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ORIGINAL PAPER

Sponge and dough bread making: genetic and phenotypic relationships with wheat quality traits

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Abstract The genetic and phenotypic relationships among wheat quality predictors and sponge and dough bread making were evaluated in a population derived from a cross between an Australian cultivar 'Chara' and a Canadian cultivar 'Glenlea'. The genetic correlation across sites for sponge and dough loaf volume was high; however, phenotypic correlations across sites for loaf volume were relatively low compared with rheological tests. The large difference between sites was most likely due to temperature differences during grain development reflected in a decrease in the percentage of unextractable polymeric protein and mixing time. Predictive tests (mixograph, extensograph, protein content and composition, micro-zeleny and flour viscosity) showed inconsistent and generally poor correlations with end-product performance (baking volume and slice area) at both sites, with no single parameter being effective as a predictor of end-product performance. The difference in the relationships between genetic and phenotypic correlations highlights the requirement to develop alternative methods of selection for breeders and bakers in order to maximise both genetic gain and predictive assessment of grain quality.

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Introduction

The sponge and dough process is a globally significant bread making method, being the predominant bread making process in Central Europe, North and South East Asia and North America. A bulk fermentation method, the sponge and dough process involves two stages: first the creation of a light, airy 'sponge' through mixing a portion of the flour (usually two-thirds), water, yeast and improving agents. Before moving to the next stage, the 'dough' stage, the 'sponge' is given an extended pre-fermentation ranging anywhere from 1 to 4 h (Sluimer 2005) or even 16 h (Cauvain 1998). The remaining ingredients are mixed

into the 'sponge' and the resulting 'dough' is then divided, moulded and given a final fermentation before baking. This procedure contrasts with other single stage processes in which all the ingredients are mixed together from the start as with straight dough bulk fermentation, mechanical dough development (MDD), Chorleywood bread making process (CBP) and activated dough development (ADD) processes. Sponges are thought to afford several advantages to the bread making process, including the following: (1) yielding a more extensible dough; (2) activation of the yeast; (3) facilitating dough formation; (4) imparting superior aroma and favour; (5) generating silk-like, soft and regular crumb textures; and (6) making the sponge and dough process more forgiving of processing delays (Cauvain 1998; Pyler 1988; Sluimer 2005).

A relationship linking flour 'strength' and the most appropriate fermentation period employed with bulk fermented breads has traditionally been observed, with 'stronger' flours requiring longer fermentation periods (Cauvain 1998). The extended fermentation periods employed in sponge and dough bread making has thus seen a preference for stronger flours by bakers (Lever et al. 2005). Flour strength has long been closely related to protein content, with flours over 12% (Cauvain 1998) and 13% (Lever et al. 2005) being favoured in sponge and dough bread making.

The relationship between bread quality and flour protein was clearly demonstrated by Finney and Barmore's (1948) observations of a linear dependence of loaf volume on protein content, with the regression line slopes varying between the American hard winter and spring wheat cultivars studied. Protein quality is considered the major contributor to these differences in regression line slope. Several compositional features of flour proteins are postulated to contribute to protein quality (Tronsmo et al. 2003), including the composition of high- and low-molecular-weight glutenin subunits (Brett et al. 1993; Payne 1987; Shewry et al. 1992) and gliadins (Flæte and Uhlen 2003; Sontag-Strohm and Juuti 1997), the relative proportions of different protein classes (Kasarda 1989; Singh et al. 1990) and the molecular weight distribution of the glutenin polymers (Southan and MacRitchie 1999). Both direct (reconstitution) and indirect (correlative) studies demonstrate that the interactions between glutenin subunits are important in determining baking performance (Bekes et al. 2004; Cornish et al. 2006; Gupta et al. 1994).

Although a globally significant bread making method, the relationship between sponge and dough bread and flour quality has received little attention (Lever et al. 2005). The majority of bread and flour quality studies have been focused upon bulk fermentation straight dough, or rapid dough bread processes like MDD, CBP and ADD. Even though the baking response for some baking methods may be correlated, the relationship between baking and protein composition and functionality will vary (Preston et al. 1992) contributing to a complex relationship between baking methods. It follows that the genetic response will also be affected by the baking procedure. This was clearly shown by Magnus et al.'s (1997) observations that baking volume was influenced by fermentation time, mixing speed and genotype, with some cultivars having a maximum baking volume at short or no fermentation times, whereas others benefited from longer fermentation times (120 min). Therefore, it is not surprising that there are many inconsistencies in the literature regarding the relationship between polymeric protein in flour (using a variety of methodologies) and loaf volume for long fermentation methods (Bean et al. 1998; Gupta et al. 1992; Gupta et al. 1993; Sapirstein and Suchy 1999). These inconsistencies are likely to be due to a range of factors including genetics, differences in production environments and baking systems.

The lack of direct investigations into sponge and dough bread making quality and the difficulty in directly transferring quality knowledge between different baking processes requires further research into the baking quality of sponge and dough bread. As a contribution to this process a double-haploid population constituting 180 lines was created from two strong bread wheat cultivars: 'Chara' an Australia wheat, and 'Glenlea' a Canadian variety.

The objective of this paper was to assess the phenotypic and genetic relationships between sponge and dough baking traits and a range of physical and rheological parameters in this double-haploid population. In doing so, such relationships can be utilised by those directly or indirectly involved in wheat processing, such as researchers, breeders, and classification panels to improve genetic selection, wheat flour quality and end product performance. The separation of the genetic factors (away from extraneous variation) allows the identification of those quality traits most amenable to genetic improvement and the identification of those traits that may be utilised as indicators of the environmental (field and processing) effects on baking quality.

Materials and methods

Plant materials

A doubled haploid population (CxG DH) consisting of 180 individuals produced from a cross between the Australian cultivar 'Chara' (Beulah Sib//Pavon'S'/Condor) and the Canadian cultivar 'Glenlea' (UM-530/(MEX)CB-100) were produced from F1 wheat using a wheat × maize (*Zea mays* L.) production technique (Kammholz et al. 2001).

'Glenlea' has unique high dough strength and good sponge and dough baking characteristics (Bushuk 1980) while 'Chara' has intermediate dough strength and intermediate baking quality attributes. This cross is therefore of interest to study the genetic basis of dough rheology (dough strength and extensibility) and sponge and dough baking performance. Both parental cultivars possess the over expressed GluB1 'al' subunit ($Bx7^{OE}$) which has been shown to increase dough strength (Butow et al. 2003; Radovanovic et al. 2002; Vawser and Cornish 2004), but not to improve sponge and dough baking parameters (Mann et al. 2009).

