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Genetic dissection of grain yield in bread wheat. I. QTL analysis

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Abstract Grain yield forms one of the key economic drivers behind a successful wheat (*Triticum aestivum* L.) cropping enterprise and is consequently a major target for wheat breeding programmes. However, due to its complex nature, little is known regarding the genetic control of grain yield. A doubled-haploid population, comprising 182 individuals, produced from a cross between two cultivars 'Trident' and 'Molineux', was used to construct a linkage map based largely on microsatellite molecular makers. 'Trident' represents a lineage of wheat varieties from southern Australia that has achieved consistently high relative grain yield across a range of environments. In comparison, 'Molineux' would be rated as a variety with low to moderate grain yield. The doubled-haploid population was grown from 2002 to 2005 in replicated field experiments at a range of environments across the southern Australian wheat belt. In total, grain yield data were recorded for the population at 18 site-year combinations. Grain yield components were also measured at three of these environments. Many loci previously found to be involved in the control of plant height, rust resistance and ear-emergence were found to influence grain yield and grain yield components in this population. An additional nine QTL, apparently unrelated to these traits, were also associated with grain yield. A QTL associated with grain yield on chromosome 1B, with no significant relationship with plant height, ear-emergence or rust resistance, was detected (LOD ≥2) at eight of the 18 environments. The mean yield, across 18 environments, of individuals carrying the 'Molineux' allele at the 1B locus was 4.8% higher than the mean grain yield of those lines carrying the 'Trident' allele at this locus. Another QTL identified on chromosome 4D was also associated with overall gain yield at six of the 18 environments. Of the nine grain yield QTL not shown to be associated with plant height, phenology or rust resistance, two were located near QTL associated with grain yield components. A third QTL, associated with grain yield components at each of the environments used for testing, was located on chromosome 7D. However, this QTL was not associated with grain yield at any of the environments. The implications of these findings on marker-assisted selection for grain yield are discussed.

Keywords Bread wheat · Grain size · Grain yield · Grain yield components · Quantitative trait locus · *Triticum aestivum*

Abbreviations

DH	Doubled-haploid
$G.M^{-2}$	Grains per square metre

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$G.H^{-1}$	Grains per head
$H.P^{-1}$	Heads per plant
MAS	Marker assisted selection
MET	Multiple environment trial
QTL	Quantitative trait locus
TGW	Thousand grain weight
T/M	Trident/molineux

Introduction

Improved grain yield has been a major focus of most wheat breeding programmes around the world. As a key component of farm profitability, genetic advancement in grain yield has helped to maintain the viability of agricultural systems both in developed and developing countries. In Australia, the production of early maturing, photoperiod-insensitive varieties allowed significant expansion away from the fringes of the environmentally favourable eastern coast. Similar examples of changes in adaptation through the introduction of photoperiod insensitivity have been described for other countries (Law and Worland 1997). In the middle of the twentieth century, major genes conferring reduced plant height were introduced to the global wheat industry. These substantially improved grain yield through increased harvest index and straw strength (Borlaug 1968). Beyond these, and similar examples of major shifts in plant phenology and morphology, most improvements in grain yield have arisen through incremental genetic advances. Breeders have often developed cultivars with superior adaptation to their target environment without a detailed knowledge of the underlying physiological mechanisms. Unfortunately, field measurements and particularly those for grain yield, are subject to significant extraneous error, which in turn reduces the effectiveness of phenotypic selection. In addition, the major stresses present in a particular year, and at any particular site, may not provide the optimum environment for selecting long-term, overall, genetic performance. With the advent of molecular genetics, it has become possible to select genes for grain yield with molecular markers [marker-assisted selection (MAS)] at any stage in the breeding process. Not limited by seed quantity, nor influenced by the environment, breeders have been able to use MAS to rapidly and efficiently select for other valuable traits on a genetic, rather than phenotypic basis (Yu et al. 2000; Yousef and Juvik 2001; Jefferies et al. 2003; Zhou et al. 2003).

Until recently, genetic studies for grain yield have largely focussed on specific chromosomes through the use of substitution lines, or the use of near isogenic lines for the characterisation of the effects of genes known to be involved in the control of important physiological traits (such as plant height reduction and flowering time) (Flintham and Gale 1983; Richards 1992; Worland 1996; Worland et al. 1998; Rebetzke and Richards 2000; Butler et al. 2005; Dyck et al. 2004). The advent of QTL mapping has allowed more complex traits, such as grain yield, to be dissected. QTL apparently unrelated to these physiological traits have been identified on chromosomes covering most of the wheat genome. However, QTL shown to be associated with grain yield across multiple sites/years are less common (Borner et al. 2002; Groos et al. 2003; Huang et al. 2004; McCartney et al. 2005; Marza et al. 2006).

The grain yield of wheat can also be dissected into its components, including the number of plants per unit area, number of spikes per plant, number of spikelets per spike, number of fertile florets per spikelet and grain weight. More generally, grain yield is considered the combination of grain number and grain weight. Not only is grain weight one of the key grain yield components, grain weight is often used as a grain receival and marketing standard. Should the genetic basis of grain yield components be dissected, MAS may be used to improve both grain yield and its individual components much earlier in the breeding process. Genetic dissection of grain yield components may also help to elucidate the physiological route from gene-to-phenotype for grain yield. Several genetic associations with grain yield components have been reported previously. In studies based on just four populations (Borner et al. 2002; Groos et al. 2003; Quarrie et al. 2005; Marza et al. 2006), regions on almost every wheat chromosome were shown to be associated with either thousand grain weight (TGW) or the number of grains per head ($G.H^{-1}$).

The aim of this study was to utilise the ‘Trident’ by ‘Molineux’ doubled-haploid population (Ranjbar 1997) to determine the genetic basis of grain yield in two southern Australian cultivars. More specifically, this study attempts to; (1) characterise the impacts of previously identified genes/QTL related to plant height, phenology and disease resistance on grain yield and grain yield components and (2) identify additional chromosomal associations with grain yield that have not been linked to other agronomically important traits in this population.

