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ORIGINAL PAPER

Molecular detection of genomic regions associated with grain yield and yield-related components in an elite bread wheat cross evaluated under irrigated and rainfed conditions

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Abstract Grain yield and grain weight of wheat are often decreased by water-limitation in the north-eastern cropping belt of Australia. Based on knowledge that CIMMYT lines are well-adapted in this region, a recombinant inbred line (RIL) population between two elite CIMMYT bread wheats (Seri M82 and Babax) was evaluated under water-limited environments. Fourteen productivity traits were evaluated in 192 progeny in up to eight trials. For three aggregations of the environments (all, high yield or low yield), multiple quantitative trait loci (QTL) were detected, each explaining <15% of variation. Co-location of multiple trait QTL was greatest on linkage groups 1B-a, 1D-b, 4A-a, 4D-a, 6A-a, 6B-a, 7A-a and an unassigned linkage group. Two putative QTL (LOD > 3) from Seri (6D-b and UA-d) increased grain yield and co-located with a suggestive (2 < LOD < 3) and a putative QTL for increased stem carbohydrate content (WSC), respectively; the latter QTL also co-located with a putative anthesis QTL for earlier flowering. Both QTL were detected only in high yield (>4t ha^{-1}) environments. A third increased grain yield QTL (7A-a) from Babax co-located with QTL for increased grain number. Six putative QTL increased grain weight and co-located with QTL for harvest index, grains per spike and spike number. Three putative QTL for increased grains per spike co-located with strong QTL for earlier flowering, increased grain weight and fewer spikes. A group of progeny that exceeded the mean grain yield and grain weight of commercial checks had an increased frequency of QTL for high WSC, large grain size, increased harvest index and greater height, but fewer stems, when compared to low yielding (20% less), low grain weight progeny. These findings were consistent with agronomic analyses of the germplasm and demonstrate that there should be opportunities to independently manipulate grain number and grain size which is typically difficult due to strong negative correlations.

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Introduction

Bread wheat (*Triticum aestivum* L.) production in Australia and globally is often limited by low seasonal rainfall which reduces grain yield and frequently results in smaller grains, especially in terminal stress. The northern region of Australia is characterised by highly variable summer-dominant rainfall. Wheat is typically planted in May/June into a soil profile with greater than 50% plant available water content (PAWC), and the crop relies on this moisture and limited within season rainfall, 200–300 mm on average between May and October. However, severe post-anthesis drought stress is a common occurrence in the northern Australian

grain region and occurs in approximately 60% of years (Chapman 2008). In addition to reducing grain yield, post-anthesis drought stress results in high screenings (% small grain); wheat with greater than 3% screenings receives a financial penalty. Breeding of wheat for increased productivity in such environments is difficult as the quantity and distribution of rainfall vary substantially in the target area. Furthermore, many relevant traits such as grain yield are difficult to select for in the field as they are slow and tedious to measure and because of low heritability caused by significant genotype × environment interactions that exist in this region (Cooper et al. 1995).

Traits that increase water use, water use efficiency or harvest index are likely to enhance grain yield, maintain grain size and reduce screenings. In this production region, Dreccer et al. (2009) demonstrated that several high WSC progeny lines had a higher grain weight under irrigated and mildly water-limited conditions than did low WSC sister lines. The high WSC lines had a higher yield under water-limitation with fewer tillers and lower grain number per unit area. It appears that they were able to utilise stored stem carbohydrates to maintain a proportionally greater number of grains per spike than the low WSC lines.

Grain yield and agronomic traits related to grain yield are controlled by many genes. Molecular markers and genetic maps assist in understanding the genetic control of these traits via the dissection of the QTL that underpin yield-related traits. A large number of studies have reported QTL for yield and yield components in wheat in different environments including water-limiting stress environments. QTL for grain yield, anthesis, plant height, grain weight, grain number have been reported (e.g. Huang et al. 2006; Marza et al. 2006; Snape et al. 2007; Rebetzke et al. 2008; and references therein).

Fewer studies have reported QTL associated with high accumulation of WSC in stems, a trait which has been also shown to be important for grain yield in water-limited environments (van Herwaarden et al. 1998; Yang et al. 2007; Ehdaie et al. 2008). Stem WSC provides a potential carbon resource during grain filling, particularly when stress is sufficient to reduce the assimilate levels below the demand of the developing grains. QTL for WSC have been detected in rice (Nagata et al. 2002; Takai et al. 2005), perennial ryegrass (Turner et al. 2006) and in wheat (Rebetzke et al. 2006; Yang et al. 2007). In rice, different QTL were detected in the two rice populations studied (Nagata et al. 2002; Takai et al. 2005). Similarly, in perennial rye grass, different QTL for WSC were detected in two seasons (Turner et al. 2006). In wheat, QTL for both WSC concentration and content have been identified in three wheat populations (Rebetzke et al. 2008), with five genomic regions identified in two of three populations and one region common to all three. QTL were detected on the same chromosomes in the study by Yang et al. 2007). While most of the QTL effects were generally small in both studies (<5% of the phenotypic variance), one QTL detected by Rebetzke et al. 2008) that co-located with a major flowering gene explained between 28 and 30% of the phenotypic variance in WSC concentration and 11–16% of the phenotypic variance in WSC content in two of the three populations.

The International Maize and Wheat Improvement Centre, CIMMYT, breeds wheat for a range of environments, including water-limited environments. In two major studies of international and Australian trials, Cooper et al. (1993) and Mathews et al. (2007) demonstrated that CIMMYT lines which perform well in irrigated and droughted conditions in north-western Mexico are typically well-adapted to the northern region of Australia. Two hexaploid wheat lines, Seri M 82 and Babax, were identified by CIMMYT as genotypes that differed in yield performance in NW Mexico under drought but possessed high yield performance (Olivares-Villegas et al. 2007). A recombinant inbred line (RIL) population was specifically developed to study drought adaptive traits and has been evaluated in Mexico and in southern Australia (Olivares-Villegas et al. 2007). In Mexico, Babax consistently out-yielded Seri and also produced larger grain. In southern Australia, Seri has out-yielded the larger grained Babax (Olivares-Villegas et al. 2007), but the lines perform similarly in the northern region (Rattey et al. 2009).

We have recently evaluated the agronomic and physiological traits in the Seri–Babax (SB) RIL population that are associated with grain yield and yield components in a broad range of northern Australian wheat production environments with different levels of drought stress and grain yield (Rattey et al. 2009). The study demonstrated that broad adaptation was best achieved by selection based on performance across the yield range of the production environments but that specific adaptation to the high- or low-yielding environments was best detected in those environments. Broadly adapted SB lines with both high yield and grain weight were identified and found to be associated with a combination of traits such as slightly earlier anthesis, higher harvest index, fewer culms, higher WSC and a high number of grains per spike.

This study was initiated to investigate the genetic basis of the high grain yield and grain weight in this population and to examine the frequency of favourable QTL for the traits associated with high yield and grain weight in the SB lines, as identified by Rattey et al. (2009). Further objectives of the study were to identify QTL with broad relevance or relevance to specific yield production environments, and to investigate the importance of the WSC trait and the effects of the 1B-1R translocation on grain yield and grain weight.

Materials and methods

Plant material and measurement of phenotypic data for yield and yield component traits

The SB population was generated from crosses between two elite CIMMYT lines, Seri M82 and Babax, in CIMMYT, Obregon, Mexico, as described by Olivares-Villegas et al. (2007), and consists of F7 sister lines from a reciprocal cross. Of the 194 progeny lines, 160 are derived from Babax × Seri and 34 are derived from Seri × Babax. Based on five generations of pedigree, the coefficient of parentage (COP) between the parents was 0.332 (Mathews et al. 2008) (a COP = 0 indicates no relationship; 1 = identical lines). Seri M 82 contains the rye translocation (Rajaram et al. 1983), annotated T1BL.1RS, on the short arm of chromosome 1B. The parental Babax line was selected from a cross of the same name developed at CIMMYT (International Maize and Wheat Improvement Centre) to not contain the rye translocation (Rajaram et al. 1983), i.e. normal 1B (1BL.1BS) chromosome. The resulting population was therefore expected to segregate for the T1BL.1RS translocation solely from the Seri M82 parent.