Field

Field trialling was conducted at two sites, Griffith (southern NSW, 34°18′S, 146°02′E) in 2005 and Biloela (central Queensland, 25°24′S, 150°31′E) in 2006. Both field trials were partially replicated, randomised incomplete block designs incorporating the 180 DH lines and two parental lines into 250 plots arranged in a rectangular array of 10 rows by 25 columns. The plot sizes were 10 × 6 m rows at Griffith and 7 × 5 m rows at Biloela.

Milling

Grain samples from the Griffith and Biloela field sites were milled at the BRI Research Australia (2006 and 2007, respectively) using a laboratory scale Buhler MLU-202 pneumatic laboratory mill (Bühler AG, Uzwil, Switzerland) according to an optimised BRI method based on the AACC method (AACC Method 26-21A). Grain samples were conditioned to 14% moisture content prior to milling. All samples were milled according to a milling design based on a resolvable, partially replicated, incomplete block design with milling days the blocks. Each design consisted of 41 days with 7 samples per day for both sites.

Starch pasting properties

Flour pasting properties were analysed using a Rapid Visco Analyser (RVA) (Newport Scientific, NSW, Australia). A 2-g flour sample suspension was equilibrated at 50°C for 2 min, heated to 95°C over 6 min, maintained at temperature for 4 min, cooled to 50°C over 4 min and finally maintained at 50°C for 5 min. A constant rotating speed of the paddle (160 rpm) was used throughout the analysis. Samples were analysed according to an experimental design based on a partially replicated, incomplete block design with RVA test days as blocks. Each design consisted of 20 days with 16 samples per day.

NIR

The protein and moisture content of the grain and flour samples from the Griffith and Biloela sites were determined by near-infrared reflectance (NIR) using a FOSS NIRSystems model 5000 spinning cup spectrophotometer (FOSS NIRSystems Inc., Laurel, MD, USA) according to AACC Method 39-11 (1999). NIR data analysis was conducted using WinISI (FOSS NIRSystems Inc., Laurel, MD, USA). Samples were analysed in the same order as the milling design.

Single-kernel characterisation system (SKCS)

Hardness and average seed diameter for 300 seeds per sample were analysed using the Perten SKCS 4100 (Perten Instruments AB, Huddinge, Sweden) (AACC method 55-31). Samples were ordered according to their field position (column × row).

Water absorption

Optimal water absorption values were obtained using a prototype Micro Z-arm Mixer (Haraszi et al. 2004) and a micro-doughLAB (Newport Scientific Pty. Ltd., Warriewood NSW, Australia) (Bason et al. 2007). Both instruments only require 4 g of flour per mix and possess identical mixer bowl and impellor geometries. A separate design was utilised and involved a partially replicated, incomplete block design where days are blocks and replicates were split across machines. For the Micro Z-arm the same settings and protocols were used as those reported by Mann et al. (2009). The micro-doughLAB was operated under the same protocols as the Micro Z-arm, with a target torque of 115 mN m. Estimated values (used for baking) were calculated using best linear unbiased predictions (BLUPs) at the Griffith site (genetic effect treated as random effect) whilst at the Biloela site they were calculated using best linear unbiased estimates (BLUEs) where the genetic effect was treated as fixed component in the model. These estimates were used in conjunction with bakers' estimate for optimal dough consistency.

Mixograph

A small-scale 10 g Mixograph (National Manufacturing Co., Lincoln, NE, USA) was used to characterise the mixing properties of 252 flour samples according to a partially replicated, randomised incomplete block design that comprised of 18 mixing days, with 14 mixes per day where days were blocks. Doughs were prepared with 2% salt (Bakers %) and using the water absorption level determined and statistically corrected measurements

conducted with the Z-arm mixers. Each sample formulation was adjusted to yield a constant dough mass of 17.5 g. Data collection and analysis was conducted with MixSmart version 1.0.438 (AEW Consulting, Lincoln, NE, USA) software with subsequent data analysis focusing on the following six parameters: Peak resistance (Pr, torque, %); Mixing time (Mt, min); Time to maximum bandwidth (Tmbw, min); Maximum bandwidth (Mbw, torque, %); Resistance at breakdown after 8 min (Rbd8, torque, %); and Bandwidth at breakdown after 8 min (Bwbd8, torque, %). The Resistance and Bandwidth breakdown values are the ratio of the difference between the peak and value at 8 min after peak divided by the peak value, expressed as a percentage.

Uniaxial extension testing

Small-scale extension testing (10 g) of 252 flour samples was carried out according to a partially replicated, randomised and spatially optimised incomplete block design (where days were blocks) that was comprised of 12 extensions per day for 21 days. Doughs were mixed on the 10 g Mixograph mixer using the procedure described earlier to peak dough development as determined from the first Mixograph mixing step. Immediately after mixing to peak development ~15–17 g dough was loaded into the Kieffer moulder, compressed, trimmed and given a coating of paraffin oil, then rested at 30°C and 90% relative humidity for 45 min before extension testing. Extensions at 1 cm/s were carried out with five or six replicates per sample on a TA.XTplus Texture Analyser (Stable Micro Systems Ltd, Surrey, UK) with the Kieffer dough & gluten micro-extensibility rig (Kieffer et al. 1998). The maximum resistance (R_{max}) and extension at R_{max} (extensibility, Ext) were recorded using Texture Exponent 32 version 4.0.12.0 software (Smewing 1995).

Size exclusion high performance liquid chromatography (SE-HPLC)

SE-HPLC was carried out on all lines according to a partially replicated incomplete block design where each sample was run in duplicate and the mean analysed for each replicate.

Twenty-five milligrams of each flour sample was extracted using the procedure of Gupta et al. (1993) with some modifications (i.e. 50% acetonitrile + 0.05% trifluoracetic acid was used as solvent and mobile phase). Sonication was performed at 25% amplitude (9 W) using a Branson digital sonifier (model 450, Branson Ultrasonics Corp., Danbury, CT, USA) equipped with a tapered micro tip (end diameter of 3.2 mm). Supernatants were filtered through 0.45 mm PVDF filters prior to HPLC analysis. Protein extracts were subjected to HPLC using a 600 Waters Controller configured with a 486 Tunable Absorbance Detector and a 717plus Autosampler (Waters Corporation, Milford, USA). Twenty microlitres of each sample was injected into the system that was fitted with a Shodex Protein KW-804 (Showa Denko K.K., Tokyo, Japan) column. Flow rate was 1.00 ml/min. Detection was performed at 214 nm.

The unextractable polymeric protein (%UPP, Upp) is based on the differential solubilization of polymeric structures under mild and stringent conditions. This trait is strongly correlated with dough quality attributes, particularly strength. The percent polymeric protein in the flour (Ppf) is a measure of the total glutenin content in the flour in relation with total flour protein content.