Materials and methods

Genetic resources

A doubled-haploid population (T/M DH) consisting of 182 individuals (Ranjbar 1997) produced from a cross between ‘Trident’ (VPM1/5*Cook//4*Spear, released in 1993 by the University of Adelaide) and ‘Molineux’ (Pitic 62/Festiguay//Warigal, released in 1988 by the University of

Adelaide) was used as the basis for this study. A genetic linkage map was produced using 260 microsatellite and protein markers (Williams et al. 2006).

Grain yield analysis

Each of the T/M DH lines (as well as the parents and other control varieties) was grown in grain yield field experiments during the years 2002–2005. A total of 18-year-site combinations (environments) were utilised to assess the performance of the population (Table 1). Grain yield component measurements were recorded at three of these environments. Grain yield field plots constituted either five or six rows and were 1.3 m wide and 5 m long. These were then reduced to 3.2 m in length prior to anthesis by herbicide application. Seed was sown on a volume basis, aiming for an average 200 seeds per square metre. Fertiliser application and management regime for each site followed local practice. Grain was harvested and then the total plot weight was recorded and converted to the units kg ha^{-1}. Two replications (three for RS04 and RS05) of each line were arranged in a randomised (nearest neighbour design) rectangular array 12 plots deep.

At RS04 the grain yield components heads per plant ($H.P^{-1}$), $G.H^{-1}$, grains per square metre ($G.M^{-2}$) and TGW were measured to partition the genetic variance for grain yield into its various constituents. The number of plants growing in a subsection, two rows, 1 m long, of each plot in the RS04 field experiment were counted, and before harvest, the number of heads in this same plot subsection were counted and from this, the number of $H.P^{-1}$ determined. Field plots were machine harvested, chaff was removed from each grain sample, and the total plot weight and TGW recorded. From this, the number of $G.M^{-2}$, and consequently the number of $G.H^{-1}$ were calculated. TGW and $G.M^{-2}$ were measured in the same way on samples from CN04 and PN04 (Table 1).

Statistical analysis

Best linear unbiased predictors (BLUPs) for grain yield and grain yield components for each of the DH lines, parent and other control varieties were determined for each environment where data was recorded, using the REML directive within GENSTAT 8 (Payne et al. 2002). A spatial model incorporating row and column effects was fitted to the data along with any other significant ($P < 0.05$) spatial terms, such as seeding or harvest direction (Gilmour et al. 1997). Grain yield data from the 18 environments were combined and analysed as a multiple-environment trial (MET). As with the single environment experiments, REML analysis was used to determine the MET BLUP for each line. The environment (site-year combination) was fitted as a random effect and the interaction between spatial error terms and environments were included as fixed and random effects as appropriate. DH line and DH line-by-environment interactions were fitted as random effects. The VFUNCTION procedure of GENSTAT was used to calculate broad sense heritabilities on a line mean basis (Nyquist 1991).

Genotypic data from markers (Ellis et al. 2002) perfectly linked to the two height reducing genes *Rht-B1b* and *Rht-D1b* were available for this population (Williams et al. 2006). Where the effects of the height loci were significantly associated with the grain yield and grain yield components, adjusted means were subsequently used in an attempt to identify genetic associations beyond those previously shown to be involved in the control of plant height. For these analyses, DH lines were classified as either dwarf (carrying both dwarfing genes), semi-dwarf (carrying one dwarfing gene) or tall (carrying neither of the dwarf genes). Similarly, the effects on grain yield and grain yield components of the allele specific marker (Seah et al. 2001) for the 'VPM1' derived rust resistance locus *Lr37/Sr38/Yr17* (Bariana and McIntosh 1993), and the predicted alleles (Whittaker et al. 1996) for QTL associated with ear-emergence (Kuchel et al. 2006) were determined by general linear regression in GENSTAT. The predicted alleles for ear-emergence QTL were determined from flanking markers where necessary, or where a single marker was located near the peak of the QTL, data from the single marker was used. Single marker data were used for the ear-emergence QTL detected on chromosomes 2AL (*Xbarc5*), 2AS (*Xbarc220*) and 5AL (*Xgwm271*), whereas flanking markers were used to predict QTL alleles for the loci on chromosomes 1AL (*Xgwm497*–35.5 cM–*Xbarc158*), 2BS (*Xgwm614*–35.5 cM–*Xbarc200*), 6DS (*Xgdm141*–17.3 cM–*Xbarc27*), 7AS (*Xbarc108*–23.4 cM–*Xbarc154*) and 7BS (*Xwmc46*–12.2 cM–*Xwmc182*). These analyses were performed using genotypic data coded between 0 ('Trident' allele) and 1 ('Molineux' allele). The mean grain yield data were then arithmetically adjusted using the regression coefficients from the general linear regression to remove any significant ($P < 0.05$) effects of the plant height loci, 'VPM' rust resistance locus and ear-emergence loci. The adjusted data is identified using the suffix '-adj'.

QTL were identified using composite interval mapping (Jansen and Stam 1994) provided by MAP MANAGER QTX (Manly and Olson 1999). A QTL with a LOD between two and three was considered suggestive, while a QTL with a LOD greater than three was considered significant. The genome wide significance ($P < 0.05$) level, as calculated by permutation test within MAP MANAGER QTX, was 3.02. The confidence interval of each QTL was

Table 1 A summary of the environments used to assess grain yield and grain yield components thousand grain weight (*TGW*), grains per square metre ($G.M^{-2}$), grains per head ($G.H^{-1}$) and heads per plant ($H.P^{-1}$) for the T/M DH population (2002–2005)

