Theor Appl Genet (2004) 109: 933–943
DOI 10.1007/s00122-004-1708-7

ORIGINAL PAPER

X. Q. Huang · H. Kempf · M. W. Ganal · M. S. Röder

Advanced backcross QTL analysis in progenies derived from a cross between a German elite winter wheat variety and a synthetic wheat (*Triticum aestivum* L.)

Received: 4 February 2004 / Accepted: 14 April 2004 / Published online: 9 July 2004

Abstract We report here the second advanced backcross quantitative trait locus (AB-QTL) analysis carried out in winter wheat. Seven agronomic traits were studied in a BC_2F_1population derived from a cross between the German winter wheat variety *Flair* and the synthetic wheat line XX86 developed in Japan. We selected 111 BC_2F_1 lines and genotyped these with 197 microsatellite markers. Field data for seven agronomic traits were collected from corresponding BC_2F_3 families that were grown at up to six locations in Germany. QTL analyses for yield and yield components were performed using single-marker regression and interval mapping. A total of 57 putative QTLs derived from XX86 were detected, of which 24 (42.1%) were found to have a positive effect from the synthetic wheat XX86. These favourable QTLs were mainly associated with thousand-grain weight and grain weight per ear. Many QTLs for correlated traits were mapped in similar chromosomal regions. The AB-QTL data obtained in the present study are discussed and compared with results from previous QTL analyses.

Communicated by G. Wenzel

X. Q. Huang (✉) · M. S. Röder
Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK),
Corrensstr. 3,
06466 Gatersleben, Germany
e-mail: huangxiuqiang@yahoo.com
Tel.: +49-394-825589
Fax: +49-394-825137
e-mail: roder@ipk-gatersleben.de

H. Kempf
Saatzucht H. Schweiger GbR,
Feldkirchen 3,
85368 Moosburg, Germany

M. W. Ganal
TraitGenetics GmbH,
Am Schwabeplan 1b,
06466 Gatersleben, Germany

Cereal Research Centre, Agriculture and Agri-Food Canada,
195 Dafoe Road,
Winnipeg, R3T 2M9, Manitoba, Canada

Introduction

Bread wheat (*Triticum aestivum* L.) is a hexaploid ($2n$=6, x=42) organism with three (A, B and D) genomes. It originated from a series of natural hybridisations, the first occurring between *T. urartu* Thum. ex Gandilyan (AA) and an unknown species (BB) closely related to *T. speltoides* (Tausch.) Gren. ex Richter (SS). The resulting tetraploid wheat—*T. turgidum* L. (AABB)—then hybridised with *T. tauschii* (Coss.) Schmal (DD) to generate the hexaploid wheat *T. aestivum* L. (AABBDD, Chapman et al. 1976; Kihara 1944; Zohary et al. 1969). Feldman et al. (1995) estimated that the latter hybridisation event occurred approximately 8,000 years ago. This hybridisation event can be repeated today by crossing tetraploid wheat (AABB) with *T. tauschii* (DD) to produce synthetic hexaploid wheat. These synthetic hexaploids have been used as an intermediate for transferring genes for biotic stresses, such as diseases (Kerber 1987; Lutz et al. 1995; Ma et al. 1995), and abiotic stresses, such as cold hardiness and salinity (Gorham et al. 1987; Limin and Fowler 1993), from wild progenitors to cultivated hexaploid wheats.

Several attempts have been made for incorporating quantitative complex traits, such as growth rate, grain yield (YLD) and product quality, from the ancestral species into crop species like oat (Lawrence and Frey 1975), sorghum (Cox et al. 1984) and pearl millet (Bramel-Cox et al. 1986). In wheat, Cantrell and Joppa (1991) found that some chromosomes from wild emmer wheat *T. dicoccoides* Korn (AABB) had significant positive effects on grain YLD and protein content. Cox et al. (1995) evaluated the agronomic and quality traits of many BC_2F_2 lines derived from direct hybrids between wheat and *T. tauschii* and detected that *T. tauschii* germplasm increased protein concentration but depressed

grain YLD in comparison to the recurrent parents. Gororo et al. (2002) reported that *T. tauschii* has an outstanding potential for improving the yield of wheat in low-yielding environments subject to drought stress, basing his conclusions on an evaluation of the yield performance of backcross populations from normal hexaploid with that from synthetic hexaploid wheat. By using BC_2F_2 lines derived from crosses between different synthetic hexaploids and spring wheat cultivars, del Blanco et al. (2001) reported that several synthetic-derived lines had significantly higher grain YLD than the recurrent wheat parent and that more than 80% of the lines were significantly superior for kernel weight. However, the quantitative trait loci (QTLs) involved in these synthetic hexaploids were not identified using molecular markers.

Although there have been some reports on the transfer of quantitative traits from unadapted wild relatives into cultivated hexaploid wheat, this approach has not been widely used in wheat improvement programmes. The reason for this is that favourable attributes are often linked to undesirable traits in unadapted wild relatives and are difficult to separate from them, the so-called linkage drag (Patterson et al. 1991; Stalker 1980). This problem can be solved by the advanced backcross QTL (AB-QTL) approach proposed by Tanksley and Nelson (1996). The AB-QTL strategy can not only reduce linkage drag, but it can also integrate the process of QTL identification and variety improvement while exploiting the potential of the genetic variation available in unadapted germplasm for the improvement of quantitative traits. Beneficial alleles from unadapted germplasm can be identified using molecular markers. This strategy has been used in detecting and transferring valuable QTLs from unadapted germplasm into elite breeding lines in tomato (Bernacchi et al. 1998; Fulton et al. 1997, 2000; Tanksley et al. 1996), rice (Brondani et al. 2002; Moncada et al. 2001; Xiao et al. 1998) and barley (Pillen et al. 2003). Results from the first AB-QTL analysis in winter wheat were published by Huang et al. (2003a). We report here the second AB-QTL analysis in winter wheat using the synthetic wheat XX86 as the donor parent and compare the QTLs detected with those detected in the first AB-QTL analysis.

Materials and methods

Plant materials

The German winter wheat variety *Flair* and a synthetic hexaploid wheat, XX86, were used as the recurrent and donor parent in this study, respectively. XX86 was provided by Dr. F.J. Zeller, Technical University Munich, Freising-Weihenstephan, Germany and was developed originally from the cross between emmer wheat (*Triticum dicoccum*) line KU 124 and *T. tauschii* accession 2047 by Dr. Ohta, Japan (F.J. Zeller, personal communication).

Population development

XX86 was crossed as the female parent to var. *Flair* to produce 60 F_1 seeds. The F_1 plants were grown in the field of Saatzucht H. Schweiger GbR, Moosburg, and the 14 most vigorous F_1plants were backcrossed to *Flair* (as the female). Seventy BC_1F_1 plants were obtained, which were grown in the field. The best 29 individuals based on phenotypic selection were backcrossed a second time to *Flair* (as the female) to produce 498 BC_2F_1 seeds. These were grown in the field and bulk-propagated to BC_2F_2 and subsequently BC_2F_3 families. The best 111 BC_2F_3 families were selected and used for measuring the agronomic traits.

