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Detection of two major grain yield QTL in bread wheat (*Triticum aestivum* L.) under heat, drought and high yield potential environments

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Abstract A large proportion of the worlds' wheat growing regions suffers water and/or heat stress at some stage during the crop growth cycle. With few exceptions, there has been no utilisation of managed environments to screen mapping populations under repeatable abiotic stress conditions, such as the facilities developed by the International Wheat and Maize Improvement Centre (CIMMYT). Through careful management of irrigation and sowing date over three consecutive seasons, repeatable heat, drought and high yield potential conditions were imposed on the RAC875/Kukri doubled haploid population to identify genetic loci for grain yield, yield components and key morpho-physiological traits under these conditions. Two of the detected quantitative trait loci (QTL) were located on chromosome 3B and had a large effect on canopy temperature and grain yield, accounting for up to 22 % of the variance for these traits. The locus on chromosome arm 3BL was detected under all three treatments but had its largest effect under the heat stress conditions, with the RAC875 allele increasing grain yield by 131 kg ha^{-1} (or phenotypically, 7 % of treatment average). Only two of the eight yield QTL detected in the current study (including linkage groups 3A, 3D, 4D 5B and 7A) were previously detected in the RAC875/Kukri doubled haploid population; and there were also different yield components driving grain yield. A number of discussion points are raised to understand differences between the Mexican and southern Australian production environments and explain the lack of correlation between the datasets. The two key QTL detected on chromosome 3B in the present study are candidates for further genetic dissection and development of molecular markers.

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Introduction

Of the 12 CIMMYT mega-environments for wheat (*Triticum aestivum* L.), half are classified as either drought and/or heat stressed at some stage of crop production (Braun et al. 1996). Breeding for yield improvement in cereal crops,

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notably bread wheat, for these regions has traditionally relied upon empirical selection methods. An understanding of major genes controlling phenology has facilitated the fine-tuning of days to ear emergence. This has ensured that crops achieve the optimum balance between vegetative and reproductive growth, aiming to minimise the impact of abiotic stress during crucial growth stages of flowering and grain fill. However, more recently there has been an increasing focus on morpho-physiological dissection of grain yield, with the aim of improving grain production, particularly under abiotic stresses such as drought and heat. Rapid, integrative measurements, such as canopy temperature (CT) and Near Differential Vegetative Index (NDVI) have been suggested as useful screening tools under these conditions (Babar et al. 2006; Olivares-Villegas et al. 2007), whilst other traits, such as water-soluble carbohydrates and flag leaf glaucousness, have been proposed as key traits supporting grain yield in stressed conditions (Blum et al. 1994; Rebetzke et al. 2008b; Richards et al. 1986).

With the exception of Pinto et al. (2010), there have been relatively few instances where managed environments have been used to screen segregating mapping populations under defined abiotic stress conditions. The International Centre for Wheat and Maize Improvement (CIMMYT) has developed a number of controlled environments at its Ciudad Obregon field station, in north-west Mexico, which were described in full by Kirigwi et al. (2007). The drought environment involves intermittent irrigation events using a drip irrigation system, to create a cyclical drought environment during vegetative growth and terminal drought conditions during grain fill. This regime mimics rain-fed production systems of many areas of the world. The heat stress environment has been designed to mimic environments where high temperatures are experienced during grain fill but water is not a limiting factor. By sowing later than conventional practice, usually in mid-February, experiments are naturally exposed to the high temperatures of the Mexican summer and this environment has been found to correlate well with some areas where heat stress during grain fill is common (Lillemo et al. 2005). Finally, growing experiments in a fully irrigated environment allows the yield potential of the germplasm of interest to be assessed. With water being a non-limiting factor and mild temperatures experienced during key growth stages, high yields can be achieved, which are directly comparable to the drought and heat stress treatments, given they are sown in close proximity, on similar soils and otherwise similar climatic conditions.

QTL mapping has been increasingly utilised as a strategy to identify genomic regions important for grain yield and other genetically complex traits in cereal species (Cuthbert et al. 2008; Rebetzke et al. 2008a). Development of populations segregating for traits of interest can permit

detection of key genomic regions. This can lead to increases in genetic progress in breeding through strategies such as marker-assisted selection (Collins et al. 2008).

The RAC875/Kukri doubled haploid (DH) population has been extensively characterised for yield and key yield components in its target population of environments of southern Australia (Bennett et al. 2012a, b), particularly under water-stressed conditions. It has also been characterised for variation in maturity and flag leaf glaucousness, with a wide range in maturity identified, which is not desirable in a population aiming to detect QTL under drought stress. However, Reynolds et al. (2009) and Bennett et al. (2012a) suggested strategies to deal with this, including reducing the population size by removing extremes of maturity and adjusting phenotypic data for maturity date; and a combination of these was successful in removing these effects from yield mapping results (Bennett et al. 2012b). This study aimed to (1) genetically dissect grain yield under high yield potential, drought and heat stressed managed environments; (2) identify key yield components associated with grain yield in these environments; (3) identify key morpho-physiological traits related to grain yield under each treatment and associated QTL; and (4) compare detected QTL to those previously identified in the RAC875/Kukri DH population.

Methods

Plant material

A doubled haploid population, derived from a cross between RAC875 and Kukri was sown in six experiments over three field seasons. The population contained 368 individuals but in the 2008 and 2009 seasons, a subset of 255 lines was sown to minimise the confounding impact of phenology and reduce resources required for phenotyping (Bennett et al. 2012a). Briefly, RAC875 is a breeders' line that has previously shown relatively stable grain yield in water-limited conditions in southern Australia, while Kukri is a variety that suffers significantly reduced grain yield under the same conditions. These two parents were described and physiologically investigated in more detail by Izanloo et al. (2008).

Field experiments and phenotypic measurements

Each field experiment was arranged in two blocks, completely randomised. The parents of the population and three locally adapted, check lines contrasting for drought tolerance were also sown (Sokoll, Weebil and Atil). Two experiments were sown under terminal drought (Drt) in 2007 and 2009, with supplementary drip irrigation (as discussed by Kirigwi et al. 2007). Two more experiments

were sown later than conventional practice to expose the plants to higher temperatures (2008, 2009), particularly during grain fill, but with supplementary irrigation to minimise the effect of water stress (heat; as discussed by Lillemo et al. 2005). The final two experiments were at a conventional sowing time in 2007 and 2008 and received full irrigation (Irr). A summary of in-season irrigation and temperature for all experiments are detailed in Tables 1 and 2. All experiments were sown in the Yaqui Valley, Mexico, on CIMMYTs' Obregon Experimental Station, located in the state of Sonora (27°25′N 109°54′W, 38 m above sea level). In 2007, plots consisted of twin two-row, 60 cm centre-to-centre raised beds, 6 m in length; whilst in 2008 and 2009, plots consisted of a single 2 m raised bed.

