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ORIGINAL PAPER

AB-QTL analysis in winter wheat: I. Synthetic hexaploid wheat (*T. turgidum* ssp. *dicoccoides* × *T. tauschii*) as a source of favourable alleles for milling and baking quality traits

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Abstract The advanced backcross QTL (AB-QTL) strategy was utilised to locate quantitative trait loci (QTLs) for baking quality traits in two BC_2F_3 populations of winter wheat. The backcrosses are derived from two German winter wheat cultivars, Batis and Zentos, and two synthetic, hexaploid wheat accessions, Syn022 and Syn086. The synthetics originate from hybridisations of wild emmer (*T. turgidum* spp. *dicoccoides*) and *T. tauschii*, rather than from durum wheat and *T. tauschii* and thus allowed for the first time to test for exotic QTL effects on wheat genomes A and B in addition to genome D. The investigated quality traits comprised hectolitre weight, grain hardness, flour yield Type 550, falling number, grain protein content, sedimentation volume and baking volume. One hundred and forty-nine SSR markers were applied to genotype a total of 400 BC_2F_3 lines. For QTL detection, a mixed-model ANOVA was conducted, including the effects DNA marker, BC_2F_3 line, environment and marker × environment interaction. Overall 38 QTLs significant for a marker main effect were detected. The exotic allele improved trait performance at 14 QTLs (36.8%), while the elite genotype contributed the favourable effect at 24 QTLs (63.2%). The favourable exotic alleles were mainly associated with grain protein content, though the greatest improvement of trait performance due to the exotic alleles was achieved for the traits falling number and sedimentation volume. At the QTL on chromosome 4B the exotic allele increased the falling number by 19.6% and at the QTL on chromosome 6D the exotic allele led to an increase of the sedimentation volume by 21.7%. The results indicate that synthetic wheat derived from wild emmer × *T. tauschii* carries favourable QTL alleles for baking quality traits, which might be useful for breeding improved wheat varieties by marker-assisted selection.

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Introduction

Wheat is one of the most important crops in the world. Together with rice and maize, it provides more than 60% of the calories and proteins for human nutrition (Gill et al. 2004). The most promising approach to increase agricultural productivity and to satisfy human needs in the future is the genetic improvement of crops, which requires a continuous allocation of new sources of genetic variation (Börner et al. 2000). The introgression of exotic genes that reduced plant height and increased disease resistance and viral resistance in wheat provided the foundation for the 'Green Revolution' and demonstrated the tremendous impact that genetic resources can have on plant production (Hoisington et al. 1999). More recently, the advanced backcross quantitative trait locus (AB-QTL) analysis was developed to identify and select new and beneficial QTL

alleles of exotic ancestors for introduction into elite gene pools (Tanksley and Nelson 1996; Xiao et al. 1996).

Hexaploid wheat (*Triticum aestivum*) has no hexaploid wild relatives, but synthetic hexaploid wheat is considered a promising source of exotic alleles for introgression into wheat (e.g. Colmer et al. 2006; Mujeeb-Kazi et al. 2006; Reynolds et al. 2007; Tadesse et al. 2007). Synthetic hexaploid wheat can be produced from interspecific crosses of tetraploid *T. turgidum* ssp. and diploid *T. tauschii*. Synthetics derived from cultivated durum (*T. turgidum* ssp. *durum*) have been used in QTL studies (Nelson et al. 1995; Mujeeb-Kazi et al. 1996; Börner et al. 2002; Huang et al. 2003, 2004; Nelson et al. 2006). Synthetics derived from tetraploid wild emmer (*T. turgidum* spp. *dicoccoides*) should also be useful, allowing detection of favourable alleles from both the tetraploid and diploid exotic parents. Wild emmer proved already as a donor of useful genetic variation for important agronomic traits in tetra- and hexaploid wheat, contributing to powdery mildew resistance, rust resistance, reduced plant height, early heading, increased number of spikes per plant, higher spike weight per plant, increased kernels per spikelet and higher yield (Peng et al. 1999, 2003; Rong et al. 2000). Wild emmer also proved to possess genes improving grain quality in wheat. Based on an initial QTL analysis in a cross between *T. turgidum* spp. *dicoccoides* and *T. turgidum* spp. *durum*, Uauy et al. (2006) cloned the *Gpc-B1* gene and showed that the wild emmer allele, which is a NAC transcription factor, accelerates senescence and, simultaneously, improves grain protein, zinc, and iron content in wheat.

The milling and baking quality of wheat involves a complex group of traits, which usually exhibit quantitative variation. Seven of these components are introduced here. (1) The hectolitre weight, also termed test weight, has long been used as an indicator of wheat quality (Hook 1984). In contrast to Marshall et al. (1986), who reported a strong positive correlation between hectolitre weight and milling yield, Hook (1984) found correlations between hectolitre weight and milling yield to be poor. Nevertheless, hectolitre weight may still be useful as a measurement of bulk density as an aid to grain storage and plant capacity (Hook 1984). (2) Grain hardness is one of the most important determinants of milling yield, having profound effects on milling, baking as well as end-use quality of bread wheat (Galande et al. 2001). Variation in grain hardness is mainly controlled by the *Ha* locus on the short arm of chromosome 5D in hexaploid wheat. Genes for puroindoline a (*Pina-D1*), puroindoline b (*Pinb-D1*) and grain softness related proteins (*Gsp-D1*) at the *Ha* locus have been associated with the expression of grain hardness (Tranquilli et al. 1999). The *Ha* locus was found to have a strong influence on milling yield (Campbell et al. 1999). Consistent with this result, Martin et al. (2001) and Nelson et al. (2006) both detected strong negative correlations between grain hardness and milling yield. (3) For economical reasons, flour yield or milling yield is also an important quality criterion (Marshall et al. 1986), which may be affected by field variation and by variation from the laboratory (Smith et al. 2001). (4) Falling number, an indicator for starch degradation, is highly correlated with α-amylase activity, due to pre-harvest sprouting, which can negatively influence the processing quality of the grains. (5) The grain protein content of wheat is important for an improved nutritional value and is one of the major factors affecting bread-making (Khan et al. 2000). The genetic components of the grain protein content have been extensively studied in bread wheat (Joppa et al. 1997; Prasad et al. 2003; Perretant et al. 2000). Although an increased yield often results in lower protein content via a dilution effect (Cox et al. 1995), Groos et al. (2003) detected no strong negative pleiotropic effect for grain protein content and yield, suggesting that it will be possible to improve these two economically important traits in the same breeding scheme. Consequently, QTLs which are involved in the control of grain protein content independent from the effects on grain yield should be identified in order to manipulate protein content (Kuchel et al. 2006). Flour proteins, particularly, glutenins and gliadins are important determinants of baking quality (Finney et al. 1987). The *Glu-1* loci, coding for high molecular weight glutenins on chromosomes 1A, 1B and 1D play an important role in this respect. (6) Sedimentation volume is an index widely used to evaluate flour quality in durum and bread wheat. Significant associations between sedimentation volume and endosperm proteins like gliadins, and high molecular weight and low molecular weight glutenin subunits have been reported (Blanco et al. 1998). (7) Baking volume or loaf volume is a major wheat quality trait since it determines the capacity of the dough to produce a loaf. The baking volume is a function of both the quantity and quality of flour proteins. These proteins are mainly represented by glutenins, considered to control dough strength, and elasticity and gliadins, considered to control dough viscosity and extensibility (Nelson et al. 2006).