Field trials and trait evaluation

The field trials were conducted at three different locations dispersed over northern and southern Germany in 2002 and 2003: Feldkirchen (FE-02), Hadmersleben (HA-02), Silstedt (SI-02), Böhnshausen (BÖ-03), Feldkirchen (FE-03) and Wohlde (WO-03). A complete randomized block design was used for the field trials. The 111 BC_2F_3 families were planted in two replications for each location. Each family was grown in 10-m^2 plots. In total, 170 kg urea (nitrogen)/ha was applied at four different growth stadiums. All trials were kept free of weeds and diseases with two applications of broad-spectrum herbicides and fungicides, respectively.

A total of seven agronomic traits were evaluated for each plot in three or more locations. Grain YLD per plot was evaluated based on the grain harvest from all plants in each plot. Ear emergence time (EET) was evaluated based on morphological characters in each plot. Plant height (HT) was calculated as the average height of ten plants in centimeters measured from the soil surface to the tip of the spike (awns excluded). Tiller number per square meter (TN) was calculated as the number of spikes per square meter from each plot. Thousand-grain weight (TGW) was measured in grams as the average weight of two independent samples of 1,000 grains from each plot. Twenty-five main spikes were cut from each of the 111 BC_2F_3 families and evaluated for grain number per ear (GNE) and grain weight per ear (GWE). GNE and GWE were measured as the average number of the 25 spikes analysed.

Trait correlations and analysis of variance (ANOVA)

Pearson's correlation coefficients between traits were calculated for each location combination based on the field data using the QGENE software (Nelson 1997). Using the package SPSS for Windows, ANOVA-general linear model (GLM) analysis was performed to determine the significances of differences between the genotypes of the population lines and between the locations (environments). Genotype-by-environment (G×E) interactions were also analysed using ANOVA-GLM.

Microsatellite marker analyses

DNA from the parents *Flair* and XX86 was used for screening for polymorphism of the microsatellite markers. The order and distribution of the microsatellite markers were based on the ITMI population of wheat described by Röder et al. (1998; unpublished data). Segregation ratios of individual markers were statistically determined for each marker locus, and deviations from the expected ratios were determined using the chi-square (χ^2) test. Six plants from each of the 111 BC_2F_3 families were bulked for DNA extraction. Total genomic DNA was extracted from young leaf tissue and frozen in liquid nitrogen as previously described by Huang et al. (2000). PCR analyses of the microsatellite markers were performed according to Röder et al. (1998), and microsatellite fragments were detected on an automated laser fluorescence (ALF) express sequencer and analysed using the computer programme FRAGMENT ANALYSER VER. 1.02 (Amersham Biosciences, UK) by comparison with internal size standards (Huang et al. 2002, 2003b).

QTL analysis

The software QGENE developed by Nelson (1997) was used for QTL analysis. The association between phenotype and marker genotype was investigated using single-marker regression. The positions of identified QTLs were determined using interval mapping. Each trait/location combination was treated separately. According to Fulton et al. (1997, 2000) and Tanksley et al. (1996), regions of the genomes were identified as putatively containing a QTL if the results met one or more of the following criteria: (1) a significant effect was observed for a single-marker/trait combination at a single location with $P<0.001$; (2) significant effects were observed in the same direction (i.e., either all positive effects or all negative effects) for a single-marker/trait combination at two or more locations with $P<0.01$; (3) significant effects were observed in the same direction for a single-marker/trait combination at three or more locations with $P<0.1$.

The percentage phenotypic variation (%PV) associated with each significant QTL was calculated from the regressions of each marker/phenotype combination. The percentage phenotypic change (A%) of each significant QTL, which is associated with the presence of the donor allele at a given marker locus, was estimated to be A% = 100(AB−AA)/AA (Fulton et al. 1997, 2000; Huang et al. 2003a), where AA is the phenotypic mean for individuals homozygous for *Flair* alleles at the specified marker(s) and AB is the phenotypic mean for heterozygotes (*Flair*/XX86).

Results

Correlations between traits and ANOVA for genotypes, environments and their interactions

Figure 1 shows the correlation coefficients between the seven traits measured in this study, calculated separately for each location. As a result of bad weather and the subsequent inavailability of data for some traits, the correlations between the traits in Hadmersleben-2002 and Silstedt-2002 were not included in the correlation matrix.

As in the first AB-QTL analysis in wheat, there was no significant correlation between YLD and YLD components at all four locations, indicating that YLD is a complex trait (Huang et al. 2003a). YLD showed a positive correlation with HT at the Feldkirchen location during 2002 and 2003 but a negative correlation with HT for the Böhnshausen location in 2003. In agreement with the results of our previous study, TGW was correlated with HT and EET (Huang et al. 2003a). A significant negative correlation was found between TGW and GNE. GWE showed a significantly positive correlation with TGW and GNE.

The *F*-value of ANOVA for genotypes and environments as well as for their interactions is presented in Table 1. Significant differences between genotypes were found for all seven traits investigated. The *F*-value ranged from 1.31 ($P<0.05$) for GWE to 5.83 ($P<0.0001$) for HT. The environment had a large influence on all seven traits. Significant G×E interaction was observed for YLD ($P<0.001$) and GNE ($P<0.05$), but there were no significant interaction between other genotypes and environment.

	Yld		Ht		Eet		Tn		Tgw		Gne	
Ht	0.224**	-0.552****										
	0.613****	-0.088										
Eet	-0.047	0.072	0.227*	-0.117								
	0.111	-0.152	0.051	0.016								
Tn	0.109	-	0.130	-	-0.261	-						
	0.070	0.292**	0.021	0.075	-0.098	-0.223**						
Tgw	0.056	0.013	-0.041	0.221*	0.023	0.429***	-0.056	-				
	-	0.099	-	0.459****	-	0.374***	-	-0.036				
Gne	-	-	-	-	-	-	-	-	-	-		
	0.004	0.095	-0.117	-0.273**	0.212*	-0.184	-0.156	-0.193*	-0.367***	-0.349****		
Gwe	-	-	-	-	-	-	-	-	-	-	-	-
	0.335***	0.158	0.385***	0.060	-0.077	0.058	-0.115	-0.216*	0.613****	0.391****	0.487****	0.675****

FE-02	BÖ-03
FE-03	WO-03

Fig. 1 Pearson's correlation coefficients between seven traits in the BC_2F_3families from the cross *Flair* × XX86. Significance levels are: **P*<0.05, ***P*<0.01, ****P*<0.001. *BÖ* Böhnshausen, *FE* Feldkirchen, *WO* Wohlde, *Eet* Ear emergence time, *Gne* grain number per ear, *Gwe* grain weight per ear, *Ht* plant height, *Tgw* thousand-grain weight, *Tn* Tiller number per square meter, *Yld* yield.− No data

Table 1 *F* values of anova-GLM for genotype and environment as well as their interaction in the BC_2F_3 families of the cross *Flair* × XX86 (*NS* not significant)

Item	Genotype (G)		Environment (E)		G × E interaction	
	df	*F*	*df*	*F*	*df*	*F*
Total yield	110	2.50***	3	676.36****	330	1.84***
Ear emergence time	110	3.98****	2	87.13****	220	1.14 NS
Plant height	110	5.83****	2	669.97****	220	0.92 NS
Tiller number/m^2	110	1.58**	2	170.35***	220	0.70 NS
Thousand-grain weight	110	4.58****	4	186.56****	440	0.92 NS
Grain number/ear	110	3.15****	3	317.55****	330	1.20*
Grain weight/ear	110	1.31*	3	131.71****	330	0.17 NS