Early vigour, ear emergence time, anthesis date and physiological maturity (Phys) were scored visually, peduncle length, plant height and flag leaf width using a ruler in the field (the average of five measurements per plot) and kernels per square metre, derived by dividing plot grain weight by 1,000 kernel weight (Tkw). Grain yield was calculated from harvested grain weight, Tkw was estimated by counting and weighing 100 grains and water soluble carbohydrates measured using the same methodology described by Pinto et al. (2010). Canopy temperature was measured twice a day as climatic conditions permitted, using a handheld infrared thermometer (Mikron M90 series, Santa Clara, CA, USA). NDVI was measured using a GreenSeeker sensor (Optical Sensor Unit, 2002 Ntech Industries Inc., Ukiah, CA, USA) at 25 days after emergence but not in the Irr treatments. SPAD was measured using a portable meter (SPAD-502, Konica-Minolta, Plainfield, IL, USA) but was not measured in the Irr treatments and Wsc was not measured in the Drt treatments. Trait abbreviations are listed in Table 3.

Statistical analysis and QTL mapping

The methods outlined by Gilmour et al. (1997) were followed to minimise or remove spatial effects of field variation. For each trait in each experiment, linear mixed-model analysis using the method of residual maximum likelihood (REML) was performed in GenStat release 8.2 (Payne et al. 2005). Genotype was firstly fitted as a random effect to calculate broad sense heritability on an experimental basis, and then the data were re-analysed with genotype as a fixed effect, to produce the best linear unbiased estimates (BLUEs). Ear emergence time was also fitted as a covariate in the analysis for each trait in each experiment. When the effect was not significant, it was excluded from the model. Utilising the BLUEs and standard errors, genetic correlations (r_g) were generated during multi-environment analysis following the methods of Mathews et al. (2008). Heritabilities were calculated on a single experiment basis and presented as the lowest achieved for a given trait under a given treatment. The weighted genotype mean for each experiment was then averaged across each treatment and this value used for QTL mapping of each trait. The QTL analysis was performed by the mixed-model based composite interval mapping (CIM) using QTLNetwork v2.0 (Yang et al. 2008), with a significance threshold of $P < 0.05$. The linkage map for the population was published by Bennett et al. (2012a) but briefly; contained 456 DArT and SSR markers forming linkage groups representing all 21 chromosomes. Trait abbreviations and QTL designations were defined adopting the nomenclature suggested by the wheat catalogue of gene symbols (McIntosh et al. 2008) or those suggested by Pinto et al. (2010).

Results

Climatic and phenotypic summary

The late-sown heat experiments were the hottest in terms of average minimum and maximum temperatures during vegetative growth and grain fill, and had the highest number of days with temperature >30 and 35 °C (Table 2). The comparison between drought and irrigated environments were performed side by side in 2007 but in different years for the 2008 and 2009 experiments, potentially introducing additional sources of variation. The use of smaller rows may also have been conducive to increased error within experiments, particularly under drought, where any edge effect (i.e. increased water availability for plants at the ends of plots) would have a proportionally larger effect than in a

Table 1 Summary of the experiment codes, treatments, years experiment was conducted, irrigation received, grain yield of the parents of the RAC875/Kukri doubled haploid population, average and range in grain yield of the population multi-environment trial average per genotype and lowest broad sense heritability of grain yield achieved under each treatment

Code	Treatment (years)	Irrigation received	Grain yield (kg ha^{-1})				
			Kukri	RAC875	Population avg	Range	H^2
Drt	Drip irrigation (2007, 2009)	150	1,511	2,048	1,867	1,041–2,546	0.58
Heat	Late sown (2008, 2009)	300	1,900	2,244	1,905	1,342–2,768	0.78
Irr	Fully irrigated (2007, 2008)	500	5,658	5,933	5,380	3,716–6,797	0.74

Table 2 Summary of the average grain yield (in kg ha^{-1}), average minimum and maximum temperatures during vegetative growth, anthesis and grain fill and the number of days below 10, >30 and >35 °C across the six experiments at Obregon, Mexico

Experiment[a]	Average grain yield (kg ha^{-1})	Temperature (°C)								
		Vegetative		Anthesis		Grain fill		Number of days		
		Min	Max	Min	Max	Min	Max	<10 °C	>30 °C	>35 °C
DRT07	1,484	7.1	23.8	4.7	25.1	8.2	28.4	93	10	0
DRT09	2,248	8.9	26.0	7.1	23.7	9.0	26.6	81	12	0
HEAT08	1,532	8.6	29.9	10.6	33.6	14.5	35.6	50	71	25
HEAT09	2,281	9.7	27.4	9.0	30.6	14.7	35.0	46	54	22
IRR07	5,642	6.5	23.7	7.7	29.5	9.7	29.2	96	19	0
IRR08	5,124	6.8	25.1	9.3	29.5	8.2	29.3	106	23	1

[a] D indicates drought treatment, H heat treatment and I irrigated treatment, followed by the last two digits of the year that that experiment was conducted

bigger size plot. The Drt environments ($r_g = 0.61$) received the lowest amount of irrigation (approximately 150 mm average total), subsequently achieved the lowest yield (average 1,867 kg ha^{-1}) and also generally had the lowest grain yield heritability (Table 1). The second lowest yielding treatment was heat ($r_g = 0.54$ between treatments, average 1,905 kg ha^{-1}) and the Irr treatment yielded more than double the other two environments on average ($r_g = 0.71$ between treatments, 5,658 kg ha^{-1}, Table 1). RAC875 yielded significantly ($P < 0.05$) more than Kukri and the population average in all three environments.

Yield under the heat and Irr treatments were positively correlated ($r = 0.45$, $P < 0.01$), as was yield under the Drt and heat treatments ($r = 0.38$, $P < 0.05$) but there was no significant correlation between the Irr and Drt treatments (data not shown). In the heat and Drt treatments, Tkw was positively correlated with yield ($r = 0.28$, $P < 0.05$ and $r = 0.44$, $P < 0.01$, respectively), but only in the Drt treatments was it correlated ($r = -0.46$, $P < 0.01$) with Kpsm (Fig. 1). Flag leaf width (Flw) was positively correlated with grain yield in the Irr and heat treatments, whilst canopy temperature-vegetative (CT-veg) and during grain fill (CT-gf) was negatively associated with yield in the same two treatments (Fig. 1), indicating genotypes with cooler canopies were higher yielding. Kpsm was positively associated with yield in each environment ($P < 0.05$) and showed a highly significant correlation with yield in the heat treatment ($r = 0.79$, $P < 0.001$). Phys was also positively correlated with yield under heat, as well as NDVI-gf, with NDVI-gf also correlated with yield, Flw, Kpsm, Ht, Pdl and CT-gf in this environment (Fig. 1).