Micro-Zeleny

An automated Sedicom System® (Lab-Intern Ltd, Budapest, Hungary) was used for determination of Zeleny values. The measurements were carried out according to the modified ICC Standard No. 116/1. The flour (0.4 g) sample was measured into a 15-ml cylinder and mixed with 4 mg/l bromophenol blue solution and shaken with the standard procedure for 5 min. After removing the cylinder from the shaker, 3.15 ml of 21.25% (v/v) lactic acid was added and then shaken for 10 min. The shaker was stopped, left to stand for 5 min and the volume of sediment (ml) was read using a digital reader. A fully replicated design was used with a mean of two measures per replicate.

Sponge and dough baking

Sponge and dough baking was conducted at BRI Research Ltd. using a two-step process (Lever et al. 2005; Mann et al. 2009). In the first step, the sponge is made by mixing part of the total flour (200 g) with water, yeast, and yeast food at 60 rpm. The sponge is then allowed to ferment for 4 h. In the second step, the sponge is incorporated with the rest of the flour (100 g), water and other ingredients to make dough and mixed at 100 rpm. Both the sponge and the dough were mixed in a 300 g Farinograph bowl (Brabender GmbH & Co., Duisburg, Germany). The water addition rate was based on the water absorption described earlier and adjusted (if required) during the sponge stage, using Easymix peak height and baker's visual assessment.

Each dough sample produced two high top pup loaves and 1 square pup loaf. Loaf volume measurements were made on two high top loaves using rape seed displacement on the day of baking. The mean of the two loaves was used for analysis at the Griffith site and a single loaf was used at the Biloela site. Ovenspring (the increase in loaf volume experienced during baking) was estimated from the height

of the tear formed between the crust and the side of the loaf. Crumb structure was measured the day after baking using a C-Cell digital image analysis system (Calibre Control International, UK) on the square sandwich style pup loaf, with the slice from each loaf being derived from the same position, 45 mm from the end of the loaf. The following C-Cell parameters were utilised in the analysis: cell number, cell area, cell wall thickness and slice area.

Experimental design

As there are 180 doubled haploid (C × G DH) progeny from the experimental cross it is inefficient to utilise a fully replicated design at each of the experimental phases. In order to overcome this problem, Smith et al. (2006) suggest the use of a partially replicated experimental design approach (Cullis et al. 2006) and extend it to a multi-phase experiment setting. Initial field trials at Biloela and Griffith were established as partial replication (*p*-rep) designs and randomised using the DiGGer design generation programme (Coombes 2002). All designs were blocked in two directions before spatial optimisation. The *p*-rep field designs replicate a proportion *p* of the genotypes of interest leaving others unreplicated. Following Smith et al. (2006), the next phase uses a *p*-*q*-rep design to process the *p* replicated varieties from the field and duplicate a further proportion *q* of unreplicated varieties. If necessary, this pattern of duplication is repeated in additional phases. Smith et al. (2006) shows that this type of partial replication allows an appropriate stratification and estimation of the non-genetic variation at each phase of the experimentation and, more importantly, the appropriate estimation of the genetic variation using linear mixed model analysis.

Statistical analysis

Before proceeding with the computation of the phenotypic correlations, raw means of each genetic line were obtained for each trait across all phases of experimentation from both sites. This aggregation was chosen to ensure an appropriate calculation of the trait correlations between sites. The phenotypic correlation matrix was then computed from the complete matrix of trait means.

A multivariate mixed model analysis was used to estimate the genetic correlations between traits from all phases of experimentation associated with the two sites, Biloela and Griffith. Due to the large number of traits and phases in the data and computational limitations of software, the analysis was undertaken in two stages using the methodology of Smith et al. (2001a).

In the first stage, individual traits from each site were analysed while accounting for extraneous environmental variation and variation due to experimental design. As a preliminary, a baseline mixed model for each trait was fitted which consisted of a fixed component for the DH lines (i.e. genetic variation) as well as non-genetic variation partitioned corresponding to the phase of experimentation during which the trait was obtained. For example, non-genetic variation associated with baking volume, as measured in the baking phase, was represented by blocks in the field, between field plots, between milling days and between milling samples within milling days (i.e. milling residual variation), between baking days and between baking samples within baking days (i.e. baking residual variation). The baseline mixed model was then extended to include possible trends in the field, trends occurring across milling samples within milling days as well as trends across baking samples within baking days. A similar modelling procedure was followed for all individual traits at each site. Following Smith et al. (2001a), a mean and an appropriate weight for each genetic line was then extracted from the individual trait analyses and used in the second stage of multivariate analysis.

In the second stage, the genetic means for all traits across the two sites were analysed simultaneously using a multivariate mixed model based on a multiplicative factor-analytic model for the trait by genotype interaction (Smith et al. 2001b). Smith et al. (2001b) show that the factor-analytic model provides an efficient mechanism with which to approximate the unstructured correlation matrix for the trait by genotype interaction. Due to the number and variability of traits across the two sites, an analysis requiring a six-factor model was found to provide the best approximation for the genetic correlation matrix.

All statistical modelling analysis was undertaken using the flexible mixed modelling software ASReml-R (see Butler et al. (2009)) that has been developed as an R package (R Development Core Team 2009).

Results

Trait summaries

The mean, range and heritability for all phenotypes are presented in Table 1. Heritability estimates for most traits were moderate to high (0.41–0.97) and consistent between sites. The exception was maximum bandwidth, which was low (0.14 and 0.2) at both sites. There are some notable differences in results at the two sites across all phases of the experimental design. The first phase of the experiment was the field, where the quality based parameters seed diameter, seed hardness and grain protein were measured. Both grain protein and grain hardness were different between sites with the Griffith site having higher protein and slightly softer grain.

Table 1 The mean, medium, range, heritability and coefficient of variation (CV) for the phenotypes measured grouped by experimental phase for the Griffith and Biloela sites