Environment	Site[a]	Year	Traits recorded
BL05	Booleroo, SA	2005	Grain yield
CM04	Coomalbidgup, WA	2004	Grain yield
CN04	Coonalpyn, SA	2004	Grain yield, TGW, $G.M^{-2}$
CN05	Coonalpyn, SA	2005	Grain yield
HR03	Horsham, Vic	2003	Grain yield
KP03	Kapunda, SA	2003	Grain yield
KP04	Kapunda, SA	2004	Grain yield
ML03	Melrose, SA	2003	Grain yield
MN03	Minnipa, SA	2003	Grain yield
MN05	Minnipa, SA	2005	Grain yield
PN04	Pinnaroo, SA	2004	Grain yield, TGW, $G.M^{-2}$
PN05	Pinnaroo, SA	2005	Grain yield
RS02	Roseworthy, SA	2002	Grain yield
RS03	Roseworthy, SA	2003	Grain yield
RS04	Roseworthy, SA	2004	Grain yield, TGW, $G.M^{-2}$, $G.H^{-1}$, $H.P^{-1}$
RS05	Roseworthy, SA	2005	Grain yield
TC04	Tuckey, SA	2004	Grain yield
WT03	Winulta, SA	2003	Grain yield

[a] The closest urban centre to the field trial environment is used as the site code. The Australian state is also indicated for each environment (*WA* Western Australia, *Vic* Victoria and *SA* South Australia)

determined using the bootstrapping option within MAP MANAGER QTX. For comparison with the gene effects estimated by REML analysis for height, rust and phenology loci, gene effects (twice the additive allele effect) are presented for each QTL.

Results

Data summary

Mean grain yield for each environment ranged from 491 to 3,035 kg ha^{-1} (Table 2) with the average grain yield across the all environments being 2,051 kg ha^{-1}. The genotype-by-environment variance for the MET was 5,209, or 12.1% of the sum of genotype and genotype-by-environment variance. Genotypic correlations between the grain yields achieved at each of the environments ranged from low and statistically not significant ($r = -0.07$) through to high and statistically significant ($r = 0.87$). No significant negative correlations were observed, while each environment showed a significant association with the MET (data not shown). 'Trident' was higher yielding ($P < 0.05$), or did not significantly differ from 'Molineux' at each of the environments used for grain yield assessment, and often achieved grain yields near the high extreme of the population (Table 2). A histogram of the MET grain yields (Fig. 1) also showed clustering of DH progeny towards the grain yield level of 'Molineux'. Of the grain yield components, TGW was most heritable, but the strongest relationship with grain yield was observed for $G.M^{-2}$. At all three locations, TGW and $G.M^{-2}$ were negatively correlated (Table 3).

The association between height reducing genes and grain yield and grain yield components

The *Rht-B1* and *Rht-D1* alleles carried by the parents of this population differed (Trident = *Rht-B1a/Rht-D1b* and Molineux = *Rht-B1b/Rht-D1a*) and consequently explained 60.2% of the phenotypic variation in mean plant height across seven environments (H. Kuchel, unpublished data). When fitted individually, the *Rht-B1* and *Rht-D1* alleles accounted for 27.9 and 26.8% of the phenotypic variation in plant height, respectively. Semi-dwarf DH lines (*Rht-B1b/Rht-D1a* or *Rht-B1a/Rht-D1b*) achieved mean MET grain yields 144 kg ha^{-1} higher ($P < 0.001$) than those lines with both dwarfing alleles (dwarf) and 150 kg ha^{-1} higher than lines with both non-dwarfing alleles (tall). The grain yield of the two semi-dwarf genotypes did not significantly differ at any of the environments and are consequently presented as a single, semi-dwarf genotypic class (Table 4). The semi-dwarf class was significantly higher yielding than the dwarf class in 12 environments, and significantly higher yielding

Table 2 A summary of the range and heritability of grain yield (kg ha^{-1}) observed in the T/M DH population across the 18 environments

Environment	'Trident'	'Molineux'	Mean grain yield (kg ha^{-1})	Heritability	Range (min–max)
BL05	1,720	1,522	1,599	0.34	1,402–1,780
CM04	3,359	2,620	2,856	0.84	1,974–3,574
CN04	2,101	1,924	1,914	0.82	1,477–2,340
CN05	2,624	2,550	2,468	0.60	1,343–3,030
HR03	2,534	1,751	1,980	0.95	1,089–2,727
KP03	2,597	2,367	2,307	0.87	1,758–2,782
KP04	3,369	2,960	2,879	0.55	2,336–3,567
ML03	1,199	1,313	1,272	0.52	974–1,516
MN03	7,47	762	748	0.87	554–865
MN05	2,106	1,931	1,955	0.53	1,709–2,125
PN04	2,100	1,772	1,903	0.61	1,332–2,326
PN05	2,561	1,354	1,825	0.85	801–2,734
RS02	2,706	2,474	2,436	0.79	1,754–2,904
RS03	3,465	2,691	2,784	0.91	1,083–3,707
RS04	2,906	2,904	2,645	0.86	1,815–3,201
RS05	4,616	2,112	3,035	0.97	1,038–5,095
TC04	612	418	491	0.90	68–752
WT03	1,817	1,415	1,480	0.79	993–1,932
MET	2,455	1,946	2,051	0.86	1,605–2,640

than the tall class in 13 environments. The height reducing genes were significantly associated with the components of grain yield at the three environments tested, RS04, CN04 and PN04 (Table 4). As with grain yield, the two semi-dwarf genotypes did not differ in their effects on grain yield components and were consequently pooled to form a single semi-dwarf genotypic class. The DH lines with a tall genotype produced a lower number ($P < 0.001$) of $G.M^{-2}$ and higher TGW ($P < 0.001$) than the semi-dwarf and dwarf genotypes. Likewise, progeny with the tall genotype had 16% fewer ($P < 0.001$) $G.H^{-1}$ than the dwarf and semi-dwarf genotypes at RS04 where complete yield component analysis was performed. However, the effects of the three height genotypes on the number of $H.P^{-1}$ at RS04 did not differ significantly.