Chromosomal regions associated with grain yield and supporting traits

A total of 116 QTL were detected across the three treatments and thirteen traits measured, with QTL detected on all

linkage groups except for 7D (Supplementary Table 1). In total, nine loci were associated with grain yield in at least one of the three treatments (Fig. 2). Under the drought treatment, all yield QTL accounted for 25 % of the genetic variance, in the heat treatment, 44 % and in the irrigated treatment, 30 %. The RAC875 allele was associated with greater grain yield at five of these loci. This included the QTL accounting for the largest percentage of genetic variance under the heat environment, which was located on the long arm of chromosome 3B (*Q.Yld.aww-3B-2*, $r^2 = 0.22$); it also accounted for a large portion of the genetic variance for grain yield in the Irr and Drt environments (Supplementary Table 1; $r^2 = 0.12$). Furthermore, QTL for canopy temperature during grain fill, again accounting for a large percentage of genetic variance, were detected in the Irr environment in the same region as *Q.Yld.aww-3B-2* ($r^2 = 0.05$) and particularly in the heat treatment ($r^2 = 0.21$); as was the case for Kpsm at this locus. Similarly, QTL were also detected for Wsc, CT-veg in the Irr environment and Flw and early vigour (EV) under heat at this locus. A QTL for Pdl also mapped to this region, with the RAC875 allele for all traits except for canopy temperature and Wsc, resulting in a greater value relative to the Kukri allele.

A second QTL detected on the short arm of chromosome 3B (*Q.Yld.aww-3B-1*) also accounted for a large percentage of the phenotypic variance for grain yield in the heat environment but particularly in the Irr environment ($r^2 = 0.14$), where the Kukri allele resulted in higher yield (Fig. 2). The Kukri allele at this locus also resulted in a cooler canopy temperature (2.4 °C cooler, $r^2 = 0.02$) during grain fill and greater Kpsm in the Irr environment and greater Tkw and NDVI in the heat environment. The QTL detected on chromosome 5B (*Q.Yld.aww-5B*) was also associated with canopy temperature during vegetative growth, where the RAC875 allele was associated with a cooler canopy and higher grain yield in the Irr environment (for both traits, $r^2 = 0.04$).

Table 3 Summary of trait performance of the RAC875/Kukri doubled haploid population and parents grown at CIMMYTs' Obregon field station, Mexico in three different treatments

Trait	Abbr.	Units	Drought				Heat				Irrigated			
			Avg	Range	Kukri	RAC875	Avg	Range	Kukri	RAC875	Avg	Range	Kukri	RAC875
1,000 kernel weight	Tkw	g	46.0	38.8–56.4	40.2	53	31.6	24–42	27.4	31.2	43.6	33.4–53.2	38.5	49.2
Anthesis date	Ad	Days after sowing	69.5	55.6–90.2	72.1	69.1	63.6	54.2–70.8	67.1	63.6	79.8	67.7–99.8	81.5	79.3
Canopy temperature: grain fill	Ct-gf	°C	35.0	31.9–38.2	33.6	35.3	34.9	32.3–37.2	36.4	34.8	28.0	27.5–28.3	28.0	27.8
Canopy temperature: vegetative	Ct-veg	°C	NR	–	–	–	27.4	26.3–28.6	26.8	27.4	19.3	19–19.6	19.4	19.2
Ear emergence time	Eet	Days after sowing	55.9	46.9–82.5	58.6	57.0	52.7	46.6–64.7	55.6	53.3	75.9	62–95.7	78.765	75.38
Early vigour	Ev	1–9 visual score	8.0	7.09–8.9	7.7	8.1	NR	–	–	–	3.2	1.1–7.8	3.5	4.5
Flag leaf width	Flw	mm	12.3	10.8–13.3	12.03	12.93	10.3	8.6–12.4	9.6	10.6	17.5	13.5–22.6	16.5	18.7
Flag leaf glaucousness	W	1–9 visual score	5.1	3.3–6.8	3.6	6.7	5.1	3.3–6.8	3.6	6.7	5.1	3.3–6.8	3.64	6.6
Grain yield	Yld	kg ha^{-1}	1,866.9	1,041–2,546.5	1,511.0	2,048.0	1,906.7	1,342–2,768	1,900.0	2,244.0	5,383.2	3,716–6,797	5,658	5,933
Kernels per metre sq	Kpsm	Number	4,207	3,397–4,904	4,057	4,167	6,023	4,232–9,441	7,299	7,580	11,961	9,331–17,511	13,761	11,457
Normalized difference vegetative index	NDVI		0.61	0.51–0.69	0.60	0.63	0.57	0.51–0.62	0.57	0.59	NR	–	–	–
Plant height	Ht	cm	54.2	44.2–67.4	55.2	50.7	61.6	47.8–78.8	64.3	58.9	84.0	71.5–105.4	87.6	76.3
Physiological maturity	Phys	Days after sowing	NR	–	–	–	78.9	76.1–81.6	77.0	77.9	122.1	119.1–125.3	122.15	122.7
Peduncle length	Pdl	mm	236.0	203.9–274.7	269.3	233.3	203.2	119.1–273.2	234.4	198.5	NR	–	–	–
SPAD	SPAD	SPAD	51.5	46.8–55.9	48.9	54.1	51.4	46.4–57.9	47.3	53.4	NR	–	–	–
Water-soluble carbohydrates	WSC	g 6 stems^{-1}	NR	–	–	–	107.6	49.4–170.5	113.1	119.4	143.4	75.1–239.7	123.5993	164.2222
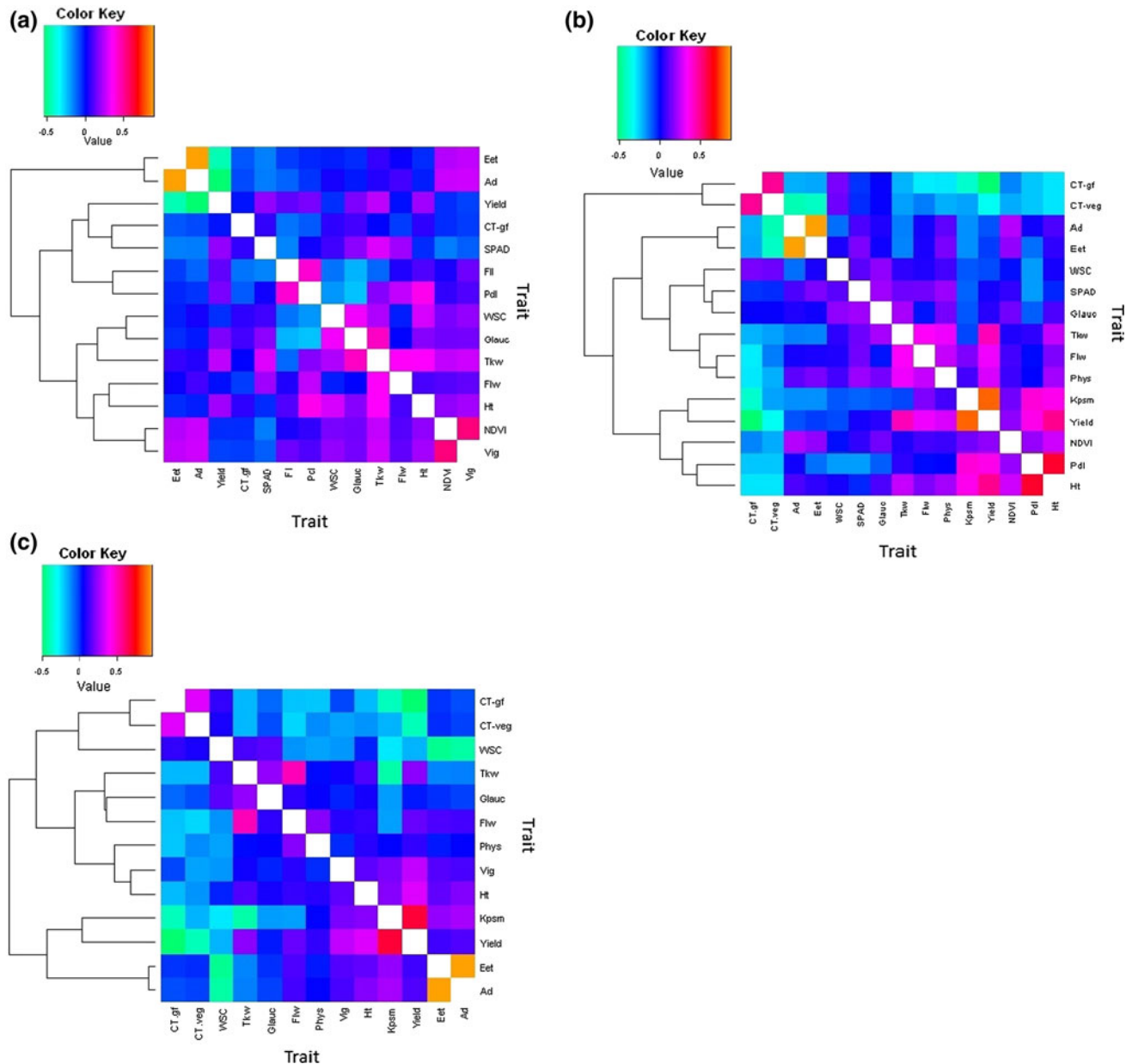
Fig. 1 Heat maps illustrating the phenotypic correlation between all traits measured in the RAC875/Kukri doubled haploid population grown under **a** drought; **b** heat; and **c** irrigated treatments at CIMMYT, in north-west Mexico. *Dendrograms on the left hand side highlight the correlation between traits, with a more recent split indicating greater correlation*