Field trials were conducted at three locations in central and south-eastern Queensland from 2002 to 2006 for the 194 progenies plus parents and the following data collected as described in Rattey et al. (2009): anthesis biomass (abi), days to anthesis (ant), grains per spike (gps), grain yield (g m^{-2}) (gy), hectolitre weight (g 0.5 L^{-1}) (hect), harvest index (hi), height (ht), grain weight (mg $grain^{-1}$) (gw), maturity biomass (mbi), grain number m^{-2} (mgn), spike number m^{-2} (msn), percent screenings (scr), WSC content (WSCc, mg g^{-1}), WSC content on an area basis (WSCa, g m^{-2}). Trait abbreviations and table order are consistent with Rattey et al. (2009). Statistical analysis of the phenotypic data was undertaken as described in Rattey et al. (2009). On the basis of mean grain yield, three of the six trials for which grain yield data were collected were classified as high-yielding environments (HiY) (>400 g m^{-2}) and three were classified as low-yielding environments (LoY) (<400 g m^{-2}). For each trait, Best Linear Unbiased Estimates (BLUEs) were calculated from analyses within each environment while Best Linear Unbiased Predictors (BLUPs) were calculated from across-environment (ALL), HiY trials and LoY trials data sets; BLUPs from the across-environment data sets were used to approximate the genetic correlations (r_g) between traits while BLUEs were used as phenotypic data input into the QTL analyses (see Rattey et al. 2009 for further details of the analysis).

Map construction and QTL analysis

DNA was isolated from leaves collected from the progeny and parents using the method of Hoisington (1992). The population was scored for SSR and AFLP markers, as described in Schmidt et al. (2005), as well as for DArT markers, using the method described in Wenzl et al. (2004). The Seri × Babax map was constructed using JoinMap 3.0 Software (van Ooijen and Voorrips 2001). Segregation ratios were examined for all markers; single markers exhibiting segregation distortion at $P < 0.01$ were removed. Marker order for each linkage group was refined using RECORD (Isidore et al. 2003). Markers that co-located were removed, with SSR markers being preferentially retained, followed by DArT markers with the fewest missing values and high call rates (Wenzl et al. 2004). Two progeny were removed from the analysis—one contained incorrect markers and is most likely a rogue progeny (data not shown) while the second progeny line contained a high number of missing values (40%) (data not shown). Linkage groups (LGs) were assigned to chromosomes on the basis of previously mapped SSR (http://wheat.pw.usda.gov/GG2/index.shtml) and DArT markers (http://www.triticarte.com.au/). LGs were named according to the chromosome to which they were assigned, followed by a suffix (a, b or c). The prefix indicated the relative chromosomal position of LGs assigned to the same chromosome (LG-a above LG-b, consistent with short arm above long arm), if known. If the position of a LG, relative to other LGs assigned to the same chromosome, could not be determined, it was assigned the next suffix in the sequence. If only one LG was assigned to a chromosome, it was labelled LG-a. Marker clustering was undertaken using the 587 markers scored on the 192 progeny and analysed using the heatmap function within R (R Development Core Team 2006).

The progeny were also screened with two rye-specific markers to identify progeny carrying the T1BL.1RS translocation. PCR was undertaken using rye 5S rDNA primers (Koebner 1995) and primers to the rye-specific repeated DNA sequence, Iag95 (Mohler et al. 2001; Mago et al. 2002), following the protocols described therein.

The map was imported into *QTLCartographer for Windows Version 2.0* (Bioinformatics Research Centre, North Carolina State University, USA) for QTL analysis. For all 14 traits, QTL analysis was undertaken for the three data sets, ALL, HiY and LoY. QTL were identified via composite interval mapping (CIM) using the program's default values, namely Forward Regression with five background markers, a window size of 10.0 cM and a walk speed of 2 cM. Other parameters were investigated, including backward and forward regressions and 3–7 background markers, but as they had little effect on the detection of QTL (data not shown) the default values were retained. Putative QTL were defined as two or more linked markers (~5 cM) associated with a trait at LOD > 3.0. Suggestive QTL were defined as QTL where two or more linked markers (~5 cM) were detected only at $2.0 < \text{LOD} < 3.0$. A customised

'heatmap' was developed to display the results of QTL with LOD > 2 using the *image* function and other plotting routines as implemented in R Development Core Team (2006).

QTL frequency in high-yielding progeny selections

Quantitative trait loci frequency in response to phenotypic selection was estimated in 31 lines selected as having either high grain number per unit area and high grain weight (nine lines); high grain number but low grain weight (eight lines); low grain number but high grain weight (nine lines); or low grain number and low grain weight (five lines). These 31 lines were grown at Gatton in 2007 and phenotyped as described in Rattey et al. (2009). For each putative QTL, flanking markers were identified. The frequency of the Seri allele for each selected marker was calculated in the four groups of progeny.

Results

Yield and yield component trait data for the Seri × Babax population

Data were collected for 14 traits in between five and eight trials. The trials sampled a range of locations from Central Queensland to northern NSW, with multiple trial-years at Gatton (southern Queensland) under different levels of water-limitation. As summarised in Table 1 and described in detail in Rattey et al. (2009), there was a substantial range among trial means for each trait, with the exception of days to anthesis (ant) and hectolitre weight (hect). Transgressive segregation was present for many of the observed traits (Rattey et al. 2009). Heritability was high (>0.70) for days to anthesis (ant), height (ht), hectolitre weight (hect) and grain weight (gw), moderately high (0.40–0.70) for grains per spike (gps), grain yield (gyp), harvest index (hi), grain number m^{-2} (mgn), spike number m^{-2} (msn), percent screenings (scr) and WSCc, and low (<0.40) for biomass at anthesis (abi), biomass at maturity (mbi) and WSCa. There was a threefold range in trial mean grain yield, from 202 g m^{-2} in the rainfed trial at Gatton in 2005 to 660 g m^{-2} in the irrigated trial at Gatton in 2006.

Genetic correlations among the 14 traits across all trials are discussed in detail in Rattey et al. (2009) and are presented in Table 2. Significant positive correlations ranged from 0.14 (grain weight and harvest index) to 0.65 (WSCc and WSCa) (Table 2). Significant negative correlations ranged from −0.14 (grains per spike and grain weight, and hectolitre weight and spike number m^{-2}) to −0.64 (grain weight and percent screenings and grain number m^{-2}) (Table 2). Across all environments, higher grain yield was

Table 1 Trait means across all environments, trait range among environments and heritability for 14 yield and yield-related components

Trait	Trait code[a]	Parental trait mean		Population trait mean		All environments	High yield environments[c]	Low yield environments[c, d]
		Seri M82	Babax	Across all environments[b]	Range among environments[c]	h^2	h^2	h^2
Anthesis biomass (g m^{-2})	abi (5)	609	616	622	505–868	0.23	0.16	0.02
Anthesis (days)	ant (7)	92.5	89.9	90.4	83.9–94.4	0.94	0.88	0.75
Grains per spike	gps (5)	46.9	44.0	44.0	34–62	0.51	0.40	0.29
Grain yield (g m^{-2})	gyp (6)	413	408	404	202–660	0.53	0.17	0.38
Hectolitre weight (g)	hect (5)	344	342	342	311–369	0.70	0.59	0.30
Harvest index	hi (6)	0.46	0.44	0.44	0.37–0.50	0.49	0.27	0.30
Height (cm)	ht (8)	78.5	82.4	80.5	61.6–92.3	0.86	0.79	0.62
Grain weight (mg)	gw (8)	28.5	31.5	29.7	19.8–36.6	0.82	0.62	0.66
Maturity biomass (g m^{-2})	mbi (5)	796	830	826	537–1405	0.23	0.05	0.08
Grain number (m^{-2})	mgn (6)	15350	14173	14676	6675–24082	0.65	0.34	0.62
Spike number (m^{-2})	msn (5)	262	247	267	188–356	0.58	0.32	0.36
Percent screenings	scr (5)	3.64	5.13	4.96	2.3–8.6	0.40	0.43	0.08
WSC content (g m^{-2})	WSCa (5)	100	91	91	42–134	0.28	0.04	0.00
WSC concentration (mg g^{-1})	WSCc (6)	166	146	149	82–223	0.43	0.14	0.05

Table adapted from Rattey et al. 2009

[a] The number of environments at which each trait was assessed is provided in parentheses

[b] BLUPs from combined analysis across environments

[c] BLUEs from analyses within each environment

[d] High- and low-yield environments are described in Rattey et al. (2009)

Table 2 Genetic correlations between 14 traits in the Seri/Babax RIL population evaluated across environments in 2002–2006