In the present study seven quality traits were investigated in two winter wheat populations consisting of 400 BC_2F_3 lines derived from two German winter wheat cultivars and two synthetic, hexaploid wheat accessions, Syn022 and Syn086. The synthetic wheat accessions were selected from hybridisation of wild emmer (*T. turgidum* spp. *dicoccoides*) and *T. tauschii* and, thus, served as the donors of wild species alleles for all three wheat genomes, A, B and D. The objective of this study was to locate quantitative trait loci for quality traits in BC_2F_3 lines carrying alleles from unadapted genetic resources and, in addition, to assess the potential of the exotic QTL alleles to improve quality traits of two elite wheat cultivars.

Materials and methods

Plant material

The development of two advanced backcross (AB) populations was conducted according to the advanced backcross strategy of Tanksley and Nelson (1996). The crosses derived from two German winter wheat cultivars (*Triticum aestivum* L.) and two synthetic, hexaploid wheat accessions. The German winter wheat cultivars Batis and Zentos, obtained from the breeders Fr. Strube Saatzucht (Batis) and Saatzucht Hadmersleben (Zentos), were selected as high performing varieties. The synthetic wheat accessions Syn022 and Syn086, kindly provided by Dr. W. Lange, Wageningen (Lange and Jochemsen 1992a, b), were developed from hybridization of *T. turgidum* spp. *dicoccoides* and *T. tauschii*. In the following, the two AB populations are designated as B22 (Batis × Syn022) and Z86 (Zentos × Syn086). In the initial crosses, Batis and Zentos, were used as the female parents and the exotic accessions were used as the male parents. A single F_1 plant (maternal) was backcrossed to the respective cultivar (paternal). The BC_1F_1 plants were backcrossed a second time with the two cultivars, followed by two cycles of selfing. The resulting AB populations comprised 250 and 150 BC_2F_3 lines for B22 and Z86, respectively. In B22, the AB lines are derived from 22 BC_1F_1 and 144 BC_2F_1 plants. In Z86, the AB lines are derived from 17 BC_1F_1 and 95 BC_2F_1 plants. In the first backcross, we tried to achieve a maximum number of offspring to avoid genetic drift. In the second backross and in the subsequent selfing generations, we sampled 1–7 offspring per parent line to keep the population fairly unbiased. The resulting seeds of each BC_2F_3 plant were bulk propagated in field plots ($BC_2F_{3:4}$). In the following two years the $BC_2F_{3:5}$ and the $BC_2F_{3:6}$ lines were grown in the field for phenotypic evaluation.

Molecular characterisation

DNA from parental and AB lines was isolated according to a modified procedure of Plaschke et al. (1995). The DNA was isolated from foliage at the BBCH 29 stage (Bleiholder et al. 1991) collected in bulk from single leaves from ten different plants per $BC_2F_{3:4}$ line grown in the field.

A total of 488 SSR markers selected for an even coverage of all three wheat genomes were utilised in a polymorphism survey of all four parents of the two crosses. The following prefixes of SSR names indicate the published sources from which the primer sequence information was taken: *BARC*, Song et al. (2005); *CFA* and *CFD*, Guyomarc'h et al. (2002) and http://www.wheat.pw.usda.gov; *GDM*, Pestsova et al. (2000); *GWM*, Röder et al. (1998) and *WMC*, Gupta et al. (2002) and http://www.wheat.pw.usda.gov. The chromosomal positions of the SSR markers were obtained from the consensus map of Somers et al. (2004) or estimated from flanking markers of the genetic map of R. Ward (2003, http://www.scabusa.org). The genotyped markers were assigned to bins according to information by Sourdille et al. (2004).

For DNA amplification of SSRs the tailed primer method was applied (von Korff et al. 2004). The PCR reaction was prepared including an IRD-labelled M13 primer, which flagged the PCR product after fusion during the amplification process. The PCR reaction was carried out in 20 µl final volume reactions containing 5 µl of DNA template (approx. 100 ng), 0.5 µl of Taq polymerase (5 U/µl), 2 µl of 10× PCR-buffer (500 mM KCl, 100 mM Tris–HCl, 1% Triton X-100, pH = 9.0), 1 µl $MgCl_2$ (25 mM), 0.75 µl of dNTP (2 mM), 0.2 µl of the forward and reverse oligonucleotide primers (10 µM) and 0.5 µl of the M13 universal forward primer (1 µM). The M13 primer was labelled with either IRD700 or IRD800 at the 5′ end for visualisation. The amplification profile started with 10 cycles of denaturing at 94°C for 1 min, annealing at 64–55°C (touch-down PCR) for 1 min and extension for 1 min at 72°C followed by 30 cycles of 1 min at 94°C, 1 min at 55°C and 1 min at 72°C with a final extension step at 72°C for 5 min. The amplified DNA fragments were separated in an electrophoresis using a Li-Cor DNA Sequencer 4200 (LI-COR, Bad Homburg) as an automated DNA detection device.

