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ORIGINAL PAPER

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AB-QTL analysis in spring barley: II. Detection of favourable exotic alleles for agronomic traits introgressed from wild barley (*H. vulgare* ssp. *spontaneum*)

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Abstract The objective of the present study was to identify favourable exotic Quantitative Trait Locus (QTL) alleles for the improvement of agronomic traits in the BC_2DH population S42 derived from a cross between the spring barley cultivar Scarlett and the wild barley accession ISR42-8 (*Hordeum vulgare* ssp. *spontaneum*). QTLs were detected as a marker main effect and/or a marker × environment interaction effect ($M \times E$) in a three-factorial ANOVA. Using field data of up to eight environments and genotype data of 98 SSR loci, we detected 86 QTLs for nine agronomic traits. At 60 QTLs the marker main effect, at five QTLs the $M \times E$ interaction effect, and at 21 QTLs both the effects were significant. The majority of the $M \times E$ interaction effects were due to changes in magnitude and are, therefore, still valuable for marker assisted selection across environments. The exotic alleles improved performance in 31 (36.0%) of 86 QTLs detected for agronomic traits. The exotic alleles had favourable effects on all analysed quantitative traits. These favourable exotic alleles were detected, in particular on the short arm of chromosome 2H and the long arm of chromosome 4H. The exotic allele on 4HL, for example, improved yield by 7.1%. Furthermore, the presence of the exotic allele on 2HS increased the yield component traits ears per m^2 and thousand grain weight by 16.4% and 3.2%, respectively. The present study, hence, demonstrated that wild barley does harbour valuable alleles, which can enrich the genetic basis of cultivated barley and improve quantitative agronomic traits.

Keywords *Hordeum vulgare* ssp. *spontaneum* · Barley · SSR · AB-QTL · Yield

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Introduction

Based on the promising results of advanced backcross quantitative trait locus (AB-QTL) analyses conducted in tomato, Gur and Zamir (2004) proposed a new paradigm in plant breeding: the use of natural variation present in the wild relatives of modern crop plants to lift yield barriers in plant breeding. They predicted that for crops with a rather narrow genetic basis, but rich biodiversity resources, the introgression of exotic germplasm could lead to dramatic improvements in yield and other quality traits. For barley, the beneficial effect of exotic genes on biotic (Backes et al. 2003; Fischbeck and Jahoor 1991; Zeller 1998) and abiotic (Jefferies et al. 1999) stresses and to some extent on quality traits (Erkkilä 1998) has already been demonstrated. The potential use of wild germplasm for the improvement of agronomic traits, however, is still a matter of controversy. Few studies on yield improvement have so far attempted to work with exotic germplasm, since the majority of genes present in exotic germplasm have strong negative effects on agronomic performance. As such, the challenge remains to identify favourable exotic alleles and to introduce them into breeding programs. As a modification of the QTL mapping approach, Tanksley and Nelson (1996) have developed the AB-QTL strategy, particularly suitable to unmask valuable exotic alleles and to introgress them into elite breeding material. Since QTL detection is carried out in advanced backcross populations, problems associated with considerable phenotypic variation and linkage drag in interspecific crosses are reduced. So far, several reports on the application of the AB-QTL strategy are available

for tomato (Tanksley et al. 1996; Fulton et al. 1997, 2000, 2002; Bernacchi et al. 1998); rice (Xiao et al. 1996, 1998; Moncada et al. 2001; Brondani et al. 2002; Septiningsih et al. 2003; Wu et al. 2004); maize (Ho et al. 2002); pepper (Rao et al. 2003); wheat (Huang et al. 2003, 2004; and barley (Pillen et al. 2003, 2004; Matus et al. 2003; Li et al. 2004). The favourable effects of the wild barley accession ISR101-23 on yield in two barley feeding varieties recorded by Pillen et al. (2003, 2004) encourage further investments in the development of AB-populations for the genetic exploitation of diverse exotic barley germplasms. The demonstrated genetic diversity in wild barley (*Hordeum vulgare* ssp. *spontaneum*, Turpeinen et al. 2001; Baek et al. 2003) suggests a not yet exploited wealth of novel exotic alleles.

Therefore, the aim of the present study was to identify favourable exotic alleles in a BC_2DH population (S42) derived from a cross of the malting barley cultivar Scarlett with the wild barley accession ISR42-8 from Israel. Favourable effects of the exotic donor accession ISR42-8 on disease resistances in S42 have already been demonstrated by von Korff et al. (2005).

Materials and methods

Plant material

The development of the population S42 with 301 BC_2DH lines originating from the cross of the German spring barley variety Scarlett with the Israeli wild barley accession ISR42-8 is described in detail in von Korff et al. (2004).

Molecular characterisation

The BC_2DH population was genotyped with 98 SSR markers as described in von Korff et al. (2004).

Phenotypic evaluation of agronomic traits

Phenotypic evaluation of yield and yield component traits of the population S42 was carried out under field conditions at four different locations during the seasons 2003 (03) and 2004 (04). The test locations were the experimental station Dikopshof (D03, D04, University of Bonn, West Germany), and the breeders' experimental stations in Gudow (G03, G04, Nordsaat Saatzucht, North Germany), Irlbach (I03, I04, Dr. J. Ackermann, South Germany) and Morgenrot (M03, M04, Saatzucht Josef Breun, East Germany). The field experiment was designed in randomised plots without replications. As a control, the recurrent parent Scarlett was tested with 20 replications per block. Net plot sizes (5.0–9.0 m^2), seed density (300–330 kernels/m^2), nitrogen fertilization (60–80 kg N/ha) taking into account the N_{min} content in the soil, and field management were in accordance with the local practice. The grain was harvested with a small plot harvester at maturity. The recorded traits and methods of measurement are listed in Table 1.