The association between the 'VPM1' derived *Lr37/Yr17/Sr38* rust resistance locus and grain yield and grain yield components

A diagnostic marker for *Lr37/Yr17/Sr38* (Seah et al. 2001) showed association ($P < 0.05$) with grain yield at CN04, CN05, HR03, ML03, KP04, PN04, PN05, RS03, RS05 and

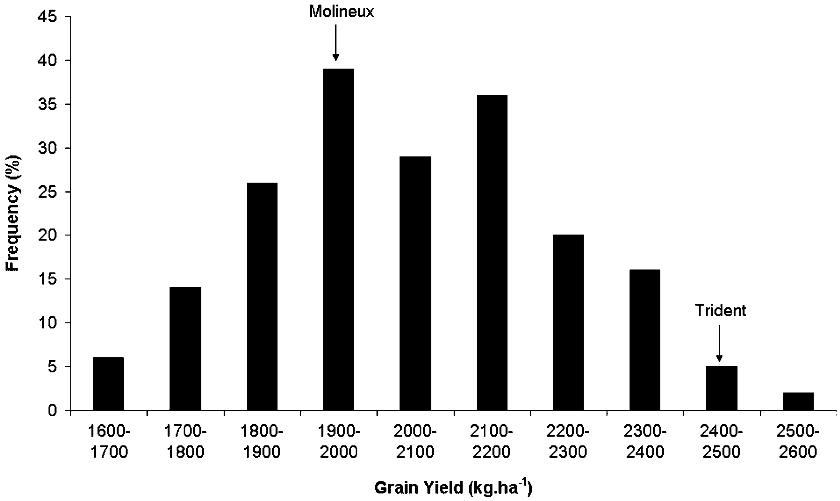

Fig. 1 Grain yield distribution of the T/M DH population across the 18 sites

Table 3 The heritabilities of the grain yield components thousand grain weight (*TGW*), grains per square metre ($G.M^{-2}$), grains per head ($G.H^{-1}$), and heads per plant ($H.P^{-1}$) measured at CN04, PN04 and RS04, along with their phenotypic correlations with grain yield and the other grain yield components at the same environments

Environment	Trait	Heritability	Grain yield	TGW	$G.M^{-2}$	$G.H^{-1}$
CN04	TGW	0.80	0.32			
	$G.M^{-2}$	0.36	0.85	–0.19		
PN04	TGW	0.71	0.34			
	$G.M^{-2}$	0.56	0.71	–0.32		
RS04	TGW	0.96	–0.19			
	$G.M^{-2}$	0.80	0.79	–0.71		
	$G.H^{-1}$	0.49	0.63	–0.49	0.75	
	$H.P^{-1}$	0.71	0.30	–0.21	0.32	0.03 ns

Results are significant ($P < 0.05$) unless otherwise stated (ns)

with the MET BLUP (Table 4). Stripe rust (causal organism *Puccinia striiformis* Westend. F. sp. *tritici*) was observed at CN04, CN05, HR03, KP04, PN04, PN05, RS03 and RS05 and at each of these environments the grain yield of lines carrying the 'Trident' allele (resistant) were significantly higher than the lines carrying the 'Molineux' allele (susceptible). In contrast, the *Lr37/Yr17/Sr38* rust resistance allele was associated with a slight reduction in grain yield at ML03 ($P = 0.032$) where no rust was observed. At the remainder of environments not exposed to rust, the *Lr37/Yr17/Sr38* locus was not associated with grain yield. The molecular marker for the *Lr37/Yr17/Sr38* rust resistance locus only showed association ($P < 0.01$) with grain yield components at PN04. Lines with the resistant ('Trident') allele produced 3.5% higher $G.M^{-2}$ and 2.9% greater TGW than lines carrying the susceptible ('Molineux') allele.

The association of chromosome regions carrying QTL for heading date with grain yield and grain yield components

Eight independent genetic associations with the timing of ear-emergence in the T/M DH population have been reported (Kuchel et al. 2006). All the QTL for time to ear-emergence reported previously showed association with grain yield at one or more environments (Table 4). Of these QTL, chromosomes 1AL, 2AS, 6DS and 7AS showed the highest degree of association with grain yield. The ear-emergence QTL on chromosome 1AL was associated with grain yield at seven of the 18 environments while the 2AS QTL was associated with grain yield at six, the 6DS QTL was found to be associated at ten environments, and the 7AS QTL was associated with grain yield at eight environments. In addition, the 1AL ($P < 0.05$), 2AS ($P < 0.01$) and 6DS ($P < 0.01$) QTL were also associated with the overall MET grain yield. For all except the chromosome 2BS photoperiod responsive ear-emergence locus (Kuchel et al. 2006), the alleles associated with earlier emergence were also associated with higher grain yield. In the case of *Ppd-B1*, the earlier maturing 'Molineux' allele was associated with higher grain yield at MN03, but lower grain yield at ML03.

The phenological loci (Kuchel et al. 2006) also exerted significant influence over the grain yield components (Table 4). Although only two weak associations were observed between grain yield and the *Ppd-B1* locus, the photoperiod-sensitive allele inherited from 'Trident' was associated with an increase (2.2 g) in TGW at RS04 ($P < 0.001$). Like the *Ppd-B1* locus, the photoperiod-sensitive alleles at the 1A and 7A loci were associated with a higher TGW at RS04. A corresponding drop in $G.M^{-2}$ was also associated with the photoperiod-sensitive alleles at these two loci. The earliness per se QTL on 6DS was found to be associated with TGW at PN04 and CN04. In both cases, the early allele from Trident was associated with heavier grain.

Novel genetic associations with the expression of grain yield and grain yield components

In total, nine different chromosomal regions showed an association with grain yield-adj (grain yield adjusted for genetic loci involved in the control of plant height, phenology and rust resistance) at one or more environments (Table 5). Three of these associations (4A, 5B and 7B) were only suggestive, failing to meet the significance criteria (LOD 3) at any of the environments. However the genetic relationship between chromosome 4A and grain yield-adj was still identified at two environments. QTL significantly associated with grain yield-adj were identified on chromosomes 1B, 2D, 3D, 4D, 6A and 6D at one or more environments. For all but the chromosome 4D locus, the same allele was favourable at all environments and 'Trident' was the donor of the high grain yield allele for all but the 1B locus. The genetic association with grain yield-adj detected on chromosome 1B (*QGyld.agt-1B*) showed the highest level of stability and was one of three QTL (1B, 3D and 4D) found to be associated with MET grain yield-adj. Although being the lower yielding parent, the 'Molineux' allele at *QGyld.agt-1B* was associated with higher grain yield. Across the 18 environments (MET) used for grain yield assessment, DH lines possessing the 'Molineux' genotype at *QGyld.agt-1B* achieved grain yields 99.0 kg ha^{-1} in excess of those with the 'Trident' genotype (LOD 4). Expressed as a percentage of MET grain yield, the Molineux *QGyld.agt-1B* allele was associated with 4.8%