Trait	abi	ant	gps	gyp	hect	hi	ht	gw	mbi	mgn	msn	scrpercent	wsc	wsca
abi		0.24**	−0.29**	0.07	−0.13	−0.37**	0.02	−0.10	0.52**	0.17*	0.25**	0.04	0.02	0.60**
ant			−0.11	−0.50**	−0.49**	−0.45**	−0.13	−0.46**	0.23**	0.02	0.15*	0.21**	−0.30**	−0.12
gps				0.36**	−0.12	0.53**	0.01	−0.14*	0.02	0.40**	−0.39**	0.24**	0.09	−0.21**
gyp					0.40**	0.47**	0.07	0.22**	0.36**	0.52**	0.08	−0.16*	0.25**	0.15*
hect						0.19**	0.25**	0.53**	−0.10	−0.21*	−0.14*	−0.48**	0.31**	0.15*
hi							−0.08	0.14*	−0.30	0.24**	−0.15*	−0.02	0.15*	−0.18**
ht								0.40**	0.04	−0.27**	−0.32**	−0.18**	0.11	0.09
gw									−0.18**	−0.65**	−0.50**	−0.64**	0.40**	0.23**
mbi										0.45**	0.42**	0.09	−0.10	0.20**
mgn											0.48**	0.46**	−0.18**	−0.07
msn												0.20	−0.33**	−0.03
scrpercent													−0.35**	−0.22**
wsc														0.65**
wsca														

Table modified from Rattey et al. (2009). See Table 1 for trait codes and the number of environments at which each trait was assessed

*, ** Genetic correlation is significantly different from zero at $P = 0.05$ and $P = 0.01$, respectively

significantly correlated with earlier flowering and higher levels of all traits except height, biomass at anthesis, and spike number m^{-2}. It was most strongly ($r_g > 0.35$) associated with earlier flowering and higher hectolitre weight, harvest index and biomass at maturity, and more grains per spike and grains m^{-2}. Higher grain weight was significantly correlated with all traits except biomass at anthesis. It was most strongly correlated with earlier flowering and taller plants, higher hectolitre weight, more grains m^{-2} and spikes m^{-2}, lower percent screenings and a higher WSCc. WSCc was positively correlated with WSCa, and negatively correlated with grains spike m^{-2}, spikes m^{-2}, and screenings. Grains m^{-2} was positively associated with spikes m^{-2} and with grains per spike; spikes m^{-2} was negatively correlated with grains per spike. Similar correlations were obtained using the HiY and LoY data (data not shown) although grain yield was less strongly correlated with grain weight, grains per spike and harvest index in the HiY environments than in the LoY environments (data not shown).

The Seri × Babax map

A total of 587 markers (74 SSRs 264 AFLPs 249 DArT markers) were scored across the 192 progeny in the SB population. Segregation ratios of all markers were compared between the 158 Babax × Seri progeny and the 34 Seri × Babax progeny. As there was no difference in segregation ratios of any marker between the two progeny groups (data not shown), the map was constructed using all 192 progeny.

The 587 markers were grouped into 39 linkage groups, of which 35 could be assigned to chromosomes on the basis of two or more mapped SSRs and/or DArT markers. After refining the marker order, co-locating markers and singleton distorted markers were removed. The final map contained 425 markers (68 SSR, 212 AFLP and 145 DArT) distributed onto the 39 LGs (Supplementary Table 1). These 39 LGs could be assigned to 20 of the 21 wheat chromosomes on the basis of mapped SSR and DArT markers; no LG was assigned to chromosome 3D. Additional 3D SSRs were tested but none were polymorphic in the SB population (data not shown). Supplementary Table 1 indicates a very uneven distribution of markers across both the wheat genomes and chromosome groups. While 41 and 48% of markers mapped to the A and B genome chromosomes, respectively, only 11% mapped to the D genome and 25 of the 45 markers mapping to LGs assigned to the D genome mapped to the two LGs assigned to chromosome 1D; the other six D genome chromosomes contained between 0 and 7 markers. In addition to the D genome chromosomes, chromosomes 2A and 7B were also poorly represented (Supplementary Table 1).

Cluster analysis of the marker data revealed two regions with unusual segregation patterns, one on LG 1B-a and the other on 4A-a (Fig. 1). The majority of markers on LG 1B-a exhibited segregation distortion with approximately 75% of the progenies receiving Babax marker alleles. In addition, 60% of the progeny possessed a parental-type 1B-a LG that consisted only of marker alleles from one or other parent. The remaining progeny (40%) possessed a 1B-a LG containing markers from both parents only in the distal 3–4 markers (data not shown); markers segregated 1:1 as expected in LG 1B-b (data not shown). For LG 4A-a, while markers from the two parents segregated 1:1 as expected,

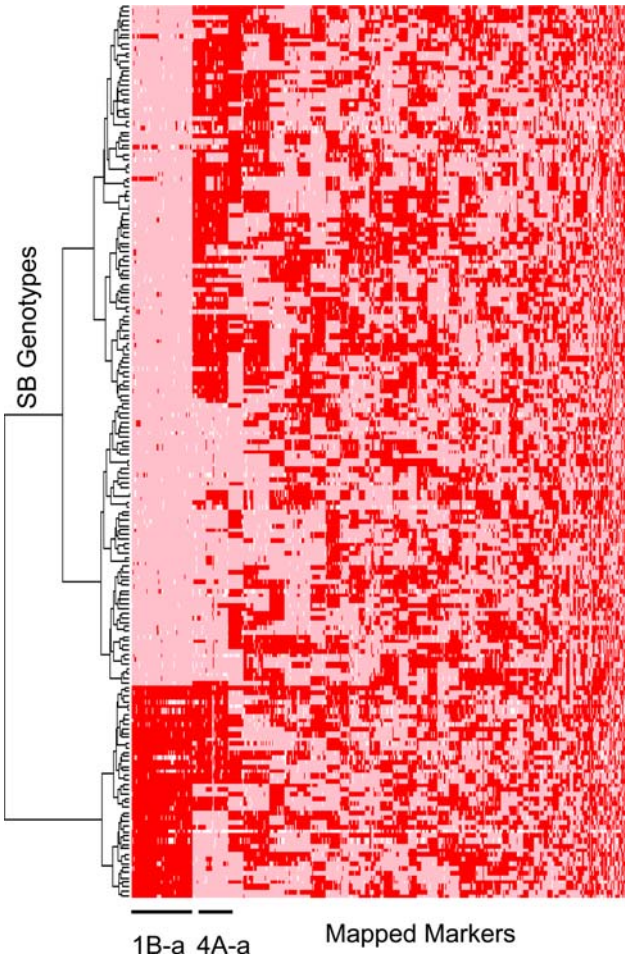

Fig. 1 Heat map illustrating the clustering of SB progeny based on marker genotypes. The *horizontal axis* is the 587 original markers scored in the SB population—the 1B-a and 4A-a markers are indicated. The *vertical axis* is the SB progeny. The markers are ordered by linkage group to reflect influence on clustering. The first two branches of the tree are driven by markers that map to 1B-a and to 4A-a. *Red* Seri alleles, *pink* Babax alleles, *white* missing data

127 of the 192 progeny (66%) inherited a parental LG with no marker alleles from the second parent (Fig. 1). For LG 4A-b, 53 of the 192 progeny (27.6%) inherited a parental-like LG with no recombination (data not shown). If recombination between parental alleles at the distal two markers on 4A-b was ignored, then the frequency of progeny with parental LGs increased to 43% (83 of the 192 progeny) (data not shown). The frequency of parental non-recombinant LG for all other linkage groups was less than 20% (data not shown) and usually less than 10%; it also did not increase beyond 25% if distal recombination was ignored (data not shown).

Identification of yield and yield component QTL

When considering data averaged across all trials, multiple putative QTL were identified for each trait, with the exception of biomass at anthesis (Fig. 2; Table 3). Between two (maturity biomass) and seven (grain weight and spikes m^{-2}) putative QTL (LOD > 3.0) were identified, with a total of 24 different genomic regions associated with the 13 traits other than yield. Alleles of QTL with increased effect were identified from both parents for each trait, with more identified from the parent with the largest trait value (Fig. 2; Tables 1, 3).

Figure 2 illustrates the relative position of putative and suggestive QTL for the 14 traits, including the identification of chromosomal regions containing putative and suggestive QTL for multiple traits. Co-location of QTL for multiple traits using the across all environment data set was greatest on LGs 1B-a, 1D-b, 4D-a, 6A-a, 6B-a, 7A-a and UA-d (Fig. 2). In the HiY data set only, QTL for grain yield (gyp), hectolitre weight (hect), harvest index (hi), height (ht) and grain weight (gw) co-located on LG 2B-a (Fig. 2).

