

## Genetic dissection of grain yield in bread wheat. II. QTL-by-environment interaction

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**Abstract** The grain yield of wheat is influenced by genotype, environment and genotype-by-environment interaction. A mapping population consisting of 182 doubled haploid progeny derived from a cross between the southern Australian varieties ‘Trident’ and ‘Molineux’, was used to characterise the interaction of previously mapped grain yield quantitative trait locus (QTL) with specific environmental covariables. Environments (17) used for grain yield assessment were characterised for latitude, rainfall, various temperature-based variables and stripe rust infection severity. The number of days in the growing season in which the maximum temperature exceeded 30°C was identified as the

variable with the largest effect on site mean grain yield. However, the greatest QTL-by-environmental covariable interactions were observed with the severity of stripe rust infection. The rust resistance allele at the *Lr37/Sr38/Yr17* locus had the greatest positive effect on grain yield when an environment experienced a combination of high-stripe rust infection and cool days. The grain yield QTL, *QGyld.agt-4D*, showed a very similar QTL-by-environment covariable interaction pattern to the *Lr37/Sr38/Yr17* locus, suggesting a possible role in rust resistance or tolerance. Another putative grain yield per se QTL, *QGyld.agt-1B*, displayed interactions with the quantity of winter and spring rainfall, the number of days in which the maximum temperature exceeded 30°C, and the number of days with a minimum temperature below 10°C. However, no cross-over interaction effect was observed for this locus, and the ‘Molineux’ allele remained associated with higher grain yield in response to all environmental covariables. The results presented here confirm that *QGyld.agt-1B* may be a prime candidate for marker-assisted selection for improved grain yield and wide adaptation in wheat. The benefit of analysing the interaction of QTL and environmental covariables, such as employed here, is discussed.

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### Abbreviations

DH	Doubled haploid
GCI	Genotype-by-environmental covariable interaction
GEI	Genotype-by-environment interaction
QCI	Quantitative trait locus-by-environmental covariable interaction
QEI	Quantitative trait locus-by-environment interaction
QTL	Quantitative trait locus
T/M	Trident/Molineux

## Introduction

Grain yield is arguably the most important economic trait in wheat improvement and is consequently a major selection target for most breeding programmes throughout the world. However, the influences of environmental variation on the performance of wheat cultivars reduces the genetic gain achieved by such selection. Changes in the relative performance of plant cultivars across environments may also complicate selection, particularly when breeding for wide adaptation to a heterogenous population of environments. This genotype-by-environment interaction (GEI) has been studied for many years, and methods have been developed to characterise GEI for cultivars and identify those with high, but stable, grain yield (Finlay and Wilkinson 1963; Eberhart and Russell 1966). However, the genetic and environmental basis for this GEI is not well understood, forcing breeders to rely on multiple-environment trials and appropriate statistical methodology to predict the performance of genotypes across years and locations (Basford and Cooper 1998).

The development of statistical methods that can assist in the detection of associations between genotype and phenotype, such as quantitative trait locus (QTL) mapping (Lander and Botstein 1989; Haley and Knott 1992), has expanded the wheat geneticist's knowledge of complex traits, including grain yield (Borner et al. 2002; Groos et al. 2003; Huang et al. 2004; McCartney et al. 2005; Marza et al. 2006). These statistical techniques have been extended to consider multiple-environment trials, which in turn provides the opportunity to examine interactions between chromosomal regions and the environment (Sari-Gorla et al. 1997; Piepho 2000; Verbyla et al. 2003). However, rather than simply detecting QTL whose expression on the phenotype varies with respect to the environment (QTL by environment interaction, QEI), the expression of QTL can be examined with reference to the edaphic and climatic features which may be responsible for such QEI. This philosophy has been applied successfully to investigate interactions between QTL for wheat grain yield, barley grain yield and maize biomass, with environmental characters such as maximum temperature and quantity of rainfall (Crossa et al. 1999; Campbell et al. 2004; Malosetti et al. 2004). Analyses of this nature are likely to help improve our understanding of the molecular and physiological pathways underlying relationships between genes and phenotypes (van Eeuwijk et al. 2005). Characterisation of QEI for existing QTL will also provide confidence to breeders prior to undertaking marker-assisted selection for complex traits.

A doubled haploid (DH) population created from a cross between the Australian cultivars 'Trident' and 'Molineux' was used previously to identify QTL involved in the control of grain yield and grain yield components in bread wheat

(Kuchel et al. 2006b). QTL/genes responsible for variation in plant height, rust resistance and the timing of ear-emergence, as well as nine QTL apparently unrelated to these agronomic traits, were associated with the expression of grain yield.

The aim of this study was to assess the relative contributions of these major genes and the QTL previously detected (Kuchel et al. 2006b) to the grain yield of wheat under the influence of a range of environmental/climatic conditions. Due to the importance of temperature related traits shown by Crossa et al. (1999), Campbell et al. (2004) and Malosetti et al. (2004), a major focus of this study was to assess the influence of major genes and QTL on grain yield under the influence of temperature related covariables in field situations in southern Australia. This in turn could lead to the development of improved grain yield selection strategies, targeted at a specific group of environments.

## Materials and methods

### Genetic resources

A doubled-haploid population Trident/Molineux (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).

For ear-emergence (Kuchel et al. 2006a) and grain yield QTL (Kuchel et al. 2006b), genotypes were calculated from flanking markers using the method of Whittaker et al. (1996). For the height reducing loci *Rht-B1* and *Rht-D1*, markers from Ellis et al. (2002) were used to classify the DHs, while the allele specific marker of Seah et al. (2001) was used for the 'VPM1' derived rust resistance locus *Lr37/Sr38/Yr17* (Bariana and McIntosh 1993) carried by 'Trident'. All genotypes (allele probabilities) were produced on a scale from 0 to 1 where 0 indicates 100% probability of the QTL allele being inherited from 'Trident' and 1 indicates that the QTL allele was inherited from 'Molineux'.

### 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. However, for reasons discussed later, data from one of the environments were

discarded for this analysis. A detailed description of the environments, the field experiments and methodology used to collect the grain yield data can be found in Kuchel et al. (2006b).