Phase/instrument	Trait	Abbreviation	Mean		Median		Range		Heritability		CV	
			Griffith	Biloela	Griffith	Biloela	Griffith	Biloela	Griffith	Biloela	Griffith	Biloela
Field	Grain yield (kg)*	Yld	5.62	3.49	5.77	3.50	0.62–9.06	1.47–5.22	0.58	0.93	28.43	23.18
	Hardness (au)	Skh	72.76	76.11	72.81	76.61	53.60–91.12	58.28–91.26	0.90	0.96	10.04	8.89
	Seed diameter (mm)	Sks	2.82	2.76	2.83	2.76	2.56–3.08	2.39–3.05	0.72	0.97	4.07	4.14
	Grain protein (%)	Gpc	14.83	13.92	14.70	13.80	12.6–19.0	11.70–17.90	0.90	0.93	7.18	7.71
Milling	Flour protein (%)	Fpc	13.44	12.58	13.35	12.42	10.86–17.75	10.09–16.59	0.89	0.94	8.46	8.60
	Milling yield (%)	Myld	76.87	72.89	77.10	73.10	72.50–80.20	66.20–77.30	0.73	0.67	1.63	2.88
Z-arm	Water absorption (%)	Wa	59.51	59.53	59.41	59.70	53.60–67.32	53.30–64.00	0.85	0.55	3.84	2.94
Mixograph	Peak resistance (% torque)	Pr	69.68	71.66	69.69	71.75	60.85–76.76	63.58–80.5	0.69	0.72	4.11	4.73
	Mixing time (min)	Mt	5.76	5.26	5.46	4.94	3.08–11.42	2.96–9.59	0.89	0.71	30.28	24.79
	Time to maximum badwidth (au)	Tmbw	4.13	3.91	3.81	3.40	1.45–9.01	1.40–13.88	0.79	0.65	37.03	36.41
	Maximum bandwidth (au)	Mbw	58.79	52.74	58.80	52.70	48.36–69.06	41.38–61.31	0.14	0.20	6.69	7.35
	Resistance at breakdown (8 min)	(auR)bd8	0.20	0.19	0.20	0.19	0.10–0.31	0.10–0.31	0.87	0.83	19.05	19.72
	Bandwidth at breakdown (8 min)	(auB)wbd8	0.64	0.53	0.70	0.51	0.08–0.91	0.06–0.85	0.67	0.80	32.91	43.52
Extensograph	Maximum resistance (N)	R_{max}	0.46	0.50	0.45	0.45	0.21–0.84	0.21–0.93	0.88	0.78	25.85	27.82
	Extensibility (mm)	Ext	132.80	129.40	134.60	129.10	71.15–184.20	66.12–181.70	0.92	0.81	16.14	15.57
RVA	Peak viscosity (au)	Rpv	199.80	182.30	199.80	181.00	137.80–236.10	147.90–217.60	0.64	0.93	6.74	7.43
	Time to peak viscosity (min)	Rtpv	8.77	8.92	8.73	8.93	8.33–9.20	8.47–9.33	0.88	0.88	1.61	1.85
	Final viscosity (au)	Rfv	256.20	253.30	256.80	254.10	166.80–292.90	186.90–291.80	0.65	0.93	7.03	6.14
Micro-zeleny	Sedimentation volume (au)	Zsv	4.16	NA	4.05	NA	2.95–7.54	NA	0.88	NA	15.13	NA
HPLC	Polymeric protein in flour	Ppf	6.86	6.55	6.82	6.51	5.77–9.00	5.39–8.44	0.88	0.87	7.76	8.10
	% Unextracted polymeric protein	Upp	55.56	53.52	55.35	53.41	47.40–64.24	44.91–61.66	0.93	0.95	5.89	6.83
Baking-hightop	Oven spring (cm)#	Bosp	1.51	1.82	1.00	2.00	0–6.00	0–7.00	0.50	0.41	97.44	73.35
	Baking volume (cc)#	Bvol	718.80	686.20	722.50	690.00	592.50–830.00	570.00–840.00	0.72	0.70	5.95	5.36
Baking-C-cell	Slice area (au)	Csa	2.64	2.48	2.65	2.50	2.16–3.03	1.93–3.06	0.72	0.61	6.10	6.42
	Cell wall thickness (au)	Ccwth	2.93	2.93	2.92	2.93	2.61–3.26	2.55–3.27	0.85	0.63	5.57	5.32
	Cell number	Cno	4110	3886	4120	3861	2753–5878	2563–5686	0.81	0.60	17.83	17.03
	Average cell area (au)	Csize	50.49	49.99	50.60	50.10	47.80–53.00	46.90–52.40	0.71	0.61	2.28	2.14

* indicates different plot sizes, # mean of two samples per replicate at Griffith, one sample per replicate at Biloela

The second phase was the milling, in which flour protein and milling yield were recorded. Flour protein differences were consistent with the grain protein content, while milling yield was four per cent higher at the site with lower hardness, Griffith.

The third phase of the experimental design involves the remainder of the traits. Rheological (mixograph and extensograph), RVA and HPLC traits showed consistent heritability estimates across sites. However, differences were observed between the mean values for a number of traits, including higher values for mixing time, bandwidth at breakdown, peak viscosity and %UPP at the Griffith site, whilst higher R_{max} values were recorded at the Biloela site.

It is interesting to note the difference in R_{max} and %UPP between sites. Typically, %UPP is associated with increased strength. Biloela samples showed a decrease in %UPP along with the anticipated decrease in mixing time; however, R_{max} increased. One possible explanation may be the differences observed in daily temperatures throughout grain filling at the two sites. Figure 1 shows the difference in the maximum temperature at the two site years (Griffith 2005 and Biloela 2006) between 1 September and 30 November, highlighting the hotter conditions at the Biloela site during the grain filling period.

Large differences between heritability estimates for quality-related traits were observed between sites, including, water absorption, ovenspring and C-Cell parameters. The Griffith site had consistently higher heritability estimates for these traits indicating the possibility of a larger environmental effect on these traits at the Biloela site. It should be noted that the 'sponge' water was estimated differently for flour derived from both sites (as described in the materials and methods), but the dough water estimation was conducted in the same manner. It is not expected that this estimation would have had any impact on baking parameters given that the dough water was adjusted by the baker to ensure an optimal dough consistency. For all baking traits, with the exception of ovenspring, the Griffith site had higher mean values.

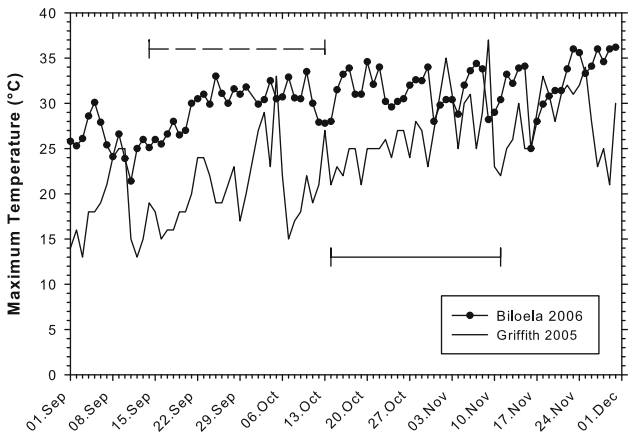

Fig. 1 The maximum daily temperatures for the Griffith (2005) and Biloela (2006) sites between 1 September and 30 November. Griffith site was sown 27 July, flowered approximately mid October and harvested 20 December. Biloela site was sown 26 April, flowered approximately early September and harvested 26 October. *Horizontal bars* indicate the period of grain filling for Griffith (*unbroken line*) and Biloela (*dashed line*)

Phenotypic correlations

The table of phenotypic correlations is provided as supplementary material (Table S1) and a heat map is presented in Fig. 2. The heat map displays colour gradations indicating the various correlations from strong negative correlations (red) through to strong positive correlations (blue). Correlations of <0.2 have been coded white to aid in contrasting the relationships.