Statistical analyses

Statistical analyses were carried out with SAS version 9.1 (SAS Institute 2003). Genetic correlation between trait values were calculated with the ls means of BC_2DH lines averaged across environments. The detection of QTLs was carried out using the following mixed hierarchical model in the GLM procedure:

$$Y_{ijkm} = \mu + M_i + L_j(M_i) + E_k + M_I \times E_k + \varepsilon_{m(jik)}$$

where μ is the general mean, M_i is the fixed effect of the ith marker genotype, $L_j(M_i)$ is the random effect of the jth BC_2DH line nested in the ith marker genotype, E_k is the random effect of the kth environment, $M_i \times E_k$ is the random interaction effect of the ith marker genotype with the kth environment, $\varepsilon_{m(jik)}$ is the error of Y_{ijkm}. Marker main effects and M×E interactions are interpreted as putative QTLs, if the P value calculated by the Type III sums of squares is less than 0.01 (Pillen et al. 2003). Linked significant markers with a distance of ≤ 20 cM and showing the same effect were interpreted as a single putative QTL, and only the most significant marker from each group of linked loci is recorded. In order to meet the ANOVA assumption of normality, the data for lodging (LOF) were transformed by calculating the inverse of the square root. The relative performance of the homozygous exotic genotype (RP[*Hsp*]) was calculated as described in von Korff et al. (2005). The genetic variance explained by a marker (R^2_M), and by an $M \times E$ interaction ($R^2_{M \times E}$) was calculated as follows:

$$R^2_M = SQ_M/SQ_g, R^2_{M \times E} = SQ_{M \times E}/SQ_g$$

SQ_M and $SQ_{M \times E}$ correspond to the sums of squares of M and $M \times E$. SQ_g was calculated as the type III sums of square of the BC_2DH lines in the following ANOVA model:

$$Y_{ijk} = \mu + L_i + E_j + \varepsilon_{jik},$$

where L_i is the fixed effect of the ith BC_2DH line and E_j is the random effect of the jth environment. SQ_g was calculated for every marker separately to account for the occurrence of missing genotype data. If both, the marker main effect and the $M \times E$ interaction effect are significant, R^2 is calculated as SQ_M/SQ_G.

Results

Correlations

A total of 34 significant correlations were detected between nine traits (Table 2). The yield exhibited negative correlations with brittleness, plant height, lodging at

Table 1 List of nine quantitative traits investigated in up to eight environments

Abbr.[a]	Trait	Method of measurement	Value [b]	Environment tested [c]
BRT	Brittleness	Visual assessment of brittleness as present (1) or absent (2) before harvest.	–	D03, D04
EAR	Ears per m^2	Number of ears counted from 50 cm (D03, D04), 2 × 1 m (G03, G04), 1 m (M03).	+	D03, D04, G03, G04, M03
HEA	Days until heading	Number of days from sowing until emergence of 50% of ears on main tillers.	–	D03, D04, G03, G04, I03, I04, M03, M04
HEI	Plant height	Average plant height measured from soil surface to tip of spike (including awns) two weeks after flowering.	–	D03, D04, G03, G04, I03, I04, M03, M04
HI	Harvest index	Ratio of generative to vegetative biomass, calculated from a single row of 50 cm at maturity.	+	D03, D04
LOF	Lodging at flowering	Visual rating of the severity of lodging at flowering, where 1 represents no lodging and 9 represents total lodging.	–	D03, D04, G03, G04, I03, I04, M03, M04
MAS	Vegetative dry biomass	Total dry biomass above ground, collected from a row of 50 cm at maturity.	+	D03, D04
TGW	Thousand grain weight	Average weight of 1,000 kernels calculated from two samples of 250 kernels.	+	D03, D04, G03, I03, I04, M04
YLD	Grain yield	Weight of barley grain, harvested per plot and dried for 1–2 days.	+	D03, D04, G03, G04, I03, I04, M03, M04

[a] Data for LOF were transformed by x^{-2} transformation of raw data prior to ANOVA.
[b] The breeding goals for the investigated traits were defined according to breeding progams for spring malting barley, where (−) indicates that a reduction and (+) that an increase of the trait values is desirable.
[c] Combination of the location [Dikopshof (D), Gudow (G), Irlbach (I), Morgenrot (M)] and the year [2003 (03), 2004 (04)].

flowering and biomass ranging from −0.31 to −0.56, and positive correlations with ears per m^2, days until heading and harvest index of 0.26, 0.33 and 0.55, respectively. Ears per m^2 showed a positive correlation with days until heading, harvest index and yield between 0.15 and 0.58 and a negative correlation with plant height, lodging at flowering and thousand grain weight of −0.60, −0.42 and −0.21, respectively. In order to test the hypothesis that a high percentage of exotic germplasm P[*Hsp*] has a negative influence on agronomic performance, the proportion of exotic alleles in a BC_2DH lines was calculated. No strong correlations between P[*Hsp*] and other traits were recorded. However, weak negative correlations of P[*Hsp*], were revealed with days until heading, biomass, thousand grain weight and yield and weak positive correlations were found with brittleness and lodging at flowering.

