37	6.78	17.1	AA	aa	aa	aa	AA
42	7.33	24.4	aa	aa	aa	aa	aa
43	7.68	8.1	AA	aa	aa	aa	aa
52	7.82	8.4	aa	aa	AA	aa	aa
53	7.22	10.7	AA	aa	aa	aa	AA
63	7.27	14.9	AA	aa	aa	aa	aa
66	6.83	13.8	AA	aa	aa	aa	aa
73	8.15	15	aa	aa	AA	aa	aa
75	7.05	8.3	AA	aa	aa	aa	aa
91	7.87	7.5	AA	aa	aa	aa	aa
92	6.91	18.9	AA	aa	aa	aa	aa
116	7.75	9.6	aa	aa	AA	aa	aa

CSCR6 (%) = percentage of chromosome segments from the hexaploid donor 'CSCR6'; 'AA' = homozygous loci from the hexaploid donor 'CSCR6'; 'aa' = homozygous loci from the recurrent parent 'Bellaroi'.

Table 5. Alleles with significant effects on spikelet per spike (SPI) in the seven BC_2F_8 lines showing longer SPI than 'Bellaroi'.

Line	SPI	CSCR6 (%)	Gwm357	Wmc177	Cfa2262	Barc141	Gwm186	Gwm156
5	16.19	21.7	AA	aa	AA	aa	aa	AA
8	16.05	21.1	aa	AA	AA	aa	aa	AA
58	15.43	16.7	aa	AA	aa	aa	aa	AA
81	17.61	11.7	AA	aa	AA	AA	AA	AA
85	16.25	16.6	AA	AA	aa	aa	aa	aa
134	17.21	26.1	aa	AA	AA	aa	aa	aa
156	16.32	11.6	aa	AA	aa	aa	aa	aa

CSCR6 (%) = percentage of chromosome segments from the hexaploid donor 'CSCR6'; 'AA' = homozygous loci from the hexaploid donor 'CSCR6'; 'aa' = homozygous loci from the recurrent parent 'Bellaroi'.

DISCUSSION

The donor hexaploid parent of the population, CSCR6, belongs to the species *T. spelta*. Because genotypes of *T. spelta* have not suffered the same breeding pressure as those of bread or durum wheat, it was expected that large segregation for agronomic-related traits would be observed in the backcross population generated, which is desirable for investigations of possible effects of hexaploid chromosome segments for yield components and grain quality in durum backgrounds. The results indicated that the two parents showed significant differences for nine of the 10 traits measured, ranging from 11.67% for GPC to approximately 1.6-fold for SV. The population means of two quality traits (GPC and GC) were increased compared with those of Bellaroi, and the same trends were found for two yield-related traits (SL and SPI). Thirteen lines showed significant increases in SL compared with Bellaroi, whereas seven lines showed significantly higher SPIs than Ballaroi. A number of studies showed that SL is positively correlated with shoot biomass, straw biomass per plant, harvest index and grain yield (Moghaddam et al., 1997; Donmez et al., 2001). Based on the above results, it can be concluded that the introgression of chromosome fragments from CSCR6 into the durum background could be a feasible way for improving yield- and quality-related traits of the durum population.

However, the genotyping results of the 13 lines with better SL values than Bellaroi showed that most of those lines (nine) also carried one or two negative loci from the donor instead of carrying only the positive donor allele detected by the SSR marker cfa2163. Similarly, five of the seven lines showing better SPI values than Bellaroi carried negative loci from the donor and carried zero to five of the six CSCR6-positive loci. Therefore, the presence of the positive or negative allele does not appear to be essential for a specific line's performance with respect to target traits. Nonetheless, for both of these traits, the lines carrying only positive loci and no negative loci ranked on top (line 81 for SPI, line 73 for SL). These results might be explained by the interaction between genes and environments, but further study is needed for confirmation.

A locus on 6BL that was associated with plant height was detected by the barc24 allele in all of the experiments. Previous studies (Cadalen et al., 1998; Cui et al., 2011; Griffiths et al., 2012) have also identified loci linked with plant height on 6BL. Although this locus only increased plant height by 4.7 cm on average, the fact that this region was found to be involved in controlling plant height in different genetic backgrounds indicated that this locus was closely related to plant height. Interestingly, the increasing allele of the 6B locus was from Bellaroi rather than CSCR6. Furthermore, this locus was the only one identified to be responsible for plant height in the population despite the fact that the donor parent CSCR6 was much taller than the recurrent parent Bellaroi. In fact, none of the loci controlling plant height previously reported from the donor (Ma et al., 2012b) were detected in this population. This suggested that the hexaploid loci for plant height failed to function once they were transferred to the durum background. This also appeared to be the case for QTLs related to resistance to crown rot and *Fusarium* head blight. These major QTLs also failed to provide resistance to crown rot and *Fusarium* head blight once transferred to the durum background (Ma et al., 2012a; Xie GQ and Liu CJ, unpublished results). Previous studies (Ma et al., 2012a) have suggested that possible reasons for the loss of function of these genes may be due to the absence of D-chromosomes, which might be essential for the proper function of the genes, or alternatively, might be due to the presence of suppressor genes in the durum.

The markers that detected loci linked with SL were located on chromosomes 2A, 5A, and 6B. Previous studies have also identified QTLs controlling SL on chromosomes 2A and 5A (Cui et al., 2011). However, to our knowledge, none of the loci conferring SL have previously been detected on 6B. In addition, the fact that the loci responsible for SL and PH were detected by the same marker (barc24) on 6B ($P < 0.01$) suggested that PH and SL might be controlled by the same QTL or by several closely located QTLs. This result differs from previous study (Cui et al., 2011), in which a weak association was found between these two traits. Therefore, although some QTLs only affected PH, other QTLs appeared to have pleiotropic effects on PH and SL. As a result, in marker-assisted selection, the introduction of alleles that could decrease PH might also lead to a decrease in SL. Using a combination of PH QTLs without effects on SL could help resolve this.

The loci linked with SPI were detected by markers on chromosomes 1A, 2A, 3A, and 5A. In previous studies, the QTL controlling SPI was mapped to 1A, 2A, and 5A (Sourdille et al., 2000; Li et al., 2007; Wang et al., 2011). As for PH and SL, a locus responsible for SPI and SL was detected by the same SSR marker, wmc177, on chromosome 2A. A previous study also identified a region on 2A with a shared QTL for SL and SPI. However, in that study, the increasing alleles for SPI and SL were from different parents (Sourdille et al., 2000). In the

present study, the increasing alleles were all from the recurrent parent, Bellaroi. The locus on 3A was a new locus, as no QTLs on this chromosome have been previously reported. The increasing allele of the marker (cfa2262) linked with this locus originated from CSCR6, which increased the SPI by 4.85 on average. The loci linked with TGW were detected by markers on chromosomes 2A, 2B, and 3A. A QTL controlling TGW was previously mapped to these same chromosomes (Huang et al., 2003; Wu et al., 2011).

Finally, because molecular markers were not used during the development of this BC_2F_8 population, a small portions of donor chromosome fragments were retained in each line of the population (varied from 2.6 to 31.9%). Therefore, the identification of the effects of loci for different traits could be biased due to interference from the genetic backgrounds. However, loci that were consistently detected in different years and environments should be stable. Using molecular markers, an F_2 population only segregating in the interval controlling the target traits could be obtained by backcrossing the lines that carried the positive allele with the recurrent parent. These F_2 populations could be valuable to fine map the loci controlling these target traits.

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