Phenotypic evaluation

The BC_2F_3 populations B22 and Z86 were grown under field conditions at a total of five locations in the seasons 2004 (04, $BC_2F_{3:5}$) and 2005 (05, $BC_2F_{3:6}$). The test locations were the Research Station Dikopshof of the University of Bonn (D04, D05, West Germany), and the breeders' experimental stations in Adenstedt (A04, A05, Limagrain-Nickerson, Central Germany), Jerxheim (J04, Fr. Strube Saatzucht, Central Germany), Morgenrot (M04, Saatzucht Josef Breun, East Germany) and Wohlde (W04, W05, Lochow-Petkus, North Germany). In each test environment, the AB lines and their recurrent parents were grown in a single randomised block, containing one plot of each AB line, 20 plots of Batis and 10 plots of Zentos. The amount of nitrogen fertiliser applied (140–220 kg N/ha) was determined according to the N_{min} content of the soil. Net plot sizes (4.5–6.3 m^2), seed density (310–360 kernels/m^2) and field management were in accordance with local practice. Grain was harvested with a plot harvester at maturity. The evaluation of quality traits was carried out at the Federal Research Centre for Nutrition and Food (BfEL), Detmold. Hectolitre weight was measured on grain samples from all eight environments. Other quality traits

were measured on grain samples from only the J04 and W04 environments as listed in Table 1.

Statistical analyses

The statistical analyses were carried out with SAS version 9.1 (SAS Institute 2004). For QTL detection, the following mixed hierarchical model described by von Korff et al. (2006) was applied:

$$Y_{ijkl} = \mu + M_i + L_j(M_i) + E_k + M_i \times E_k + \varepsilon_{l(ijk)},$$

where μ is the general mean, M_i is the fixed effect of the i-th marker genotype, $L_j(M_i)$ is the random effect of the j-th BC_2F_3 line nested in the i-th marker genotype, E_k is the random effect of the k-th environment, $M_i \times E_k$ is the random interaction effect of the i-th marker genotype with the k-th environment and $\varepsilon_{l(jik)}$ is the error of Y_{ijkl}. At each marker locus only the homozygous genotypes were included in the calculation, because according to Pillen et al. (2003), the repeated selfing of heterozygous genotypes leads to a mix of both homozygous genotypes in the derived $BC_2F_{3:5}$ and $BC_2F_{3:6}$ field plots, resulting in a false estimate of the performance of true heterozygous genotypes. Marker main effects were accepted as putative QTLs, if the P value was less than 0.001. Markers detecting the same significant effect were combined to a single QTL, if linked with ≤20 cM (Pillen et al. 2003). The relative performance of the homozygous exotic genotype (RP[aa]) was calculated as described by Pillen et al. (2003). The genetic variance explained by a marker (R^2_M) was calculated as described by von Korff et al. (2006). The proportion of the exotic genome (P[exot]) was calculated as the percentage of exotic alleles present in a single BC_2F_3 line according to the formula:

$$P[exot] = (2[aa] + [Aa])/(2([AA] + [Aa] + [aa]))$$

where [AA], [Aa] and [aa] represent the frequencies of the homozygous elite, the heterozygous and the homozygous exotic genotypes, calculated from all investigated marker loci. Deviations of the observed ratio of elite to heterozygous to exotic genotype (AA:Aa:aa) from the expected ratio of 84.38:6.25:9.38 in a BC_2F_3 generation were calculated by Chi-square tests.

Data archiving

The QTL data will be archived on the GrainGenes website (http://www.wheat.pw.usda).

Results

Marker data

Of 163 SSR markers selected for genotyping, genomic regions at 5 (B22) and 13 (Z86) SSR markers revealed fewer than five individuals, which carry the homozygous exotic genotype. These markers were excluded from the statistical analyses, since the numbers of exotic genotypes were considered too low for QTL detection. Overall, one (B22) and five (Z86) SSR markers were assigned to more than one chromosome and were excluded as well. In all, 149 SSRs were subjected to the statistical analyses. Segregation distortion was recorded at $P < 0.05$ for 19 (B22) and 27 (Z86) SSR markers. For B22, eight and six markers revealed an excess of the exotic and elite homozygous classes, respectively. In Z86, 12 and 10 SSR markers revealed an excess of the exotic and elite homozygous

Table 1 List of seven traits measured in populations B22 and Z86 in up to eight environments

Abbr.	Trait (Units)	Method of measurement[a]	Environment[b]
HLW	Hectolitre weight (= test weight) (kg/hl)	Weight of 100 l of wheat, calculated from a sample of 250 ml by a hectolitre weight-measuring funnel (Nr. 6218, Wilhelm Jäger, Königswinter, Germany)	A04, A05, D04, D05, J04, M04 (B22), W04, W05
GH	Grain hardness (-)	Near infrared reflectance (NIR), measured from whole grain groats	J04, W04
FY_{550}	Flour yield, Type 550 (=milling yield) (%)	Percentage of flour recovered from milling 2000 g of grain. Flour yield type 550 is adjusted to a mineral content of 510–630 mg per 100 g flour	J04, W04
FN	Falling number (s)	ICC Standard No.107/1 according to Hagberg-Perten	J04, W04
GPC	Grain protein content (%)	ICC Standard No.105/2 according to Kjeldahl	J04, W04
SED	Sedimentation volume (ml)	ICC Standard No.116/1 according to Zeleny	J04, W04
BVO	Baking volume (=loaf volume) (ml/100 g flour)	Rapid-Mix-Test (RMT), calculated from total volume of 30 small bread loaves measured in a bread volumeter	J04, W04

[a] ICC (International Association for Cereal Science and Technology), see ICC (2004)

[b] Abbreviation of the location [Adenstedt (A), Dikopshof (D), Jerxheim (J), Morgenrot (M), Wohlde (W)] and the year [2004 (04), 2005 (05)]

classes, respectively. The percentage of exotic germplasm present in a BC_2F_3 line (P[exot]), calculated as explained in materials and methods, ranged from 0.6 to 33.1% (B22) and from 1.6 to 25.3% (Z86). The average percentage of exotic germplasm across all AB lines was 12.7% in B22 and 13.0% in Z86. Both values are close to the expected percentage of 12.5% donor germplasm in a BC_2F_3 generation. The size of single introgressions per line ranged from 0.5 to 97.9 cM in B22 and from 0.5 to 108.5 cM in Z86. On average, a B22 line carried 1.5 introgressions with 23.4 cM of size. A Z86 line carried on average 2.1 introgressions with 17.7 cM of size.