Another grain yield QTL on 3A co-located with QTL for Tkw under Drt, as well as Pdl and Wsc in the Irr and heat environments. Here, the RAC875 allele resulted in a greater Yld, Tkw and Wsc but a shorter Pdl. The Kukri allele at *Q.Yld.aww-3D* resulted in higher grain yield (up to 65 kg ha^{-1}, $r^2 = 0.03$) and Kpsm under Drt and heat but was associated with lower early vigour ($r^2 = 0.06$). A yield QTL detected in the Irr environment on linkage group 4A appeared to be associated with lower NDVI and EV scores in the Drt environment whilst the Kukri allele at

Q.Yld.aww-4D was associated with greater grain yield ($r^2 = 0.04$) and SPAD ($r^2 = 0.10$) in the heat environment. On linkage group 7A, a QTL on the short arm (*Q.Yld.aww-7A-1*) did not appear to co-locate with any other QTL and was distinct from a second QTL on the long arm. The two loci had opposite allele effects and were detected under different treatments. The RAC875 allele at *Q.Yld.aww-7A-2* resulted in greater grain yield (up to 74 kg ha^{-1}, $r^2 = 0.06$), Tkw, glaucousness and fewer Kpsm and days to ear emergence.
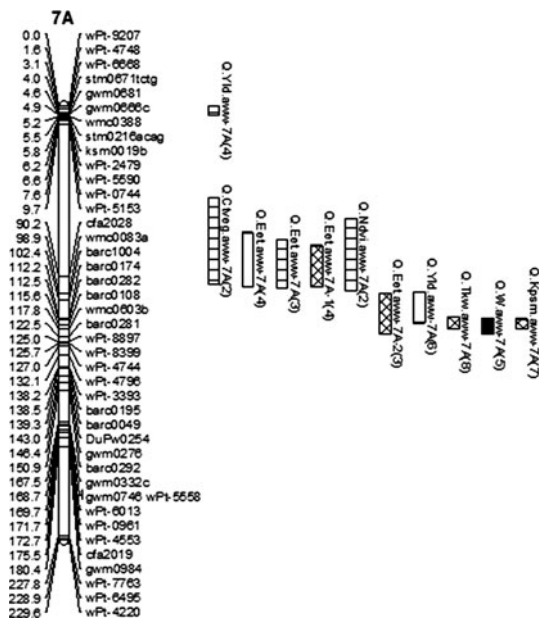
Fig. 2 Linkage groups in the RAC875/Kukri-derived doubled haploid population, showing quantitative trait loci for grain yield and co-locating traits across drought, heat and fully irrigated experiments grown at Obregon, Mexico. QTL detected in the drought treatment (*white bars*), heat treatment (*horizontal-lined bars*), irrigated environments (*cross hatched*) and QTL detected by the mean across all environments (*solid black bars*), with the length of the bar determined by a 95 % confidence threshold. The r^2 of each QTL is provided in *parentheses* after each QTL name

Fig. 2 continued

QTL detected in the present study associated with QTL previously identified in the RAC875/Kukri doubled haploid population

Previous studies of the RAC875/Kukri doubled haploid population have identified a number of key genomic regions, where QTL were detected for grain yield, yield components, Eet and glaucousness in southern Australia. A comparison of co-locating QTL and their positive allele effects are summarised in Table 4. Only two QTL in the present study have been detected previously for grain yield in this population (Bennett et al. 2012b). While the effect of *Q.Yld.aww-7A-2* was consistent across studies, the allele effect of *Q.Yld.aww-4D* was opposite in the current study. Interestingly, previously identified QTL affecting grain yield on 2A, 2B, 2D and 6D were detected in the current study for a variety of other morpho-physiological traits (Wsc, CT, NDVI and SPAD), suggesting potential physiological roles for yield determination under southern Australian conditions. QTL detected on linkage group 3B for grain yield were of large effect in the present study but only affected harvest index (3BS) and grain screenings (3BL) in southern Australian field experiments. Similarly, QTL detected on 7AS and 3A had a significant effect on grain yield in the present study but failed to exert any influence on grain yield in southern Australia. In the case of 3A, nevertheless, a significant positive effect on physical grain quality had been identified in southern Australia (Bennett et al. 2012b).