For grain yield (gyp), four putative and seven suggestive QTL were detected using the ALL data set (Fig. 2; Table 3; Supplementary Table 2). The four putative QTL were detected on LGs 6D-a, 6D-b, 7A-a and an unassigned linkage group, UA-d, and explained between 3 and 7% of the additive effect variation (Table 3), with increased grain yield at three QTL originating from Seri (6D-a, 6D-b and UA-d) and one from Babax (7A-a). All four QTL co-located with putative and/or suggestive QTL for other traits, with higher grain yield usually associated with earlier flowering (ant), increased grain weight (gw), WSCc, hectolitre weight (hect), harvest index (hi) and grains m^{-2} (mgn) and reduced percent screenings (scr) (Table 3); the QTL on 7A-a for increased grain yield from Babax co-located with a suggestive QTL from Babax for decreased WSCc while the grain yield QTL on UA-d from Seri co-located with a putative QTL from Seri for a reduction in grains m^{-2} (Table 3). Grain yield QTL analysis was also undertaken using the HiY and LoY data sets to identify QTL × E effects. All four putative grain yield QTL detected using the ALL data set were also detected in the HiY data set but only the 7A-a QTL was detected in the LoY data set, with an increased LOD score (Supplementary Table 2); it was the strongest LoY grain yield QTL detected and the only LoY grain yield QTL in common with putative QTL detected using either the ALL or the HiY data sets (Fig. 2; Supplementary Table 2). Six of the ALL trials suggestive QTL co-located with putative QTL for other traits; increased grain yield was associated with increases in height (ht), hectolitre weight (hect), spikes m^{-2} (msn) and WSCa. All six of these suggestive QTL were also detected in the HiY data set, with three of these regions detected at LOD > 3. In the LoY data set, two additional putative QTL were detected on 1B-a and 5A-a. The high yield QTL on 1B-a was derived from Babax and co-located with a strong QTL for earlier flowering. The high yield QTL on 5A-a was

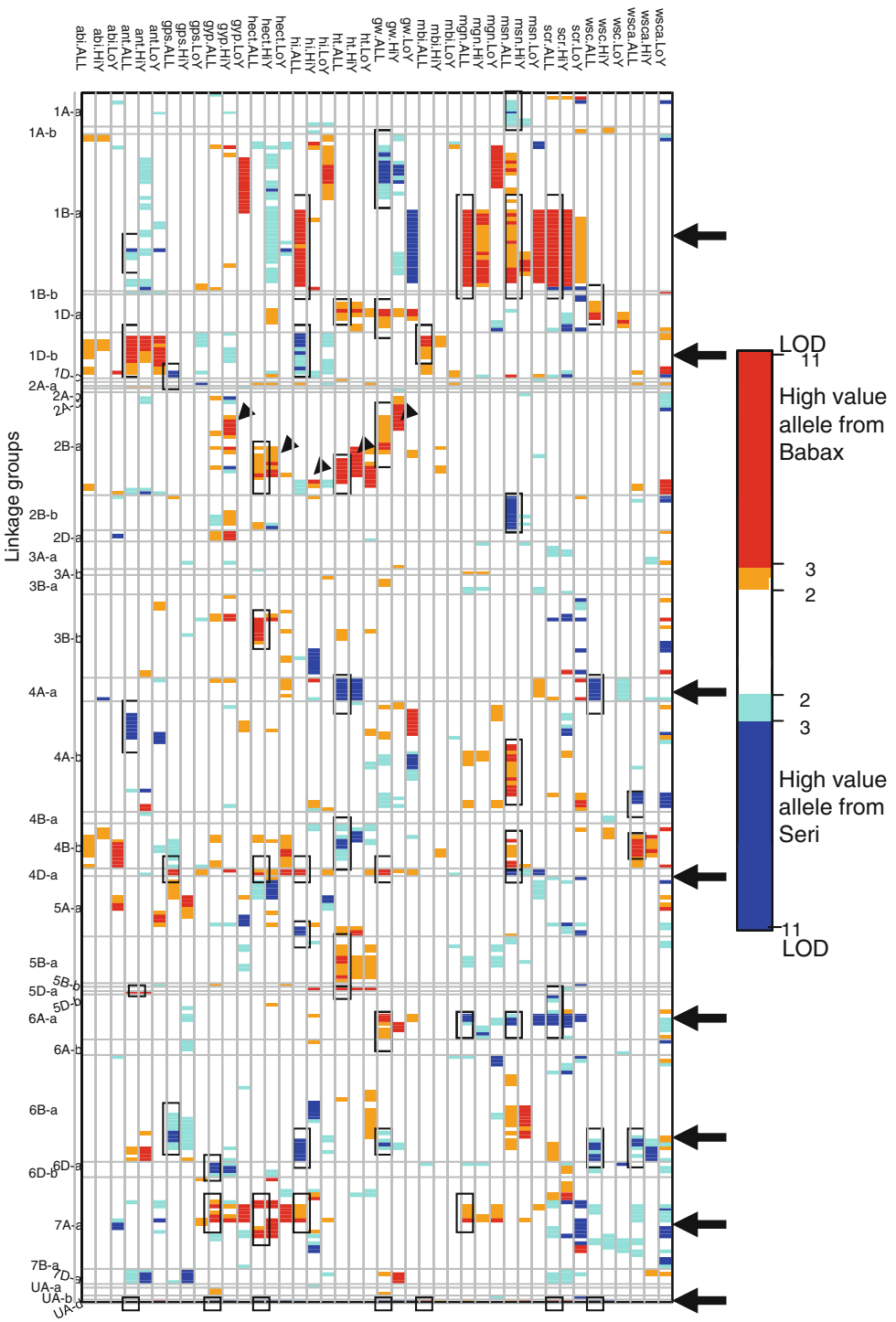

Fig. 2 Customised heat map illustrating location of marker-trait associations for 14 traits using ALL, HiY and LoY data sets. The *vertical axis* is the 39 LGs with all non-significant markers omitted. The *horizontal axis* is the 42 trait data sets. Trait abbreviations are as listed in Table 1. *Orange* and *red* lines indicate markers associated with the data set at a 2 < LOD < 3 and LOD > 3, respectively, as detected using CIM, with the high trait value allele derived from Babax. *Light blue* and *blue lines* indicate markers associated with the data set at a 2 < LOD < 3 and LOD > 3, respectively, as detected using CIM, with the high trait value allele derived from Seri. Putative QTL, as defined in "Materials and methods", in the ALL data set are *boxed*. *Arrows* to the right of the figure indicate the position of co-locating QTL for multiple traits using the across all environment data sets. *Arrow heads* indicate the position of co-locating QTL for multiple traits using the HiY data set

from Seri, and co-located with a strong QTL for increased harvest index (hi) (Fig. 2; Supplementary Table 2).

For the yield component or related traits with a high genetic correlation with grain yield (Table 2), viz. grains per spike (gps), grains m^{-2} (mgn), grain weight (gw), spike m^{-2} (msn), WSCc and WSCa, three to seven putative QTL were detected, with individual QTL explaining less than 15% of the phenotypic variation (Fig. 2; Table 3). Seven putative QTL were detected for grain weight (gw) (Fig. 2; Table 3) in the ALL data set with high grain weight alleles for four QTL originating from Babax, the parent with the larger grain weight (Table 1); a further six suggestive QTL (four from Babax) were also detected. Each putative QTL explained up to 11% of the additive effect variation (Table 3). QTL for increased grain weight co-located with QTL for increased hectolitre weight (three of seven QTL),

Table 3 Location, direction of additive effect, and % phenotypic variation explained for putative QTL for 13 grain yield and yield-related traits detected in the SB population

Chr	ant[a]			gps			gyp			hect			hi			ht			gw		
	Position[b]	Effect[c]	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)
1A-a																					
1B-a	90 (90–99)	−0.59	3.4										88 (79–99)	0.49	7.3				62 (46–71)	−0.47	6.3
1D-a																39 (23–67)	0.74	4.8	47 (39–64)	0.45	4.9
1D-b	2 (0–6)	0.80	6.7	6 (6–16)	−1.01	8.0							0 (0–6)	−0.41	7.1						
2B-a										60 (38–64)	1.11	4.1				60 (49–65)	1.13	8.4	37 (27–44)	0.43	5.0
2B-b																					
3B-b										40 (40–82)	1.45	5.2									
4A-a																15 (0–18)	−0.99	7.0			
4A-b	46 (25–46)	−0.68	4.8																		
4B-b																35 (0–42)	−0.67	5.5			
4D-a				0 (0–2)	0.86	4.9				2 (0–2)	1.40	4.1	2 (0–2)	0.51	7.2				0 (0–2)	0.56	7.4
5A-a													100 (92–103)	−0.37	5.4						
5B-a																21 (11–30)	0.70	4.0			
5D-a																0 (0–10)	1.22	9.5			
5D-b	0 (0–1)	0.82	6.3																		
6A-a																			55 (35–91)	0.51	6.5
6B-a				97 (86–104)	−0.82	5.6							110 (99–113)	−0.47	8.7				102 (93–104)	−0.20	1.0
6D-a							6 (1–10)	−3.21	3.2												
6D-b							0 (0–11)	−2.73	2.4												
7A-a							92 (55–212)	4.73	7.2	92 (55–174)	2.24	12.0	110 (92–110)	0.30	3.6						
UA-d	0 (0–3)	1.35	18.9				0 (0–3)	−4.63	6.7	0 (0–3)	−2.70	19.3							0 (0−3)	−0.66	11.4

