

Quantifying the value to grain yield of QTL for adaptation and tolerance to abiotic stress in bread wheat

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INTRODUCTION

Drought stress is a pervasive feature of wheat production in many of the world's major cereal-growing regions. To improve the productivity in these areas the importance of traits associated with tolerance to drought needs to be quantified. Yield is a complex trait and many physiological, morphological and developmental characteristics have been suggested as being important to yield in water limited environments. However, yield can be considered in terms of a few fundamental processes: the ability of the crop to use the available moisture for the efficient production of biomass and the partitioning of this into yield. Consequently, to achieve high yields a variety needs to have a pattern of development appropriately tuned to the seasonal trends in moisture availability, a healthy root system that enables it to exploit soil moisture and nutrient reserves and tolerance to important soil nutrient deficiencies and toxicities. Secondary traits such as glaucousness or leaf rolling may also contribute to yield by alleviating the severity of stress and helping to maintain growth during periods of water or heat stress.

Yield shows large Genotype x Environment (GE) interactions, yet our understanding of the genetic and physiological bases of adaptation is poor. Few studies have analysed the relative importance of different physiological and agronomic characteristics that may contribute to improved drought tolerance^{1, 2, 3}. QTL analysis of yield provides a means of describing the genes and the physiological processes that influence GE interactions. In this study, we have used trials from a wide range of sites to assess the value of specific traits to yield under water-limited conditions. The aim is to identify QTL that are associated with high yield under drought and broad adaptation, to assess their agronomic value in different environments and to use the analysis to dissect the GE interaction.

METHODS

The study used a doubled haploid population derived from a cross between two elite genotypes, Berkut and Krichauff. Berkut is a broadly-adapted CIMMYT variety whilst Krichauff is well-adapted to the winter-dominant rainfall pattern and the alkaline soils that are widespread in southern Australia. The population was

grown under rainfed conditions in a number of sites in Australia, Mexico, India, Morocco and Kazakhstan and under irrigation in Pakistan and Mexico in 2006 and 2007. Measurements were made of crop development (using Zadok's growth stages) and time of flowering, canopy temperature prior to and after anthesis (to indicate the ability to maintain transpiration), plant height, the severity of leaf rolling and drought-induced head tipping (death of distal spikelets), grain yield and yield components. Composite interval mapping QTL analysis was conducted using the Windows QTL Cartographer 2.5 application⁴. 1000 permutation tests were performed to establish an experiment-wise significance value at the 0.05 significance level defined as a minimum LOD threshold for each trait in CIM⁵.

RESULTS AND DISCUSSION

Yields at all non-irrigated sites were less than 2t/ha, with many less than 1 t/ha (Table 1). However, despite the low yields heritabilities were relatively high at most of the sites.

Table 1. Mean grain yield (kg/ha) and heritabilities (h^2) for selected sites in 2006 and 2007.

(Irr) - Irrigated trial; NA – data not available

Year	Site	Mean yield	h^2
2006	Booleroo, S. Aust	469	0.08
	Minnipa, S. Aust.	416	0.45
	Roseworthy, S. Aust	1919	0.26
	Obregon, Mexico (Irr)	5555	0.47
	Obregon, Mexico	1105	0.32
2007	Balaklava, S. Aust	666	0.48
	Booleroo, S. Aust	1428	0.37
	Minnipa, S Aust.	571	0.57
	Narrabri, NSW	1405	0.49
	Roseworthy, S Aust.	1905	0.30
	Obregon, Mexico (Irr)	6139	0.47
	Obregon, Mexico	1486	0.60
	Faisalabad, Pakistan (Irr)	3507	NA

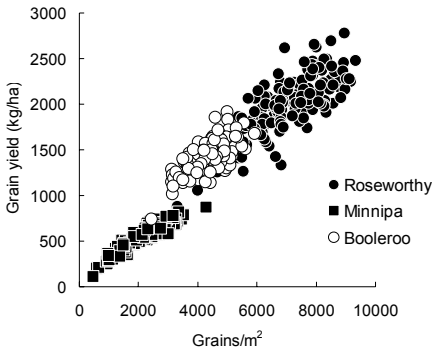


Figure 1. The relationship between grain yield and grains/m² in the Berkut x Krichauff doubled haploid population at three rainfed sites in South Australia in 2007.

In general, grain yield was strongly correlated with the number of grains/m² rather than kernel weight. Data from three sites in 2007 are shown in Fig 1 and this shows that the relationship was tightest at Minnipa, the lowest yielding site. The relative importance of kernel weight to grain yield increased from the lowest yielding to the highest yielding site, suggesting a shift in the sink-source relationships as the severity of the stress and the length of the growing season changed.

Under southern Australian conditions, most of the lines flower within about a 7-day period, but this range was up to 2-3 weeks at CIMMYT. Maturity QTL were consistently identified in the regions of the vernalisation genes on chromosomes 5A (*Vrn-A1*), 5B (*Vrn-B1*) and 5D (*Vrn-D1*) across environments and these explained 10-40% of the phenotypic variation in maturity. In the CIMMYT drought trials, grain yield was strongly affected by the days to anthesis ($r = -0.78, P < 0.001$) and maturity ($r = -0.77, P < 0.001$). A component of grain yield at CIMMYT collocated with maturity QTL on 5A and yield at Minnipa partially collocated with the QTL on 5B. At CIMMYT, pre-anthesis canopy temperature and leaf waxiness at anthesis also collocated to the maturity QTL on chromosomes 5A and 5D suggesting the expression of these traits were influenced by the range in maturity among the lines.