QTL analysis

The ANOVA revealed 248 significant marker trait associations with 175 marker main effects and 24 marker environment interaction effects. For 49 markers trait associations both, the marker main and the M × E interaction effects were significant. Due to linkage between markers, these effects were summarised to 86 putative QTLs for nine agronomic traits (Table 3, Fig. 1). At 60 QTLs the marker main effect, at five QTLs the M × E interaction effect, and at 21 QTLs both effects

Table 2 Correlation coefficients (*r*) according to Pearson between nine traits and the percentage of exotic germplasm (P[*Hsp*]) in the BC_2DH population S42

Traits	EAR	HEA	HEI	HI	LOF	MAS	TGW	YLD	P[*Hsp*]
BRT	−0.26 ***	−0.24 ***	0.32 ***	−0.43 ***	0.34 ***	−0.06	0.03	−0.50 ***	0.23 ***
EAR		0.15 *	−0.60 ***	0.58 ***	−0.42 ***	0.10	−0.21 ***	0.26 ***	0.08
HEA			−0.46 ***	0.43 ***	−0.65 ***	0.17 *	−0.15 **	0.33 ***	−0.13 *
HEI				−0.85 ***	0.87 ***	0.56 ***	0.10	−0.56 ***	0.02
HI					−0.80 ***	−0.61 ***	−0.09	0.53 ***	−0.07
LOF						−0.47 ***	−0.07	−0.55 ***	0.14 *
MAS							0.16	−0.31 ***	−0.07 *
TGW								0.07	−0.23 ***
YLD									−0.35 ***

The quantitative traits are defined in Table 1. For calculating correlations, the least square means of the trait performance of each BC_2DH line was averaged across environments. The significance thresholds for *r* values are * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3 List of 86 putative QTLs for nine traits detected in S42