*, **, ***, ****Significant at $P<0.05$, $P<0.01$, $P<0.001$ and $P<0.0001$, respectively

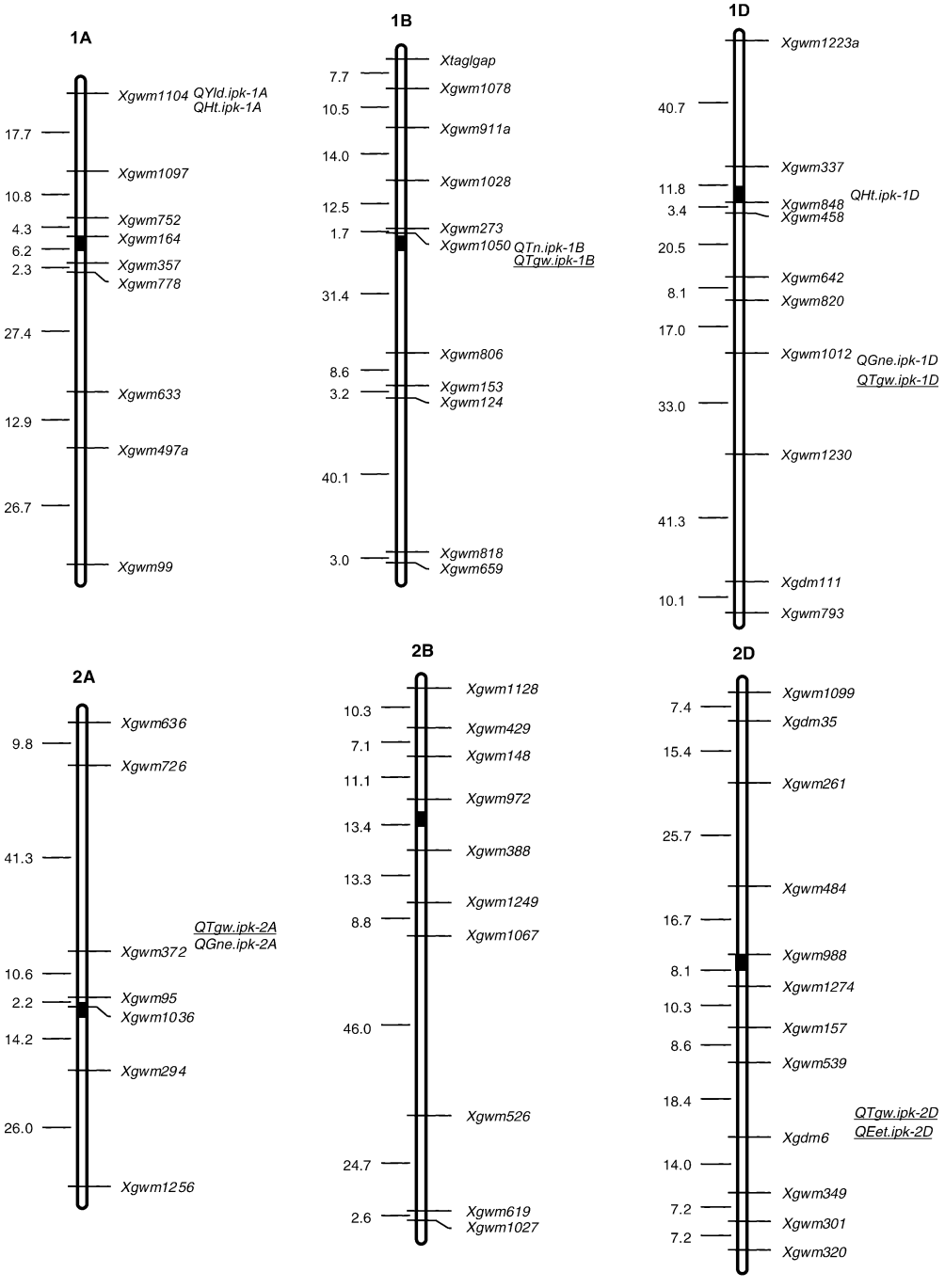


Fig. 2 Linkage map of microsatellite markers used for BC_2 QTL analysis. The marker order and relative distances (in Kosambi mapping units) are based on the ITMI population. The centromeres are indicated as a *solid black bar*. Putative QTLs are shown on the *right*. *Underlined* QTL represents an allele from synthetic wheat XX86 that is favourable for the traits

Microsatellite polymorphism and marker segregation

We tested 404 microsatellite markers for polymorphisms between the two parents *Flair* and XX86. Of these, 252 (62.4%) simple sequence repeat (SSR) markers were polymorphic between the parents. Polymorphisms in the A, B and D genomes were 57.66%, 60.83% and 69.35%, respectively. Chromosomes 5A and 7B showed the least polymorphism–40.91% and 42.86%, respectively—whereas chromosome 7D showed the highest polymorphism—83.33%. A total of 197 marker loci were used for genotyping the 111 BC_2F_1plants. The remaining polymorphic marker loci, which produced fragments only in the recurrent parent *Flair* but not in the donor parent XX86, were not used for AB-QTL analysis (Huang et al. 2003a). The average marker distance was 15 cM. Large regions (more than 45 cM) without polymorphic markers were found on chromosomes 2B, 3B, 3D, 4D, 5A, 6A, 7A and 7B (Fig. 2).

On the basis of the 197 microsatellite markers, the average number of heterozygotes per locus was 15.85%, which was much lower than the expected average of 25% heterozygotes in the BC_2F_1 population. The segregation ratio at 89 loci (45.18%) deviated from the expected ratio (χ^2>3.84, P<0.05) with all of these loci skewed toward the recurrent parent *Flair*. These observations can be explained by the selection that was applied in the BC_1 and BC_2 generations during population development.

QTLs detection

Putative QTLs for each trait that were detected at least in two locations are listed in Table 2 and their map positions

Fig. 2 (continued)