#### Environmental covariables

Data retrieved (<http://www.bom.gov.au>) from the closest meteorological station(s) were used to derive the climatic (temperature and rainfall) covariables for each of the environments used for grain yield testing. As the specific dates of ear emergence and physiological maturity for the population were not available for each of the environments, two calendar-based surrogates were used to partition the growing seasons into two major growth stages. The period from June to August (winter) was classed as the ‘vegetative’ stage and the period from September to November (spring) classed as the ‘reproductive’ phase. Table 1 provides a description of the 11 covariables assessed in this study. Table 2 provides the detailed data on each covariable for each environment. The mean grain yield for the T/M DH population was calculated for each of the environments to determine the correlation of the environmental covariables with grain yield. The latitude of the urban centres located closest to the sites used for grain yield assessment was used as a measure of variation in photoperiod. Naturally occurring stripe rust (*Puccinia striiformis* Westend. F. sp. *tritici*) infection was noted at seven environments and a score was assigned to each environment based on the relative severity of rust infection observed. However, RS05 was so heavily infected with stripe rust that some susceptible genotypes failed to produce grain. Consequently, this environment

was removed from further analysis to reduce the likelihood of false positive associations through bias.

#### Statistical analysis

Best linear unbiased predictors (BLUPs) for grain yield were determined for each DH in each environment where data were 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). These BLUPs provided the raw data for the subsequent multi-environment analyses.

The characterisation of QTL-by-environmental covariable (QCI) interaction in this population progressed through four stages.

1. The effects of the environmental covariables on site mean grain yield were determined by simple linear regression and correlation.
2. The genotype-by-environmental covariable interaction (GCI) was determined for each of the environmental covariables measured.
3. The QEI was assessed for each of the genes/QTL being investigated.
4. The QCI was determined for each of the genes/QTL being investigated and each of the environmental covariables measured.

Mixed models consisting of both fixed and random effects (see Bernardo 2002 for a detailed description of mixed models) were used for these analyses. Solutions were

**Table 1** Description of the environmental covariables used to investigate QEI

Environmental covariable	Units	Description
Mean_grain yield	kg ha <sup>-1</sup>	The site mean grain yield for the DH population
Latitude	Degrees (decimal)	The latitude (south) of the closest urban centre
Max_J-A	°C	Average maximum daily vegetative temperature (June–August)
Max_S-N	°C	Average maximum daily reproductive temperature (September–November)
Min_J-A	°C	Average minimum daily vegetative temperature (June–August)
Min_S-N	°C	Average minimum daily reproductive temperature (September–November)
Rain_A	mm	The annual rainfall
Rain_J-A	mm	The vegetative rainfall (June–August)
Rain_S-N	mm	The reproductive rainfall (September–November)
Yr_severity	0–10 Relative scale	Relative stripe rust infection
<10 Days_J-N	Days	The number of cold nights (<10°C min) from June to November
>30 Days_J-N	Days	The number of hot days (>30°C max) from June to November

**Table 2** Classification of the each of the 17 environments for the covariables under examination

Environment	Mean grain yield (kg ha <sup>-1</sup> )	Latitude south (°)	Max J-A (°C)	Max S-N (°C)	Min J-A (°C)	Min S-N (°C)	Rain A (mm)	Rain J-A (mm)	Rain S-N (mm)	Yr severity (0–10)	<10°Days		>30°Days	
											J-N (days)	J-N (days)	J-N (days)	J-N (days)
BL05	1,599	32.9	17.9	25.8	5.5	10.0	355	146	132	0	120	22	22	
CM04	2,856	33.7	17.3	21.5	9.0	11.0	550	209	92	0	95	6	6	
CN04	1,914	35.7	15.7	21.1	8.3	9.7	424	198	112	2	120	7	7	
CN05	2,468	35.7	16.4	21.0	7.6	10.4	412	184	148	5	106	5	5	
HR03	1,980	36.7	13.8	20.0	3.7	5.1	463	201	105	10	172	8	8	
KP03	2,307	34.3	13.6	20.7	5.1	8.2	536	198	124	0	156	8	8	
KP04	2,879	34.3	14.0	21.4	5.9	8.6	497	244	123	5	148	9	9	
ML03	1,272	32.8	18.8	26.3	4.8	11.6	548	203	135	0	109	26	26	
MN03	748	32.8	17.0	24.6	7.2	9.5	240	113	44	0	139	19	19	
MN05	1,955	32.8	17.5	24.4	7.7	10.3	286	128	112	0	117	18	18	
PN04	1,903	35.3	15.9	23.5	5.7	8.6	258	54	122	5	149	15	15	
PN05	1,825	35.3	16.8	22.8	5.8	8.9	293	115	111	10	140	8	8	
RS02	2,436	34.5	16.5	24.4	5.2	8.4	308	98	67	0	126	13	13	
RS03	2,784	34.5	15.5	21.5	5.9	7.5	417	174	104	1	144	9	9	
RS04	2,645	34.5	15.9	24.1	6.9	7.7	375	173	96	0	131	13	13	
TC04	491	33.7	17.2	25.7	6.2	9.3	242	128	41	0	136	25	25	
WT03	1,480	34.3	15.0	21.4	7.7	10.1	473	241	92	1	139	11	11	

provided by the REML directive within GESTAT 8 (Payne et al. 2002). For these mixed-model analyses, the random terms consisted of genotypes, environments and their interactions (GEI). For analysis Stage 2 the fixed effects consisted of each of the possible GCIs, and for Stage 3 they consisted of all QTL and all QEIs. The proportion of  $V_{\text{GEI}}$  (GEI variance) explained by each QEI was determined from the changes in the random GEI term as each of the QEIs were dropped in turn. The fourth stage of analysis was performed in three parts. In the first part of analysis Stage 4 the fixed effects consisted of a QTL and its interaction with an environmental covariable. This analysis was repeated for each QTL, also fitting the remaining QTL and their QEIs as fixed effects to account for additional genetic variation not explained by the interaction between the target QTL and environmental covariables. The significance of each QCI was determined from this analysis, and the proportion of  $V_{\text{GEI}}$  explained by each QCI was taken from the change in the random GEI term after the inclusion of the QCI term. The proportion of  $V_{\text{QEI}}$  (QEI) explained by each QCI term was calculated arithmetically from the proportion of  $V_{\text{GEI}}$  attributable to the corresponding QEI (from the Stage 3 analysis). In the second part of Stage 4, all QCIs for a given QTL were fitted as fixed effects in a combined mixed-model to determine which QCI remained significant ( $P < 0.05$ ) when all QCIs for a QTL were fitted simultaneously. The QTL and QEI effects were retained as fixed effects for the remaining QTL. The proportion of  $V_{\text{GEI}}$  and  $V_{\text{QEI}}$  explained by the combination of all QCIs for a given QTL were determined in this analysis. Finally, all significant QCIs for all QTL were fitted as fixed effects, allowing the total proportion of  $V_{\text{GEI}}$  and  $V_{\text{QEI}}$  explained by the QCIs to be determined. The analyses used here are similar to the method proposed by

Malosetti et al. (2004), except that for practical purposes, means for each DH in each environment after spatial adjustment were analysed.