Trait performance and correlations

For the assessment of trait performance, i.e. the performance of a population in regard to a certain trait, the least-squares means of the traits were calculated for the backcross populations and the recurrent parents (Table 2). The comparison of the least squares means revealed significant differences of the means for the traits BVO, GPC and SED, where the performance of B22 was above that of Batis. In addition, significant differences were observed for FN and HLW, with B22 below that of Batis. The comparison of the performances of Z86 with Zentos displayed a significantly stronger performance of Z86 for the trait GPC. For the traits FN, HLW and SED, the least-squares means showed a weaker performance of Z86 compared to the recurrent parent Zentos (Table 2). The genetic correlation between the seven investigated traits was calculated using the least-squares means of the BC_2F_3 lines averaged across all environments. Significant correlations ($P < 0.05$) were detected for 20 (B22) and 15 (Z86) trait combinations. In B22, the trait BVO revealed moderate positive correlations with GPC ($r = 0.57$) and SED, ($r = 0.57$). In addition, moderate positive correlations were detected between FY_{550} and HLW ($r = 0.57$) and for GPC and SED ($r = 0.51$). In Z86, the trait BVO exhibited a moderate positive correlation of 0.53 with SED. In order to test the effect of the portion of exotic germplasm on baking quality traits, the correlation between the percentage of exotic germplasm present in each BC_2F_3 line and the measured line performance was observed. For this calculation the estimated percentage of exotic alleles P[exot] present in a BC_2F_3 line was used. In B22, P[exot] showed weak negative correlations with FY_{550} ($r = –0.24$) and HLW ($r = –0.32$). Weak positive correlations were found between P[exot] and BVO ($r = 0.13$), GPC ($r = 0.38$) and SED ($r = 0.19$). For Z86, P[exot] exhibited weak negative correlations with HLW ($r = –0.27$) and SED ($r = –0.23$). In addition, a weak positive correlation was measured for P[exot] with GPC ($r = 0.20$).

QTL detection

A single-point marker analysis by means of a three-factorial ANOVA revealed 55 significant marker trait associations with 53 marker main effects and two effects where both, the marker main effect as well as the marker environment interaction effect were significant. The significant marker main effects corresponded to 38 putative QTLs for seven traits, due to linkage between markers (Table 3; Fig. 1). At 36 QTLs the marker main effect and at two QTLs the marker main effect as well as the M × E interaction effect were significant. The exotic genotype improved trait performance at 14 (36.8%) QTLs, while the elite genotype contributed to the favourable effect at 24 QTLs (63.2%). In the following the QTLs are presented for each trait separately.

Table 2 Least squares means for seven traits calculated across all environments for B22 and Z86 and the recurrent parents Batis and Zentos

Trait[a]	Lsmeans			SD[b]		Lsmeans			SD[b]	
	B22	Batis	Sig[c]	B22	Batis	Z86	Zentos	Sig[c]	Z86	Zentos
HLW	80.1	81.8	***	3.0	2.2	80.5	81.2	**	3.1	2.2
GH	56.3	56.6	NS	2.5	2.9	55.8	55.3	NS	2.3	2.4
FY_{550}	73.4	73.9	NS	2.5	0.7	74.4	73.8	NS	2.2	1.6
FN	276.3	307.4	*	58.1	27.7	342.9	374.2	**	42.9	21.1
GPC	12.9	12.0	***	0.9	0.5	13.8	13.1	***	1.0	0.5
SED	48.5	43.2	*	10.9	1.9	54.3	62.3	***	10.3	3.3
BVO	630.1	601.6	**	40.1	27.7	694.5	694.7	NS	39.1	20.3

[a] HLW (hectolitre weight), GH (grain hardness), FY_{550} (flour yield Type 550), FN (falling number), GPC (grain protein content), SED (sedimentation volume), BVO (baking volume)

[b] Standard deviation

[c] Significant differences between Lsmeans were compared with a *t* test. Level of significance: NS: not significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Table 3 List of 38 putative QTLs significant for a marker main effect for seven traits detected in populations B22 and Z86