QTL[a]	SSR	Chr[b]	Pos[c]	Range[d] (cM)	Bin[e] Range	Effect[f]	R^{2g} %	[*Hv*][h]	[*Hsp*][i]	RP[*Hsp*][j]	Cand genes[k] Corresp. QTL
BRT											
QBrt.S42-3H.a	HVITR1	3H	49	25–70	3–6	M	39.6	1.1	2.0	42.2	*btr1*, *btr2*[1]
QBrt.S42-3H.b	HVM62	3H	165	165	14	M	2.1	1.9	2.0	3.7	
QBrt.S42-5H.a	MGB338	5H	85	85	8	M	3.8	1.8	2.0	7.2	*Hst-7L*[2]
QBrt.S42-6H.a	Bmag613	6H	112	112–135	9–10	M	5.2	1.9	2.0	4.8	
QBrt.S42-7H.a	BMS64	7H	146	93–178	6–12	M	5.6	1.9	2.0	7.8	
EAR											
QEar.S42-1H.a	GBMS143	1H	162	162	14	M + I	3.7	776.4	717.9	−7.5	
QEar.S42-2H.a	HVM36	2H	17	17	2	M + I	6.6	760.7	831.0	9.2	
QEar.S42-2H.b	GMS3	2H	86	67–86	6–8	M + I	28.0	738.3	859.4	16.4	
QEar.S42-3H.a	MGB410	3H	65	65–70	5–6	M	7.4	778.6	673.7	−13.5	
QEar.S42-3H.b	HV13GEIII	3H	155	130–190	10–16	M	6.5	783.4	712.7	−9.0	
QEar.S42-4H.a	HVOLE	4H	21	21–25	3	M	5.1	780.7	708.6	−9.2	
QEar.S42-4H.b	MGB396	4H	95	95	8	M	5.7	759.6	820.1	8.0	
QEar.S42-4H.c	HVM67	4H	180	125–190	9–13	M + I	27.7	737.4	853.1	15.7	HVBAMY×Ear[4]
QEar.S42-5H.a	MGB384	5H	0	0	2	M	6.9	781.0	702.0	−10.1	
QEar.S42-5H.b	Bmag337	5H	43	24–85	4–8	M	5.5	781.2	714.9	−8.5	
QEar.S42-6H.a	GBM1008	6H	135	112–155	9–14	M	5.9	784.2	724.8	−7.6	
HEA											
QHea.S42-1H.a	GBMS12	1H	130	130–144	13	M + I	4.7	72.1	73.4	1.8	*Vrn-H3*[5]
QHea.S42-2H.a	GBM1052	2H	42	17–86	2–8	M + I	17.4	72.7	67.0	−7.9	*Ppd-H1*[5]Qhd.2.1[6]GMS3×Hea[3,4]
QHea.S42-2H.b	EBmac415	2H	146	143–146	13	M + I	3.5	72.7	70.5	−3.0	Ebmac415×Hea[3,4]
QHea.S42-3H.a	HVLTPPB	3H	25	25–30	3	M + I	4.3	72.6	69.6	−4.2	EBmac705×Hea[4]
QHea.S42-3H.b	HV13GEIII	3H	155	155–175	13–15	M + I	8.2	72.9	70.7	−3.0	*denso*[5]
QHea.S42-4H.a	HDAMYB	4H	190	180–190	12–13	M + I	6.3	72.1	73.6	2.2	*Vrn-H2*[5]HVM67×Hea[3,4]
QHea.S42-6H.a	Bmac316	6H	6	6	1	M	2.3	72.7	71.2	−2.0	HvW1×Hea[4]
QHea.S42-6H.b	EBmac624	6H	107	96–107	5–7	M	4.6	72.8	71.3	−2.1	*eps6L.1*[5]GMS6×Hea[4]
QHea.S42-7H.a	Bmag206	7H	19	19	1	M	3.1	72.6	70.6	−2.7	*eps7S*[5]
QHea.S42-7H.b	BMS64	7H	146	146	8	M + I	4.3	72.7	70.7	−2.7	*eps7L*[5] BMS64×Hea[3] EBmac755×Hea[4]
HEI											
QHei.S42-1H.a	HVABAIP	1H	144	144	13	M + I	3.1	81.6	77.1	−5.6	*Vrn-H3*[5]
QHei.S42-1H.b	GBMS143	1H	162	162	14	M + I	2.8	80.5	86.1	6.9	
QHei.S42-2H.a	GBM1052	2H	42	17–42	2–4	M + I	3.1	81.0	71.5	−11.7	*Ppd-H1*[5]
QHei.S42-2H.b	GMS3	2H	86	80–107	7–9	M	14.8	83.3	73.6	−11.5	*sdw3*[7], GMS3×Hei[4]
QHei.S42-3H.a	HVITR1	3H	49	25–70	3–6	M + I	7.4	81.1	100.0	23.4	EBmac705×Hei[4]
QHei.S42-3H.b	HV13GEIII	3H	155	130–175	10–15	M + I	19.9	78.5	92.0	17.2	*denso*[5]
QHei.S42-4H.a	HVM67	4H	180	125–190	9–13	M + I	12.0	83.1	74.8	−10.0	*Vrn-H2*[5] HvBamy×Hei[3,4]
QHei.S42-5H.a	Bmag337	5H	43	43–48	5	M	5.8	79.5	86.9	9.3	Qph5.1[6]
QHei.S42-7H.a	Bmag7	7H	27	27	2	M	3.3	80.1	89.0	11.2	
QHei.S42-7H.b	HVSS1	7H	62	62	5	M	2.8	80.3	92.0	14.6	
QHei.S42-7H.c	BMS64	7H	146	146	8	I	0.9	80.2	83.9	4.6	BMS64×Hei[3]
HI											
QHi.S42-1H.a	HVABAIP	1H	144	144	13	M	8.7	0.59	0.63	7.6	
QHi.S42-1H.b	GBMS143	1H	162	162	14	M	3.9	0.60	0.56	−6.1	
QHi.S42-2H.a	HVM36	2H	17	17–27	2–3	M	5.5	0.59	0.63	6.9	HVM36×Hi[4]
QHi.S42-2H.b	Ebmac684	2H	80	67–92	6–8	M	9.9	0.59	0.63	7.6	GMS3×Hi[4]
QHi.S42-3H.a	Bmag603	3H	70	49–70	4–6	M	18.4	0.60	0.53	−12.2	Bmag209×Hi[4]
QHi.S42-3H.b	HV13GEIII	3H	155	155–190	13–16	M	18.4	0.61	0.53	−12.5	*denso*[5]
QHi.S42-4H.a	HVOLE	4H	21	21	3	M	2.2	0.60	0.57	−5.0	HVB23D×Hi[3]
QHi.S42-4H.b	EBmac701	4H	130	125–150	9–11	M	4.1	0.59	0.62	5.5	
QHi.S42-4H.c	HVM67	4H	180	180–190	12–13	M	12.7	0.58	0.63	8.6	*Vrn-H2*[5],
QHi.S42-5H.a	Bmag357	5H	48	12–48	3–5	M	8.8	0.61	0.55	−8.6	
QHi.S42-6H.a	HVM74	6H	103	103–107	6–76	M	2.6	0.60	0.58	−4.3	
QHi.S42-7H.a	Bmag7	7H	27	19–27	1–2	M	6.5	0.60	0.53	−11.9	HVM4×Hi[3]
LOF											
QLof.S42-2H.a	GMS3	2H	86	80–86	7–8	M	4.4	2.7	1.6	−39.9	*Ppd-H1*[5]GMS3×Lof[3]
QLof.S42-2H.b	GBM1016	2H	139	139–146	12–13	M	3.5	2.4	3.9	62.9	Qlg2.1[6]
QLof.S42-3H.a	HVITR1	3H	49	25–70	3–6	M	5.6	2.5	6.4	154.7	
QLof.S42-3H.b	HV13GEIII	3H	155	130–175	10–15	M	20.2	1.9	5.1	166.7	*denso*[5]
QLof.S42-4H.a	HVM67	4H	180	180	12	M	5.7	2.8	1.6	−41.4	*Vrn-H2*[5],
QLof.S42-5H.a	Bmag337	5H	43	43	5	M	4.2	2.2	3.7	68.2	Bmag337×Lof[4] Qlg5.1[6]
QLof.S42-6H.a	HVM74	6H	103	96–107	5–7	M	3.3	2.2	3.3	47.1	
QLof.S42-7H.a	Bmag7	7H	27	27	2	M	2.6	2.3	4.1	79.8	
QLof.S42-7H.b	BMS64	7H	146	146	8	M	3.0	2.3	3.5	49.5	

Table 3 (Contd.)