For each of these analyses the significance ( $P < 0.05$ ) of the fixed terms was determined from the Wald statistic and for models containing multiple terms, insignificant terms were dropped by backward selection beginning with the least significant. For the height reducing loci, *Rht-B1* and *Rht-D1*, the interaction effect between the loci was also fitted. As mentioned previously, the proportion of variation in GEI explained by each of the fixed terms in the models was taken from the change in the estimated variance component of the GEI term from the random part of the mixed-model. However it should be noted that the GEI term is fitted as the residual in this analysis and will consequently contain some of the intra-environmental variance. The proportions of GEI explained by the various QEI and QCI are therefore likely to be underestimated. However, the relativeity of these proportions should remain true.

For graphical representation of QCI, the VPREDICT directive within GENSTAT 8 (Payne et al. 2002) was used to predict the grain yield of the genotypic classes at the various levels of the environmental covariables.

## Results

### Environmental covariables

Across the 17 environments used in this study, the number of growing season days with a maximum temperature  $>30^{\circ}\text{C}$ , and the highly correlated Max\_S-N, were the only covariables significantly associated with the average grain yield achieved in an environment (Table 3). The high-

**Table 3** Correlation matrix for the environmental covariables used for QCI analysis

	Mean grain yield kg ha <sup>-1</sup>	Latitude decimal	Max J-A ( $^{\circ}\text{C}$ )	Max S-N ( $^{\circ}\text{C}$ )	Min J-A ( $^{\circ}\text{C}$ )	Min S-N ( $^{\circ}\text{C}$ )	Rain A (mm)	Rain J-A (mm)	Rain S-N (mm)	Yr severity (0–10)	<10 $^{\circ}$ Days J-N (days)
Latitude	0.37										
Max_J-A	-0.41	<b>-0.63</b>									
Max_S-N	<b>-0.56</b>	<b>-0.71</b>	<b><u>0.79</u></b>								
Min_J-A	0.10	-0.18	0.23	-0.13							
Min_S-N	-0.25	<b>-0.61</b>	<b>0.70</b>	0.40	<b>0.57</b>						
Rain_A	0.46	0.11	-0.33	<b>-0.51</b>	-0.02	0.09					
Rain_J-A	0.32	0.10	-0.39	<b>-0.53</b>	0.15	0.06	<b><u>0.87</u></b>				
Rain_S-N	0.45	0.24	-0.10	-0.28	-0.14	0.13	0.48	0.31			
Yr_Severity	0.14	<b><u>0.74</u></b>	-0.38	-0.47	-0.35	-0.47	-0.03	-0.02	0.31		
<10 $^{\circ}$ Days_J-N	-0.07	0.42	<b>-0.74</b>	-0.33	<b>-0.62</b>	<b>-0.83</b>	-0.11	-0.05	-0.14	0.46	
>30 $^{\circ}$ Days_J-N	<b>-0.72</b>	<b>-0.71</b>	<b>0.65</b>	<b><u>0.92</u></b>	-0.24	0.33	-0.39	-0.37	-0.28	-0.46	-0.14

Correlation coefficients are in normal font if  $P > 0.05$ , bold if  $P < 0.05$ , bold italic if  $P < 0.01$  and bold italic underline if  $P < 0.001$

temperature covariable >30 days<sub>J-N</sub>, was also correlated with the latitude of the environment and Max<sub>J-A</sub>. There was no significant correlation between quantities of winter and spring rainfall. However, environments with high-average maximum temperatures tended to experience lower annual and vegetative rainfall. The stripe rust severity at an environment was only correlated with Latitude. The covariable >30 days accounted for 49.2% of the variation in grain yield among sites. Mean grain yield reduced by  $75.8 \pm 19 \text{ kg ha}^{-1}$  ( $P = 0.001$ ) for every day with a maximum temperature exceeding 30°C.

The effect of the environmental covariables on the relative grain yield of the DH individuals and the interaction of QTL with environments

When included in a combined model, highly significant ( $P < 0.001$ ) interactions were detected between the grain yield of the DHs and all of the environmental covariables except Latitude (data not shown). The final model excluding the not significant genotype-by-Latitude interaction term, explained 54.8% of the total variation in GEI.

Significant ( $P < 0.05$ ) interactions between the environments used for grain yield assessment and QTL associated with plant height (*Rht-B1* and *Rht-D1*), rust resistance (*Lr37/Sr38/Yr17*), plant phenology (Kuchel et al. 2006a) and grain yield per se (Kuchel et al. 2006b) were detected (Table 4). The largest QEI was observed for the ‘VPM’ derived rust resistance locus, *Lr37/Sr38/Yr17*, explaining 11.9% of the variation in total GEI. Of the remaining QEI, the *Rht-B1*, *Rht-D1* and grain yield QTL on chromosome 4D (*QGyld.agt-4D*) showed the largest interactions with the environment. Overall, 29.8% of the variation in GEI was accounted for by the final model for QEI (terms listed in Table 4).

The grain yield interaction effects between QTL and environmental covariables

The marker for the *Lr37/Sr38/Yr17* locus showed a high-level of interaction with each of the environmental covariables, except annual and vegetative rainfall (Table 5). The largest interaction observed for *Lr37/Sr38/Yr17* was with the severity of stripe rust infection (Yr<sub>Severity</sub>). No cross-over interaction for grain yield was observed between the *Lr37/Sr38/Yr17* locus and Yr<sub>severity</sub>. The grain yield of DHs with the resistant (‘Trident’) allele remained equal or superior to those with the susceptible (‘Molineux’) allele across the range of stripe rust infection severities (Fig. 1). The grain yield advantage of the *Lr37/Sr38/Yr17* resistance allele, inherited from ‘Trident’, was also strongly ( $P < 0.001$ ) reduced at lower Latitude environments. When each of the covariable interactions with *Lr37/Sr38/Yr17*

**Table 4** Proportion of the grain yield genotype-by-environment variance attributed to QTL-by-environment interaction for each of the gene/QTL shown to be associated with grain yield (Kuchel et al. 2006b)