Trait[a]	QTL[b]	SSR[c]	Chr[d]	Pos[e]	Range[f]	Bin range[g]	R^2_G [h] (in %)	[AA][i]	[aa][j]	RP [aa][k] (in %)	P/N[l]	Candidate Gene/ Corresponding QTL[m]
B22												
HLW	QHlw.B22–3B.a	Xgwm285	3B	60.9	60.9	C-3BS1-0.33	6.0	80.2	78.8	–1.7	–	
	QHlw.B22-4A.a	Xwmc722	4A	83.9	83.9		8.3	80.3	78.8	–1.8	–	
	QHlw.B22-6B.a	Xgwm626	6B	47.7	47.7	C-6BS5-0.76	7.9	80.2	78.4	–2.2	–	Xgwm88xTW[2]
	QHlw.B22-7A.a	Xwmc596	7A	72.2	41.7–72.2	C-7AS8-0.45*	12.1	80.3	78.7	–2.0	–	QTw.crc-7A[12]
	QHlw.B22-7A.b	Xgwm282	7A	99.8	99.8	7AL16-0.86-0.90	7.5	80.3	78.8	–1.9	–	
	QHlw.B22-7B.a	Xgwm46	7B	53.5	40.0–53.5	(C-7BS1-0.27)-(7BS1-0.27–1.00)*	17.8	80.4	78.3	–2.6	–	
FY_{550}	QFy550.B22-2A.a	Xgwm636	2A	11.0	11.0	2AS5-0.78–1.00	11.2	73.7	71.7	–2.8	–	
	QFy550.B22-2A.b	Xwmc522	2A	45.0	45.0–52.5	C-2AS5–0.78*	8.1	73.6	71.9	–2.3	–	
	QFy550.B22–6B.a	Xgwm626	6B	47.7	47.7	C-6BS5–0.76	5.6	73.5	71.2	–3.1	–	
	QFy550.B22–7A.a	Xcfa2028	7A	41.7	41.7–72.2	C-7AS8–0.45*	11.9	73.7	71.3	–3.3	–	
	QFy550.B22–7B.a	Xgwm46	7B	53.5	40.0–53.5	(C-7BS1–0.27)-(7BS1–0.27–1.00)*	13.8	73.7	70.8	–3.9	–	
FN	QFn.B22–1B.a	Xbarc80	1B	106.3	106.3	1BL3–0.83–1.00	4.7	269.4	301.1	11.7	+	
	QFn.B22–2D.a	Xgwm261	2D	23.2	23.2	C-2DS1–0.33	5.3	278.2	239.5	–13.9	–	
	QFn.B22–4B.a	Xgwm113	4B	24.5	21.6–40.6	(4BS8–0.57–0.81)-(4BL1–0.86–1.00)*	9.9	271.1	324.2	19.6	+	*Rht-B1*[3]
	QFn.B22–7B.a	Xbarc65	7B	48.0	48.0		6.0	280.9	204.4	–27.2	–	*α-Amy-B2*[4]
	QFn.B22-7B.b	Xwmc276	7B	141.9	141.9		9.7	285.0	238.5	–16.3	–	
GPC	QGpc.B22-3A.a	Xbarc1060	3A	84.7	83.3–84.7		22.4	12.7	13.9	9.0	+	
	QGpc.B22-4A.a	Xgwm610	4A	12.1	12.1	C-4AS1-0.20	7.3	12.9	13.6	5.5	+	QGpc.ccsu-4A.2[9]
	QGpc.B22-4A.b	Xwmc722	4A	83.9	83.9		10.1	12.8	13.6	6.5	+	
	QGpc.B22-5D.a	Xgwm583	5D	44.0	44.0	C-5DL1-0.60	4.5	13.0	12.6	–3.3	–	
	QGpc.B22-7B.a	Xgwm569	7B	7.9	7.9		5.1	12.8	13.3	3.9	+	
	QGpc.B22-7D.a	Xbarc352	7D	66.0	66.0		7.8	12.9	13.6	5.6	+	
SED	QSed.B22-5D.a	Xgwm190	5D	8.9	8.9	C-5DS1–0.63	17.3	50.3	32.8	–34.7	–	
	QSed.B22-6D.a	Xbarc204	6D	72.8	72.8		6.2	47.7	58.0	21.7	+	
BVO	QBvo.B22-6B.a	Xgwm626	6B	47.7	47.7	C-6BS5-0.76	5.6	628.4	662.8	5.5	+	
	QBvo.B22-7B.a	Xgwm569	7B	7.9	7.9		4.5	626.8	648.7	3.5	+	
Z86												
HLW	QHlw.Z86-3B.a	Xgwm493	3B	11.8	11.8	3BS8-0.78–1.00	7.8	80.6	78.8	–2.3	–	
	QHlw.Z86-3B.b	Xbarc139	3B	66.3	66.3		24.3	80.7	78.3	–3.0	–	
	QHlw.Z86-6B.a	Xbarc24	6B	55.3	47.7–59.3	(C-6BS5-0.76)-(6BL5–0.40–1.00)	17.2	80.7	78.9	–2.3	–	Xgwm88xTW[2]

Table 3 continued

Trait[a]	QTL[b]	SSR[c]	Chr[d]	Pos[e]	Range[f]	Bin range[g]	R^2_G [h] (in %)	[AA][i]	[aa][j]	RP [aa][k] (in %)	P/N[l]	Candidate Gene/ Corresponding QTL[m]
GH	QGh.Z86-2D.a	Xgwm157	2D	73.1	73.1	2DL3-0.49–0.76	8.7	55.5	57.2	3.2	+	Xbcd120xKernel hardness
	QGh.Z86-5D.a	Xgwm190	5D	8.9	8.9	C-5DS1-0.63	13.1	56.0	53.0	–5.4	–	*Ha*/ Xmta9xKernel hardness[11] Xmta10xHard [8] Xmta9xPina-D1[5] Xmta10xPinb-D1[5] QHa.ksu-5D[6]
FY_{550}	QFy550.Z86-5D.a	Xbarc143	5D	23.4	23.4	C-5DS1-0.63	6.5	74.6	72.9	–2.2	–	*Ha*[1]
FN	QFn.Z86-3A.a	Xgwm5	3A	44.9	44.9	C-3AL3-0.42	7.1	346.8	312.3	–9.9	–	
	QFn.Z86-6B.a	Xgwm626	6B	47.7	47.7	C-6BS5-0.76	9.4	337.2	376.1	11.5	+	*α-Amy-B1*[7]
GPC	QGpc.Z86-4B.a	Xgwm251	4B	35.7	35.7	4BL1-0.86–1.00	17.6	13.7	15.1	10.0	+	
SED	QSed.Z86-1D.a	Xgwm642	1D	75.4	75.4	1DL2-0.41–1.00	32.8	57.5	44.7	–22.2	–	*Glu-D1*/ Glu-D1xSDSsed[10]
	QSed.Z86-5D.a	Xgwm190	5D	8.9	8.9	C-5DS1-0.63	11.9	55.6	41.5	–25.4	–	
BVO	QBvo.Z86-4B.a	Xgwm251	4B	35.7	35.7	4BL1-0.86–1.00	7.7	693.9	737.1	6.2	+	

[a] BVO (baking volume), FN (falling number), FY_{550} (flour yield Type 550), GH (grain hardness), GPC (grain protein content), HLW (hectolitre weight), SED (sedimentation volume)

[b] Linked significant markers were interpreted as a single QTL

[c] Representative marker for a significant QTL effect, selected by the highest *F*-value

[d] Chromosomal localisation of the marker

[e] Position of the listed marker in cM, taken from Somers et al. (2004)

[f] CentiMorgan position from the first to the last significant marker in a linkage group

[g] Markers were assigned to bins according to Sourdille et al. (2004). In case of linked significant markers, the bin range is given. An asterisk (*) indicates that not every significant marker was assigned to a bin

[h] Proportion of the genetic variance, explained by the marker main effect. R^2_M was calculated as SQ_M/SQ_g for a marker main effect

[i] Lsmeans of trait values across all investigated environments for BC_2F_3 lines carrying the elite genotype at the given marker locus

[j] Lsmeans of trait values across all investigated environments for BC_2F_3 lines carrying the exotic genotype at the given marker locus