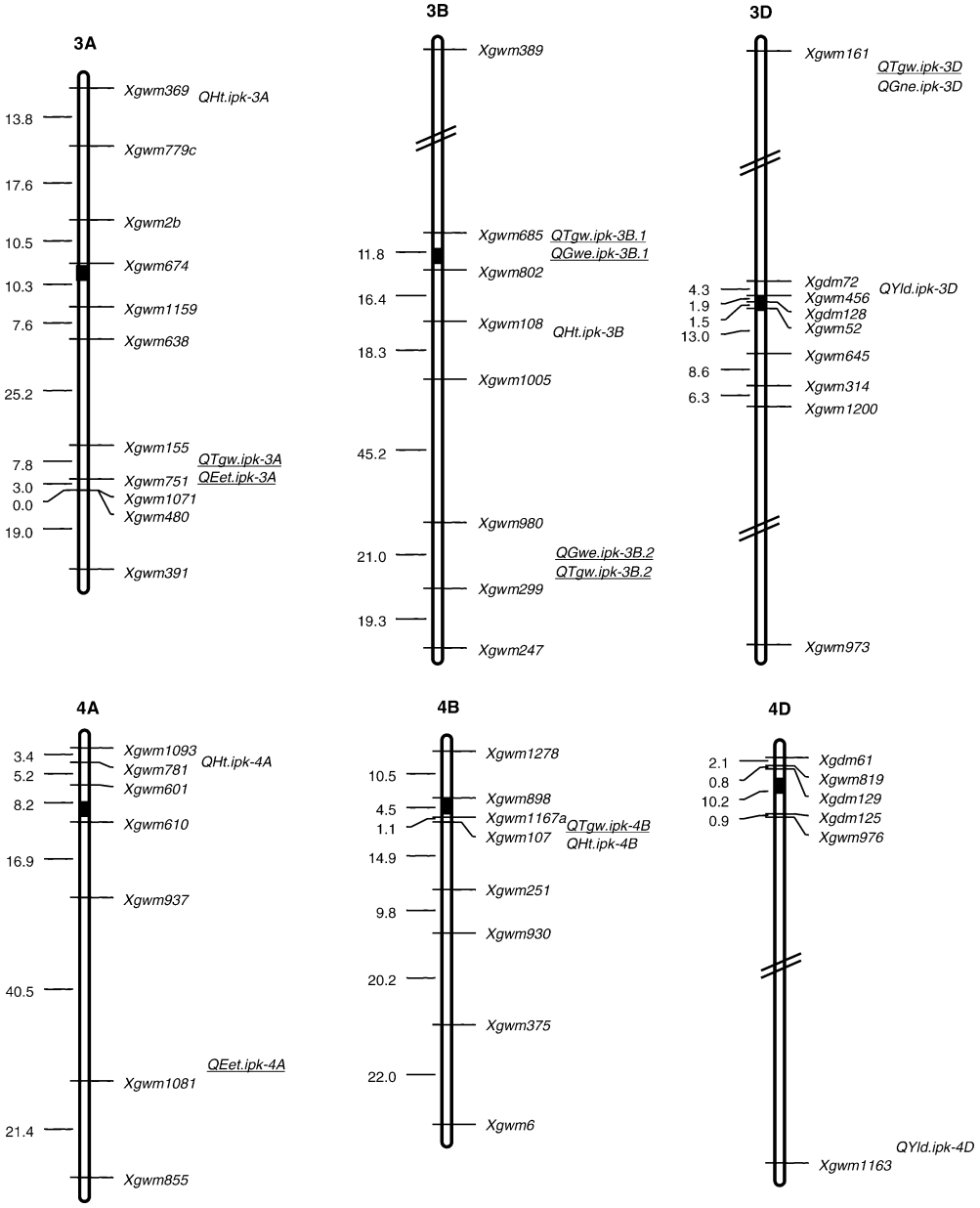
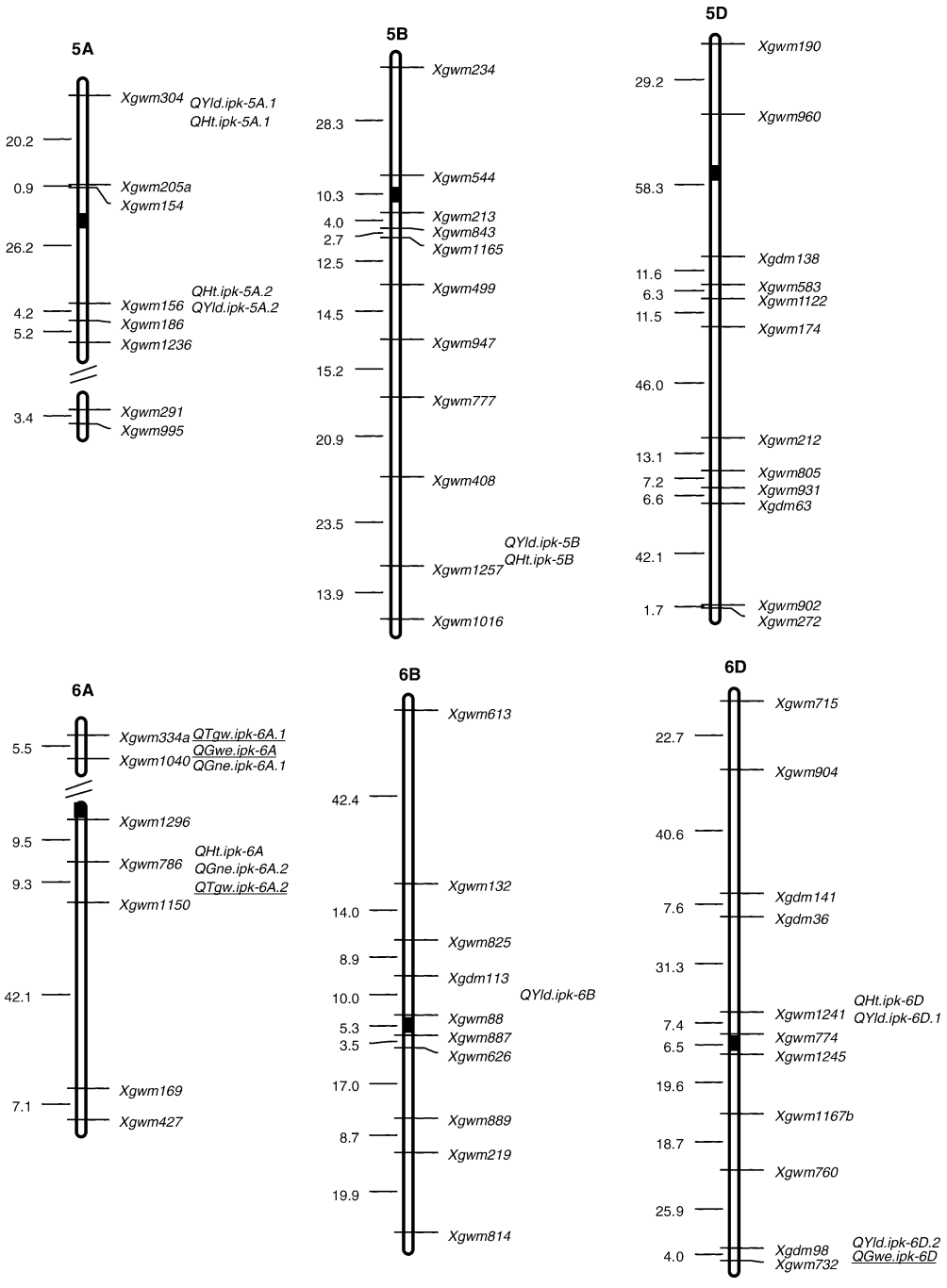


Fig. 2 (continued)



are shown in Fig. 2. A total of 57 putative QTLs were identified, ranging from two to 14 QTLs for each trait.