Discussion

Phenotypic differences between experiments

The ability to manage water availability and sowing time created three distinct environment treatments for the RAC875/Kukri doubled haploid population. The phenotypic response to these environments within the population has been genetically dissected by QTL analysis. The Drt environment was the lowest yielding on average for the population, although the heat experiments, despite receiving double the amount of irrigation, yielded a similar level. The late sowing resulted in the shortest time to ear emergence, which would most likely be due to both the long day length and elevated temperatures, increasing the degree days received by the experiment per calendar day. Due to the longer growing season under fully irrigated conditions, the grain filling period was actually warmer than that for the drought treatment; although it was not as hot as the late sowing. During the week around anthesis (based on population average), which is well documented as being sensitive to abiotic stress such as high temperature (Dolferus et al. 2011; Gibson and Paulsen 1999), the average daily maximum in the fully irrigated experiment was not significantly different to that of the heat experiment. The drought experiments were climatically significantly cooler during the same growth stage (although in the drought treatment, plant temperatures, as measured by canopy temperature, were warmer than air temperature) and should have permitted us to genetically dissect the impact of drought and heat stress as separate factors, although they often occur together in the field.

QTL dissection of grain yield under well-watered, late-sown/heat and drought treatments

Q.Yld.aww-3B-2 was one of nine QTL detected for yield, but the only one to impart an effect on this trait in all three contrasting treatments. The effect of the RAC875 allele was very large, particularly in the heat environment, accounting for 22 % of the genetic variance for grain yield. This appears to be one of the largest QTL influencing grain yield identified to date, apparently not related to maturity, or plant height. The RAC875 allele also increased Flw, Kpsm, Pdl and resulted in a cooler canopy temperature during the vegetative and grain fill growth stages. Zhang et al. (2010) identified a META-QTL for grain yield in this region, of minor effect, whilst Pinto et al. (2010) also detected a QTL of relatively large effect in a similar region under similar heat stress conditions. The yield QTL detected by Kumar et al. (2007) was in a very similar region on 3BL to the QTL detected by Ma et al. (2012) for *Fusarium* resistance, as well as QTL detected for root knot

Table 4 Summary of QTL detected in the RAC875/Kukri doubled haploid population in the present study to QTL detected in similar regions (within 10 cM) in the same population when grown in southern Australia

Current study (treatment in first parenthesis) QTL	Bennett et al. (2012b)		
	Source of positive allele	Comparable QTL	Source of positive allele
Q.Ndvi.aww-1B (Drt) (172)	Kukri	Q.Yld.aww-1B (165)	RAC875
Q.W.aww-2A, Q.Phys.aww-2A (heat) (83)	Kukri	Q.Yld.aww-2A (94)	Kukri
Q.Tkw.aww-2B, Q.Vig.aww-2B, Q.Flw.aww-2B (heat, Drt) (76)	RAC875	Q.Yld.aww-2B (62)	RAC875
Q.Ndvi.aww-2B (heat) (131)	RAC875	Q.Tkw.aww-2B-2 (139)	RAC875
Q.Wsc.aww-2D, Q.Tkw.aww-2D, Q.Flw.aww-2B (Irr), Q.Vig.aww-2D (heat, Drt) (70)	RAC875	Q.Yld.aww-2D-2 (79)	Kukri
Q.Tkw.aww-3A, Q.Yld.aww-3A, Q.Wsc.aww-3A (Drt) (60)	RAC875	Q.Twt.aww-3A, Q.Ht.aww-3A, Q.Wsc-c.aww-3A, Q.Wsc-a.aww-3A, Q.Wsc-t.aww-3A (64)	RAC875
Q.Pdl.aww-3A (ALL) (60)	Kukri	Q.Pdl.aww-3A, Q.Kps.aww-3A, Q.Kpsm.aww-3A (60)	Kukri
Q.Yld.aww-3B-1, Q.Kpsm.aww-3B-1, Q.Tkw.aww-3B, Q.Ndvi.aww-3B (Irr) (74)	Kukri	Q.Hi.aww-3B (84)	Kukri
Q.Ctgf.aww-3B-1 (Irr) (74)	RAC875		
Q.Wsc.aww-3B, Q.Kpsm.aww-3B-2, Q.Flw.aww-3B, Q.Kpsm.aww-3B, Q.Pdl.aww-3B, Q.Vig.aww-3B, Q.Yld.aww-3B-2 (Irr, Drt, heat) (190)	RAC875		
Q.Ctgf.aww-3B-2, Q.Ctveg.aww-3B-2 (Irr, Drt, heat) (190)	Kukri	Q.Scr.aww-3B-2 (190)	Kukri
Q.Yld.aww-4A (Irr) (0)	RAC875	Q.Tn.aww-4A (15)	RAC875
Q.Ndvi.aww-4A, Q.Vig.aww-4A (Drt) (15)	KUKRI	Q.Twt.aww-4A, Q.Fll.aww-4A (15)	Kukri
Q.Spad.aww-4D (heat, Drt), Q.Yld.aww-4D (heat) (5)	Kukri	Q.Yld.aww-4D, Q.Scr.aww-4D, Q.Kpsm.aww-4D (6)	RAC875
		Q.Twt.aww-4D, Q.Hi.aww-4D (6)	Kukri
Q.Spad.aww-6D (ALL), Q.Phys.aww-6D (Irr) (90)	RAC875	Q.Yld.aww-6D, Q.Kpsm.aww-6D (85)	RAC875
Q.Yld.aww-7A-1 (heat) (0)	Kukri	Q.Kps.aww-7A (4)	Kukri
Q.Eet.aww-7A-2 (Irr, Drt, heat), Q.Kpsm.aww-7A (Irr) (110)	Kukri	Q.Scr.aww-7A (127)	Kukri
Q.Yld.aww-7A-2 (Drt), Q.Tkw.aww-7A (Irr), Q.W.aww-7A (ALL) (110)	RAC875	Q.Yld.aww-7A-1, Q.Ev.aww-7A (116)	RAC875

Approximate position of QTL peak (in cM) provided in parentheses (second parentheses for current study) and trait abbreviations in Table 3

nematode resistance (Coriton et al. 2009), aluminium tolerance (Navakode et al. 2010) and stem solidness (Houshmand et al. 2007). However, after comparison with the wheat consensus map (Somers et al. 2004), the region of interest in those studies appeared to be approximately 15 cM distal to the locus detected in the present study. Given the large phenotypic effect of this locus on yield, particularly under heat stress, it should be given high priority for fine mapping and candidate gene identification, so that diagnostic molecular markers can be developed and deployed within breeding programs, particularly those targeting heat prone regions.