[k] Relative performance of the exotic genotype: ([aa] – [AA]) × 100/[AA], where [aa] and [AA] are the least squares means of the homozygous exotic [aa] and the homozygous elite [AA] genotypes of the BC_2F_3 lines at a given marker locus

[l] The marker main effect of the exotic genotype [aa] is favourable (+) or, respectively, unfavourable (–) in all environments

[m] Candidate genes or corresponding QTLs published in: 1. Campbell et al. (1999), 2. Elouafi and Nachit (2004), 3. Flintham et al. (1997), 4. Gale et al. (1983), 5. Igrejas et al. (2002), 6. Narasimhamoorthy et al. (2006), 7. Nishikawa et al. (1981), 8. Perretant et al. (2000), 9. Prasad et al. (2003), 10. Rousset et al. (2001), 11. Sourdille et al. (1996), 12. Huang et al. (2006)

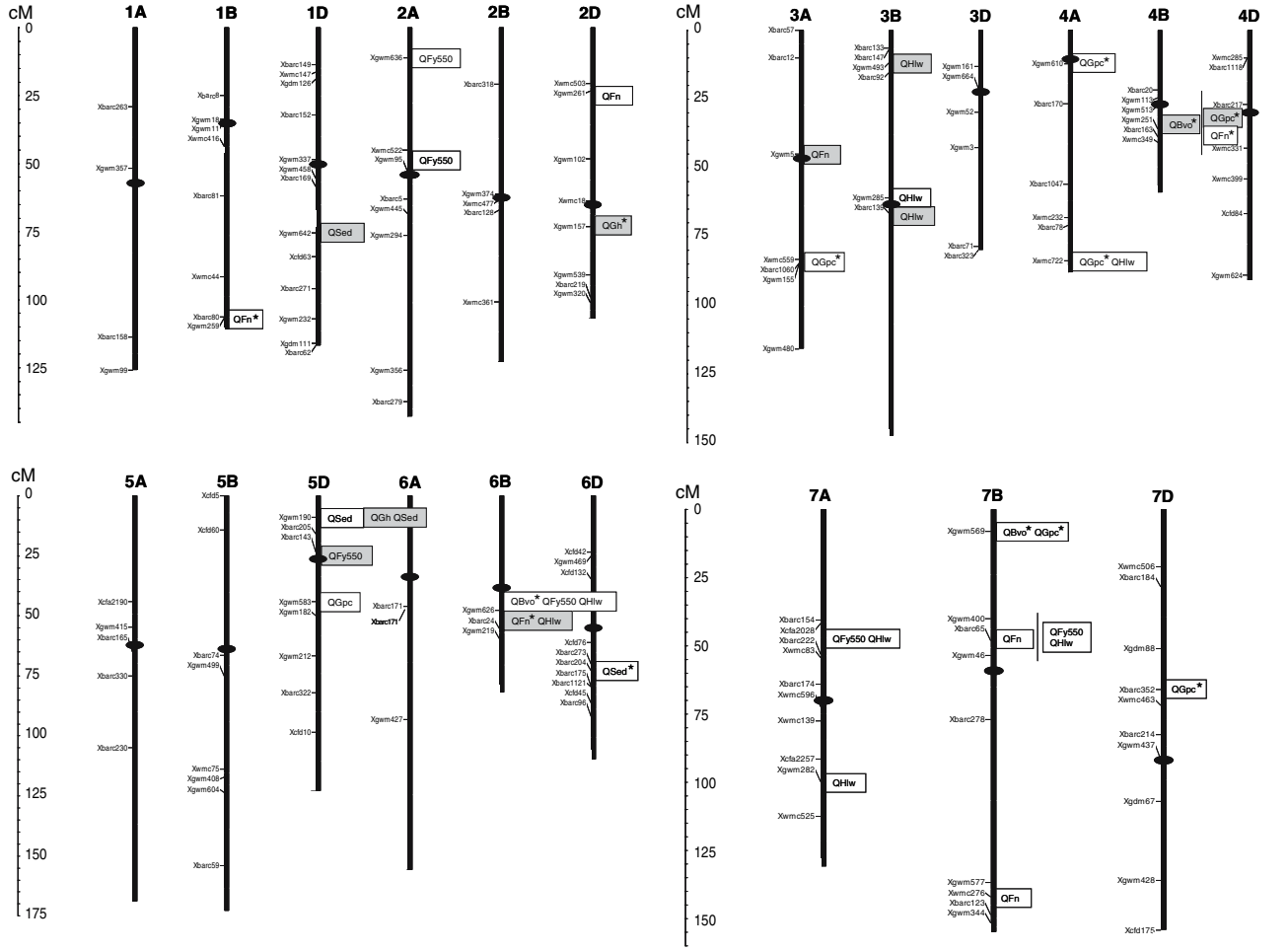

Fig. 1 QTL map showing 38 putative QTLs for seven traits detected in populations B22 and Z86. QTLs with white background were detected in B22 and QTLs with grey background were detected in Z86. The putative QTLs are indicated to the right of the marker or the linked markers that showed a significant effect for the respective trait. A *vertical line* represents the marker interval where the QTL was located. Abbreviations of the QTLs: see Table 1. An *asterisk* (*) indicates exotic QTL alleles showing a favourable effect. The map is based on Somers et al. (2004)

Hectolitre weight (HLW)

Altogether six putative QTLs were localised for HLW in B22. At all QTLs, the exotic allele diminished HLW by up to 2.6%. The strongest QTL effect explained 17.8% of the genetic variance. In Z86, three putative QTLs for HLW were found. The presence of the exotic allele led to a decrease of HLW by up to 3.0% at all three QTLs. The strongest effect was detected at QTL QHlw.Z86–3B.b, which explained 24.3% of the genetic variance.

Grain hardness (GH)

In B22, no QTL for GH was located. Overall two putative QTLs were found for GH in Z86. The presence of the exotic allele increased grain hardness by up to 3.2% at the marker $Xgwm157_{[2D]}$. This marker explained 8.7% of the genetic variance. At the QTL QGh.Z86-5D.a, the exotic allele caused softer grains by 5.3%. The marker $Xgwm190_{[5D]}$ explained 13.1% of the genetic variance.