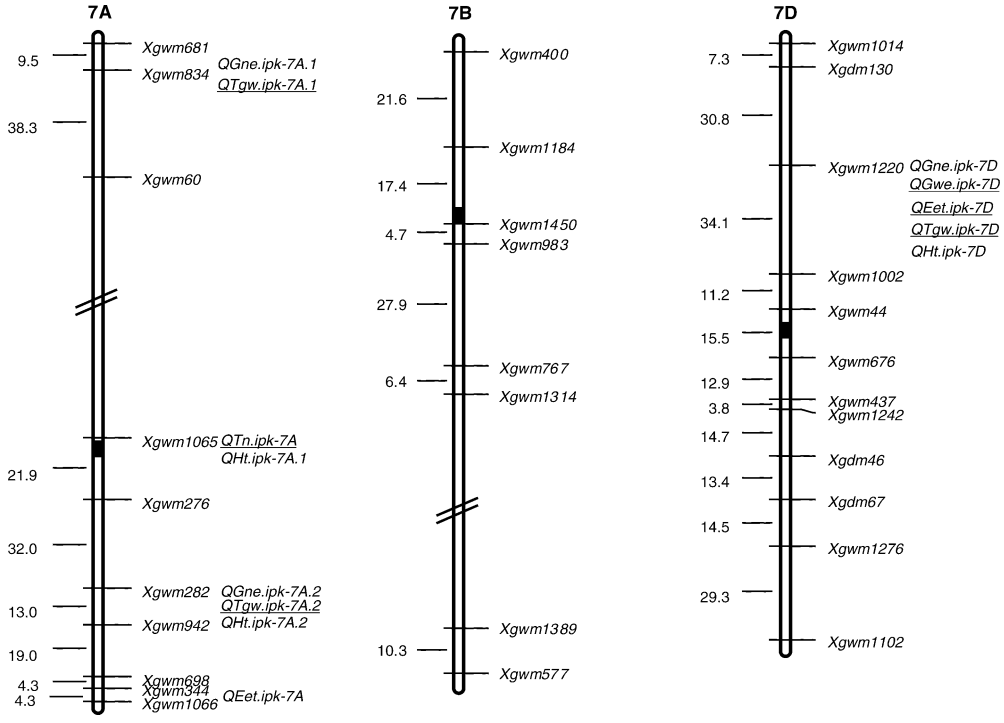
Total yield

Nine QTLs were detected for total YLD, explaining from 10.0% to 23.0% of the phenotypic variation with a LOD of 2.6–6.2. For all nine QTLs, the *Flair* allele increased total YLD. No QTLs for total YLD were identified from the donor synthetic line XX86 that produced a significant increase of total YLD.

Ear emergence time

Five QTLs were detected with an effect on EET. Four QTLs on chromosomes 2D, 3A, 4A and 7D explained from 12.8% to 22.7% of the phenotypic variation for reducing the number of days to ear emergence from the XX86 alleles, whereas one QTL on chromosome 7A, *QEet.ipk-7A*, explained 11.8% of the variance for increasing number of days to ear emergence from the XX86 allele.

Fig. 2 (continued)



Plant height

Fourteen QTLs were associated with HT. For the QTLs that were located on chromosomes 1A, 1D, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6D, 7A and 7D, the XX86 allele increased HT with a negative effect from an agronomic perspective. The variation explained by these individual QTLs ranged from 10.0% to 37.3%. All of these QTLs were detected in all four locations investigated.

Tiller number per square meter

Tiller number per square meter was evaluated only at three locations—FE-02, FE-03 and WO-03. Two putative QTLs were detected for TN. These two QTLs explained 7.0% and 13.9% of the phenotypic variation with a LOD of 1.8 and 3.6, respectively. For the QTL *QTn.ipk-1B*, the wild allele decreased TN, whereas for the QTL *QTn.ipk-7A*, the allele from XX86 increased TN by 7.5%.

Thousand-grain weight

Fourteen QTLs significantly influenced TGW and mapped on 11 chromosomes, of which two QTLs each were identified on chromosomes 3B, 6A and 7A. All QTLs explained more than 8.0% of the phenotypic variation and were identified in all of the locations investigated. For all of the QTLs, the XX86 alleles increased TGW by 5.2–8.0%.

Grain number per ear

Eight significant QTLs were identified for GNE. For all these QTLs, the wild alleles caused a decrease in GNE with a phenotypic effect of 5.7–8.4%. The phenotypic variation explained by these individual QTLs was 8.2–15.0%. No favourable effects of the XX86 alleles on GNE were observed.

Grain weight per ear

Five genomic regions were associated with GWE. These QTLs explained 8.0–12.2% of the phenotypic variation. All of these QTLs showed the positive effect coming from the wild alleles with an increase in GWE by 5.2%–8.1%.

Discussion

Distribution of the detected QTLs in the genomes and chromosomes

Using single-marker analysis and interval mapping, we detected 57 putative QTLs in the present study. The highest number of QTLs was found in the A genome, with 27 QTLs (47.4%); 12 (21.1%) and 18 (31.6%) QTLs were found in genomes B and D, respectively (Table 2, Fig. 2). Similarly, the YLD-related QTLs were also predominant in the A genome of wild emmer wheat *T. dicoccoides* Korn (AABB; Peng et al. 2003). The number of QTLs from homoeologous groups 1 to 7 were seven (12.28%), four (7.0%), 11 (19.3%), five (8.8%), six (10.5%), 11 (19.3%) and 13 (22.8%), respectively. Except for

Table 2 Putative QTLs detected in the BC_2F_1 population from the cross Flair × XX86. (FE = Feldkirschen, HA = Hadmersleben, SI = Silstedt, BÖ = Böhnshausen, WO = Wohlde, NS = not significant, ND = no data)