Phenotypic correlations within sites

The phenotypic correlations between baking volume and predictive tests within sites were relatively low and inconsistent between sites. At the Biloela site (Fig. 2a) significant positive correlations associated with baking volume were identified with seed diameter, bandwidth and resistance at breakdown whilst significant negative correlations were identified with milling yield, mixing time and maximum bandwidth. This was in contrast with the phenotypic correlations at the Griffith site (Fig. 2b) where mixing time, time to maximum bandwidth and R_{max} displayed significant positive correlations as did %UPP. The only trait that had a significant negative correlation with baking volume at the Griffith site was extensibility. Notably, given the importance in grain price determination, the relationship between protein content and baking volume was low at both sites. This relationship is displayed in Fig. 3.

Phenotypic correlations between baking volume and C-Cell slice area were high and so for the purposes of this discussion these traits are considered essentially equivalent traits. However, the relationship between baking volume/slice area with the individual C-Cell parameters varied particularly between sites; cell number had the highest correlation with baking volume (0.70 and 0.39) at Griffith and Biloela, respectively. An interesting relationship was observed between %UPP and the C-Cell parameters, cell number, cell size and cell wall thickness. All traits were significantly correlated with %UPP, cell number high and positively correlated and cell size and cell wall thickness negatively correlated. These relationships were consistent across sites; however, higher correlations were observed at the Griffith site.

A very significant correlation with baking volume/slice area and ovenspring was observed for both sites, with the correlations being higher at the Griffith site.

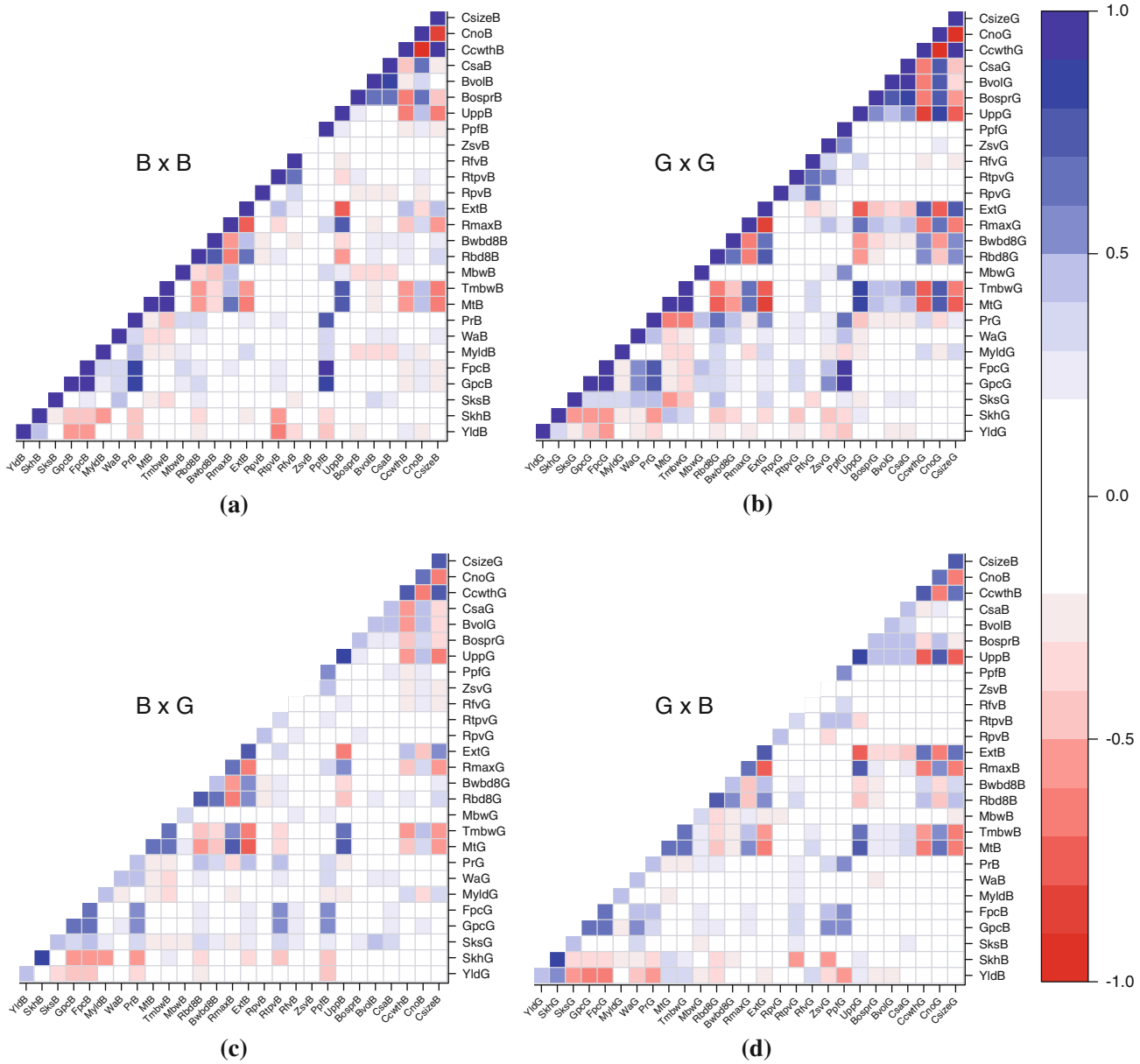

Fig. 2 Phenotypic correlation table for 26 measured traits for both Griffith and Biloela sites displayed as four separate heat maps: within site correlations for Biloela (**a**), and Griffith (**b**), and between site correlations (**c**) and (**d**). *Red colour* represents a strong negative correlation and *blue* a strong positive correlation. To improve contrast correlations between −0.2 and 0.2 have been coloured *white*. Trait abbreviations as per those listed in Table 1, with the last character indicating the measurement site (*G* Griffith, *B* Bileola). See Table 1 for abbreviations

Phenotypic correlations between sites

The phenotypic correlations between sites for all traits (Fig. 2c, d) with the exception of final paste viscosity were significant (Table S1) and varied from moderate to very high. The field traits seed hardness and grain protein displayed very high correlations between sites, whilst seed size and grain yield displayed a more moderate correlation. Milling yield had a moderate correlation between sites, while the final phase traits varied considerably.