Table 4 Estimates of grain yield and grain yield component genotype effects (kg ha^{-1}) of QTL associated with rust resistance and ear-emergence (using predicted QTL alleles from flanking markers) in the T/M DH population for each of the environments and the MET

Environment	Trait	%[a]	Height loci[b]			Rust locus	Phenology loci							
			Dwarf	Semi-dwarf	Tall	Lr37/ Sr38/ Yr17	QPpd.agt-1A M[c]	QEps.agt-2AL T	QEps.agt-2AS T	Ppd-B1 M	Vrn-A1 T	QEps.agt-6D T	QPpd.agt-7A T	QPpd.agt-7B T
BL05	Grain yield	11.4					28.4*	–29.6**				–45.7***		
CM04	Grain yield	30.4	3,128.9^{x}	3,103.0^{x}	2,665.3^{y}				–143.6**			–132.4*		
CN04	Grain yield	15.5	1,901.9^{x}	1,984.4^{y}	1,905.6^{x}	–52.1*	109.1***					–62.2*	–54.5*	
CN05	Grain yield	16.9	2,318.8^{x}	2,566.3^{y}	2,534.3^{y}	–102.6**								
HR03	Grain yield	31.0	2,171.3^{x}	2,285.0^{y}	2,184.6^{x}	–407.6***			–98.7*					
KP03	Grain yield	23.8	2,219.0^{x}	2,424.0^{z}	2,308.7^{y}		79.7*					–105.7**	–71.2*	
KP04	Grain yield	17.7	2,839.5^{x}	2,985.2^{y}	2,880.9^{x}	–153.3***	123.4**						–89.2*	
ML03	Grain yield	8.8	1,251.1^{x}	1,289.7^{y}	1,245.5^{x}	37.9*				–50.5***				
MN03	Grain yield	13.8	711.0^{x}	744.8^{y}	740.6^{y}		28.5*			20.2*			–29.3**	
MN05	Grain yield	3.1	1,957.2^{x,y}	1,979.5^{x}	1,948.3^{y}							–34.9*		
PN04	Grain yield	9.4	1,936.5^{x}	1,998.3^{y}	1,899.7^{x}	–113.7***								
PN05	Grain yield	35.4				–593.5***								
RS02	Grain yield	34.7	2,444.7^{x}	2,587.4^{y}	2,453.4^{x}		88.2**		–74.4***			–76.8**	–116.5***	
RS03	Grain yield	36.1	2,756.2^{x}	3,226.1^{z}	3,049.2^{y}	–109.9*			–127.2*			–207.5***	–202.3***	
RS04	Grain yield	26.5	2,750.4^{x}	2,813.7^{x}	2,540.9^{y}				–78.4*			–131.3**		
RS05	Grain yield	37.2	3,692.1^{x}	3,815.4^{x}	3,410.0^{y}	–1,238.0***								
TC04	Grain yield	30.3					73.8***	–42.2**			–39.5*	–51.1**	–67.6***	–46.1**
WT03	Grain yield	31.5	1,472.1^{x}	1,665.2^{y}	1,659.0^{y}				–65.1**			–91.3**	–114.8***	–55.4*
MET	Grain yield	38.6	2,100.5^{x}	2,243.1^{y}	2,080.5^{x}	–170.5***	71.8*		–66.7**			–86.8**		
CN04	TGW	6.9	35.9^{x}	37.2^{y}	36.9^{y}							–0.9*		
PN04	TGW	15.1	35.6^{x}	37.4^{y}	37.5^{y}	–1.2***						–1.1*		
RS04	TGW	31.2	29.8^{x}	30.9^{y}	33.2^{z}		–1.6*			–2.2**			1.5**	
CN04	G.M^{-2}	5.5					247.0***							
PN04	G.M^{-2}	12.2	5,267.8^{x}	5,182.5^{x}	4,916.1^{y}	–197.8**	183.7*							
RS04	G.M^{-2}	28.8	9,156.1^{x}	9,055.4^{x,y}	7,793.2^{y}				414.0**				–382.0*	
RS04	G.H^{-1}	23.6	29.2^{x}	28.9^{x}	24.3^{y}									
RS04	H.P^{-1}	6.0							0.1*				–0.1**	

Higher relative grain yield and grain yield components are indicated by a positive effect if the allele is inherited from ‘Molineux’ and negative if inherited from ‘Trident’. The genotypic means of the dwarf, semi-dwarf and tall genotype classes are also presented. The effects of all significant ($P < 0.05$) marker alleles at the agronomic loci were fitted simultaneously and the proportion of phenotypic variance accounted for by the model is presented for each environment

[a] The percentage phenotypic variation in grain yield and grain yield components accounted for by the chromosome regions associated with plant height, rust resistance and ear-emergence

[b] The mean plant height of the dwarf, semi-dwarf and tall genotypic classes are significantly different if followed by a different letter

[c] The parent contributing the earliness allele is presented for each phenological QTL as either a *T* ‘Trident’ or an *M* ‘Molineux’

*$P < 0.05$

**$P < 0.01$

***$P < 0.001$

higher grain yield. Although not reaching significance at as many environments (six), the 'Trident' allele at *QGyld.agt-4D* was still associated with higher (5.1%) MET grain yield.

Three chromosome regions were shown to be associated with the grain yield components (Table 5). Significant relationships were observed between a region on chromosome 7D (*QTgw.agt-7D*) and the grain yield components at all three environments. In each case, the 'Molineux' allele was associated with higher TGW-adj. At RS04 and PN04, this same allele reduced the number of G.M^{-2}-adj, but had no significant effects on any of the other grain yield components. A LOD of 1.9 was observed for a non-significant association between this chromosomal region and the number of G.H^{-1}-adj at RS04 (not presented). A second QTL located at *QGyld.agt-6A*, was found to be associated with TGW-adj at CN04 and PN04. A third QTL, on chromosome 5B, was associated with tillering (H.P^{-1}-adj) at RS04 and with G.M^{-2}-adj at CN04.