Trait	QTL	Marker	HA-02	SI-02	FE-02	FE-03	WO-03	BÖ-03	LOD[b]	A[c]%	%PV[d]
Total yield	*QYld.ipk-1A*	*Xgwm1104*	NS	ND	NS	***– [e]	*–	****–	4.1	−7.2	15.8
	QYld.ipk-3D	*Xgwm456*	NS	ND	****	NS	*–	NS	6.2	−5.7	23.0
	QYld.ipk-4D	*Xgwm1163*	NS	ND	****–	NS	*–	NS	5.2	−5.7	19.3
	QYld.ipk-5A.1	*Xgwm304*	*–	ND	NS	***–	NS	****–	3.7	−6.8	14.2
	QYld.ipk-5A.2	*Xgwm156*	*–	ND	NS	***–	NS	****–	3.3	−7.9	12.7
	QYld.ipk-5B	*Xgwm1257*	*–	ND	NS	NS	*–	***–	2.6	−5.4	10.0
	QYld.ipk-6B	*Xgdm113*	NS	ND	*–	**–	*–	***–	2.7	−5.7	11.8
	QYld.ipk-6D.1	*Xgwm1241*	NS	ND	NS	***–	*–	****–	3.4	−7.2	13.0
	QYld.ipk-6D.2	*Xgdm98*	**–	ND	***–	NS	NS	NS	2.9	−3.1	11.4
Ear emergence time	*QEet.ipk-2D*	*Xgdm6*	ND	ND	**+	*+	NS	****+	3.4	3.4	16.7
	QEet.ipk-3A	*Xgwm751*	ND	ND	**+	**+	*+	***+	2.7	3.8	12.8
	QEet.ipk-4A	*Xgwm1081*	ND	ND	****+	****+	****+	****+	6.2	4.3	22.7
	QEet.ipk-7A	*Xgwm1066*	ND	ND	***–	NS	**–	**–	3.0	−1.6	11.8
	QEet.ipk-7D	*Xgwm1220*	ND	ND	*+	****+	****+	***+	4.4	3.1	16.7
Plant height	*QHt.ipk-1A*	*Xgwm1104*	ND	ND	****+	****+	****+	**+	4.8	5.5	24.0
	QHt.ipk-1D	*Xgwm848*	ND	ND	*+	**+	*+	****+	3.3	3.8	15.9
	QHt.ipk-3A	*Xgwm369*	ND	ND	**+	**+	***+	*+	2.3	4.1	10.9
	QHt.ipk-3B	*Xgwm108*	ND	ND	**+	****+	***+	**+	3.8	6.0	18.4
	QHt.ipk-4A	*Xgwm781*	ND	ND	**+	**+	***+	**+	2.5	5.2	11.8
	QHt.ipk-4B	*Xgwm1167a*	ND	ND	***+	****+	****+	***+	4.0	6.2	19.7
	QHt.ipk-5A.1	*Xgwm304*	ND	ND	****+	****+	****+	****+	5.8	6.5	29.7
	QHt.ipk-5A.2	*Xgwm156*	ND	ND	****+	****+	****+	****+	7.1	8.6	37.3
	QHt.ipk-5B	*Xgwm1257*	ND	ND	**+	**+	*+	***+	2.1	3.1	10.0
	QHt.ipk-6A	*Xgwm786*	ND	ND	****+	****+	****+	****+	4.1	7.0	15.6
	QHt.ipk-6D	*Xgwm1241*	ND	ND	**+	****+	***+	**+	3.9	5.4	19.0
	QHt.ipk-7A.1	*Xgwm1065*	ND	ND	***+	***+	**+	**+	2.9	4.1	13.9
	QHt.ipk-7A.2	*Xgwm942*	ND	ND	**+	***+	**+	NS	2.6	5.5	12.3
	QHt.ipk-7D	*Xgwm1002*	ND	ND	**+	***+	****+	**+	4.0	7.3	19.6
Tiller number/m^2	*QTn.ipk-1B*	*Xgwm1050*	ND	ND	**–	NS	*–	ND	1.8	−8.2	7.0
	QTn.ipk-7A	*Xgwm1065*	ND	ND	****+	NS	*+	ND	3.6	7.5	13.9
Thousand-grain weight	*QTgw.ipk-1B*	*Xgwm1050*	NS	NS	NS	**+	**+	****+	3.3	7.8	12.6
	QTgw.ipk-1D	*Xgwm1012*	NS	*+	NS	***+	**+	*+	2.4	6.5	9.3
	QTgw.ipk-2A	*Xgwm372*	*+	***+	*+	***+	**+	*+	2.6	5.4	10.3
	QTgw.ipk-2D	*Xgdm6*	**+	**+	NS	****+	****+	****+	4.1	6.4	15.8
	QTgw.ipk-3A	*Xgwm751*	NS	*+	**+	*+	**+	*+	2.1	5.2	8.4
	QTgw.ipk-3B.1	*Xgwm685*	*+	*+	NS	***+	**+	*+	2.9	6.2	11.5
	QTgw.ipk-3B.2	*Xgwm299*	*+	***+	NS	**+	**+	*+	2.8	6.3	10.9
	QTgw.ipk-3D	*Xgwm161*	**+	**+	NS	**+	**+	NS	2.3	6.1	9.2
	QTgw.ipk-4B	*Xgwm107*	**+	***+	NS	**+	***+	*+	3.2	7.0	12.3
	QTgw.ipk-6A.1	*Xgwm334a*	**+	****+	NS	**+	**+	*+	3.9	6.9	15.8
	QTgw.ipk-6A.2	*Xgwm1150*	*+	***+	NS	****+	***+	*+	6.2	7.6	22.6
	QTgw.ipk-7A.1	*Xgwm834*	*+	***+	NS	****+	***+	**+	3.3	7.0	12.7
	QTgw.ipk-7A.2	*Xgwm282*	*+	***+	NS	****+	****+	**+	4.6	8.0	16.9
	QTgw.ipk-7D	*Xgwm1220*	**+	****+	*+	****+	****+	****+	7.0	7.8	25.2
Grain number/ear	*QGne.ipk-1D*	*Xgwm1012*	NS	NS	ND	**–	**–	ND	2.3	−8.0	9.3
	QGne.ipk-2A	*Xgwm372*	**–	*–	ND	NS	**–	ND	2.4	−8.4	9.8
	QGne.ipk-3D	*Xgwm161*	**–	NS	ND	****–	***–	ND	3.9	−6.8	15.0
	QGne.ipk-6A.1	*Xgwm1040*	**–	*–	ND	***–	***–	ND	3.0	−5.7	11.8
	QGne.ipk-6A.2	*Xgwm786*	**–	*–	ND	*–	***–	ND	2.5	−7.4	9.9
	QGne.ipk-7A.1	*Xgwm834*	*–	NS	ND	***–	**–	ND	2.9	−5.7	11.3
	QGne.ipk-7A.2	*Xgwm282*	*–	NS	ND	*–	***–	ND	3.0	−7.9	11.6
	QGne.ipk-7D	*Xgwm1220*	NS	NS	ND	*–	**–	ND	2.1	−6.0	8.2

Table 2 (continued)

Trait	QTL	Marker	HA-02	SI-02	FE-02	FE-03	WO-03	BÖ-03	LOD[b]	A[c]%	%PV[d]
Grain weight/ear	*QGwe.ipk-3B.1*	*Xgwm685*	NS	*+	ND	**+	NS	ND	2.0	5.2	8.0
	QGwe.ipk-3B.2	*Xgwm980*	*+	**+	ND	NS	NS	ND	2.3	8.1	9.3
	QGwe.ipk-6A	*Xgwm334a*	NS	**+	ND	NS	*+	ND	2.2	8.1	8.6
	QGwe.ipk-6D	*Xgwm732*	NS	*+	ND	***+	NS	ND	2.6	6.3	10.2
	QGwe.ipk-7D	*Xgwm1220*	NS	**+	ND	***+	NS	ND	3.1	7.9	12.2

Significance levels: *P<0.1, **P<0.01, ***P<0.001, ***** P<0.0001
[a]LOD score from the location with the underline P-value
[b]A (%) = 100(AB−AA)/AA, where AA is the phenotypic mean for individual homozygous for Flair alleles at specified markers and AB is the phenotypic mean for heterozygotes Flair/XX86
[c]%PV = phenotypic variance estimated from marker regression against phenotype
[d]+/– indicate positive or negative effect from XX86 allele
[e]Underlined P-value indicates location for which A (%) and %PV were calculated

chromosomes 2B, 5D and 7B, these QTLs were distributed on the other 18 chromosomes. The highest number of QTLs—eight (14.0%)— was identified on chromosome 7A. Of 57 QTLs, 24 (42.1%) were found to have a positive effect from the synthetic wheat XX86. Most of the favourable QTLs were located on chromosomes 3B, 6B, 7A and 7D (four, three, three and three, respectively), while no beneficial QTLs were detected on chromosomes 1A, 4D, 5A, 5B and 6B.

In five cases, the QTLs for total YLD and HT mapped to the same positions on chromosomes 1A, 5A (two positions), 5B and 6D (Fig. 2). For these five genomic regions, the alleles from XX86 increased HT but decreased the total YLD, indicating that the total YLD is negatively correlated with HT. This is consistent with the negative correlation coefficient between total YLD and HT observed in Böhnshausen 2003 (Fig. 1). EET showed a positive correlation with TGW (Fig. 1). For three regions on chromosomes 2D, 3A and 7D, the wild alleles reduced number of days to ear emergence and increased TGW (Fig. 2). There were significantly negative correlation between TGW and GNE. This can be confirmed by the results that six favourable QTLs for TGW and six unfavourable QTLs for GNE were located in the same positions on chromosomes 1B, 1D, 2A, 3D, 6A (two positions) and 7D (Fig. 2). Three specific marker regions associated with more than two traits were observed on chromosomes 6A (two regions) and 7D. This is likely to indicate either pleitropic or linkage effects. For example, in the approximate 30-cM interval between *Xgwm1220* and *Xgwm1002* on the short arm of chromosome 7D, there were five QTLs for GNE, GWE, EET, TGW and HT.