MAS											
QMas.S42-2H.a	GMS3	2H	86	67–107	6–9	M	8.4	29.6	25.2	−15.0	
QMas.S42-3H.a	HVM62	3H	165	130–190	10–16	M	9.0	27.6	33.0	19.6	
QMas.S42-4H.a	MGB396	4H	95	95	8	M	2.8	29.0	26.2	−9.8	Ebmac679×Mas[4]
QMas.S42-4H.b	HVM67	4H	180	170–190	12–13	M	4.9	29.5	26.2	−11.1	
QMas.S42-5H.a	Bmag337	5H	43	43	5	M	6.8	27.7	32.6	17.4	
QMas.S42-7H.a	Bmag7	7H	27	19–27	1–2	M	4.1	28.2	34.0	20.8	
TGW											
QTgw.S42-2H.a	GBM1035	2H	27	17–86	2–8	M	7.7	42.7	44.1	3.2	GMS3×Tgw[3] HVM36xTgw[4]
QTgw.S42-3H.a	HVM60	3H	110	110–130	9–10	M	8.4	42.7	44.0	3.0	HVM60×Tgw[4]
QTgw.S42-3H.b	MGB358	3H	175	165–175	14–15	M	11.8	43.2	41.6	−3.6	
QTgw.S42-4H.a	MGB396	4H	95	95	8	M + I	10.2	43.3	41.9	−3.3	
QTgw.S42-4H.b	EBmac701	4H	130	125–190	9–13	M	33.6	43.5	40.9	−5.9	HvBAMY×Tgw[4]
QTgw.S42-5H.a	MGB357	5H	165	165	14	M	4.6	43.0	41.0	−4.7	Bmag337×Tgw[3] GMS27×Tgw[4]
QTgw.S42-6H.a	GBM1049	6H	40	40	3	I	4.2	43.1	42.1	−2.4	
QTgw.S42-6H.b	HVM74	6H	103	96–103	5–6	I	3.6	43.1	42.3	−1.9	Qtgw6.1[6]
QTgw.S42-7H.a	BMS64	7H	146	146–181	8–12	M	8.5	43.1	41.4	−4.1	Bmag135×Tgw[3]
YLD											
QYld.S42-1H.a	Bmag105	1H	75	52–85	6–8	M	6.2	60.3	49.6	−17.7	Qyld.1.1[6]
QYld.S42-2H.a	GBM1035	2H	27	17–27	2–3	I	1.0	59.1	60.4	2.3	*Ppd-H1*[5] *Qyld2.1*[6] HVM36×Yld[4]
QYld.S42-2H.b	HVTUB	2H	92	86–92	8	I	1.7	59.0	60.2	2.0	GMS3 × Yld[4]
QYld.S42-2H.c	GBM1016	2H	139	122–146	10–13	M	3.3	60.0	51.0	−15.0	HVM54×Yld[3]
QYld.S42-3H.a	HVLTPPB	3H	25	25–70	3–6	M + I	13.7	60.2	39.9	−33.7	*btr1*, *btr2*[1]
QYld.S42-3H.b	HV13GEIII	3H	155	155–175	13–15	M + I	9.8	60.9	51.9	−14.8	*denso*[5]Qyld.3.1[6]
QYld.S42-4H.a	GBM1015	4H	170	125–190	9–13	M + I	3.1	58.4	62.5	7.1	EBmac679×Yld[4]
QYld.S42-5H.a	Bmag337	5H	43	43	5	M	4.4	60.3	54.0	−10.4	
QYld.S42-5H.b	MGB338	5H	85	85	8	M	2.1	60.1	53.9	−10.2	HvUDPGPP×Yld[4]
QYld.S42-5H.c	AF04394A	5H	137	126–137	10–11	M	3.1	60.2	53.5	−11.2	GMS27×Yld[3,4]
QYld.S42-6H.a	Bmag613	6H	112	96–112	5–9	M	4.9	60.7	55.4	−8.7	
QYld.S42-7H.a	Bmag7	7H	27	27	2	M	2.2	60.0	52.8	−12.0	
QYld.S42-7H.b	BMS64	7H	146	146	8	M	4.0	60.2	53.2	−11.6	EBmac755×Yld[3]

[a] QTL names consist of the qualifier "Q", the trait abbreviation, the population name, the chromosomal location and a consecutive character to discriminate two or more QTLs per chromosome. Linked significant markers (≤ 20 cM) were interpreted as one QTL.
[b] Chromosomal localisation of the marker
[c] Position of the listed SSR marker in cM taken from von Korff et al. (2004)
[d] CentiMorgan range from the first to the last significant marker in a group
[e] Genotyped markers were assigned to bins according to information by Kleinhofs and Graner (2001) and the OWB mapping population (Costa et al. 2001, http://www.barleyworld.org). If several linked markers are significant, the bin range is given
[f] A putative QTL was assumed in the vicinity of a marker locus, if the marker main effect (M) or the M × E interaction (I) was significant in the 3-factorial ANOVA with $P < 0.01$
[g] R^2_M and $R^2_{(M \times E)}$: Proportion of the genetic variance, which is explained by the marker main effect (if Effect contains 'M') or explained by the M × E interaction effect (if Effect = 'I'), respectively.
[h] Least square means of trait value across all tested environments for BC_2DH lines carrying the elite genotype (*Hv*) at the given marker locus
[i] Least square means of trait value across all tested environments for BC_2DH lines carrying the exotic genotype (*Hsp*) at the given SSR marker locus
[j] Relative performance: (*Hsp-Hv*) × 100/*Hv*), where *Hv* and *Hsp* are the least square means of lines with the elite and exotic genotype, respectively, at the given SSR marker locus
[k] Candidate genes or corresponding QTLs published in: 1 Franckowiak (1997), 2 Kandemir et al. (2000), 3 Pillen et al. (2003), 4 Pillen et al. (2004), 5 Laurie et al. (1995), 6 Li et al. (2004), 7 Gottwald et al. (2004). At underlined QTLs, the exotic allele showed the same qualitative effect as in this study.

were significant. The exotic genotype improved the trait performance at 31 (36.0 %) of 86 QTLs. In the following, the QTLs are presented for each trait separately.