Discussion

Statistical considerations

Extraneous and systematic field variation in southern Australia has a large effect on the accuracy of grain yield measurements and will therefore impact on the power of QTL detection. Consequently, this study employed mixed model based data analysis (Gilmour et al. 1997), as used in local breeding programmes, to produce predicted means for grain yield prior to genetic analysis. Using this analysis type, either estimates or predictions of the true DH line performance can be produced, depending on whether DH line is fitted as a fixed or random effect. Here, we have chosen to use BLUPs for genetic analysis. One may argue that the use of BLUPs of line means as input will result in estimates of gene effects that are underestimated due to 'shrinkage' of means towards zero. However, rather than posing a problem for QTL detection, the more conservative nature of BLUP line effects may act to balance against the well documented over estimation of QTL effects that often occurs within relatively small mapping populations (Bernardo 2002). In either case, QTL analysis was also performed on best linear unbiased estimates (BLUEs) from a subset of the environments to test that no substantial differences in QTL detection would arise from the analysis employed (data not shown). As expected, environments with a lower heritability showed larger gene/QTL effects when estimated on BLUEs rather than BLUPs. However, the set of QTL detected were almost identical with the two analysis methods and very similar significance levels were achieved.

The association of loci involved in the control of plant height, rust resistance, and phenology with grain yield and grain yield components

The grain yield superiority of semi-dwarf wheat varieties under favourable growing conditions is well documented (Borlaug 1968; Nizam Uddin and Marshall 1989). The shorter stature of wheat plants has provided resistance to lodging, high-harvest index and has also been shown to be related to high numbers of fertile florets (Syme 1970). However, the grain yield benefit of the height reduction conferred by the *Rht-B1b* and *Rht-D1b* alleles in lower yielding environments, such as those experienced in Australia, has been questioned (Richards 1992). Although the semi-dwarf genotype has generally led to greater improvements in grain yield at high yield potential environments, the results presented here suggest that even at environments with mean grain yields less that 2,000 kg ha^{-1}, semi-dwarf lines achieve grain yields equal to or higher than tall lines. This result is in contrast to the study of Butler et al. (2005) in the USA who reported an increase in grain yield of the semi-dwarf class over tall lines only under full irrigation. In Australia, Nizam Uddin and Marshall (1989) concluded that semi-dwarf genotypes were superior to tall genotypes under both irrigated and dry land conditions, although the tall lines did not suffer the same relative drop in grain yield at environments of lower water availability. The results presented here also confirm the rise in spikelet fertility that is coupled with the introduction of these gibberellic acid-insensitive dwarfing alleles (Flintham et al. 1997). For the three environments where G.M^{-2} and TGW were recorded, the dwarf and semi-dwarf genotypes achieved a higher number of G.M^{-2} than the tall genotypes, but did not significantly differ from one another. However, in the case of the dwarf lines, the higher GM^{-2} was associated with small grain size suggesting the dwarf genotypes were not able to provide adequate substrate to fill the greater number of grains, leading to lower overall grain yield. In contrast, the semi-dwarf class was capable of maintaining a TGW equal to that of the tall lines at CN04 and PN04. At RS04, the grain yield of the semi-dwarf class was not adversely affected by lower TGW due to the large number of grains filled. These results suggest that the semi-dwarf genotypic class achieves higher relative grain yield in southern Australia through increases in grain set and little compensatory loss in grain weight.

The introgression of genes for rust resistance into wheat from related species has afforded effective protection against potential grain yield losses across the world for many decades. However, either through pleitropy or linkage drag, these genes from wild relatives have sometimes been associated with reductions in grain yield (The et al. 1988). The 'VPM' derived compound rust resistance locus,

Table 5 The chromosome location and significance of QTL for grain yield-adj and grain yield components-adj at each of the environments used for grain yield assessment as determined by interval mapping

Environment	Chromosome→	1B		2D		3D		4A		4D	
	QTL→	QGyld.agt-1B		QGyld.agt-2D		QGyld.agt-3D		QGyld.agt-4A		QGyld.agt-4D	
	Closest marker→	Xgwm11		Xgwm311		Xgwm314		Xgwm397		Xgwm194	
	Location[a]→	*26.7–54.1–85.6*		*161.2–175.0–183.4*		*141.1–142.9–167.7*		*14.9–25.3–41.1*		*28.7–63.5–75.9*	
	Trait	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff
BL05	Grain yield	2.7	38.2			2.6	–41.8				
CM04	Grain yield										
CN04	Grain yield	2.2	70.6			3.7	–97.2				
CN05	Grain yield			3.1	–133.2					2.3	–116.8
HR03	Grain yield									2.0	–176.6
KP03	Grain yield	4.9	120.2			2.2	–87.8	2.3	–84.6		
KP04	Grain yield	4.1	142.4								
ML03	Grain yield	3.4	55.6								
MN03	Grain yield										
MN05	Grain yield	2	35.2								
PN04	Grain yield									2.3	–83.2
PN05	Grain yield									3.2	–248.2
RS02	Grain yield										
RS03	Grain yield	4.1	204.6	2.5	–170.4						
RS04	Grain yield										
RS05	Grain yield									3.3	–556.2
TC04	Grain yield							2.1	–44.6	2.2	47.8
WT03	Grain yield	3.3	94.4								
MET	Grain yield	4.0	99.0			2.2	–70.2			3.3	–104.2
CN04	TGW										
PN04	TGW										
RS04	TGW										
CN04	G.M^{-2}										
PN04	G.M^{-2}										
RS04	G.M^{-2}										
RS04	G.H^{-1}										
RS04	H.P^{-1}										