Comparison with AB-QTL and other QTL analyses in wheat

The study of QTLs in wheat has a long history and is based on the use of morphological markers with cytogenetically derived single chromosome substitution lines (Berke et al. 1992; Law 1966, 1967; Law et al. 1978; Snape et al. 1985). However, QTLs can only be located onto individual chromosomes using this method, while the employment of molecular markers enables the researcher to map QTLs to specific chromosomal regions. Due to the lack of sufficient polymorphic marker loci, there have been fewer studies on QTLs for YLD and fewer YLD components detected in the whole wheat genome. QTLs for YLD and its components have been identified only on chromosomes 3A (Shah et al. 1999), 4A (Araki et al. 1999) and 5A (Kato et al. 2000) of wheat using single chromosome recombinant substitution lines in combination with restriction fragment length polymorphic (RFLP) markers. Hyne et al. (1994) performed a partial genome assay for QTLs in wheat, paying the most attention to the short arms of chromosomes 6B, 7A, 7B and 7D. The high-density RFLP map developed in the ITMI mapping population enabled the identification of YLD-related QTLs (Börner et al. 2002). Huang et al. (2003a) recently reported an AB-QTL analysis in wheat using microsatellite markers and a different population.

Of the seven traits evaluated in the present study, five were also measured our previous AB-QTL analysis (Huang et al. 2003a). For these traits, 88 QTLs were detected, and only eight (9.1%) of them are potentially orthologous between the two synthetic wheat lines—*QHt.ipk-4B, QYld.ipk-4D*, *QTgw.ipk-2D* and *QTgw.ipk-7D* (Huang et al. 2003a; Fig. 2). For the QTL *QHt.ipk-4B* on chromosome 4B, the wild alleles from both synthetic wheat lines increased HT with the negative effect. For the QTLs *QTgw.ipk-2D* and *QTgw.ipk-7D* on chromosomes 2D and 7D, both wild alleles had a positive effect on increasing TGW. For the QTL *QYld.ipk-4D* associated with microsatellite marker *Xgwm1163* on chromosome 4D, the alleles from two synthetic wheat lines had a negative effect and total decreased LD. For EET and TN, no common QTLs were identified. The few common QTLs between the two synthetic wheat lines could be explained by the fact that these synthetic wheat lines might have very different genetic backgrounds, with W-7984 developed from Mexico and XX86 from Japan.

We compared the AB-QTLs obtained in this study with QTLs obtained from classical QTL analyses by comparing the positions of QTLs and reference RFLP markers in the microsatellite map of wheat (Röder et al. 1998, unpublished data). A total of ten QTLs—two for HT on chromosomes 1AS and 4BL, two for EET on chromosomes 4AL and 7DS, four for TGW on chromosomes 3AL, 3BL, 6AL and 7DS and one for GNE on chromosome 7AL (Fig. 2)—were mapped in similar positions to QTLs reported in the ITMI population by Börner et al. (2002). For HT, six QTLs were common to one population; two of these—*QHt.ipk-1A* and *QHt.ipk-4B*—were identified in two other QTL studies (Börner et al. 2002; Cadalen et al. 1998). *QHt.ipk-3A* on chromosome 3AS in this study may be associated with the earliness per se (*Eps*) locus that was identified by Shah et al. (1999). Another common QTL, *QHt.ipk-5A*, is probably a pleiotropic effect of the vernalisation response gene *Vrn-A1* on chromosome 5AL (Kato et al. 1999). The same QTLs, *QEet.ipk-4A* and *QEet.ipk-7D*, were also identified by Araki et al. (1999) and Hyne et al. (1994), respectively. For total YLD, the QTL on chromosome 5AL, *QYld.ipk-5A.2*, is in a similar position to the one detected by Kato et al. (2000).

Although the favourable alleles for total YLD were not identified from the synthetic wheat line, we found 14 significantly positive QTLs for TGW that were conserved across different locations and years (Table 2). In particular, two QTLs, *QTgw.ipk-2D* and *QTgw.ipk-7D* on chromosomes 2D and 7D, respectively, were conserved between the two different synthetic wheat lines (Fig. 2; Huang et al. 2003a). In order to confirm their significant effects, we are developing near-isogenic lines (NILs) for single QTLs from BC_4F_1 plants. Once NILs for TGW-QTLs are isolated, they can be inherited as single Mendelian factors (Yamamoto et al. 1998) and transferred into high-yielding wheat cultivars using the molecular markers associated with these QTLs for improving the YLD trait of the cultivated varieties of wheat.

Acknowledgements We would like to thank E. Ebmeyer at Lochow-Petkus GmbH, H. Cöster at Monsanto Agrar Deutschland GmbH, T. Hammann at Saatzucht Hadmersleben GmbH and R. Schachschneider at Nordsaat Saatzucht GmbH for the field experiments and evaluations described in this study; J. Schondelmaier at Saaten-Union Resistenzlabor GmbH for the coordination of this project; and A. Heber for excellent technical assistance. This research was supported by a grant from Arbeitsgemeinschaft industrieller Forschungsvereinigungen (AiF). [Das Forschungsvorhaben (AiF-Nr. 12572 BR) wurde aus Haushaltsmitteln des Bundesministeriums für Wirtschaft und Arbeit (BMWA) über die Arbeitsgemeinschaft industrieller Forschungsvereinigungen "Otto von Guericke" e.V. (AiF) gefördert.]

References

Araki E, Miura H, Sawada S (1999) Identification of genetic loci affecting amylose content and agronomic traits on chromosome 4A of wheat. Theor Appl Genet 98:977–984

Berke TG, Baenziger PS, Morris R (1992) Chromosomal location of wheat quantitative trait loci affecting agronomic performance of seven traits, using reciprocal chromosome substitutions. Crop Sci 32:621–627

Bernacchi D, Beck-Bunn T, Eshed Y, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley S (1998) Advanced backcross QTL analysis in tomato. I. Identification of QTLs for traits of agronomic importance from *Lycopersicon hirsutum*. Theor Appl Genet 97:381–397

Börner A, Schumann E, Fürste A, Cöster H, Leithold B, Röder MS, Weber WE (2002) Mapping of quantitative trait loci for agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). Theor Appl Genet 105:921–936

Bramel-Cox PJ, Andrews DJ, Frey KJ (1986) Exotic germplasm for improving grain yield and growth rate in pearl millet. Crop Sci 26:687–690

Brondani C, Rangel P, Brondani R, Ferreira M (2002) QTL mapping and introgression of yield-related traits from *Oryza glumaepatula* to cultivated rice (*Oryza sativa*) using microsatellite markers. Theor Appl Genet 104:1192–1203

Cadalen T, Sourdille P, Charmet G, Tixier MH, Gay G, Boeuf C, Bernard S, Leroy P, Bernard M (1998) Molecular markers linked to genes affecting plant height in wheat using a doubled-haploid population. Theor Appl Genet 96:933–940