Chr	mbi			mgn			msn			scr			wsca			wscc		
	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)
1A-a							33 (15–47)	−4.66	7.9									
1B-a				92 (79–99)	484	14.1	62 (58–62) 89 (73–96)	5.00 5.14	7.0 6.1	90 (79–116)	3.93	12.1						
1D-a																54 (23–54)	2.00	6.0
1D-b	0 (0–6)	9.79	7.8															
2B-a																		
2B-b							0 (0–21)	−5.39	6.5									
3B-b										40 (40)	−2.06	3.8						
4A-a																13 (13–18)	−2.11	7.1
4A-b							97 (76–98)	4.38	5.7				101 (98–114)	−2.59	6.8			
4B-b							44 (33–45)	2.95	4.3				37 (33–45)	2.74	6.6			
4D-a							2 (0–2)	−7.31	4.5									

Table 3 continued

Chr	mbi			mgn			msn			scr			wsca			wscc		
	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)	Position	Effect	r^2(%)
5A-a																		
5B-a																		
5D-a																		
5D-b																		
6A-a				55 (35–65)	−308	6.9				0 (0–18)	−0.45	1.7						
										55 (35–65)	−1.79	3.0						
6B-a													102 (99–111)	−1.66	4.1	111 (99–113)	−2.05	6.5
6D-a																		
6D-b																		
7A-a				110 (92–110)	266	5.6												
UA-d	0 (0–3)	6.06	3.1							0 (0–3)	3.44	10.0				0	−2.04	6.3

No putative QTL (LOD > 3.0) were detected for biomass at anthesis (abi)

[a] QTL detected using across all environment BLUPs

[b] Marker with highest LOD score (position of flanking markers detected at LOD > 2). Marker distances are in cM from the end of the short arm

[c] Additive genetic effect with highest LOD marker. Positive value indicates Babax allele with larger trait value

WSCc (three of seven QTL) but reduced grains m^{-2} (two of seven QTL), spikes m^{-2} (three of seven QTL) and percent screenings (three of seven QTL) (Fig. 2; Table 3). All putative grain weight QTL, with the exception of the QTL on 6B-a, were detected as putative or suggestive QTL in both the HiY and LoY data sets (Fig. 2; Supplementary Table 2); the 6B-a grain weight QTL was only detected as a suggestive QTL in the HiY data set. Furthermore, three of the suggestive grain weight QTL identified in the ALL data set were detected at higher LOD scores (LOD > 3) in the HiY (7B-a) and LoY (2 QTL on 4A-b) data sets. No new grain weight QTL was detected in the HiY or LoY data sets (Fig. 2; Supplementary Table 2).

For grains per spike (gps), three putative QTL were detected with high grains per spike alleles originating from both parents (Fig. 2; Table 3). All three high grains per spike QTL co-located with QTL for increased harvest index, with two high grains per spike QTL also co-locating with QTL for increased grain weight or decreased spikes m^{-1}. Only one of these grains per spike QTL was detected in the HiY data set while two were detected in the LoY data set and all were at a lower LOD score (<3.0) (Supplementary Table 2). Grains per spike QTL explained between 5 and 8% of the variation (Table 2). Two additional putative QTL were detected in the HiY data set with one co-locating with a QTL for earlier flowering and the other for decreased hectolitre weight. One putative QTL for grains per spike was detected in the LoY data set on LG 2A-a; it did not co-locate with any other putative QTL (Fig. 2; Supplementary Table 2).

For grains m^{-2} (mgn), three putative QTL were detected with high grains m^{-2} alleles originating from both parents (Fig. 2; Table 3); these QTL were also detected in the HiY and LoY data sets (Fig. 2, Supplementary Table 2). Each grains m^{-2} QTL explained between 5 and 14% of the variation (Table 3). Two of the high grains m^{-2} QTL co-located with QTL for increased spikes m^{-1}, percent screenings but lower grain weight, with one QTL also co-locating with a QTL for increased harvest index. The third grains m^{-2} QTL also co-located with QTL for increased harvest index, grain yield, and hectolitre weight. Two additional putative high grains m^{-2} QTL were detected in the LoY data sets on chromosomes 1D-a and 6B-a; both originated from Seri and co-located with QTL for increased percent screenings (Fig. 2; Supplementary Table 2).

Seven putative QTL, each explaining between 4 and 8% of the additive effect variation were detected for spike m^{-2} (msn) (Fig. 2; Table 3) with high msn QTL originating from both parents. QTL for msn co-located with QTL for reduced hectolitre weight, harvest index and grain weight. Only two of the putative QTL were detected in both the HiY and LoY data sets (Fig. 2; Supplementary Table 2). Three were also detected in the HiY data set only at a

Table 4 Performance (BLUEs) for traits of grain weight (GW)–grain number (GN) groups of Seri/Babax RILs from analyses across 2002–2007 environments

Classification	abi[a]	ant	gps	gyp	hi	ht	gw	mbi	mgn	msn	scrpercent	WSCc
High GW_High GN	647	90.2	40.7	365	0.45	77.7	31.2	795	12314	271	4.60	142
High GW_Low GN	639	91.6	37.1	341	0.43	80.1	32.9	771	10839	267	4.24	139
Low GW_High GN	642	93.8	42.0	349	0.44	75.5	26.5	810	13643	302	6.85	130
Low GW_Low GN	637	95.6	39.4	304	0.42	76.3	27.0	766	11988	297	6.04	123
Parents (Seri and Babax)	649	93.6	41.2	345	0.44	79.1	29.8	795	12269	269	4.92	141
LSD[b] ($P = 0.05$)	14	0.3	1.3	7	0.01	0.9	0.4	13	315	6	0.36	4

Table modified from Rattey et al. (2009)

[a] See Table 1 for trait codes

[b] The least significant difference for declaring two groups of Seri/Babax RILs different at $P = 0.05$

reduced LOD (<3.0) and one was detected in the LoY data set only (Fig. 2; Supplementary Table 2).

Four putative QTL were detected in the ALL data set for WSCc, three of which were derived from Seri, the high WSC parent (Fig. 2; Table 3). One was also detected in the HiY data set while two were detected in the LoY data set. Only one suggestive QTL for WSCc was detected in all three data sets with high WSCc from Seri (Fig. 2; Supplementary Table 2). Three putative and two suggestive QTL were detected in the ALL data set for WSCa, of which three were derived from Seri, the high WSC parent (Fig. 2; Table 3). Only one putative QTL was detected in all three data sets and the high WSC QTL originated from Seri; three were detected in the LoY data set and one in the HiY dataset (Fig. 2; Supplementary Table 2). QTL for increased WSCc and WSCa often co-located with QTL for increased grain weight.

Putative height QTL were detected on chromosomes 1D-a, 2B-a, 4A-a, 4B-b, 5B-a and 5D-a, with four of the six tall QTL derived from the slightly taller parent, Babax (Fig. 2; Tables 1, 2). Interestingly, two QTL tall alleles were derived from different parents in the HiY data set when compared with the ALL and LoY datasets (Fig. 2; Supplementary Table 2). Five putative anthesis QTL were detected with earlier flowering for three QTL derived from Babax (Fig. 2; Table 3).

QTL response to selection for high grain number and large grain weight

Despite the negative correlation between grain weight (gw) and grain number (mgn) (Table 2), progeny lines were identified that fell broadly into four categories: (1) low gw_low mgn, (2) low gw_high mgn, (3) high gw_low mgn and (4) high gw_high mgn (Table 4; Rattey et al. 2009). A comparison between the highest yielding group, high gw_high mgn, and the lowest yielding group, low gw_low mgn, suggested that the grain yield and grain weight in these high-yielding lines was associated with a combination of traits, including slightly earlier flowering and taller plants with fewer and heavier culms, a higher harvest index, higher water soluble carbohydrates reserves in the stem and a higher number of grains per spike. The two high grain number groups have significantly greater grain yield than the other two groups, a higher harvest index and more grains per spikelet. The two high grain weight groups have a lower percent screenings, fewer but heavier spikes m^{-2} and a higher level of WSCa and WSCc than the two low gw groups (Table 4).