Environment	Chromosome→	5B		5B		6A		6D		7B		7D	
	QTL→	QGno.agt-5B		QGyld.agt-5B		*QGyld.agt-6A*		*QGyld.agt-6D*		*QGyld.agt-7B*		*QTgw.agt-7D*	
	Closest marker→	Xbarc004		Xgwm371		*Xwmc163*		*Xbarc204*		*Xbarc279*		*Xbarc172*	
	Location[a]→	*0.0–15.1–35.3*		*36–89.7–118.0*		58.0–67.5–75.7		37.5.0–43.0–91.6		0.0–0.0–12.3		63.9–91.5–99.1	
	Trait	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff
BL05	Grain yield					3.2	–60.0						
CM04	Grain yield							2.2	–167.0				
CN04	Grain yield												
CN05	Grain yield									2.3	–172.2		
HR03	Grain yield												
KP03	Grain yield			2.4	–83.0								
KP04	Grain yield												
ML03	Grain yield												

Table 5 continued

Environment	Chromosome→	5B		5B		6A		6D		7B		7D	
	QTL→	QGno.agt-5B		QGyld.agt-5B		*QGyld.agt-6A*		*QGyld.agt-6D*		*QGyld.agt-7B*		*QTgw.agt-7D*	
	Closest marker→	Xbarc004		Xgwm371		*Xwmc163*		*Xbarc204*		*Xbarc279*		*Xbarc172*	
	Location[a]→	*0.0–15.1–35.3*		*36–89.7–118.0*		58.0–67.5–75.7		37.5.0–43.0–91.6		0.0–0.0–12.3		63.9–91.5–99.1	
	Trait	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff	LOD	Eff
MN03	Grain yield												
MN05	Grain yield												
PN04	Grain yield												
PN05	Grain yield												
RS02	Grain yield												
RS03	Grain yield												
RS04	Grain yield							3.1	–137.0				
RS05	Grain yield												
TC04	Grain yield												
WT03	Grain yield												
MET	Grain yield												
CN04	TGW					5.6	–1.5					4.0	1.38
PN04	TGW					3.2	–1.4					3.3	2.3
RS04	TGW											2.1	2.2
CN04	G.M^{-2}	2.8	–246.6										
PN04	G.M^{-2}											2.2	–201.3
RS04	G.M^{-2}											2.0	–471.6
RS04	G.H^{-1}												
RS04	H.P^{-1}	2.5	–1.2										

The LOD is presented for any associations that achieved a value of two or greater. The closest marker to the peak of the QTL and the confidence interval for each QTL is displayed for positional reference and an increase in grain yield is indicated by a positive gene effect (Eff) if inherited from ‘Molineux’ and negative if inherited from ‘Trident’

[a] The position and confidence interval (QTL left margin—QTL peak—QTL right margin) of each QTL on the TMDH population linkage map (Williams et al. 2006) are presented for the environment showing the strongest association

Lr37/Yr17/Sr38 (derived from *Triticum ventricosum*), has been successfully deployed in several Australian cultivars and helps to form the basis of genetic resistance to some rust races in Australia. At environments where stripe rust was present, the *Lr37/Yr17/Sr38* locus was associated with substantially higher grain yield. This was most evident at RS05 where lines carrying the resistance allele (‘Trident’) achieved 50% higher grain yield than their susceptible counterparts. Perhaps, more important than the confirmation of the effectiveness of this locus at protecting wheat against grain yield losses caused by rust, the ‘VPM’ derived resistance locus was not associated with consistent grain yield *losses* in the *absence* of disease. Beyond the effects on grain yield due to protection against stripe rust infection, the ‘VPM’ derived resistance locus did not appear to confer any adaptive function. In general, this resistance locus can apparently be utilised by breeders without concern for any undesirable change in grain yield or grain yield components in the absence of rust, or if the genes on the ‘VPM’ derived resistance locus are ineffective against an alternative race of rust.

The introduction to Australia of the key adaptive trait, earliness, through the selection of photoperiod insensitivity had a major role in the expansion of the local wheat industry (Law and Worland 1997). This is particularly the case in southern Australian where the end of the growing season is erratically punctuated by high temperatures and a rapid progression towards water shortage. It is perhaps not surprising then, that for all but one of the 41 associations between ear-emergence QTL and grain yield at individual environments in southern Australia, the early allele led to an increase in grain yield. Interestingly, although having a large impact on phenology, the two well characterised ear-emergence loci on chromosomes 5A (*Vrn-A1*) and 2B (*Ppd-B1*) did not appear to be as strongly associated with grain yield as many other phenological loci. The two putatively photoperiod-sensitive loci *QPpd.agt-1A* and *QPpd.agt-7A* were both shown in this study to exert significant control over grain yield in southern Australia. In a study of the *Ppd-B1* and *Ppd-D1* loci in Europe, Worland et al. (1998) concluded that, although there was large variation from year-to-year, photoperiod sensitivity tended to be desirable under the cool climates of higher European latitudes and insensitivity was favoured in the southern latitudes. Likewise, in the higher latitudes of North America, Dyck et al. (2004) showed that lines carrying the photoperiod-sensitive allele at *Ppd-D1* achieved higher grain yield than their insensitive counterparts. In contrast, this study has demonstrated an increase in grain yield associated with photoperiod insensitivity conferred by *QPpd.agt-1A* and *QPpd.agt-7A*. Although having a similar influence on the timing of ear-emergence, the *Ppd-B1* locus was not consistently associated with grain yield. The unique cross-over gene-by-environment interaction effects observed at ML03 and MN03 for this locus, may indicate additional linked genes that are obscuring the effects of *Ppd-B1* on grain yield. However, given its small and infrequent association with grain yield, shown in this study, this cross over interaction would not appear likely to pose problems in breeding for wide adaptation to the southern Australian environment.