Brittleness (BRT)

For BRT, the analysis revealed five QTLs with marker main effects located on chromosomes 3H, 5H, 6H and 7H. The exotic allele was responsible for brittleness at all detected QTLs. The QTL QBrt.S42-3H.a exerted the strongest effect on brittleness. This QTL explained 39.6% of the genetic variance and the exotic allele at this locus increased BRT by 42.2% relative to the elite genotype.

Ears per m^2 (EAR)

For EAR, eleven QTLs with a marker main effect were detected on all chromosomes with the exception of 7H. At four loci the marker main effect and the M × E interaction effect were significant. At four QTLs the exotic allele increased EAR by up to 16.4% at QEar.S42-2H.b. The latter QTL explained 28.0% of the genetic variance. At the remaining QTLs, the exotic

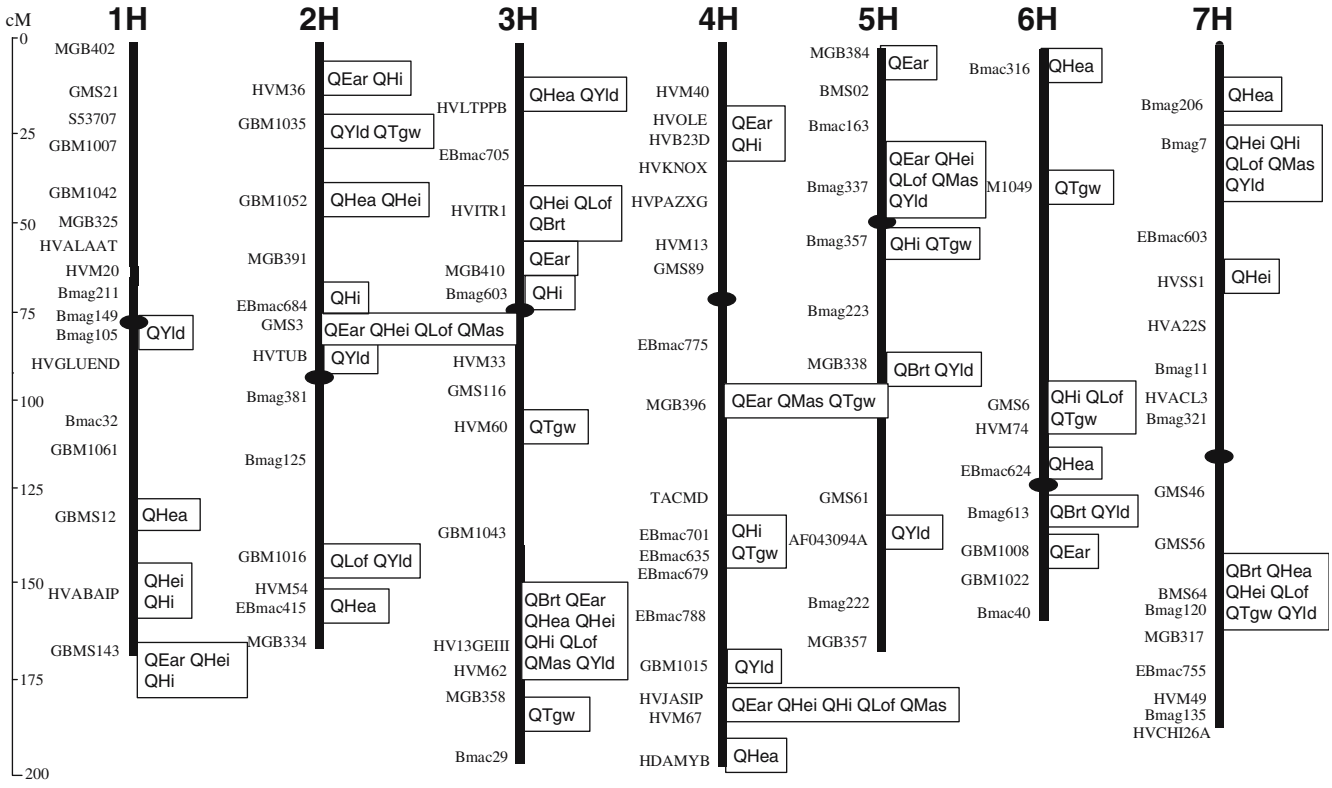

Fig. 1 QTL map of the population S42 showing 86 putative QTLs detected for nine agronomic traits. The putative QTLs are indicated to the right of the SSR marker, which showed the highest *F*-value of a group of linked significant markers (see Table 3). Trait abbreviations of QTLs follows Table 1

allele was associated with a reduced number of EAR of up to 13.5% at QEar.S42-2H.c.

Days until heading (HEA)

Ten QTLs for HEA were located on all chromosomes with the exception of chromosome 5H. All loci revealed a significant marker main effect, while seven loci exhibited in addition a significant M × E interaction effect. At eight QTLs the exotic allele reduced the number of days until heading. At the QTL QHea.S42-2H.a, explaining 17.4% of the genetic variance, the exotic allele was associated with a reduced heading time of 7.9%.

Plant height (HEI)

Eleven QTLs were detected for HEI. Six of the ten QTLs with marker main effect also exhibited an M × E interaction effect. At one QTL only the $M \times E$ interaction effect was significant. At four QTLs the exotic allele displayed a desirable decrease in plant height of up to 11.7% (QHei.S42-2H.a). At seven QTLs the exotic allele increased plant height by up to 23.4% (QHei.S42-3H.a). A maximum of explained genetic variance was found at QHei.S42-3H.b (19.9%).