QTL allele frequency at the 24 genomic regions associated with QTL for the 14 traits (Table 3) was assessed in the 31 SB progenies present in the four progeny groups. QTL allele frequencies for six regions (Table 5) varied significantly ($P < 0.05$) between the highest (high GW_high GN) and lowest (low GW_low GN) yielding progeny groups (Table 5); allele frequencies varied at two more QTL regions at a higher P value (Table 5). The high-yielding progenies were enriched for QTL that resulted in increased grain yield (one QTL), grains per spike (two QTL), harvest index (three QTL), grain weight (five QTL), hectolitre weight (three QTL), WSCa (three QTL) and WSCc (three QTL), reduced spikes m^{-2} (two of three QTL reduced spikes m^{-2}), earlier flowering (one QTL) and taller plants (two of three QTL increased height). Of these eight regions, four varied in frequency between the high and low GW groups, resulting in an increased frequency of QTL for higher grain yield (one QTL), grain weight (three QTL), WSCc (two QTL), harvest index (one QTL), and hectolitre weight (two QTL), fewer spikes m^{-2} (two QTL), lower percent screenings (one QTL) and biomass at maturity (one QTL), earlier flowering (one QTL) and taller plants (one QTL) (Table 5). Only one of the other four regions varied between the high and low GN groups; this region was associated with more spikes m^{-2}, shorter plants and more WSCa in the high grain number groups (Table 5).

Table 5 Proportion of progeny with Seri M 82 allele at QTL for yield and yield-related component traits in four grain weight-grain number groups[a]

QTL markers	HighGW_high GN	High GW_low GN	Lo2 GW_high GN	Low GW_low GN	Significance	Favourable allele
1D-a.aca/caa-2	0.33	0.13	0.78	1.00	***	Babax
1D-a.wPt-5503	0.33	0.13	0.78	0.80	**	Babax
2B-a.agc/cag-4	0.33	0.13	0.33	0.80	*	Babax
2B-a.wPt5680	0.22	0.25	0.22	0.80	***	Babax
2B-b.acg/cac-7	0.44	0.25	0.89	0.80	*	Babax
2B-b.acc/ctc-9	0.44	0.25	0.56	0.80	*	Babax
4B-b.gwm375	0.33	0.63	0.22	0.80	**	Babax
4B-b.barc020	0.44	0.63	0.22	1.00	**	Babax
4D-a.wmc048b	0.11	0.25	0.67	0.60	**	Babax
4D-a.cfd023	0.11	0.25	0.67	0.60	***	Babax
5A-a.aac/caa-8	0.44	0.50	0.67	0.00	**	Seri
5A-a.wPt-3563	0.33	0.50	0.89	0.00	*	Seri
6B-a.agc/cta-4	0.89	0.50	0.56	0.20	***	Seri
6B-a.agg/ctg-8	0.89	0.50	0.33	0.20	***	Seri
UA-d.gwm130	0.78	0.75	0.22	0.40	*	Seri

Frequency of Seri allele in the four GW–GN classifications for those regions significantly different between the hi gw_hi mgn and lo gw_lo mgn groups

*,**,*** Significance at the $P < 0.1$, 0.05, 0.01 levels, respectively, calculated between the hi gw_hi mgn and lo gw_lo mgn groups

[a] Frequency of Seri allele in the 9, 8, 9 and 5 SB progenies representing the four GW–GN classifications, respectively

Discussion

Variable genome coverage in the SB map

Although almost 600 markers were scored and mapped in this population, significant gaps in the map remain; the 39 LGs formed could be assigned to 20 of the 21 chromosomes with no markers mapped to chromosome 3D; this was unexpected. A map constructed in a population from a cross between Seri M 82 and Hartog (a selection from the CIMMYT line Pavon F76), with a slightly lower COP of 0.274 (McLaren et al. 2004), contained only 189 markers but linkage groups containing these markers could be assigned to all 21 wheat chromosomes (Dwi, Nadella and Godwin, unpublished obs). Furthermore, polymorphic markers were identified for other D genome chromosomes in the SB population even though fewer markers were screened. For example, the wheat DArT array used in this study (http://www.triticarte.com.au/) contains approximately 40 DArT markers that have been mapped to each of chromosomes 1D, 2D and 3D, while considerably fewer markers have been mapped to the other four D genome chromosomes (30 to 7D, and 8, 15 and 11 to 4D, 5D and 6D, respectively. Nevertheless, 12 1D and two 2D DArT markers were polymorphic and mapped in the SB population as were three of the 15 5D DArT markers. These results suggest that the difficulty in identifying polymorphic 3D markers may be due to large regions of chromosome 3D in common between the two parental lines, Seri M82 and Babax.

A high level of segregation distortion was observed on the 1B chromosome with approximately 75% of the progenies receiving the Babax marker alleles on LG 1B-a; this occurred in both the Seri–Babax progeny as well as the Babax–Seri progeny. Other studies have also reported similar segregation ratios in progeny of crosses between 1BL.1BS and T1BL.1RS parents, suggesting selective transmission against gametes carrying the translocation. However, reduced transmission has been observed previously only when the parent containing the rye translocation chromosome is used as a male (Lukaszewski et al. 1982; Singh 1985, cited in Koebner et al. 1986). To our knowledge, this is the first report of reduced transmission of the T1BL.1RS translocation chromosome through the female as well as the male gametes.

A low level of recombination was observed in linkage groups 1B-a, 4A-a and 4A-b, resulting in a large number of progenies with parental-like chromosomes. Reduced levels of recombination are commonly observed between translocated and non-translocated chromosomes, which may explain the 1B-a observation as the population is segregating for T1BL.1RS. However, while chromosome 4A has been shown to be involved in three inversions and two translocations (Miftahudin et al. 2004), these chromosomal rearrangements appear to predate the formation of hexaploid wheat and are thus present in all bread wheat lines. The low level of recombination and resulting high frequency of parental-like chromosomes observed in Seri–Babax population for linkage groups 1B-a, 4A-a and 4A-b

has major implications for both the accuracy of marker order and for QTL detection on these linkage groups; the effective population size for these three LGs was much smaller. A small population size restricts the number of recombination events between markers that can be detected and thus marker order is less precise. This may explain why two QTL were detected for spikes m^{-2} on LG 1B-a, or why two regions of co-locating QTL were apparently detected on LG 1B-a. In addition, a small population size has also been shown to affect the number of QTL detected, the accuracy with which they are detected and to result in an overestimation of the additive effect of the QTL detected (Doerge 2002; Bernardo 2004; and references therein).

The T1BL.1RS wheat–rye translocation

The T1BL.1RS wheat–rye translocation has been reported to confer yield and biotic and abiotic stress advantages and is widely used in plant breeding programs (Villareal et al. 1995). Using this population, Mathews et al. (2008) and Rattey et al. (2009) found that the translocation had a negative impact on grain yield; a similar result was found by Peake (2003) using other crosses involving the Seri parent. The results of this study are consistent with the agronomic results. Putative QTL for numerous traits but not for grain yield, were found to co-locate to this QTL. In particular, the translocation from Seri M82 was found to increase grain weight and promote early flowering, but decrease harvest index, grain number, spikes m^{-2} and percent screenings. No grain yield QTL was detected on this LG in the ALL or HiY data set, but a putative QTL was detected on LG 1B-a in the LoY data set. The latter result is consistent with the suggestion by Rattey et al. (2009) that the effect of this translocation varies with the environment sampled.

Detection of broadly adapted and environment-specific QLT for grain yield and yield-related traits

Substantial yield variation has been observed in wheat in the north-eastern region of Australia as a result of water stress (Brennan and Byth 1979). Rattey et al. (2009) had previously shown that in the SB population broad adaptation was best achieved by selection based on performance across the yield range of the production environments but that specific adaptation to the high- or low-yielding environments was also observed. One of the objectives of this paper was to identify broadly relevant QTL for yield and yield-related traits for this cropping region, using the phenotypic data derived from the "across-all-trials" analysis, and to investigate the extent and type of production environment-specific QTL using data from environments subsetted into high-yielding (HiY) and low-yielding (LoY). While most QTL were detected in all three datasets, a small number of QTL were detected that were specific to one or other production environment type, or that had a strong influence on the detection of the across-environment QTL. For example, a QTL for grain yield was detected on LG 7A-a in all three data sets, whereas the QTL on LGs 6D-b and UA-d were only detected in the ALL and HiY data sets and the QTL on 1B-a in the LoY data set only. Similarly, a HiY QTL hotspot was detected on LG 2B-a with co-locating putative QTL for grain yield, hectolitre weight, harvest index, height and grain weight detected only in this dataset These QTL could be useful for large niche environments that had some consistency in being high or low yielding due to water-limitation.