Although the inheritance of photoperiod-sensitive alleles at *QPpd.agt-1A*, *Ppd-B1* and *QPpd.agt-7A* was generally associated with lower grain yield, the later flowering alleles were also associated with larger grain at RS04. This is in agreement with the results of Worland et al. (1998) who showed an increase in TGW in the favourable climate of England for near isogenic lines possessing the photoperiod-sensitive *Ppd-B1* allele. However, the association of the photoperiod-sensitive alleles at *QPpd.agt-1A*, *Ppd-B1* and *QPpd.agt-7A* with grain size and grain yield components is counter intuitive for the southern Australian environment. In the sharp finishing seasons experienced in southern Australia, one would expect drought avoidance conferred by photoperiod insensitivity to result in larger grain. However, it may be possible that delayed flowering is related to deeper rooting and consequently greater soil-water extraction during grain fill, as considered by Foulkes et al. (2004). Alternatively, the later flowering phenotype may have been favoured by some specific environmental stress. In this case, field plots at RS04 were subjected to a sudden rise in daily temperature (42.5; 17°C above the previous week's average maximum) accompanied by strong winds for a 2-day period during the middle of anthesis. However, this does not explain the lack of association observed at CN04 and PN04, where similar heat stress was experienced on the same days.

From a breeding perspective, the considerable impact of the regions associated with earliness per se on grain yield is intriguing. Particularly the two QTL associated with time to ear-emergence on chromosomes 2A and 6D, which showed strong and consistent association with grain yield, and were related to 3.2 and 4.2% higher MET grain yield, respectively. Although these QTL were strongly associated with grain yield, their effects on time to ear-emergence were only minor, and certainly less than that observed for the photoperiod and vernalisation-sensitive loci (Kuchel et al. 2006). This may indicate that their primary influence on grain yield was not mediated through earliness but rather through some alternative pleiotropic effects on grain yield. The results from this study suggest that further research on the role of genes for earliness per se on adaptation is warranted.

The influence of chromosomal regions, not shown to be associated with plant height, rust resistance and phenology, on grain yield and grain yield components

Similar to the studies of Borner et al. (2002), Groos et al. (2003), Huang et al. (2004), McCartney et al. (2005) and Marza et al. (2006), a large number (nine) of genetic associations with grain yield were observed in the T/M DH population in this study. However, only half the QTL were detected at more than two environments. Although this may be partly due to variations in QTL detection power at the various environments, it may also support the generally accepted belief that genotype-by-environment interaction dictates that breeding for wide adaptation requires testing and selection across multiple sites and years (Basford and Cooper 1998). Interestingly, only one crossover gene-by-environment interaction was observed for the loci associated with grain yield when adjusted for the effects of loci controlling plant height, rust resistance and phenology. The QTL on chromosome 1B (*QYld.agt-1B*) that was also significantly associated with MET grain yield showed a consistent, stable association with grain yield, but variation for the magnitude of its effects. On the other hand, the QTL on chromosome 4D (*QYld.agt-4D*) showed a small degree of crossover genotype-by-environment interaction. The 'Trident' allele was superior to the 'Molineux' allele at all sites showing association with *QYld.agt-4D*, except at TC04 where lines with the 'Molineux' allele achieved higher grain yields. Quarrie et al. (2005) also reported a QTL for grain yield on chromosome 1B near the *Glu-B1* locus and, although the QTL reported here was mapped closer to the centromere, it is possible they are equivalent. The same authors also reported QTL associated with grain yield on chromosomes 3D, 5B and 7B that may coincide with those presented here. Likewise, in the study of McCartney et al. (2005), QTL for grain yield were detected in a similar position to the QTL presented in this report on chromosome 4A. Groos et al. (2003) reported a QTL on chromosome 5B that was associated with grain yield as well as grain size and protein content. However, the breadth of that QTL makes assessment of coincidence with the QTL identified in this study difficult. It is interesting to note that a QTL not too distant from this region was associated with some grain yield components in this study. At CN04 and RS04, the higher yielding allele ('Trident') was associated with a larger number of $G.M^{-2}$ and $H.P^{-1}$, perhaps suggesting that this QTL mediates its effects on grain yield through the control of tillering. Although *QYld.agt-6A* was only associated with grain yield at BL05, coincident chromosomal associations were detected at CN04 and PN04 with grain weight. The 'Trident' allele, which conferred higher relative grain yield, was also associated with larger grain.

One locus (*QTgw.agt-7D*) showed a stable association with grain yield components across environments, with the 'Molineux' allele strongly related to low $G.M^{-2}$ and high TGW. Unlike the effects of the ear-emergence QTL, the effects of this locus on grain yield components were consistent, showing little gene-by-environment interaction. Previous reports exist for association between chromosome 7D and both TGW (Borner et al. 2002) and test weight (McCartney et al. 2005). However, McCartney et al. (2005) did not identify any association between this chromosome and TGW. The detection of association between *QTgw.agt-7D* and grain yield component traits at the three environments used in this study, and its likely coincidence with previously mapped QTL for related traits, makes this a candidate for further investigation. Although influencing both the number of $G.M^{-2}$ and TGW, no association between this region and grain yield was detected. Consequently, MAS at this locus may make it possible to manipulate TGW without substantial affects on grain yield, although this will require further investigation.

Ideally, further research would be undertaken to dissect the mode of action of *QYld.agt-1B* and *QYld.agt-4D* on grain yield and any environmental interactions they may possess. Unfortunately, these QTL were only associated with grain yield at one environment used for grain yield component analysis, making it difficult to determine the route through which high-grain yield is conferred. The strong and generally consistent effects of these loci on grain yield in southern Australia reported in this study suggest that, despite the lack of knowledge regarding their mode of action on grain yield, MAS for these loci would be valuable for breeding programmes.

Conclusions

In this study the genetic foundation of grain yield in a population generated from a cross between two Australian cultivars was partially deciphered. The large number of site-year combinations used for grain yield assessment allowed the contribution of genes for plant height, phenology and rust resistance to be dissected. Genes involved in the control of these traits were strongly associated with grain yield and grain yield components, and lines carrying alleles conferring semi-dwarf stature, rust resistance and early ear-emergence achieved the highest grain yield. Two additional genomic regions were associated with grain yield at several environments as well as with MET grain yield, while a third region was strongly associated with grain yield components, but not grain yield. These genomic regions (*QYld.agt-1B*, *QYld.agt-4D* and *QTgw.agt-7D*) not only provide potential targets for future MAS, but the information regarding the chromosome location of these important QTL can also be used tactically by breeders for cross design and development of selection methodology.

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