Cantrell RG, Joppa LR (1991) Genetic analysis of quantitative traits in wild emmer (*Triticum turgidum* L. var. *dicoccoides*). Crop Sci 31:645–649

Chapman V, Miller TE, Riley R (1976) Equivalence of the A genome of bread wheat and that of *Triticum urartu*. Genet Res 27:69–76

Cox TS, House LR, Frey KJ (1984) Potential of wild germplasm for increasing yield of grain sorghum. Euphytica 33:673–684

Cox TS, Sears RG, Bequette RK (1995) Use of winter wheat × *Triticum tauschii* backcross populations for germplasm evaluation. Theor Appl Genet 90:571–577

del Blanco IA, Rajaram S, Kronstad WE (2001) Agronomic potential of synthetic hexaploid wheat-derived populations. Crop Sci 41:679–676

Feldman M, Lupton FGH, Miller TE (1995) Wheats. In: Smartt J, Simmonds NW (eds) Evolution of crops. Longman, London

Fulton TM, Beck-Bunn T, Emmatty D, Eshed Y, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley SD (1997) QTL analysis of an advanced backcross of *Lycopersicon peruvianum* to the cultivated tomato and comparisons with QTLs found in other wild species. Theor Appl Genet 95:881–894

Fulton TM, Grandillo S, Beck-Bunn T, Fridman E, Frampton A, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley SD (2000) Advanced backcross QTL analysis of a *Lycopersicon esculentum* × *Lycopersicon parviflorumcross*. Theor Appl Genet 100:1025–1042

Gorham J, Hardy C, Wyn Jones RG, Joppa LR, Law CN (1987) Chromosomal location for a K:Na discrimination character in the D genome of wheat. Theor Appl Genet 74:584–588

Gororo NN, Eagles HA, Eastwood RF, Nicolas ME, Flood RG (2002) Use of *Triticum tauschii* to improve yield of wheat in low-yielding environments. Euphytica 123:241–254

Huang XQ, Hsam SLK, Zeller FJ, Wenzel G, Mohler V (2000) Molecular mapping of the wheat powdery mildew resistance gene *Pm24* and marker validation for molecular breeding. Theor Appl Genet 101:407–414

Huang XQ, Börner A, Röder MS, Ganal MW (2002) Assessing genetic diversity of wheat (*Triticum aestivum* L.) germplasm using microsatellite markers. Theor Appl Genet 105:699–707

Huang XQ, Cöster H, Ganal MW, Röder MS (2003a) Advanced backcross QTL analysis for the identification of quantitative trait loci alleles from wild relatives of wheat (*Triticum aestivum* L.). Theor Appl Genet 106:1379–1389

Huang XQ, Wang LX, Xu MX, Röder MS (2003b) Microsatellite mapping of the wheat powdery mildew resistance gene *Pm5e* in common wheat (*Triticum aestivum* L.). Theor Appl Genet 106:858–865

Hyne V, Kearsey MJ, Martinez O, Gang W, Snape JW (1994) A partial genome assay for quantitative trait loci in wheat (*Triticum aestivum*) using different analytical techniques. Theor Appl Genet 89:735–741

Kato K, Miura H, Sawada S (1999) QTL mapping of genes controlling ear emergence time and plant height on chromosome 5A of wheat. Theor Appl Genet 98:472–477

Kato K, Miura H, Sawada S (2000) Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. Theor Appl Genet 101:1114–1121

Kerber ER (1987) Resistance to leaf rust in hexaploid wheat: *Lr32*, a third gene derived from *Triticum tauschii*. Crop Sci 27:204–206

Kihara H (1944) Die Entdeckung des DD Analysators beim Weizen. Agric Hortic 19:889–890

Law CN (1966) The locations of genetic factors affecting a quantitative character in wheat. Genetics 53:487–498

Law CN (1967) The locations of genetic factors controlling a number of quantitative characters in wheat. Genetics 56:445–461

Law CN, Snape JW, Worland AJ (1978) The genetic relationship between height and yield in wheat. Heredity 40:133–151

Lawrence PK, Frey KJ (1975) Backcross variability for grain yield in oat species crosses (*Avena sativa* L. × *A. sterilis* L.). Euphytica 24:77–85

Limin AE, Fowler DB (1993) Inheritance of cold hardiness in *Triticum aestivum* × synthetic hexaploid wheat crosses. Plant Breed 110:103–108

Lutz J, Hsam SLK, Limpert E, Zeller FJ (1995) Chromosomal location of powdery mildew resistance genes in *Triticum aestivum* L. (common wheat). 2. Genes *Pm2* and *Pm19* from *Aegilops squarrosa* L. Heredity 74:152–156

Ma H, Singh RP, Mujeeb-Kazi A (1995) Resistance to stripe rust in *Triticum turgidum, T. tauschii*, and their synthetic hexaploids. Euphytica 82:117–124

Moncada P, Martínez CP, Borrero J, Chatel M, Gauch H Jr, Guimaraes E, Tohme J, McCouch SR (2001) Quantitative trait loci for yield and yield components in an *Oryza sativa* × *Oryza rufipogon*BC_2F_2 population evaluated in an upland environment. Theor Appl Genet 102:41–52

Nelson J (1997) QGENE: software for marker-based genomic analysis and breeding. Mol Breed 3:239–245

Patterson AH, Tanksley SD Sorrells ME (1991) DNA markers in plant improvement. Adv Agron 46:39–90

Peng JH, Ronin Y, Fahima T, Röder MS, Li YC, Nevo E, Korol A (2003) Domestication quantitative trait loci in *Triticum dicoccoides*, the progenitor of wheat. Proc Natl Acad Sci USA 100:2489–2494

Pillen K, Zacharias A, Léon J (2003) Advanced backcross QTL analysis in barley (*Hordeum vulgare* L.). Theor Appl Genet 107:340–352

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Shah MM, Gill KS, Baenziger PS, Yen Y, Kaeppler SM, Ariyarathne HM (1999) Molecular mapping of loci for agronomic traits on chromosome 3A of bread wheat. Crop Sci 39:1728–1732

Snape JW, Law CN, Parker BB, Worland AJ (1985) Genetical analysis of chromosome 5A of wheat and its influence on important agronomic characters. Theor Appl Genet 71:518–526

Stalker HT (1980) Utilization of wild species for crop improvement. Adv Agron 33:112–149

Tanksley SD, Nelson JC (1996) Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. Theor Appl Genet 92:191–203

Tanksley SD, Grandillo S, Fulton TM, Zamir D, Eshed T, Petiard V, Lopez J, Beck-Bunn T (1996) Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. pimpinellifolium*. Theor Appl Genet 92:213–224

Xiao JH, Li JM, Grandillo S, Ahn SN, Yuan LP, Tanksley SD, McCouch SR (1998) Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon*. Genetics 150:899–909

Yamamoto T, Kuboki Y, Lin SY, Sasaki T, Yano M (1998) Fine mapping of quantitative trait loci *Hd-1, Hd-2* and *Hd-3*, controlling heading date of rice, as single Mendelian factors. Theor Appl Genet 97:37–44

Zohary D, Harlan JR, Vardi A (1969) The wild diploid progenitors of wheat and their breeding value. Euphytica 18:58–65