Gene/QTL	Gene/QTL type	%V <sub>GEI</sub>	Wald/df	Significant
<i>Lr37/Sr38/Yr17</i>	Rust resistance	11.9	30.1	<0.001
<i>Rht-B1</i>	Plant height		4.4	<0.001
<i>Rht-D1</i>		8.9	8.9	<0.001
<i>Rht-B1.Rht-D1</i>			9.0	<0.001
<i>QPpd.agt-1A</i>	Plant phenology			ns
<i>QEps.agt-2AL</i>				ns
<i>QEps.agt-2AS</i>		0.2	2.8	<0.001
<i>Ppd-B1</i>				ns
<i>Vrn-A1</i>		0.6	1.9	0.016
<i>QEps.agt-6D</i>				ns
<i>QPpd.agt-7A</i>		1.0	3.4	<0.001
<i>QPpd.agt-7B</i>				ns
<i>QGyld.agt-1B</i>	Grain yield	1.0	1.7	0.037
<i>QGyld.agt-2D</i>		0.5	2.3	0.002
<i>QGyld.agt-3D</i>				ns
<i>QGyld.agt-4A</i>		0.3	1.7	0.039
<i>QGyld.agt-4D</i>		2.1	6.3	<0.001
<i>QGyld.agt-5B</i>				ns
<i>QGyld.agt-6A</i>				ns
<i>QGyld.agt-6D</i>		1.9	4.6	<0.001
<i>QGyld.agt-7B</i>				ns
Total <sup>a</sup>		29.8		

Refer to the Stage 3 analysis in the Materials and methods for a description of the models used. The additive and interactive effects of the two height loci were fitted in a combined model, and consequently, only one %V<sub>GEI</sub> is presented for these two loci

<sup>a</sup> The total is calculated from mixed-model analyses incorporating each of the QTL, not the sum of the individual %V<sub>GEI</sub> values

were included in the model; Latitude, Max<sub>J-A</sub>, Yr<sub>Severity</sub>, <10 days<sub>J-N</sub> and >30 days<sub>J-N</sub> remained significant ( $P < 0.05$ ) and accounted for 11.3% of the variance of GEI and 95.2% of the variance of QEI for the *Lr37/Sr38/Yr17* locus.

The impact of the alleles at the *Rht-B1* and *Rht-D1* loci on grain yield showed significant ( $P < 0.05$ ) variation with respect to all of the environmental covariables except Rain<sub>S-N</sub> (Table 5). The two- (*Rht-B1* and *Rht-D1*) and three-way (*Rht-B1.Rht-D1*) interactions with Max<sub>J-A</sub> had a significant ( $P < 0.05$ , 0.01 and <0.001, respectively), effect on grain yield (Fig. 2). A cross-over interaction effect was observed for the dwarf and tall genotypes with respect to Max<sub>J-A</sub>. The grain yield of the dwarf genotypes was generally lower than that of the tall genotypes, but when Max<sub>J-A</sub> was 17.2°C or greater, the grain yield of the dwarf genotypes was higher. The two semi-dwarf genotypes achieved grain yields higher than the tall and dwarf

**Table 5** Effects of significant QTL by covariable interactions (non-significant interactions are not presented)

Gene/QTL	Covariable	%V <sub>GEI</sub>	%V <sub>GEI</sub> <sup>b</sup>	Effect	Wald statistic	Probability
<i>Lr37/Sr38/Yr17</i>	<b>Latitude</b>	4.7	39.4	-86.8 ± 6.8	162.9	<0.001
	<b>Max_J-A</b>	1.4	11.6	36.8 ± 5.4	46.6	<0.001
	Max_S-N	2.0	16.8	31.8 ± 3.9	68.0	<0.001
	Min_J-A	1.8	14.9	43.8 ± 5.6	60.2	<0.001
	Min_S-N	3.1	26.4	52.7 ± 5.1	107.5	<0.001
	Rain_S-N	0.5	4.3	-1.1 ± 0.3	17.64	<0.001
	<b>Yr_Severity</b>	10.4	87.5	-42.5 ± 2.2	389.6	<0.001
	<b>&lt;10 Days_J-N</b>	3.0	25.4	-4.1 ± 0.4	103.5	<0.001
	<b>&gt;30 Days_J-N</b>	2.3	20.0	10.4 ± 1.2	79.5	<0.001
Sub-total <sup>a</sup>		11.3	95.2			
<i>Rht-D1</i>	<b>Latitude</b>	0.5	6.0	16.8 ± 6.6	6.6	0.010
<i>Rht-B1.Rht-D1</i>	<b>Latitude</b>			51.0 ± 13.5	14.3	<0.001
<i>Rht-B1</i>	Max_J-A	0.7	7.9	10.5 ± 5.2	4.1	0.044
<i>Rht-D1</i>	<b>Max_J-A</b>			-15.0 ± 5.1	8.7	0.003
<i>Rht-B1.Rht-D1</i>	<b>Max_J-A</b>			-42.4 ± 10.5	16.4	<0.001
<i>Rht-B1.Rht-D1</i>	Max_S-N	1.0	11.0	-44.3 ± 7.5	35.0	<0.001
<i>Rht-B1</i>	<b>Min_J-A</b>	0.7	7.3	16.9 ± 5.4	9.6	0.002
<i>Rht-D1</i>	<b>Min_J-A</b>			-21.6 ± 5.3	16.3	<0.001
<i>Rht-D1</i>	<b>Min_S-N</b>	0.4	4.7	-9.7 ± 4.8	4.0	0.046
<i>Rht-B1.Rht-D1</i>	<b>Min_S-N</b>			-35.8 ± 10.0	12.8	<0.001
<i>Rht-D1</i>	<b>Rain_A</b>	0.7	7.9	-0.2 ± 0.1	10.4	0.001
<i>Rht-B1.Rht-D1</i>	<b>Rain_A</b>			0.6 ± 0.1	15.4	<0.001
<i>Rht-B1.Rht-D1</i>	Rain_J-A	0.2	2.5	0.9 ± 0.3	8.6	0.003
<i>Rht-D1</i>	Yr_Severity	0.6	6.2	9.7 ± 2.2	20.2	<0.001
<i>Rht-B1</i>	<10 Days_J-N	1.0	10.8	-1.1 ± 0.4	8.5	0.004
<i>Rht-D1</i>	<10 Days_J-N			2.0 ± 0.4	28.8	<0.001
<i>Rht-B1.Rht-D1</i>	<b>&gt;30 Days_J-N</b>	1.3	14.4	-15.4 ± 2.3	45.5	<0.001
Sub-total <sup>a</sup>		4.0	44.8			
<i>QEps.agt-2AS</i>	<b>Min_S-N</b>	0.1	45.2	9.3 ± 4.6	4.1	0.042
	<b>&gt;30 Days_J-N</b>	0.1	61.9	2.4 ± 1.0	5.3	0.021
Sub-total <sup>a</sup>		0.2	92.9			
<i>Vrn-A1</i>	Latitude	0.1	18.4	14.8 ± 6.5	5.2	0.022
	Rain_S-N	0.1	21.6	0.6 ± 0.2	6.0	0.014
	<b>Yr_Severity</b>	0.4	65.2	8.5 ± 2.1	16.0	<0.001
Sub-total <sup>a</sup>		0.4	65.2			
<i>QPpd.agt-7A</i>	<b>Max_J-A</b>	0.1	11.9	14.0 ± 6.0	5.6	0.018
	Min_S-N	0.1	8.0	11.5 ± 5.7	4.1	0.042
	<10 Days_J-N	0.1	9.4	-1.0 ± 0.4	4.6	0.032
Sub-total <sup>a</sup>		0.1	11.9			
<i>QGyld.agt-1B</i>	Latitude	0.3	29.4	22.1 ± 6.2	12.6	<0.001
	<b>Max_J-A</b>	0.3	30.8	-17.6 ± 4.9	13.2	<0.001
	Max_S-N	0.5	50.1	-15.8 ± 3.5	20.8	<0.001
	Min_J-A	0.1	7.8	-10.3 ± 5.1	4.1	0.042
	Min_S-N	0.2	21.4	-14.2 ± 4.6	9.4	0.002
	Rain_A	0.1	11.1	0.2 ± 0.1	5.4	0.020
	<b>Rain_J-A</b>	0.1	10.1	0.3 ± 0.1	5.0	0.026