On the short arm of linkage group 3B, previous studies detected QTL for traits such as Tkw, plant height (Ht), harvest index (HI) and carbon isotope discrimination but none appeared to have detected QTL for grain yield (Cuthbert et al. 2008; Kumar et al. 2007; Rebetzke et al. 2008a). *Q.Yld.aww-3B-1* was detected with co-locating QTL for canopy temperature during grain fill and Kpsm under the fully irrigated treatment and Tkw and NDVI under heat treatment. Interestingly, this locus not only increased Kpsm but also Tkw, which was unexpected given these two traits have previously shown an inverse relationship in this population (Bennett et al. 2012b). Further to

these two loci, *Q.Yld.aww-3A* was only detected in the drought environment and *Q.Yld.aww-7A-1* only in the heat-stressed environment. *Q.Yld.aww-5B* was only detected under fully irrigated conditions and these three loci were detected in regions where previous reports of loci affecting grain yield are lacking. The locus on 3A is of particular interest, where Cuthbert et al. (2008) reported a minor Eet locus, although it did not appear that there was any such effect in this population. However, the higher yielding allele (from RAC875) was associated with a shorter peduncle length and as previously detected, greater plant height (Bennett et al. 2012b). In the previous study, the RAC875 allele was also associated with greater Wsc, test weight and Kpsm; although no yield effect. Griffiths et al. (2012) detected QTL in this region for plant height, which confirms that this is a height influencing region, with positive pleiotropic effects on other traits and these effects do not appear to have been identified previously.

Q.Yld.aww-3D was detected under both heat and drought conditions and appears to be in a similar region to the QTL reported by Naruoka et al. (2011), for tiller number. The effect observed by these authors is probably the same in the RAC875/Kukri population. *Q.Kpsm.aww-3D* was detected in the present study, again under heat and drought conditions, which is a trait that could be expected to respond to an increase in tiller number. However, characterisation of appropriately contrasting population tails for tiller number (i.e. individuals with high and low extremes for tiller number per plant) would be required to confirm this relationship.

Q.Yld.aww-7A-2 was detected in most ENV clusters identified by Bennett et al. (2012b), again with the RAC875 allele resulting in a slightly later Eet but accounting for a relatively large proportion of the genetic variance for grain yield. The above study concluded that, although the Eet effects at all other loci had been removed, the same could be expected at this locus. However, the large yield effect detected indicates the presence of either another closely located locus or a pleiotropic effect not accounted for by Eet. Interestingly, Kinoshita et al. (2011) recently found that the *Flowering Time* (*FT*) locus in *Arabidopsis* also affected stomatal aperture, keeping guard cells turgid for longer. Bennett et al. (2012a) concluded that the locus *QEet.aww-7A-3*, as well as *QEet.aww-7B*, were in a similar deletion bin and location to the *TaFT* series of genes (or *VRN3*) and this was potentially the gene causing the later ear emergence time. In both of these regions, we detected QTL for CT-veg in the heat treatment, suggesting that this mechanism may be present in wheat. Future work should aim to confirm whether the Eet loci detected in the population are indeed *TaFT* through the use of the published within-gene polymorphisms (Bonnin et al. 2008; Sun et al. 2008).

To date, there are few examples where SPAD and NDVI have been dissected by QTL analysis in bread wheat. Pinto et al. (2010) mapped NDVI during both vegetative and grain fill growth stages but the QTL detected during vegetative growth co-located with loci for height or ear emergence/flowering time, as was the case with the single locus detected for SPAD. More extensive genetic mapping of SPAD has been carried out in rice (*Oryza sativa* L.) (Fu et al. 2011) and maize (*Zea Mays* L.) (Nourse et al. 1999), where up to five loci were detected. In the present study, ten QTL were detected for this trait, with one instance where it co-located with yield (*Q.Yld.aww-4D*) and three examples where it co-located with Flw (1A, 2B and 6A). The latter relationship is interesting because the allele increasing FLW was associated with a larger SPAD score on 1A and 2B, but on 6A, where this locus is known to increase grain size, among other traits, the allele effects between Flw and SPAD score were opposite (Bennett et al. 2012b). QTL detected for SPAD on linkage groups 3BS and 4B were located near loci for canopy temperature, although a consistent relationship between the two traits is not clear (and *Q.Spad.aww-4B* was located in a region associated with Eet effects, Bennett et al. 2012a). The remaining loci for SPAD were not co-located with known QTL, which was also the case for NDVI loci on linkage groups 1B, 2A, 2B, 2D and 3D. However, QTL for NDVI detected on 3BS and 5B were positively associated with yield, although on 4A an inverse relationship was found, indicating that this trait may have some value in selecting for grain yield. Olivares-Villegas et al. (2007) also reached this conclusion, since they found small positive associations between grain yield and SPAD as well as NDVI, pre- and post-anthesis, under drought conditions.

Knowledge of the genetic basis of canopy temperature is also lacking, with only a couple of reports of QTL for this trait in bread wheat. Whilst Pinto et al. (2010) detected up to ten loci for this trait in their study, Mason et al. (2011) detected eight loci for spike and leaf temperature depression and Diab et al. (2008) detected numerous loci in a durum wheat population. The only other crop where this trait appears to have been genetically dissected is rice (Anitha et al. 2008; Liu et al. 2005). The canopy temperature QTL detected in the present study were generally independent of ear emergence time (except for *Q.Ctve-g.aww-2D* and *Q.Ctgf.aww-2D*) and most have not been previously reported. *Q.Ctgf.aww-1B*, *Q.Ctgf.aww-3B-2* and possibly *Q.Ctveg.aww-7A* were in similar locations to those reported by Pinto et al. (2010), suggesting the detection of robust, repeatable loci for this trait; with the locus on 3B having a large effect on grain yield as discussed above. With the exception of loci on chromosomes 3B and 5B, most canopy temperature loci did not co-locate with any other traits.

Understanding the key differences between the Mexican and southern Australian production environments

As highlighted above, there were only two common QTL detected between the present investigation and that of Bennett et al. (2012b), with one of these having opposite allele effects depending on the environment. There may be a range of reasons for this result, starting with the pattern of water availability. In the irrigated and heat-stressed experiments, water was non-limiting and as such, would have been unlike any of the ENV clusters identified by Bennett et al. (2012b). In the drought environment, the experiment was sown into a soil profile with 50 mm of irrigation applied, with two subsequent irrigation events of approximately 50 mm before the end of vegetative growth. No further irrigation was applied, inducing terminal drought from anthesis onwards, potentially rewarding those individuals in the doubled haploid population with deep rooting ability, that were able to follow moisture deep into the soil profile. However, in southern Australia, soil profiles are shallow, often with hostile subsoils, which would prevent such a deep rooting phenotype from being advantageous. There is evidence that a shallow, fibrous root system; better able to capture moisture from the small and increasingly infrequent rainfall events post-anthesis is evident in genotypes better adapted to this environment (Manschadi et al. 2008). This observation may also explain some of the difficulties in collecting meaningful canopy temperature data on the population in southern Australia (Bennett, unpublished data) and explain the lack of correlation between grain yield and canopy temperature under the drought treatment in the current study. Cloud cover and greater average wind speeds, which were also observed by Olivares-Villegas et al. (2007) as confounding effects, indicate that accurate measurement of this trait may be limited to specific environments.