The grain yield, height and anthesis data from this population have been previously analysed using a mixed-model approach that accounts for genetic correlations among trials and individual trial variance heterogeneity, as well as enabling the fitting of genotypic factors such as the T1BL.1RS translocation (Mathews et al. 2008). In general, similar regions were detected for all three traits using both approaches. Using the mixed-model approach, eight QTL were detected, with one QTL on 6D-a being a main effect QTL and the other seven having significant QTL-by-environment interactions (QEI) (Mathews et al. 2008). The main effect QTL and six of the seven QTL with QEI were detected in the present study with the 6D-a QTL and three other QTL detected in the ALL dataset and two QEI QTL detected in the HiY or the LoY data set only. Similarly, the mixed-model approach detected three QTL for anthesis (Mathews et al. 2008), of which two were found in all three datasets and one QTL that was detected only in the LoY dataset. Six QEI QTL (no main effect QTL were detected) were detected for height (Mathews et al. 2008) of which two were detected in the three datasets in the present study; two were detected in the ALL and HiY data sets only and one was detected in ALL and the LoY data set.

QEI for other traits were detected in the current analysis as different QTL were detected or QTL were detected at varying significance in low versus high production environments or in the across all environment data set. While most of the QTL detected in the ALL, HiY and/or LoY data sets displayed the same direction of additive effect, different parental alleles were associated with high grain yield for four suggestive gyp QTL in the ALL and HiY data sets. Co-locating suggestive QTL for harvest index, on LGs 2A-a, 2B-a and 5A-a, and hectolitre weight, on LG 2B-b, also have an altered direction of additive effect between the ALL and HiY datasets.

Co-locating QTL detected for grain yield and yield-related component traits

Most of the QTL regions detected in this population have been reported previously (for example, see Huang et al.

2006; Marza et al. 2006; Snape et al. 2007; Rebetzke et al. 2008 and references therein). However, possibly novel QTL were also detected for several traits. For example, a QTL for increased grain yield associated with the Seri allele was detected on chromosome 6D. This co-located only with a suggestive QTL for increased WSCc and was apparently independent of other traits. QTL associated with increased grain weight were identified on chromosomes 1B, 1D, and 6A and QTL for increased grain number were detected on chromosomes 1B, 6A and 7A. A QTL for high WSCc was detected on chromosome 1D and QTL for increased spikes m^{-2} were detected on chromosomes 1A 2B, 4B, and 6A. For days to anthesis, a QTL was reported on chromosome 1B and for plant height, QTL were reported on chromosomes 1D and 5B.

Co-location of QTL for yield and for yield components is common (e.g. Huang et al. 2006; Marza et al. 2006; Snape et al. 2007; Rebetzke et al. 2008; and references therein). Further work with more markers or more precisely defined populations is required to investigate the extent to which this co-location represents pleiotropy or genetic linkage of separate loci. Nevertheless, co-location of QTL has implications for the use of these markers. Previous papers have demonstrated the value of selection for high levels of particular traits (Rebetzke et al. 2008) or the identification of traits to manipulate for increased yield (Quarrie et al. 2005; Snape et al. 2007). In physiological studies of changes in wheat cultivars over decades, increased grain yield has been frequently associated with increased grain number (reviewed in Miralles and Slafer 2007), accompanied by a negative relationship between grain number and grain weight (Miralles and Slafer 2007). In the study by Quarrie et al. (2005), grain number was the yield component most frequently associated with yield QTL clusters while Snape et al. (2007) reported that grain size was the trait most highly correlated with grain yield; other studies have also indicated a high correlation between grain yield and grain number (Marza et al. 2006; Kumar et al. 2007) or grain yield and grain size (Huang et al. 2006; Narasimhamoorthy et al. 2006; Li et al. 2007). Using several lines from the Seri–Babax population, Dreccer et al. 2009) showed that the typically inverse relationship between grain number and grain size across environments could be broken in lines that had lower tiller numbers and higher WSC accumulation in stems, i.e. the higher WSC lines directly contributed up to 15% of the WSC to yield, and allowed the filling of grain under mild terminal stress. Prior to flowering, these lines had initiated more florets per spike and were also consequently better able to fill the terminal grains (grain 3) on each spikelet, reducing the proportion of 'screenings'. The co-location of WSCc and grain weight QTL in the present study supports the relevance of WSC to promote grain fill, increase grain weight and ultimately improve grain yield.

High-yielding lines are enriched for QTL for yield-related traits

In the Seri–Babax population, progeny lines with both a greater grain yield and larger grain weight than a group of commercial cultivars were identified (Rattey et al. 2009). Their performance was associated with a combination of traits, including slightly earlier flowering and taller plants with fewer and heavier culms, a higher harvest index, higher water soluble carbohydrates reserves in the stem and a higher number of grains per spike. QTL analysis of these lines indicated an altered frequency of QTL alleles consistent with the agronomic data. The high-yielding progeny had an increased frequency of QTL for earlier flowering, increased harvest index, grain weight, WSC concentration and content, grains per spike and fewer spikes m^{-2} than the low grain yielding progeny. Compared to low yielding (20% less), low grain weight progeny, the superior lines had a higher frequency of Babax alleles on 1D-a, 2B-a, 2B-b, 4B-b and 4D-a and Seri alleles on 5A-a, 6B-a and UA-d. Physiological and breeding studies, similar to those described by Dreccer et al. (2009), are on-going to try to dissect some of these trait effects. The high grain weight progeny had an increased frequency of QTL that were associated with increased grain weight, WSCc, hectolitre weight, height, and fewer spikes m^{-2}, again supporting the role of WSC in filling grain, increasing grain weight and improving grain yield. The high grain number groups were enriched for QTL associated with more spikes m^{-2}, shorter plants and a higher harvest index.

These results are promising as they suggest that both grain size and grain number can be manipulated independently in this population to increase grain yield in this cropping region. Furthermore, they suggest that it would be possible to select high-yielding lines with large grain weight using DNA markers associated with QTL for earlier flowering, increased harvest index, grain weight, WSC, grains per spike and spikes m^{-2}.

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References

Bernardo R (2004) What proportion of declared QTL in plants are false? Theor Appl Genet 109:410–424

Brennan JP, Byth DE (1979) Genotype × environmental interactions for wheatyields and selection for widely adapted wheat genotypes. Aust J Agric Res 30:221–232

Chapman SC (2008) Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. Euphytica 161:195–208

Cooper M, Byth DE, DeLacy IH, Woodruff DR (1993) Predicting grain yield in Australian environments using data from CIMMYT international wheat performance trials. I. Potential for exploiting correlated responses to selection. Field Crops Res 32:305–322

Cooper M, Woodruff DR, Eisemann RL, Brennan PS, DeLacy IH (1995) A selection strategy to accommodate genotype-by-environment interaction for grain yield of wheat: managed-environments for selection among genotypes. Theor Appl Genet 90:492–502

Doerge R (2002) Mapping and analysis of quantitative trait loci in experimental populations. Nat Rev Genet 3:43–52

Dreccer MF, van Herwaarden AF, Chapman SC (2009) Grain number and grain weight in wheat lines contrasting for stem water soluble carbohydrate concentration. Field Crops Res 112:43–54

Ehdaie B, Alloush GA, Waines JG (2008) Genotypic variation in linear rate of grain growth and contribution of stem reserves to yield in wheat. Field Crops Res 106:34–43

Hoisington DA (1992) Laboratory protocols. CIMMYT Applied Molecular Genetics Laboratory. CIMMYT, Mexico, D.F.