**Table 5** continued

Gene/QTL	Covariable	%V <sub>GEI</sub>	%V <sub>QEI</sub> <sup>b</sup>	Effect	Wald statistic	Probability
	<b>Rain_S-N</b>	0.2	20.1	0.7 ± 0.2	9.0	0.003
	Yr_Severity	0.5	51.7	9.5 ± 2.0	21.5	<0.001
	<b>&lt;10 Days_J</b>	0.3	25.3	1.2 ± 0.4	11.0	<0.001
	<b>&gt;30 Days_J-N</b>	0.5	40.7	-4.4 ± 1.0	17.1	<0.001
Sub-total <sup>a</sup>		1.0	99.0			
<i>QGyld.agt-4A</i>	Latitude	0.1	36.4	-13.6 ± 6.3	4.6	0.032
	<b>Max_J-A</b>	0.2	80.2	14.7 ± 4.9	9.0	0.003
	<b>Max_S-N</b>	0.2	83.4	10.7 ± 3.5	9.3	0.002
	Min_J-A	0.1	48.8	12.5 ± 5	5.9	0.015
	Min_S-N	0.2	64.5	12.7 ± 4.7	7.4	0.006
	Rain_A	0.1	33.1	-0.14 ± 0.07	4.3	0.038
	<10 Days_J-N	0.1	52.1	-0.9 ± 0.4	6.2	0.013
	>30 Days_J-N	0.1	47.1	2.5 ± 1.1	5.7	0.017
Sub-total <sup>a</sup>		0.3	100			
<i>QGyld.agt-4D</i>	Latitude	0.9	42.3	-37.9 ± 6.5	34.6	<0.001
	Max_J-A	0.2	9.7	14.7 ± 5.0	8.6	0.003
	Max_S-N	0.6	26.1	16.8 ± 3.6	21.7	<0.001
	Min_J-A	0.2	11.0	16.4 ± 5.3	9.6	0.002
	Min_S-N	0.3	15.2	17.3 ± 4.8	13.3	<0.001
	Rain_S-N	0.4	20.5	-1.0 ± 0.2	17.2	<0.001
	<b>Yr_severity</b>	2.1	100.0	-19.1 ± 2.1	82.6	<0.001
	<10 Days_J-N	0.3	12.0	-1.2 ± 0.4	10.5	0.001
	>30 Days_J-N	0.7	31.9	5.6 ± 1.1	26.3	<0.001
Sub-total <sup>a</sup>		2.1	100			
<i>QGyld.agt-6D</i>	Latitude	0.1	5.4	15.7 ± 7.3	4.7	0.030
	<b>Min_J-A</b>	0.2	12.7	-18.5 ± 5.9	9.8	0.002
	<b>Rain_A</b>	0.3	13.5	-0.25 ± 0.08	10.4	0.001
	<b>Rain_J-A</b>	0.1	7.2	-0.4 ± 0.2	6.0	0.014
	<b>Yr_Severity</b>	0.9	46.6	13.8 ± 2.4	33.8	<0.001
	<b>&lt;10 Days_J-N</b>	0.1	4.3	0.8 ± 0.4	4.0	0.047
Sub-total <sup>a</sup>		1.3	70.5			
Total <sup>a</sup>		22.8	76.8			

Refer to the Stage 4 analysis in the Materials and methods for a description of the models used. Covariables showing significant interactions when included in a combined mixed-model for each QTL are in bold type. The additive and interactive effects of the two height loci were fitted in a combined model. Consequently, only one %V<sub>GEI</sub> and %V<sub>QEI</sub> are presented for each of the environmental covariable interactions with these interactive loci

<sup>a</sup> Totals are calculated from mixed-models incorporating each of the QCI and consequently will not equal the sum of the individual components