With the exception of maximum bandwidth all rheological traits measured on both the mixograph and extensograph had moderate to high phenotypic correlations across sites. The phenotypic correlation for RVA parameters between sites was relatively low with the exception of peak viscosity which had a moderate correlation, suggesting that these traits were influenced strongly by their environments. The number of gas cells, cell size and cell wall thickness all had high phenotypic correlations between sites. However, ovenspring, baking volume

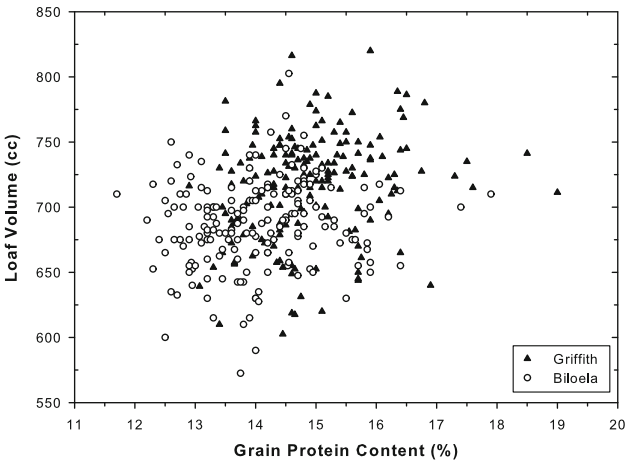

Fig. 3 Relationship between grain protein content and sponge and dough loaf volume for both the Griffith and Biloela sites

and slice area showed low moderate correlations between sites.

The correlation between sites for %UPP was relatively high (0.89); however, the mean values were lower at the Biloela site indicating the possibility of an environmental influence affecting %UPP.

Genetic correlations

The genetic correlations between baking traits were on average much higher than those for the phenotypic correlations. The full matrix of genetic correlations is supplied as supplementary material (Table S2), and Fig. 4 displays the genetic correlations as a heat map with colour gradations the same as for the phenotypic correlations.

Genetic correlations within sites

A striking difference in the table of genetic correlations is the difference between sites. At the Griffith site (Fig. 4b), strength-related traits such as $R_{max,}$ mixing time and %UPP had moderate to high genetic correlations with all baking traits. However, at the Biloela site (Fig. 4a), these relationships did not persist and there were only weak genetic correlations with any of the predictive measures and baking volume. The Biloela traits with the highest genetic correlations with baking volume were water absorption and time to peak viscosity. However, these correlations were relatively low ($\sim$0.4). Similar to the phenotypic correlations, protein content had a low (0.19–0.27) correlation with baking parameters for both sites.

Genetic correlations between sites

Genetic correlations for each trait across sites (Fig. 4c, d) were moderate to very high for all baking, rheological, protein, water absorption and HPLC traits. However, RVA traits, grain yield and seed size had relatively low correlations across sites indicating traits with a high environmental dependence.

Comparison of phenotypic and genetic correlations

We expected the comparison between genetic and phenotypic correlations to reflect heritability. Figure 5 displays the absolute differences between phenotypic and genetic correlations. It is clear that many of the major differences are due to a trait having a lower heritability at one or both sites. However, there are some interesting observations; the heat map clearly identifies a large difference observed between the phenotypic and genetic correlations for the baking and C-Cell parameters between sites (Fig. 5c, d). This is due to lower phenotypic correlations between sites but reasonably strong genetic correlations (Figs. 2c, d, 4c, d, respectively). Such a contrast reflects the difficulties of selecting for these traits using raw data alone and the importance of design parameters in partitioning the non-genetic variation across phases to accurately identify the genetic components for selection.

An additional feature of Fig. 5 is the large difference that occurred between a range of traits at the Griffith site and time to peak viscosity at the Biloela site (Fig. 5c, d). Time to peak viscosity at both sites had a high heritability (0.88) and hence it was not expected that it would have such a large change between phenotypic and genetic correlations. The phenotypic correlation between baking traits at Griffith and time to peak viscosity at Biloela was close to zero and the genetic correlations revealed moderate correlations with baking traits.

The other trait to show a large difference between genetic and phenotypic correlations was ovenspring. Importantly, ovenspring was moderately correlated to baking volume and C-Cell parameters at the phenotypic level but relatively highly correlated at the genetic level. This reflects that whilst this trait is influenced by environmental factors the genetic control is similar to baking traits.

Extensograph traits also showed a large difference between phenotypic and genetic correlations due mainly to much stronger genetic correlations compared with the phenotypic.

Discussion

Bread making is a multi-faceted process that is dependent upon both complex genetics and environmental influences (Williams et al. 2008). Assessing the bread making quality of wheat ultimately involves baking; however,