Harvest index (HI)

For HI, twelve QTLs with a marker main effect were identified on all seven chromosomes. At five loci the exotic allele increased HI by up to 8.6% (QHi.S42.4H.c). At seven QTLs, the exotic allele decreased HI. The strongest QTLs, QHi.S42.3H.a and QHi.S42.3H.b, explained 18.4% of the genetic variance each and reduced HI by 12.2% and 12.5%, respectively.

Lodging at flowering (LOF)

Nine QTLs with a marker main effect were detected for LOF on chromosomes 2H to 7H. At two QTLs, QLof.S42-2H.a and QLof.S42-4H.a, which explained 4.4% and 5.7% of the genetic variance, the exotic allele reduced lodging by 39.9% and 41.4%, respectively. At the remaining QTLs the exotic allele increased lodging by up to 166.7% (QLof.S42-3H.b).

Vegetative dry biomass (MAS)

For the trait MAS, six QTLs with marker main effects were detected on chromosomes 2H to 5H and 7H. At three QTLs the exotic allele increased MAS by up to

20.8% at QMas.S42-7H.a. A maximum of explained genetic variance was found at QMas.S42-3H.a (9.0%).

Thousand grain weight (TGW)

Nine QTLs were detected for TGW and located on chromosomes 2H to 7H. For seven QTLs the marker main effect, for two QTLs only the $M \times E$ interaction effect and for one QTL both effects were significant. At two QTLs, QTgw.S42.2H.a and QTgw.S42-3H.a, the exotic allele increased TGW by 3.2% and 3.0%, respectively. At the remaining QTLs the exotic allele reduced TGW. A maximum of explained genetic variance was found at QTgw.S42-4H.b (33.6%).

Yield (YLD)

Altogether 13 QTLs for yield were located on all seven chromosomes. Eleven loci exhibited a significant marker main effect, two loci a significant M × E interaction and three loci both, a marker main and a M × E interaction effect. The exotic allele increased yield at three QTLs by up to 7.1 % (QYld.S42-4H.a). At the majority of QTLs the exotic allele reduced grain yield by up to 33.7% (QYld.S42-3H.a). A maximum of explained genetic variance was found at QYld.S42-3H.a (13.7%).

Discussion

QTL analysis: statistical model

The QTL model used in this study accounted for $M \times E$ interaction and thereby provided a test for estimates regarding the relative importance of the QTL by environment interaction in the total genetic variation. According to Haldane (1947) genotype environment interactions have only important implications for marker assisted selection if genotypes switch ranks from one environment to another. In this study, several $M \times E$ interactions were obviously crossover interactions, with favourable effects of the exotic allele in some environments, but negative effects in other environments (indicated with 'I' in Table 2). However, the majority of $M \times E$ interaction effects (80.7%), coincided with marker main effects ('$M+I$' in Table 2) and were only due to changes in the magnitude of the effects. These QTLs may, therefore, still be used for marker assisted selection across environments. Compared to Pillen et al. (2003 and 2004), the factor BC_2DH line nested in the marker genotype was included into the model. This factor accounted for the variation within the two genotype classes at a marker locus due to the presence of additional introgressions in the BC_2DH lines. The inclusion of this additional factor allowed us, thus, to reduce the residual variance in the ANOVA and to increase the power of QTL detection.

QTL analysis: comparison with candidate genes and other QTL analyses in barley

The results of the present QTL analysis in S42 were compared with studies of candidate genes in barley and three AB-QTL analyses carried out in barley by Pillen et al. (2003, 2004) and Li et al. (2004). Pillen et al. (2003, 2004) conducted two separate AB-QTL analyses to assess agronomic performance in two BC_2F_2 populations 'A101' and 'H101' derived from crosses between the wild barley accession ISR101-23 with the feeding barley cultivars Apex (A) and Harry (H), respectively. Li et al. (2004) conducted an AB-QTL analysis in a BC_3DH population derived from the spring barley cultivar Brenda and the exotic accession HS213. For 48 of 86 QTLs detected in this study, at least one corresponding quantitative or qualitative locus from the literature was recorded (Table 3). Although the donor and recipient germplasm differed between the present and the above mentioned AB-QTL studies, the exotic alleles exhibited the same qualitative effect at 31 out of 43 (72.1%) corresponding QTL locations. The exotic alleles are thus often similar in their effects and clearly different from the elite alleles. The effectiveness of the exotic introgressions in different genetic backgrounds gives a first indication that alleles from these donors might not yet be present in adapted germplasm.

The QTLs for different traits were often mapped on the same or adjacent locations, forming several clusters (Figure 1). The strong effects of exotic introgressions on chromosome 2H on almost all analysed quantitative traits was also found by Pillen et al. (2003, 2004) and Li et al. (2004). And at the QTL on chromosome 4H the exotic allele increased EAR, HI and YLD and decreased HEI, LOF, MAS and TGW. These findings were in agreement with the reported positive correlations between EAR, HI and YLD and the negative correlation of EAR with HEI. In the following, the QTL results for the analysed traits will be discussed separately.

Brittleness

Wild barley carries two complementary and dominant genes on chromosome 3H, *Btr1* and *Btr2*, for the formation of a brittle rachis, whereas cultivated barley carries recessive alleles at either of the loci, resulting in a non-brittle rachis (Franckowiak 1997). We detected a corresponding major QTL (QBrt.S42-3H.a) on the short arm of chromosome 3H, albeit spanning 45 cM. This QTL explained 39.6% of the genetic variance, while the remaining loci had minor effects on brittleness. Indeed, several studies have reported segregation ratios for brittleness, which do not fit the two complementary gene models, but suggested the presence of additional loci (Matus et al. 2003). Komatsuda et al. (2004) detected two minor QTLs for brittleness on chromosomes 5H and 7H coinciding with the position of the QTLs QBrt.S42-5H.a and QBrt.S42-7H.a. The QTL on

chromosome 5H may also be identical to the weak rachis QTL *Hst-7L* detected by Kandemir et al. (2000).