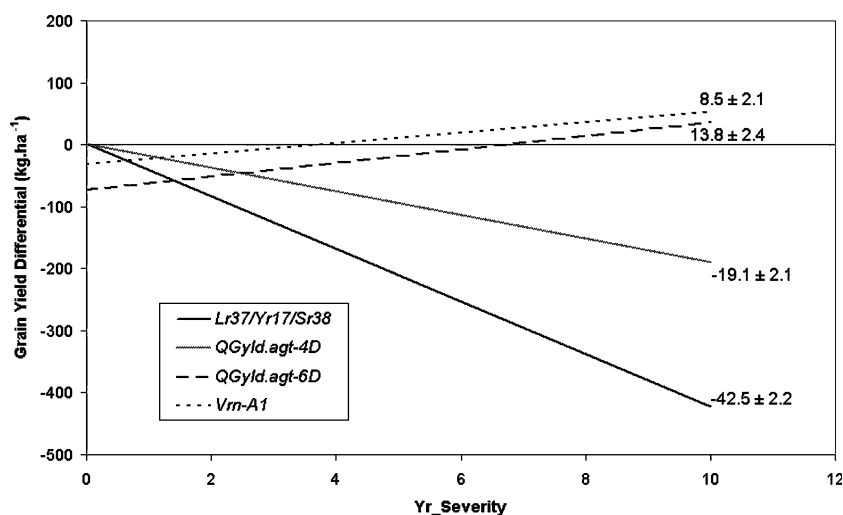
<sup>b</sup> The proportions of V<sub>QEI</sub> for the individual QCI, and the sub-totals, are expressed as a percentage of the QEI for the locus under investigation. However, the total V<sub>QEI</sub> explained by the model refers to the proportion of QEI for all loci showing interaction with environments (Table 4)

genotypes at all annual rainfall levels, although at lower levels of annual rainfall the grain yield of the tall lines neared that of the semi-dwarfs. The largest interaction effect was observed between the height reducing genes (*Rht-B1*, *Rht-D1*) and >30 days\_J-N ( $P < 0.001$ ), accounting for 1.3% of the total GEI and 14.4% of the QEI for the *Rht-B1* and *Rht-D1* loci.

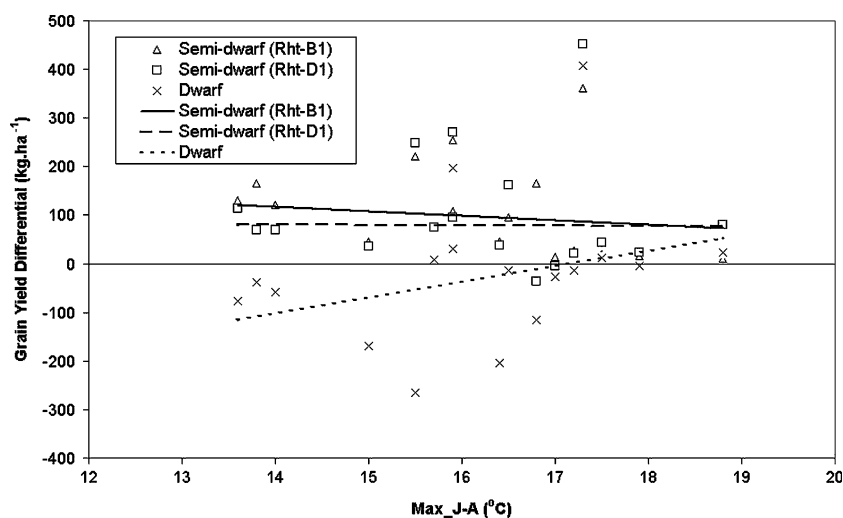
Of the eight chromosome regions identified by Kuchel et al. (2006a) to be involved in the control of plant phenology in the T/M DH population, only the minor time to ear-emergence QTL on 2AS (*QEps.agt-2AS*), the vernalisation gene, *Vrn-A1*, and the putative photoperiod sensitivity locus *QPPd.agt-7A* showed interaction with environmental covariables. *QEps.agt-2AS* and *QPPd.agt-7A* both interacted



**Fig. 1** Prediction of the grain yield differential (‘Molineux’–‘Trident’) for the *Lr37/Sr38/Yr17*, *Vrn-A1*, *QGyld.agt-4D* and *QGyld.agt-6D* loci across the range of stripe rust severities experienced at the environments use for grain yield assessment



**Fig. 2** Predictions of the grain yield interaction effects between the plant height loci *Rht-B1* and *Rht-D1*, and the average vegetative maximum daily temperature on grain yield in the T/M DH population. The grain yield differential for the two semi-dwarf (*Rht-B1b/Rht-D1a* and *Rht-B1a/Rht-D1b*) genotypes and the dwarf (*Rht-B1b/Rht-D1b*) genotype is presented relative to the tall (*Rht-B1a/Rht-D1a*) genotype for each of the environments



with temperature variables. In both cases, DH lines with the allele associated with earlier ear-emergence (‘Trident’) produced higher relative grain yield in cooler environments. However, the *Vrn-A1* locus showed a different QCI pattern, showing significant interactions with Latitude ( $P < 0.05$ ), reproductive rainfall (Rain\_S-N) ( $P < 0.05$ ) and stripe rust severity (Yr\_Severity) ( $P < 0.001$ ). When included in a combined model, only the interaction with Yr\_Severity remained significant. When Yr\_Severity was higher, the lines with the vernalisation sensitive (‘Molineux’) allele produced higher grain yield in comparison to DH lines with the insensitive allele (‘Trident’).

The putative grain yield per se QTL with the largest and most frequent effect on grain yield (Kuchel et al. 2006b), *QGyld.agt-1B* and *QGyld.agt-4D*, showed significant QCI, along with two other QTL on chromosomes 4A (*QGyld.agt-4A*) and 6D (*QGyld.agt-6D*), that had smaller grain yield main effects. Although the grain yield effects of the *QGyld.agt-2D* locus interacted with the environment, no QCI interactions for this locus were observed. Of the grain

yield QTL, *QGyld.agt-4D* was the most responsive to environmental covariables, with the relative impact of the two alleles on grain yield varying with respect to all covariables except Rain\_J-A and Rain\_A. *QGyld.agt-4D* also had the single largest QCI effect behind the rust resistance locus *Lr37/Sr38/Yr17*. Its interaction with Yr\_Severity accounted for 2.1% of the variation in total GEI (Fig. 1). When each of the covariable interactions were fitted for this locus in a combined model, only the interaction with Yr\_Severity remained significant, explaining 100% of the QEI for this QTL. Of the QCI effects observed for *QGyld.agt-6D*, its interaction with Yr\_Severity was the most significant (Fig. 1). In this case, a cross-over interaction at stripe rust severity score 6.7 meant that the DH lines possessing the ‘Molineux’ allele produced higher grain yield at higher stripe rust infection levels and the grain yield of lines with the ‘Trident’ allele were superior at lower stripe rust levels. Interactions involving *QGyld.agt-1B* did not lead to any cross-over in grain yield allele advantage within the bounds of the observed values for the environmental covariables. After fitting a model incorporating each

of the environmental covariable interactions for grain yield with *QGyld.agt-4A*, the two maximum temperature traits (Max\_J-A and Max\_S-N) were the only two that remained significant. Interactions with these climatic covariables, accounted for 100% of the QEI effects recorded for the *QGyld.agt-4A* locus.