Flour yield Type 550 (FY_{550})

Five putative QTLs were identified for FY_{550} in B22. At these QTLs, which explained between 5.6 and 13.8% of the genetic variance, a substitution of the elite allele by the exotic allele decreased flour yield Type 550 by up to 3.9%. For FY_{550}, one putative QTL was localised in Z86. The QTL QFy550.Z86-5D.a reduced flour yield Type 550 due to the exotic allele by 2.2%. This locus explained 6.5% of the genetic variance.

Falling number (FN)

For the trait FN, five putative QTLs were found in B22. Of these QTLs, two loci showed an increase in trait performance by 11.7–19.6%, if the exotic allele was present. These loci explained 4.7–9.9% of the genetic variance. At the other three loci, the exotic allele reduced FN. At two QTLs, QFn.B22-7B.a and QFn.B22-7B.b, the exotic allele reduced FN by 27.2 and 16.3%. These QTLs explained 6.0 and 9.7% of the genetic variance. Two putative QTLs were detected for FN in Z86. At the QTL QFn.Z86-6B.a, the exotic allele led to a desired increase in FN by 11.5%. This QTL explained 9.4% of the genetic variance. At the QTL QFn.Z86-3A.a, the presence of the exotic allele reduced FN by 9.9%.

Grain protein content (GPC)

Six QTLs were detected for grain protein content in B22. At five loci, the exotic allele increased the grain protein content by up to 9.0% (QGpc.B22-3A.a). The latter QTL explained 22.4% of the genetic variance. In Z86, one putative QTL was located for GPC. At the QTL QGpc.Z86-4B.a, the exotic allele increased grain protein content by 10.0%. This effect, displayed by $Xgwm251_{[4B]}$, explained 17.6% of the genetic variance.

Sedimentation volume (SED)

For the trait SED two putative QTLs were found in B22. The individual QTLs explained 6.2 and 17.3% of the genetic variance. At the QTL QSed.B22-6D.a, the exotic allele increased SED by 21.7%. At the other QTL (QSed.B22-5D.a), the exotic allele reduced sedimentation volume by 34.7%. This QTL explained 17.3% of the genetic variance. In Z86, two putative QTLs were found for SED. The exotic allele decreased SED at both loci by 22.2 and 25.4%. The strongest effect, located at $Xgwm642_{[1D]}$, explained 32.8% of the genetic variance.

Baking volume (BVO)

In B22, the QTL analysis revealed two putative QTLs significant for a marker main effect for the trait BVO. The exotic allele improved trait performance at both QTLs. The QTL QBvo.B22-6B.a had the strongest effect on baking volume, explaining 5.6% of the genetic variance. The exotic allele at this locus increased BVO by 5.5%. In Z86, one putative QTL was located for the trait BVO. The QTL QBvo.Z86-4B.a explained 7.7% of the genetic variance. At this locus the exotic allele increased BVO by 6.2%.

Discussion

QTL analysis and comparison with candidate genes and other QTL analyses

The results of the present QTL analysis were compared to other QTL analyses and to studies of candidate genes in wheat. Altogether four AB-QTL analyses of wheat have been published so far (Huang et al. 2003, 2004; Narasimhamoorthy et al. 2006; Liu et al. 2006). In all cases, the synthetic exotic donor parent originated from hybridisation of durum with *T. tauschii*, thus lacking exotic alleles on genomes A and B. All four AB-QTL analyses were used to identify QTLs for agronomic traits, except Narasimhamoorthy et al. (2006) who also investigated grain protein content and kernel hardness. Their AB-QTL analysis was conducted in a $BC_2F_{2:4}$ population developed from a cross between the hard red winter wheat variety Karl 92 and the synthetic wheat line TA 4152-4, originating from a durum × *T. tauschii* cross.

In the following, the comparison of detected QTLs with other QTL studies is presented separately for each trait. A QTL overview is given in Table 3.

Hectolitre weight (HLW) and flour yield (FY_{550})

A moderate positive correlation was observed for HLW and FY_{550} in B22. At three QTLs (50.0%) for FY_{550}, also a significant QTL effect for HLW was detected. The marker density in this study was not sufficient to decide whether these QTLs revealed pleiotropic effects or were due to linked QTLs. In total, six (B22) and three (Z86) QTLs for hectolitre weight were detected. In B22 and Z86, the position of a QTL for HLW on chromosome 6B corresponds to a QTL detected by Elouafi and Nachit (2004). In population B22, the QTL at Xwmc596 also corresponds to QTw.crc–7A, a QTL located by Huang et al. (2006) on chromosome 7A.

Grain hardness (GH)

In this study, GH showed a weak positive correlation with BVO in B22 and a weak positive correlation with FY_{550} in Z86. Sourdille et al. (1996) located a QTL for kernel hardness on chromosome 2DL in RILs from a cross between synthetic and cultivated wheat. At this locus kernel hardness was associated with the synthetic alleles. Considering the position of the QTL as well as the effect of the synthetic allele, this locus might correspond to the QTL QGh.Z86-2D.b in Z86. The QTL for grain hardness on chromosome 5D, QGh.Z86-5D.a, in Z86 is at the same position as the *Ha* locus. In addition, Igrejas et al. (2002) found that marker *Xgwm190*, which is located at our

QTL, was only 5.8 cM distant to *Xmta9* and *Xmta10*. The latter RFLP markers were very tightly linked, giving the same major QTL for grain hardness, puroindoline-a content and puroindoline-b content. Their results confirm the relationship of the *Xmta9* locus to Pin-a (*Pina-D1*) and the *Xmta10* locus to Pin-b (*Pinb-D1*). Three further studies revealed significant QTL effects for grain hardness linked to *Xmta9*, *Xmta10* and *Xcfd18* at the *Ha* locus on the short arm of chromosome 5D, respectively (Sourdille et al. 1996; Perretant et al. 2000; Narasimhamoorthy et al. 2006). At the QTL QGh.Z86-5D.a, the exotic allele led to softer grains, which was also discovered by Sourdille et al. (1996) and the AB-QTL study of Narasimhamoorthy et al. (2006).