Two yield QTL were identified at Roseworthy in 2006, on chromosomes 4A and 6A, and one at Minnipa on chromosome 6B (Table 2). While these QTL were not identified at other sites, they did significantly affect yield at a number of them (Table 2). Kirigwi et al.¹ found that a region on chromosome 4A near *wmc48* was associated with phenotypic variation in yield under drought, yield components and drought susceptibility index and this same region may also have been detected in the present work. In Canada McCartney et al.³ also identified a yield QTL very close to *wmc48* and Kuchel et al.⁶ identified a region on chromosome 4A that was

Table 2. Effects of the 3 molecular markers identified in 2006 on grain yield at seven sites. Effects calculated in REML with the markers fixed and where possible a random spatial model for ranges and rows. Proportion of the genotypic variance accounted for by the 3 markers is also shown.

Allele	<i>wmc-048b</i>	<i>wPt-492</i>	<i>wPt-7063</i>	% var
	4A	6B	6A	
	R'worthy	Minnipa	R'worthy	
Booleroo 2007				
Bkt	1394	1418	1415	
Kri	1456	1432	1434	
sed	25	26	26	
sig	*	ns	ns	3.7
Minnipa 2007				
Bkt	600	542	559	
Kri	548	606	589	
sed	21	22	22	
sig	*	*	ns	12.2
Roseworthy 2007				
Bkt	1951	1836	1772	
Kri	1842	1957	2021	
sed	64	67	67	
sig	ns	ns	*	22.9
Balaklava 2007				
Bkt	681	644	613	
Kri	624	661	692	
sed	35	36	36	
sig	ns	ns	*	4.9
Minnipa 2006				
Bkt	417	385	397	
Kri	408	440	427	
sed	15	16	16	
sig	ns	*	ns	21.3
Roseworthy 2006				
Bkt	1969	1864	1800	
Kri	1819	1924	1989	
sed	61	64	63	
sig	*	ns	*	21.2
Pakistan 2006				
Bkt	3902	3663	4144	
Kri	3758	3997	3516	
sed	198	206	206	
sig	ns	ns	*	23.4

weakly associated with grain yield in the Trident/Molineux doubled haploid population of wheat. The fact that a yield QTL has been identified in different populations and in different environments suggest this region of chromosome 4A may be a useful target for further study.

The yield QTL on 6A (near *wPt-7063*) was associated with yield differences at Roseworthy, Balaklava and in Pakistan (Table 2). This QTL was also associated with plant height at Roseworthy (2006, 2007) and at Booleroo (2006) and with canopy temperature during grain filling at CIMMYT. The Krichauff allele contributed to higher yield, taller plants and a cooler canopy. Yield was positively related to height at CIMMYT under drought ($r = 0.62$, $P < 0.001$) and at Booleroo in 2006 ($r = 0.21$, $P < 0.05$). There was also a significant negative correlation between height and canopy temperature at CIMMYT ($r = -0.21$, $P < 0.05$) and at Roseworthy in 2007 ($r = -0.63$, $P < 0.001$). Together the results suggest that this region of chromosome 6A is associated with an ability to maintain water uptake and growth (expressed as height) as water availability diminishes. The cooler canopies may reflect a deeper or more extensive root system providing better access to water⁷ leading to better plant performance. A region on chromosome 6A was also found to be associated with grain yield and in particular kernel weight in a number of mapping populations grown under drought stress in Europe⁴. The effect of this QTL was also significant in the irrigated trial in Pakistan although the effect was opposite to that observed under rainfed conditions (Table 2), suggesting the trait may be a specific adaptation to low rainfall environments.

The QTL on 6B near *wPt-492* which was associated with yield at Minnipa had no significant effect at other sites, although it was associated with head tipping at Roseworthy. The Krichauff allele contributed to greater tipping and 12% higher grain yield. Both years at Minnipa were very low yielding (< 500 kg/ha) and this QTL may be useful for yield under severe stress. A significant QTL for head tipping near *cfa-2155* was also identified on chromosome 5A in trials at CIMMYT with the Krichauff allele conferring greater tipping. Although not identified in the Australian trials, this QTL was associated with significant differences in yield at a number of Australian locations, with the largest effect observed at Narrabri in the northern cereal belt (Table 3). The Krichauff allele contributed to higher yields. This marker is about 20cM from *Vrn-1* on chromosome 5A, so the yield difference observed in the Australian trials may be related to the effect of crop development, rather than head tipping *per se*.

The population segregated for waxiness and leaf rolling and QTL were identified for both these traits: on chromosome 5A and 7D (waxiness) and 4A (leaf rolling). The regions on chromosomes 7D and 4A were

Table 3. Effects on grain yield (kg/ha) of the QTL near *cfa-2155* associated with head tipping at seven sites in Australia.

Site	Allele		sed	Sig.
	Berkut	Krichauff		
Booleroo 2007	1417	1432	26	ns
Minnipa 2006	381	424	20	*
Minnipa 2007	549	579	19	ns
NarrabriA 2007	1217	1522	53	*
NarrabriB 2007	1140	1449	49	*
NarrabriC 2007	1222	1570	46	*
Balaklava 2007	605	697	28	*

strongly associated with crop growth stage and *Vrn-1*. Therefore, it would appear that in this population neither leaf rolling nor waxiness provides any yield advantage

CONCLUSION

Although the population flowered within a relatively narrow range at the Australian sites, maturity was still an important cause of variation in a number of the traits. This suggests that either yield and its components are very sensitive to time of flowering in this environment or that there are pleiotrophic effects associated with the vernalisation genes that we do not fully understand. Nevertheless, yield QTL independent of crop development were identified. The regions on chromosomes 4A and 6A warrant further investigation as they have shown significant effects across a number of environments and the results are consistent with reports from earlier studies that have suggested these regions contribute to high yields.

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