## Discussion

### Impact of environmental covariables on grain yield

Studies on the interaction between environmental covariables and wheat grain yield, barley grain yield and maize biomass by Campbell et al. (2004), Malosetti et al. (2004) and Crossa et al. (1999), respectively, showed the largest QTL interaction effects with temperature related traits. In the case of Campbell et al. (2004), a marker linked to a QTL for grain yield on wheat chromosome 3A (Campbell et al. 2003) was found to interact significantly with the temperature from emergence to anthesis. Malosetti et al. (2004), who concentrated their report on chromosome 2H of barley, also found the largest QCI with temperature during ear-emergence. Crossa et al. (1999) found QTL for maize biomass were also most responsive to maximum temperatures. In this study, the number of growing season days exceeding 30°C had a substantial impact on the mean grain yield at a site, explaining almost 50% of the variance in grain yield among the environments. This, and the other temperature related covariables showed large interactions with genotypes. Therefore, the T/M DH population may be segregating for several genes controlling tolerance of high temperatures. High-daily temperatures may be an important factor determining grain yields achieved across southern Australia (Panozzo and Eagles 1998). However, the interaction with the temperature covariables were mainly the result of a scale effect. The detrimental effect of high temperatures on grain yield resulted in a smaller difference between the performance of alleles, but few cross-overs in relative performance. True genetic tolerance of high temperatures, a desirable feature for wheat cultivars in many Australian environments, would arise from the presence of alleles that either maintained, or even improved, their relative grain yield advantage in high-temperature environments. Unfortunately, none of the loci shown to be associated with grain yield in this population (Kuchel et al. 2006b) showed such an interaction.

### QTL by environmental covariable interactions

The largest QCI were observed for the ‘VPM’ derived rust resistance locus *Lr37/Sr38/Yr17*. DH lines with the resistant (‘Trident’) allele produced higher grain yields relative

to lines with the susceptible allele in environments with higher reproductive rainfall (Rain\_S-N), a greater number of cold nights (<10 days\_J-N) and fewer hot days (>30 days\_J-N). This fits with the expected model, where the benefit of resistance is greatest in the environments that are the most conducive to the development of a stripe rust epidemic. The strong relationship between Yr\_Severity and alleles at the *Lr37/Sr38/Yr17* locus confirm that the grain yield advantages conferred by the ‘Trident’ allele were largely due to stripe rust resistance. However, even when Yr\_Severity was included in the model, Latitude and some temperature related covariables (Max\_J-A, <10 days\_J-N and >30 days\_J-N) also remained significant. It is possible that the grain yield effects of the *Lr37/Sr38/Yr17* locus, or genes linked to it, also alter with respect to latitude and temperature.

For the height reducing genes, the results from the QCI analysis support the conclusions of Kuchel et al. (2006b) who found that the grain yield of the semi-dwarf genotypes was equal, or superior, to both the tall and dwarf genotypes. Here, the results suggest that the grain yield of the dwarf and tall genotypes are always inferior to the grain yield of semi-dwarf genotypes, regardless of the environmental covariable being considered. However, based on the model developed in this study, if an environment was encountered that received <200 mm of annual rain, it is predicted (albeit relying on the modelled linear relationship) that the grain yield of the tall genotypes would exceed that of the *Rht-B1a/Rht-D1b* semi-dwarf genotype. This result supports the findings of Fischer and Maurer (1978), who suggest that tall lines perform better than semi-dwarf types only under severe drought stress.

The lack of significant grain yield QEI and QCI for the QTL associated with the time to ear-emergence (Kuchel et al. 2006a) is surprising. Significant associations have been detected between each of the time to ear-emergence QTL and grain yield (Kuchel et al. 2006b). As one would expect for an environment suffering from terminal drought and heat stress, the alleles leading to earlier ear-emergence were also associated with high-grain yield. However, in this QCI analysis, one may have assumed that as the number of days that exceeded 30°C decreased and the quantity of rainfall increased, later ear-emerging genotypes would have performed relatively better than genotypes with early ear-emergence. However this was not the case in this study. The alleles conferring early ear-emergence (‘Trident’), at *QPpd.agt-7A* and *QEps.agt-2AS* were associated with higher grain yields at the full range of temperatures experienced across the environments in this study. This result suggests that even in the environments with high-relative rainfall and cool relative temperatures, the rapid decline in moisture availability, and rise in spring and therefore flowering temperatures, results in the superior grain yield

of genotypes with early ear-emergence. In contrast, *Vrn-A1* strongly interacted with *Yr\_Severity*. It is possible that the vernalisation sensitive allele, or genes closely linked to it, also contribute a level of resistance to stripe rust. However this was not detected in QTL mapping of foliar disease reaction data (H. Kuchel, unpublished data). It may also be possible that the environmental factors that favoured the development of stripe rust also favoured a later maturing phenotype. However, if this were the case, a similar interaction with *Yr\_Severity* may be expected for the other loci involved in the control of time to ear-emergence. It is surprising that the loci on chromosomes 1A, 2B, 7A and 7B, shown to be associated with photoperiod responsiveness (Kuchel et al. 2006a), showed no interaction with Latitude. This may have arisen due to the relatively narrow range of latitudes (<4°), and therefore low level of variation in photoperiod, sampled in this multiple-environment trial. It is also possible that variable seeding dates (due to soil moisture availability) between years acted to reduce the interaction effects with Latitude. Further experimentation covering a wider range of latitudes would be required to confidently determine the relationship between these loci and latitude.