Falling number (FN)

Two QTLs for falling number, one detected in B22 and one in Z86, were located in genome regions carrying genes for α-amylase activity. The QTL detected in Z86 on chromosome 6B may correspond to the α-*Amy-B1* locus (Nishikawa et al. 1981), while the QTL detected in B22 on chromosome 7B (QFn.B22-7B.b) is in vicinity of the α-*Amy-B2* gene (Gale et al. 1983). At QFn.B22-7B.b, the exotic allele reduced falling number by 27.2%. This might be the result of high α-amylase activity leading to starch degradation influenced by the α-*Amy-B2* gene. The QTL QFn.B22-4B.a is close to the *Rht-B1* dwarfing gene. As the dwarfing alleles *Rht-B1* and *Rht-D1* were shown to reduce α-amylase activity, without affecting germination (Mrva and Mares 1996), the QTL effect on chromosome 4B might be a pleiotropic effect of *Rht-B1* (Flintham et al. 1997). In addition, a QTL for plant height was located at the same position on chromosome 4B in B22 (A. Kunert et al., in preparation).

Grain protein content (GPC)

In B22, one QTL for grain protein content (QGpc.B22-7B.a) was located, which revealed an improved trait performance of the exotic allele without decreasing yield (A. Kunert et al., in preparation). This QTL appears to be promising because of the lack of association with low grain yield. It might be suggested that the microsatellite *Xgwm569* is a possible candidate for the improvement of protein content in wheat through marker-assisted selection (MAS). In general, the negative yield-protein correlation can be attributed to environmental factors, genetic components, dilution of grain nitrogen with a much larger grain biomass accumulation, or to bio-energetic requirements for synthesis of carbohydrates and proteins (Bathia and Rabson 1987). The QTL for GPC on chromosome 4A, QGpc.B22-4A.a, was located in vicinity of a QTL detected by Prasad et al. (2003). Recently, the gene responsible for a QTL for grain protein content, *Gpc-B1*, was cloned from wild emmer by Uauy et al. (2006). The gene is located on chromosome arm 6BS and corresponds to a transcription factor, conferring accelerated senescence and increased grain protein, zinc, and iron content. In population Z86, we found a weak marker associated effect ($P = 0.005$) on GPC in the same region at Xgwm626 (position 47.7 cM). Here, the exotic allele was associated with an increase in grain protein content as observed by Uauy et al. (2006).

Sedimentation volume (SED)

The SSR marker *Xgwm642* on 1DL identified a QTL for SED. The position indicates an influence of the *Glu-D1* locus. Also Rousset et al. (2001) detected a major QTL for sedimentation volume on 1DL, clearly corresponding to the *Glu-D1* locus.

Baking volume (BVO)

In both populations, no QTL was located for BVO in vicinity of the *Glu-1* loci at $P < 0.001$. However, marker associated effects on BVO were detected on chromosome 1B at Xgwm11 (position 34.3 cM) and Xwmc416 (position 43.5 cM) in population B22 and Z86, respectively. Here, the exotic alleles reduced BVO by 4.0 and 4.8% with P values of 0.009 and 0.003, respectively. The effects may be attributed to the *Glu-B1* locus (Payne 1987).

Comparison of detected QTLs between B22 and Z86

Of 149 markers utilised in this study, 51 SSRs were genotyped in both populations. At the common SSRs, two (18.2%) marker main effects from a total of eleven were detected in both populations. At these QTL regions, the exotic alleles showed also similar effects in the two populations. Most QTL effects (81.8%) were not reproducible between the two populations. This could be due to genetic differences between the elite parents and/or between the two donor accessions. Population size may also have been a factor with the B22 population of 250 BC_2F_3 lines (in which 26 QTLs were detected) providing greater power for QTL detection than the Z86 population of 150 BC_2F_3 lines (in which only 12 QTLs were detected).

Utilisation of the AB lines and favourable exotic QTL alleles

The evaluated AB lines from population B22 and Z86 represent potential donors of favourable alleles with a limited number of additional inferior exotic alleles. The

portion of the exotic genome as well as the average size and number of introgressions present in the two BC_2F_3 populations are already drastically reduced compared to an F_1-derived population. However, the actual size and number of introgressions might be underestimated since, firstly, introgressions are calculated only from the first to the last SSR locus in an introgression without knowledge how far an introgression extends beyond the last marker investigated. Secondly, introgressions characterized by only one locus are omitted from the calculation since their minimum size cannot be estimated. The question remains open, whether a further round of backcrossing would have been beneficial for the QTL analysis. Most likely, the size and number of introgressions would have further reduced in this case. The occurrence of deleterious side-effects due to linkage drag present in the advanced backcross lines could also be reduced by a further round of backcrossing, but this would require doubling of the number of AB lines in order to maintain the same number of AB lines having the exotic genotype at any given SSR locus. In the case of our experiments, this would have led to very large field experiments, so we chose to evaluate 400 BC_2F_3 lines rather than 800 BC_3F_3 lines. Another alternative would have been to produce doubled haploids (DH) from the BC_2F_1 generation. This would have been an improvement over our advanced backcross design. First, the genotype of the evaluated AB lines would be fixed. Secondly, homozygous exotic genotypes would increase in number due to a complete lack of heterozygotes in the doubled haploid population. Theoretically, a BC_2DH generation carries 12.5% homozygous donor genotypes at each SSR locus whereas the BC_2F_3 generation possesses only 9.38% homozygous donor genotypes.

In future, the trait-improving effect of the exotic QTL alleles can be exploited by two strategies of backcrossing. The BC_2F_3 lines could be backcrossed twice to the recurrent parent Batis or Zentos to produce a BC_4 population and create near-isogenic lines. Secondly, the AB lines could be crossed with other winter wheat varieties to transfer the favourable alleles into new genetic backgrounds. The latter strategy risks the possibility of non-reproducible QTL effects in the new genetic background. This could be due to new intra-locus interaction or due to epistatic interactions between the detected QTLs and the genetic background. Both strategies would lead to a recombination of alleles and a further reduction of linkage drag. In addition, the best BC_2F_3 lines could also be crossed to each other followed by marker-assisted selection with linked markers in order to combine a series of favourable exotic QTL alleles in single lines (gene pyramiding). The identified wheat SSR markers might allow using the QTLs of interest more precisely to manipulate traits than it would be possible based on phenotypic selection alone. The general utility of these QTLs will depend on their stable expression in other genetic backgrounds and environments and on whether they are associated with undesirable traits, either because of pleiotropic effects or because of tight linkage.

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