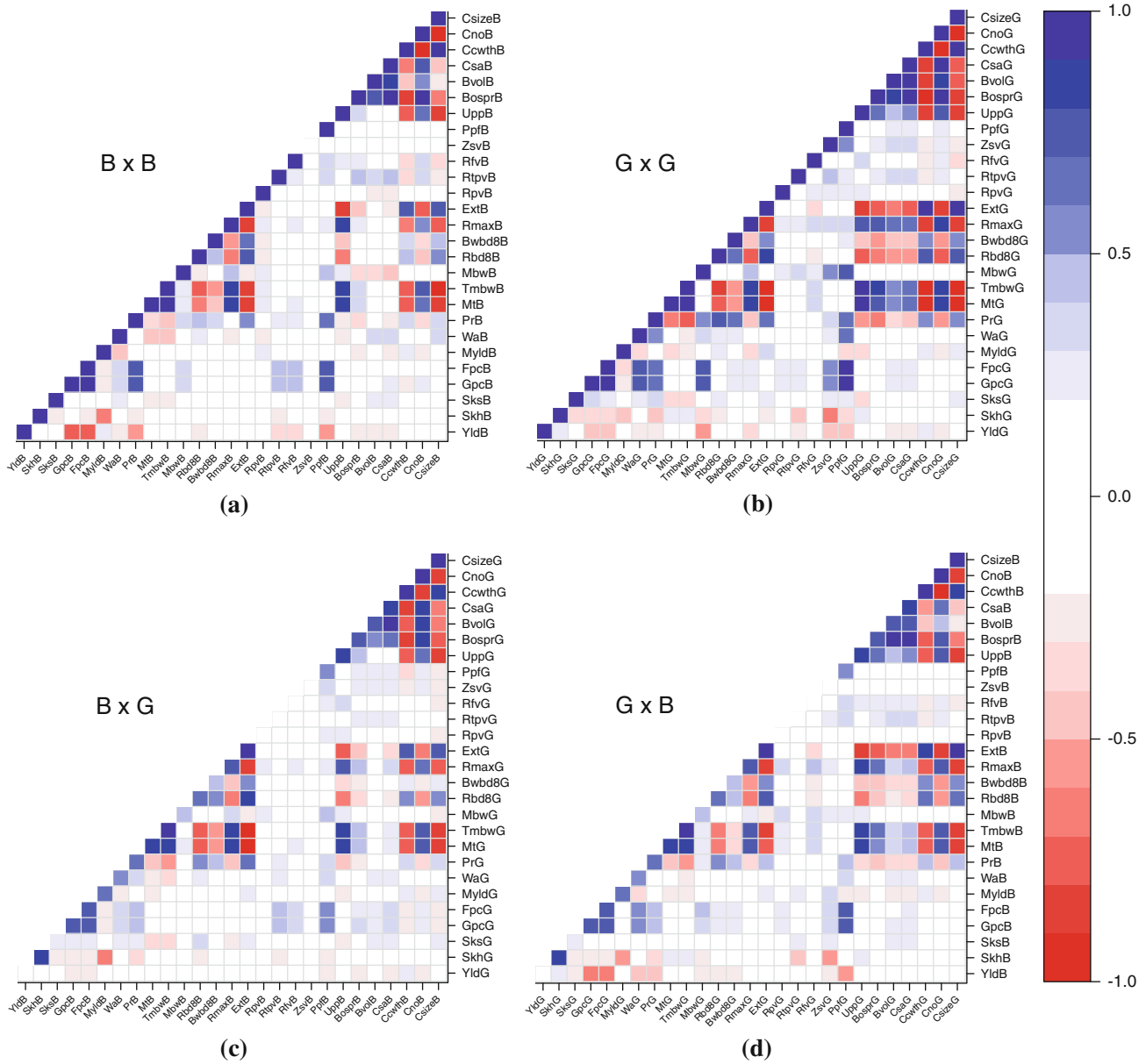

Fig. 4 Genotypic correlation table for 26 measured traits for both Griffith and Biloela sites displayed as four separate heat maps: within site correlations for Biloela (**a**), and Griffith (**b**), and between site correlations (**c**) and (**d**). *Red colour* represents a strong negative correlation and *blue* a strong positive correlation. To improve contrast correlations between −0.2 and 0.2 have been coloured *white*. Trait abbreviations as per those listed in Table 1, with the last character indicating the measurement site (*G* Griffith, *B* Bileola). See Table 1 for abbreviations

bake testing is expensive in terms of cost, time and resources. Furthermore, the requirement for large quantities of grain restricts this testing to later stages in the breeding process. To alleviate these demands, numerous predictive tests are utilised around the world as a proxy to end-product testing (Sluimer 2005). We have reported on 26 phenotypic traits across multiple phases of experimentation from two sites to determine phenotypic and genetic relationships between sponge and dough bread quality and a range of predictive traits. Separate assessment of genetic and phenotypic correlations provides a means of identifying those traits that are most amenable to genetic improvement and those most susceptible to environmental perturbations.

Genetic correlations were higher than phenotypic correlations across all traits. None of the predictive traits had high genetic or phenotypic correlations with baking volume at both sites. There were, however, very strong correlations between mixing time, R_{max}, %UPP and extensibility at the Griffith site. Similarly, the phenotypic

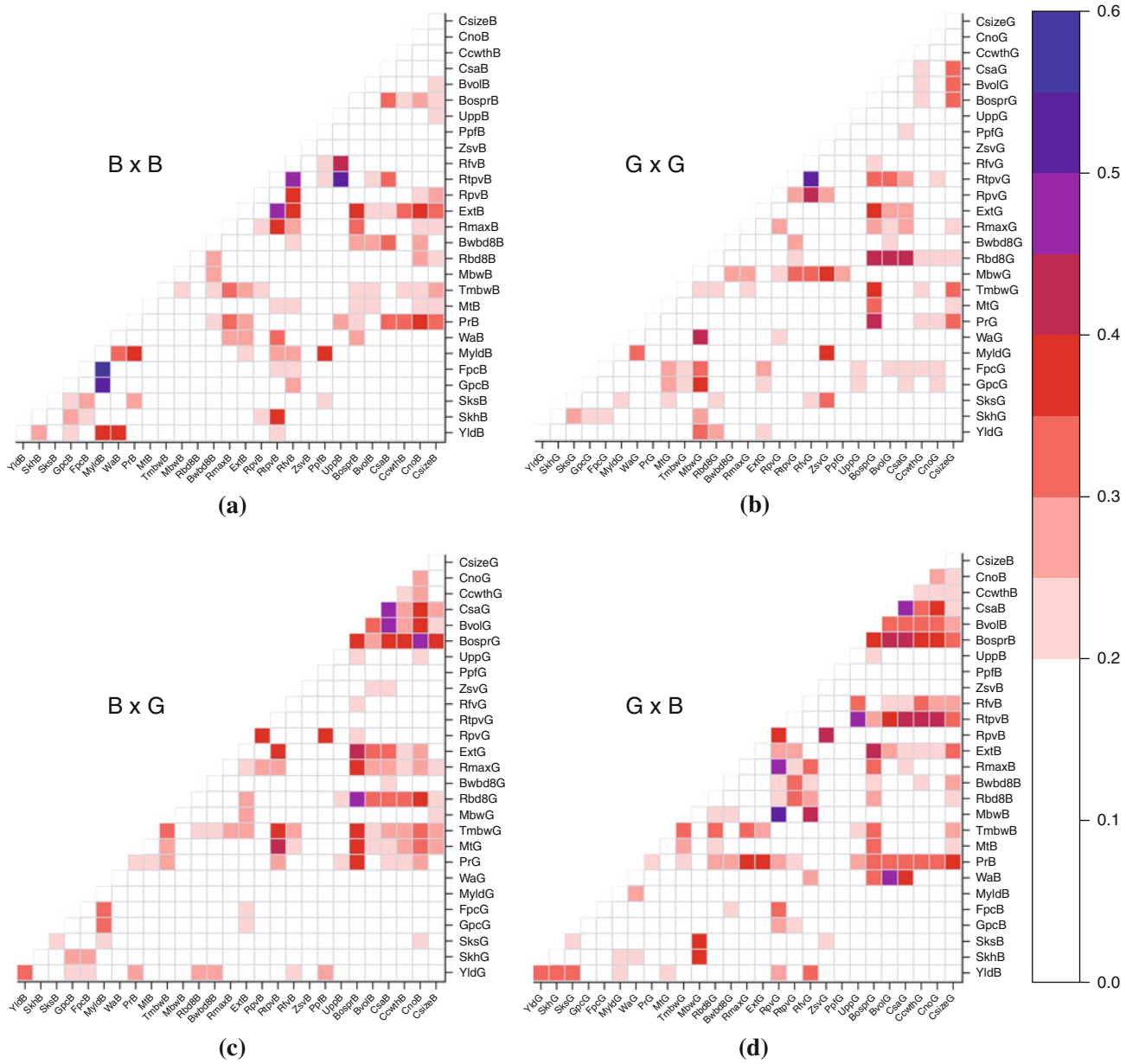

Fig. 5 Absolute differences between phenotypic and genotypic correlations for 26 measured traits for both Griffith and Biloela sites displayed as four separate heat maps: within site correlations for Biloela (**a**), and Griffith (**b**), and between site correlations (**c**) and (**d**). *Red colour* represents a strong negative correlation and *blue* a strong positive correlation. To improve contrast absolute differences <0.2 have been coloured *white*. Trait abbreviations as per those listed in Table 1, with the last character indicating the measurement site (*G* Griffith, *B* Bileola). See Table 1 for abbreviations