Of particular interest in this study is the QCI effects for the putative grain yield per se QTL identified by Kuchel et al. (2006b). Of all the grain yield QTL identified by Kuchel et al. (2006b) *QGyld.agt-1B* was significant at the most number of environments. Although significant interactions with low and high temperatures, rainfall, *Yr\_severity* and Latitude were observed for this QTL, no cross-over interaction was seen. The genotypes carrying the ‘Molineux’ allele at this locus were higher yielding than those with the ‘Trident’ allele for the full range of temperatures and rainfall levels encountered in this experiment. This further supports the conclusion that *QGyld.agt-1B* would be a suitable target for marker-assisted selection (Kuchel et al. 2006b). A very similar response pattern was observed for *QGyld.agt-4A*, where the largest interactions were with maximum vegetative (Max\_J-A) and reproductive (Max\_S-N) temperatures. Lines carrying the ‘Trident’ allele at this locus achieved grain yields in excess of those with the ‘Molineux’ allele across all temperature ranges experienced in this study. The relative superiority of the ‘Trident’ allele was diminished in hotter environments. For *QGyld.agt-1B* and *QGyld.agt-4A*, the very large percentages of QEI explained by their interactions with the environmental covariables (99 and 100%, respectively), suggests that biotic stresses and edaphic features, not tested in this experiment, are unlikely to alter the relative grain yield superiority of lines possessing the favourable alleles at these two loci. This conclusion assumes that the environments sampled in this study covered the entire gamut of stresses possible. Obviously this is not the case, but should hold largely true for the southern Australia mega-environment. However

it should also be remembered that these estimates of QEI variances are subject to substantial error, and so additional interactions with these loci may still be identified.

*QGyld.agt-4D* displayed a similar QCI profile to the *Lr37/Sr38/Yr17* locus. In fact, when all covariable interaction terms were included in a model for this locus, only the interaction with *Yr\_Severity* remained, explaining 100% of the QEI expected for *QGyld.agt-4D*. Consequently, it seems likely that this locus may be involved in the control of grain yield through either direct or indirect effects on rust resistance. However, subsequent QTL analysis of data from four rust resistance screening nurseries only detected one weak (LOD 2.5) association between *QGyld.agt-4D* and stripe rust resistance (H. Kuchel, unpublished data). Given the weak association with rust resistance but the strong association with grain yield (Kuchel et al. 2006b), it does not seem plausible that the grain yield effects of *QGyld.agt-4D* are solely due to rust resistance. However, it may be possible that *QGyld.agt-4D* either contributes to some level of tolerance to stripe rust, changes the type of rust infection (level of chlorosis, necrosis or pustule size), or perhaps alters the rate and/or timing of rust development. Alternatively, the expression of *QGyld.agt-4D* may vary in response to some other environmental characteristic that is correlated with the severity of stripe rust infection. In either case, further research is required to dissect the obvious interaction between the *QGyld.agt-4D* locus and *Yr\_Severity* (or the environmental conditions that were related to *Yr\_Severity*). This could lead to improvements in the efficiency of grain yield selection or selection for rust resistance, or both.

The effects of *QGyld.agt-6D* on grain yield were also strongly associated with the level of stripe rust infection (*Yr\_Severity*). In contrast to *QGyld.agt-4D* and *Lr37/Yr17/Sr38*, a cross-over interaction was observed between *QGyld.agt-6D* and *Yr\_Severity*. Genotypes with the ‘Molineux’ allele produced higher grain yields than genotypes with the ‘Trident’ allele when an environment experienced severe stripe rust pressure, although at lower levels of stripe rust infection the ‘Trident’ allele was associated with higher grain yield. However, less than half the QEI was explained by this interaction, and interactions with rainfall (Rain\_A and Rain\_J-A) and temperature (Min\_J-A and <10 days\_J-N) remained significant when added to the model. A small association (LOD 2.4) between *QGyld.agt-6D* and stripe rust resistance was observed at one of the four stripe rust resistance screening nurseries (H. Kuchel, unpublished data). Given the relatively low proportion of QEI explained by the interaction of this locus with *Yr\_Severity*, it seems that either the effects of this locus are not restricted to stripe rust resistance or that stripe rust resistance is perhaps a secondary feature of the QTL. This conclusion is supported by the lower grain yields associated

with the ‘resistance’ conferring allele at environments not suffering from stripe rust infection. In the context of plant breeding, this locus presents a philosophical dilemma. If the environmental target for a breeding programme were likely to be heavily infected with stripe rust on a regular basis, then the ‘Molineux’ allele would be desirable. However, given the positive interaction of the ‘Trident’ allele with rainfall, selection for this allele would be an obvious objective, particularly in target environments that do not suffer regularly from stripe rust infection and experience high rainfall.

It is interesting to note that although *QGyld.agt-2D*, *QGyld.agt-4A* and *QGyld.agt-6D* had much smaller main effects on grain yield, in comparison to *QGyld.agt-1B* and *QGyld.agt-4D*, the magnitude of their QEI effects were comparable. This highlights the importance of extending QTL mapping of grain yield in a multi-environment context to allow the identification of loci with predominantly environmentally interactive effects. Not only will this help in the identification of additional genetic elements influencing grain yield and ultimately adaptation, it should also assist in the dissection of the physiological and molecular basis of gene-to-phenotype (Malosetti et al. 2004; van Eeuwijk et al. 2005). By way of example, this QCI analysis highlights the remarkable similarity between the covariable interactions observed for *Lr37/Sr38/Yr17* and *QGyld.agt-4D*. Although it seems unlikely that the substantial associations with grain yield for this locus could be attributed to rust resistance alone, the pattern of QCI observed for this locus suggests that this QTL, or genes linked to this QTL, may influence resistance or tolerance to stripe rust infection. Although by no means certain, and requiring further investigation, this example highlights the *predictive* potential of genetic analyses incorporating specific environmental covariables.

## Conclusions

Characterisation of QTL previously identified to be associated with grain yield has shown that a substantial proportion (22.8%) of total GEI could be explained by the interactions of these QTL with specific climatic covariables. However, given that the majority of GEI is not explained by the QCI characterised here, it would be reasonable to assume that further QTL interacting with these and/or other environmental covariables could be detected in this population. The characterisation of environments for factors other than climatic covariables, including potential abiotic (e.g. nutrient toxicities or deficiencies) and biotic stresses (e.g. root disease and foliar disease), may assist in the identification of further QTL-by-environment interactions.

Quantitative trait locus analysis as employed by Kuchel et al. (2006b) is restricted to the detection of effects in specific environments, and although successful in improving our understanding of the genetic basis to complex traits such as grain yield, conclusions drawn are limited by the scope of the environments selected for examination. A QCI-based analysis, such as undertaken here, may facilitate the prediction of QTL effects beyond the set of environments used for testing. A detailed understanding of QTL-by-environment should therefore assist breeders in the design and implementation of breeding strategies targeted at improving the grain yield and adaptation of wheat to both specific and mega environments. In this study, substantial QCI effects were identified. However very few cross-over interaction effects were observed. This provides confidence that genotypic-based molecular marker selection for favourable grain yield alleles (Kuchel et al. 2006b) should afford higher grain yield across southern Australia and similar environments.

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