Huang XQ, Cloutier S, Lycar L, Radovanovic N, Humphreys DG, Noll JS, Somers DJ, Brown PD (2006) Molecular dissection of QTLs for agronomic and quality traits in a doubled haploid population derived from two Canadian wheats (*Triticum aestivum* L.). Theor Appl Genet 113:753–766

Isidore E, van Os H, Andrzejewski S, Bakker J, Barrena I, Bryan GJ, Caromel B, van Eck H, Ghareeb B, de Jong W, van Koert P, Lefebvre V, Milbourne D, Ritter E, van der Voort JR, Rousselle-Bourgeois F, van Vliet J, Waugh R (2003) Toward a marker-dense meiotic map of the potato genome, lessons from linkage group I. Genetics 165:2107–2116

Koebner RMD (1995) Generation of PCR-based markers for the detection of rye chromatin in a wheat background. Theor Appl Genet 90:740–745

Koebner RMD, Shepherd KW, Appels R (1986) Controlled introgression to wheat of genes from rye chromosome arm 1RS by induction of allosyndesis. 2. Characterization of recombinants. Theor Appl Genet 73:209–217

Kumar N, Kulwal PL, Balvan HS, Gupta PK (2007) QTL mapping for yield and yield contributing traits in two mapping populations of bread wheat. Mol Breed 19:163–177

Li S, Jia J, Wei X, Zhang X, Li L, Chen H, Fan Y, Sun H, Zhao X, Lei T, Xu Y, Jiang F, Wang H, Li L (2007) A intervarietal genetic map and QTL analysis for yield traits in wheat. Mol Breed 20:167–178

Lukaszewski AJ, Gustafson JP, Apolinarska B (1982) Transmission of chromosomes through the eggs and pollen of triticale × wheat F1 hybrids. Theor Appl Genet 63:49–55

Mago R, Spielmeyer W, Lawrence GJ, Lagudah ES, Ellis JG, Pryor A (2002) Identification and mapping of molecular markers linked to rust resistance genes located on chromosome 1RS of rye using wheat-ray translocation lines. Theor Appl Genet 104:1317–1324

Marza F, Bai G-H, Carver BF, Zhou W–C (2006) Quantitative trait loci for yield and related traits in the wheat population Ning7840 × Clark. Theor Appl Genet 112:688–698

Mathews KL, Chapman SC, Trethowan R, Pfeiffer W, van Ginkel M, Crossa J, Payne T, DeLacy I, Fox PN, Cooper M (2007) Global adaptation patterns of Australian and CIMMYT spring bread wheat. Theor Appl Genet 115:819–835

Mathews KL, Malosetti M, Chapman SC, McIntyre CL, Reynolds M, Shorter R, van Eeuwijk F (2008) Multi-environment QTL mixed models for drought stress adaptation in wheat. Theor Appl Genet 117:1077–1091

McLaren CG, Ramos L, Lopez C, Eusebio W (2004) Applications of the genealogy management system. ICIS Technical Manual

Miftahudin RK, Ma XF, Mahmoud AA, Layton J, Milla MAR, Chikmawati T, Ramalingam J, Feril O, Pathan MS, Momirovic GS, Kim S, Chema K, Fang P, Haule L, Struxness H, Birkes J, Yaghoubian C, Skinner R, McAllister J, Nguyen V, Qi LL, Echalier B, Gill BS, Linkiewicz AM, Dubcovsky J, Akhunov ED, Dvorák J, Dilbirligi M, Gill KS, Peng JH, Lapitan NLV, Bermudez-Kandianis CE, Sorrells ME, Hossain KG, Kalavacharla V, Kianian SF, Lazo GR, Chao S, Anderson OD, Gonzalez-Hernandez J, Conley EJ, Anderson JA, Choi DW, Fenton RD, Close TJ, McGuire PE, Qualset CO, Nguyen HT, Gustafson JP (2004) Analysis of expressed sequence tag loci on wheat chromosome group 4. Genetics 168:651–663

Miralles DJ, Slafer GA (2007) Sink limitations to yield in wheat, how could it be reduced? J Agric Sci 145:139–149

Mohler V, Hsam SLK, Zeller FJ, Wenzel G (2001) An STS marker distinguishing the rye-derived powdery mildew resistance alleles at the *Pm8/Pm17* locus of common wheat. Plant Breed 120:448–450

Nagata K, Shimizu H, Terao T (2002) Quantitative trait loci for non-structural carbohydrate accumulation in leaf sheaths and culms of rice (*Oryza sativa* L.) and their effects on grain filling. Breed Sci 52:275–283

Narasimhamoorthy B, Gill BS, Fritz AK, Nelson JC, Brown-Guedira GL (2006) Advanced backcross QTL analysis of a hard winter wheat × synthetic wheat population. Theor Appl Genet 112:787–796

Olivares-Villegas JJ, Reynolds MP, McDonald GK (2007) Drought-adaptive attributes in the Seri/Babax hexaploid wheat population. Funct Plant Biol 34:189–203

Peake A (2003) Inheritance of grain yield and effect of the 1BL/1RS translocation in three bi-parental wheat (*Triticum aestivum* L.) populations in production environments of north eastern Australia. School of Land and Food Sciences, The University of Queensland, Brisbane

Quarrie SA, Steed A, Calestani C, Semikhodskii A, Lebreton C, Chinoy C, Steele N, Pljevljakusic D, Waterman E, Weyen J, Schondelmaier J, Habash DZ, Farmer P, Saker L, Clarkson DT, Abugalieva A, Yessimbekova M, Turuspekov Y, Abugalieva S, Tuberosa R, Sanguineti M-C, Hollingon PA, Aragues R, Royo A, Dodig D (2005) A high-density genetic map of hexaploid wheat (*Triticum aestivum* L.) from the cross Chinese Spring × SQ1 and its use to compare QTLs for grain yield across a range of environments. Theor Appl Genet 110:865–880

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rajaram S, Mann CE, Ortiz-Ferrara G, Mujeeb-Kazi A (1983) Adaptation, stability and high yield potential of certain 1B/1R CIMMYT wheats. In: Sakamoto S (ed) The 6th international wheat genetics symposium. CIMMYT, Mexico City, Kyoto, Japan, pp 613–621

Rattey A, Shorter R, Chapman SC, Dreccer MF, van Herwaarden AF (2009) Variation for biomass and grain components, and traits conferring improved yield and grain weight, in an elite recombinant inbred wheat population grown under variable drought conditions. Aust J Agric Res 60:717–729

Rebetzke GJ, Condon AG, Richards RA, Farquhar GD (2006) Inheritance of reduced carbon isotope discrimination in bread wheat (*Triticum aestivum* L.). Euphytica 150:97–106

Rebetzke GJ, van Herwaarden AF, Jenkins C, Weiss M, Lewis D, Ruuska S, Tabe L, Fettel NA, Richards RA (2008) Quantitative trait loci for soluble stem carbohydrate production in wheat. Aust J Agric Res 59:891–905

Schmidt AL, McIntyre CL, Thompson J, Seymour NP, Liu CJ (2005) Quantitative trait loci for root lesion nematode (*Pratylenchus thornei*) resistance in Middle-Eastern landraces and their potential for introgression into Australian bread wheat. Aust J Agric Res 56:1059–1068

Singh NK (1985) The structure and genetic control of endosperm proteins in wheat and rye. PhD thesis. University of Adelaide

Snape JW, Foulkes MJ, Simmonds J, Leverington M, Fish LJ, Wang Y, Ciavarrella M (2007) Dissecting gene × environmental effects on wheat yields via QTL and physiological analysis. Euphytica 154:401–408

Takai T, Fukata Y, Shiraiwa T, Horie T (2005) Time-related mapping of quantitative trait loci controlling grain-filling of rice (*Oryza sativa* L.). J Exp Bot 56:2107–2118

Turner LB, Cairns AJ, Armstead IP, Ashton J, Skot K, Whittaker D, Humphreys MO (2006) Dissecting the regulation of fructan metabolism in perennial ryegrass (*Lolium perenne*) with quantitative trait locus mapping. New Phytol 169:45–58

Van Herwaarden AF, Angus JF, Richards RA (1998) 'Haying off', the negative grain yield response of dryland wheat to nitrogen fertiliser. II. Carbohydrate and protein dynamics. Aust J Agric Res 49:1083–1093

Van Ooijen JW, Voorrips RE (2001) JoinMap 3.0, software for the calculation of genetic linkage maps. Plant Research International B_V, Wageningen

Villareal RL, DelToro E, Mujeeb-Kazi A, Rajaram S (1995) The 1BL/1RS chromosome translocation effect on yield characteristics in a *Triciticum aestivum* L. cross. Plant Breed 114:497–500

Wenzl P, Carling J, Kudrna D, Jaccoud D, Huttner E, Kleinhofs A, Kilian A (2004) Diversity Arrays Technology (DArT) for whole-genome profiling of barley. Proc Natl Acad Sci 101:9915–9920

Yang DL, Jing RL, Chang XP, Li W (2007) Identification of quantitative trait loci and environmental interactions for accumulation and remobilization of water-soluble carbohydrates in wehat (*Triticum aestivum* L.) stems. Genetics 176:571–584