Olivares-Villegas et al. (2007) studied Seri, Babax and a population from a cross between the two lines under the CIMMYT drought treatment and an experiment in southern Australia. Not only did the two parents have an inverse yield response to one another in the two environments, but also there was a change in the relative proportion of grain yield that these could account for under the two environments. In addition, these authors identified the longer growing season of southern Australia and differences in soil abiotic constraints as two key differences between the environments, which was also noted by Mathews et al. (2007) and Dreccer et al. (2007). The latter authors also suggested that the average temperature during flowering (see also Table 2 for a comparison of growing season temperatures) and evaporative demand of the two environments may further explain some of the difference in adaptation. Mathews et al. (2007) found that germplasm that performed well across southern Australia was the germplasm more adapted to CIMMYTs' Mega Environment (ME) 9, where facultative wheats are grown in semi-arid conditions. This suggests that this environment is poorly selected for, when utilising the CIMMYT managed drought environment. Brennan and Fox (1998) identified that South and Western Australian varieties had a lower coefficient of parentage from CIMMYT-derived germplasm, as well as relying on different CIMMYT parental germplasm, suggesting that north-west Mexico has historically been a poor selection environment for adaptation to southern Australia.

However, previous studies have found that CIMMYT-derived germplasm is best adapted to eastern and in particular, north-eastern Australia (Brennan and Quade 2006; Dreccer et al. 2007; Mathews et al. 2007), where crops are grown on deep, fertile soil profiles, at times relying on stored soil moisture for the majority of the growing season. Whilst it may not be feasible to conduct further field trials on the whole doubled haploid population, particularly because it is now well characterised in the target environment, a series of trait 'tails' could be selected, as discussed by Rebetzke et al. (2012), to validate the value of some of the QTL detected in the present study in this environment. Further validation could be through a backcrossing program to incorporate key QTL into differing; but otherwise well-adapted genetic backgrounds and develop pairs of lines differing only in the chromosomal regions of interest. This would provide breeders targeting the eastern Australian grain belt with confidence in the value and precise effect that the QTL identified in the present study could have in a marker-assisted selection program. Breeders in countries where the CIMMYT late sowing treatment correlates well (such as Iran, Iraq and regions of South Africa, Syria and India; Lillemo et al. 2005) could deploy a similar strategy to confirm the value of these loci.

Conclusion

We have genetically dissected yield performance under distinct drought and heat stress treatments, through QTL analysis and a number of morpho-physiological measurements. Whilst the performance of the population was not correlated with grain yield in the drought-stressed target population environment (South Australia), the QTL detected could have implications for breeders targeting environments where CIMMYT-derived material has traditionally shown good adaptation, such as in the north-eastern grain belt of Australia. As identified by previous studies in similar heat and drought-stressed environments, canopy temperature was able to explain a significant proportion of

variation in yield, particularly under the late sown heat treatment. The RAC875 allele at *Q.Yld.aww-3B-2* accounted for a very large proportion of the genetic variance for grain yield and was co-located with QTL for Kpsm, canopy temperature, early vigour, flag leaf width and peduncle length under heat stress and also had a positive effect on grain yield under the other two treatments. Priority should be given to fine mapping efforts, to identify potential candidate genes underlying this locus, with subsequent marker development giving breeders another tool to maintain or improve grain yield in regions around the world traditionally prone to heat stress. A second yield QTL on chromosome arm 3BS, detected under fully irrigated and heat stress conditions, again accounted for a relatively large proportion of the genetic variance and does not appear to have been previously reported. This QTL and those detected on linkage groups 3A, 3D, 4D and 7A, which were also associated with yield under stress conditions, warrant further physiological and genetic dissection to ultimately aid breeders' efforts to improve yield through marker-assisted selection.

References

Anitha R, Saranya G, Gomez SM, Biji KR, Kumar SS, Babu RC (2008) Identification of microsatellite markers associated with drought tolerance in rice (*Oryza sativa* L.) using bulked line analysis. Plant Arch 8:93–96

Babar MA, van Ginkel M, Klatt AR, Prasad B, Reynolds M (2006) The potential of using spectral reflectance indices to estimate yield in wheat grown under reduced irrigation. Euphytica 150:155–172

Bennett D, Izanloo A, Edwards J, Kuchel H, Chalmers K, Tester M, Reynolds M, Schnurbusch T, Langridge P (2012a) Identification of novel quantitative trait loci for days to ear emergence and flag leaf glaucousness in a bread wheat (*Triticum aestivum* L.) population adapted to southern Australian conditions. Theor Appl Genet 124:697–711

Bennett D, Izanloo A, Reynolds M, Kuchel H, Langridge P, Schnurbusch T (2012b) Genetic dissection of grain yield and physical grain quality in bread wheat (*Triticum aestivum* L.) under water limited environments. Theor Appl Genet. doi: 10.1007/s00122-012-1831-9

Blum A, Sinmena B, Mayer J, Golan G, Shpiler L (1994) Stem reserve mobilization supports wheat grain filling under heat stress. Aust J Plant Physiol 21:771–781

Bonnin I, Rousset M, Madur D, Sourdille P, Dupuits L, Brunel D, Goldringer I (2008) FT genome A and D polymorphisms are

associated with the variation of earliness components in hexaploid wheat. Theor Appl Genet 116:383–394

Braun HJ, Rajaram S, van Ginkel M (1996) CIMMYT's approach to breeding for wide adaptation. Euphytica 92:175–183

Brennan JP, Fox PN (1998) Impact of CIMMYT varieties on the genetic diversity of wheat in Australia, 1973–1993. Aust J Agric Res 49:175–178

Brennan JP, Quade KJ (2006) Evolving usage of materials from CIMMYT in developing Australian wheat varieties. Aust J Agric Res 57:947–952

Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? Plant Physiol 147:469–486

Coriton O, Barloy D, Huteau V, Lemoine J, Tanguy AM, Jahier J (2009) Assignment of *Aegilops variabilis* Eig chromosomes and translocations carrying resistance to nematodes in wheat. Genome 52:338–346