correlations between end-product performance and the predictive tests revealed relatively low correlations and inconsistent effects between environments. Mixing time was the only trait significantly correlated phenotypically at both sites, but were low to moderate correlations (−0.29 and 0.39) at Biloela (Fig. 2a) and Griffith (Fig. 2b), respectively. The opposing correlations are indicative of an environmental interaction on mixing time. It should be noted that mixing parameters are still a valuable tool for predicting the mixing performance in bakeries, but less useful for baking performance.

The contradictory evidence in this study regarding strength *per se* influencing sponge and dough baking is an area of much discussion within the breeding community (Lever et al. 2005). Mann et al. (2009) found a poor relationship between strength (R_{max}) and baking volume. In the current study the over expression of the GluB1 *al* (over expressed Bx7) subunit was fixed in the population.

The mechanistic difference between this subunit and baking quality has been highlighted by Mann et al. (2009). This may be due to an imbalance between high- and low-molecular-weight glutenin subunits within the polymer creating stronger dough without a positive effect on loaf volume. As this subunit was fixed within the population the only conceivable way that this subunit would be involved in altering baking performance is through either an epistatic interaction, expression differences or altered accumulation. A more comprehensive HPLC analysis is underway to characterise the protein composition.

The poor predictive power of protein content (Fig. 3) supports previous work in this area (Lever et al. 2005; Mann et al. 2009). Current market classifications pay a premium for higher protein content wheat grain. However, such a system may be indirectly restricting genetic progress achievable by breeders for the sponge and dough bread making market in Australia. In contrast to protein content, at the Griffith site %UPP was directly and highly correlated, both genetically and phenotypically, with baking.

Lever et al. (2005) found an association with flour swelling volume in a set of 30 genotypes grown at two sites. In our work the RVA was utilised to study this relationship further by using final viscosity as a substitute for flour swelling volume as they are known to be highly correlated (Konik-Rose et al. 2001). The phenotypic correlation between most of the RVA traits and baking volume was poor both within and across sites. Interestingly, time to peak viscosity was positively correlated to baking volume at both sites based on the genetic correlations. The heritability estimates are high for this trait even though the phenotypic correlations between sites are low to moderate. The mechanism behind the association of time to peak viscosity and baking volume is unknown; however, one possibility is a longer gelatinisation process provides additional time for the dough to expand during the ovenspring phase of baking before gelatinisation and 'setting' of the dough foam into the final bread crumb structure.

A significant difference between sites was observed between sponge and dough bread making performance along with other predictive tests (Table 1). However, the genetic correlations between sites for baking traits was high, indicating that the expression of the genetic components controlling baking were altered rather than alternative genetic mechanism or interactions being responsible; this is consistent with Williams et al. (2008).

One environmental factor observed was exposure to high daily maximum temperatures during grain filling at the Biloela site; with few days below 30°C post mid-September (Fig. 1). By contrast, maximum temperatures at the Griffith site were rarely above 30°C. Wardlaw et al. (2002) reported that strength (as indicated by mixing time) and flour quality measured by %UPP were dramatically reduced under chronic heat stress (>30°C) for prolonged periods, while Randall and Moss (1990) showed that R_{max} increases with heat stress. These reports concur with the findings that R_{max} was higher at the Biloela site while mixing time and %UPP were lower. Given different planting dates, varying flowering times and alternative kernel filling responses within the population, it is difficult to accurately quantify the effect of heat stress during grain filling on individual lines. While the effect of this postulated heat stress at Biloela did not have a catastrophic effect on the baking response, it will be useful in further studies to monitor daily temperatures during grain filling to further explore this influence.

The surprisingly low genetic correlations at the Biloela site between loaf volume and the objective measures of crumb structure, derived from C-Cell image analysis parameters, may indicate that the difference in overall loaf volume is manifested during fermentation. In this study, we did not measure final proof height and hence do not have a quantitative trait to explain the difference between proof height and baking volume other than that approximated by the ovenspring measure.

Ovenspring at the Biloela site was higher (on average) than at the Griffith site; hence, it may be concluded that the lower loaf volumes at the Biloela site were due to underperformance during fermentation compared with the Griffith site. An adequate level of strength may be required within the fermenting sponge to withstand the softening effects of the extended fermentation. The differential ovenspring and baking volume responses between the two sites suggest that different stability mechanisms may operate during fermentation and ovenspring. Dough expansion during fermentation and ovenspring involve very different time scales, in the order of hours for fermentation, and minutes for oven spring.

The complex rheological nature of wheat flour doughs leads to non-linear rheological responses that impede prediction of flour performance under dissimilar conditions (Dobraszczyk and Morgenstern 2003). The observations of differential fermentation and ovenspring behaviour of the Bileola and Griffith sites suggest that a potentially more fruitful avenue for the development of relevant alternatives to traditional predicative tests should focus upon use of temperatures (Dobraszczyk et al. 2003), formulations (Newberry et al. 2002) and conditions (Gandikota and MacRitchie 2005) that more closely resemble those experienced during sponge and dough bread making.

Elucidation of genetic and environmental factors influencing sponge and dough bread making also requires more diverse, relevant wheat populations. A constraining factor in this study (and others) is the limited diversity sampled and the inability to contrast more than two alleles in bi-parental populations. A more comprehensive comparison of allelic effects within existing germplasm and their behaviour under varied environments will require more

advanced genetic resources presently being developed (Cavanagh et al. 2008).

Conclusions

Correlation analysis of sponge and dough bread, grain and dough quality parameters revealed significant correlations between traits. The genetic correlations were consistently stronger than the phenotypic correlations, highlighting the importance of identifying predictive tests that are able to identify the manifestation of environmental influences on baking quality. The poor correlations between baking quality and predictive quality traits, such as protein content, extension and mixing parameters, mean that quality evaluation remains reliant upon costly and time-consuming bake testing. The development of rapid quality tests capable of substituting for sponge and dough baking in wheat breeding operations will require the identification of tests that more closely resemble the sponge and dough bread making process, which requires a better understanding of the fermentation step and the development of molecular markers for marker-assisted breeding.

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