Cuthbert JL, Somers DJ, Brule-Babel AL, Brown PD, Crow GH (2008) Molecular mapping of quantitative trait loci for yield and yield components in spring wheat (*Triticum aestivum* L.). Theor Appl Genet 117:595–608

Diab AA, Kantety RV, Ozturk NZ, Benscher D, Nachit MM, Sorrells ME (2008) Drought-inducible genes and differentially expressed sequence tags associated with components of drought tolerance in durum wheat. Sci Res Essays 3:9–26

Dolferus R, Ji XM, Richards RA (2011) Abiotic stress and control of grain number in cereals. Plant Sci 181:331–341

Dreccer AF, Borgognone AG, Ogbonnaya FC, Trethowan RM, Winter B (2007) CIMMYT-selected derived synthetic bread wheats for rainfed environments: yield evaluation in Mexico and Australia. Field Crop Res 100:218–228

Fu JD, Yan YF, Kim MY, Lee SH, Lee BW (2011) Population-specific quantitative trait loci mapping for functional stay-green trait in rice (*Oryza sativa* L.). Genome 54:235–243

Gibson LR, Paulsen GM (1999) Yield components of wheat grown under high temperature stress during reproductive growth. Crop Sci 39:1841–1846

Gilmour AR, Cullis BR, Verbyla AP (1997) Accounting for natural and extraneaus variation in the analysis of field experiments. J Agric Biol Environ Stat 2:269–293

Griffiths S, Simmonds J, Leverington M, Wang YK, Fish L, Sayers L, Alibert L, Orford S, Wingen L, Snape J (2012) Meta-QTL analysis of the genetic control of crop height in elite European winter wheat germplasm. Mol Breed 29:159–171

Houshmand S, Knox RE, Clarke FR, Clarke JM (2007) Microsatellite markers flanking a stem solidness gene on chromosome 3BL in durum wheat. Mol Breed 20:261–270

Izanloo A, Condon AG, Langridge P, Tester M, Schnurbusch T (2008) Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. J Exp Bot 59:3327–3346

Kinoshita T, Ono N, Hayashi Y, Morimoto S, Nakamura S, Soda M, Kato Y, Ohnishi M, Nakano T, Inoue S, Shimazaki K (2011) FLOWERING LOCUS T regulates stomatal opening. Curr Biol 21:1232–1238

Kirigwi FM, Van Ginkel M, Brown-Guedira G, Gill BS, Paulsen GM, Fritz AK (2007) Markers associated with a QTL for grain yield in wheat under drought. Mol Breed 20:401–413

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

Lillemo M, van Ginkel M, Trethowan RM, Hernandez E, Crossa J (2005) Differential adaptation of CIMMYT bread wheat to global high temperature environments. Crop Sci 45:2443–2453

Liu HY, Zou GH, Liu GL, Hu SP, Li MS, Yu XQ, Mei HW, Luo LJ (2005) Correlation analysis and QTL identification for canopy

temperature, leaf water potential and spikelet fertility in rice under contrasting moisture regimes. Chin Sci Bull 50:317–326

Ma J, Yan GJ, Liu CJ (2012) Development of near-isogenic lines for a major QTL on 3BL conferring *Fusarium* crown rot resistance in hexaploid wheat. Euphytica 183:147–152

Manschadi AM, Hammer GL, Christopher JT, de Voil P (2008) Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.). Plant Soil 303:115–129

Mason RE, Mondal S, Beecher FW, Hays DB (2011) Genetic loci linking improved heat tolerance in wheat (*Triticum aestivum* L.) to lower leaf and spike temperatures under controlled conditions. Euphytica 180:181–194

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

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

McIntosh RA, Yamazaki Y, Dubcovsky J, Rogers J, Morris C, Somers DJ, Appels R, Devos KM (2008) Catalogue of gene symbols for wheat. In: 11th international wheat genetics symposium. Sydney University Press, Brisbane

Naruoka Y, Talbert LE, Lanning SP, Blake NK, Martin JM, Sherman JD (2011) Identification of quantitative trait loci for productive tiller number and its relationship to agronomic traits in spring wheat. Theor Appl Genet 123:1043–1053

Navakode S, Weidner A, Varshney RK, Lohwasser U, Scholz U, Roeder MS, Boerner A (2010) A Genetic Analysis of Aluminium Tolerance in Cereals. Agriculturae Conspectus Scientificus 75:191–196

Nourse SM, Elings A, Brewbaker JL (1999) Quantitative trait loci associated with lime-induced chlorosis in recombinant inbred lines of maize. Maydica 44:293–299

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

Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Welham SJ, Kane AF, Gilmour AR, Thompson R, Webster R, Tunnicliffe WG (2005) GenStat® release 8.2 reference manual. VSN International, Oxford

Pinto RS, Reynolds MP, Mathews KL, McIntyre CL, Olivares-Villegas JJ, Chapman SC (2010) Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theor Appl Genet 121:1001–1021

Rebetzke G, Condon A, Farquhar G, Appels R, Richards R (2008a) Quantitative trait loci for carbon isotope discrimination are repeatable across environments and wheat mapping populations. Theor Appl Genet 118:123–137

Rebetzke GJ, van Herwaarden AF, Jenkins C, Weiss M, Lewis D, Ruuska S, Tabe L, Fettell NA, Richards RA (2008b) Quantitative trait loci for water-soluble carbohydrates and associations with agronomic traits in wheat. Aust J Agric Res 59:891–905

Rebetzke G, Barrett-Lennard E, Bennett D, Biddulph B, Chenu K, Deery D, Mayer J, Moeller C, Rattey A (2012) A multi-site, Managed Environment Facility (MEF) for targeted trait and germplasm phenotyping. Funct Plant Biol (in review)

Reynolds M, Manes Y, Izanloo A, Langridge P (2009) Phenotyping approaches for physiological breeding and gene discovery in wheat. Ann Appl Biol 155:309–320

Richards RA, Rawson HM, Johnson DA (1986) Glaucousness in wheat—its development and effect on water use efficiency, gas exchange and photosynthetic tissue temperatures. Aust J Plant Physiol 13:465–473

Somers DJ, Isaac P, Edwards K (2004) A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor Appl Genet 109:1105–1114

Sun D, Feng Y, Wang H, Min D, Li X (2008) Polymorphism of wheat TaFT gene expressional sequence and the impact to flowering dates. Acta Agronomica Sinica 34:1953–1957

Yang J, Hu C, Hu H, Yu R, Xia Z, Ye X, Zhu J (2008) QTLNetwork: mapping and visualizing genetic architecture of complex traits in experimental populations. Bioinformatics 24:721–723

Zhang LY, Liu DC, Guo XL, Yang WL, Sun JZ, Wang DW, Zhang AM (2010) Genomic distribution of quantitative trait loci for yield and yield-related traits in common wheat. J Integr Plant Biol 52:996–1007