Time to heading

Wild barley is characterised by early and heterogeneous flowering, presumably as an adaptation strategy to drought prone environments. Indeed, in the majority of QTLs in S42, the exotic allele decreased time to heading. The QTL QHea.S42-2H.a, explaining 17.4% of the genetic variance, coincides with the major flowering QTL on chromosome arm 2HS detected by Pillen et al. (2003) and Li et al. (2004). The same region harbours the photoperiod response gene *Ppd-H1*, which promotes early flowering under long day conditions (Laurie et al. 1995). The QTLs QHea.S42-1H.a and QHea.S42-4H.a mapped to the same location as the vernalisation response genes *Vrn-H3* and *Vrn-H2* on chromosomes 1H and 4H, respectively (Laurie et al. 1995). It is interesting to note, that at these two QTLs, which coincide with known vernalisation response genes, the elite alleles reduced time to heading compared to the exotic alleles. Although vernalisation response is commonly displayed by winter forms of cereals, our data indicate, that vernalisation response may have also been selected in German spring barley cultivars as an adaptation to low temperatures at the beginning of the vegetation period. The QTL QHea.S42-3H.b mapped close to the *denso* gene, which is known to be associated with a delay in flowering time (Barua et al. 1993; Laurie et al. 1995). The elite parent Scarlett carries the *denso* gene and as such contributed the allele, which delayed time to heading. Laurie et al. (1995) mapped a number of flowering QTLs termed *earliness per se* (*eps*) QTLs, which act independently from environmental cues. In S42, three QTLs on chromosomes 6H and 7H could be identified which correspond to the genes *eps6L.1*, *eps7S* and *eps7L* (see Table 3).

Plant height and lodging

The majority of QTLs for lodging coincided with QTLs for plant height according to the strong positive correlation found between plant height and lodging. The QTLs QLof.S42-2H.a and QHei.S42-2H.b, located on the short arm of chromosome 2H, for example, reduced lodging by 39.9% and plant height by 11.5%. A corresponding candidate gene for QHei.S42-2H.b is the dwarfing gene *sdw3* which has been mapped by Gottwald et al. (2004). This gene conveys insensitivity to gibberellic acid and might be homoeologous to the *Rht* series of dwarfing genes in wheat (Börner et al. 1998). Further upstream on the short arm of chromosome 2H, Laurie et al. (1994) mapped the *Ppd-H1* gene in the Igri × Triumph DH population and reported a strong pleiotropic effect of the region on plant height. The *Ppd-H1* gene is thus a candidate gene for the corresponding QTL QHei.S42-2H.a. The QTL QHei.S42-3H.b, which coincides with the strongest QTL for lodging (QLof.S42-3H.b), maps to the same genomic region as the dwarfing gene *denso*. It has been shown that this gene, which is present in Scarlett, reduces height and lodging (Bezant et al. 1996; Yin et al. 1999). The genomic region on 4H affecting plant height and lodging also exerted a significant effect on height in the populations A101 and H101 (Pillen et al. 2003, 2004). The exotic allele reduced height in the present study by 10.0% in S42 and by 10.4 and 5.9% in A101 and H101, respectively.

Yield

The majority of QTLs analyses for yield and yield component traits in barley were conducted with early balanced populations (Hayes et al. 1993, 1996, Thomas et al. 1995; Tinker et al. 1996; Bezant et al. 1997, Yin et al. 1999, 2002, Marquez-Cedillo 2000), while only four QTLs analyses have so far been conducted in advanced backcross barley populations (Matus et al. 2003; Pillen et al. 2003, 2004, Li et al. 2004). Some QTLs in classical QTL studies consistently mapped to the same genomic regions despite a wide range of different germplasms used. These are predominantly yield QTLs identified on chromosome arms 2HS, 3HL and 6HL. Their effect on yield are commonly explained by pleiotropic effects of the photoperiod response gene *Ppd-H1* on 2HS (Li et al. 2004), the dwarfing gene *denso* on 3HL (Thomas et al. 1995), and linkage to the *Amy1* locus on 6HL (Powell et al. 1990; Bezant et al. 1997). These genomic regions also revealed significant effects on yield in this study (QYld.S42-2H.a, QYld.S42-3H.b and QYld.S42-6H.a) with the favourable QTL allele contributed by the elite parent. Other yield QTLs detected in this study obviously did not coincide with yield QTLs identified in classical QTL studies. The QTL QYld.S42-3H.a, where the exotic allele reduced yield by 33.7%, coincided with the major QTL for brittleness (QBrt.S42-3H.a) and the candidate genes *btr1* and *btr2* on the short arm of chromosome 3H. Further yield QTLs on chromosomes 3H (QYld.S42-3H.b), 5H (QYld.S42-5H.b), 6H (QYld.S42-6H.a) and 7H (QYld.S42-7H.b), mapped to corresponding QTLs identified for brittleness. The negative effect of these exotic QTL alleles on yield may, therefore, be due to exotic alleles coding for brittleness.

A maximum yield increase of 7.1% due to the presence of an exotic allele was recorded at the QTL QYld.S42-4H.a on chromosome 4H. Interestingly, a comparison with other AB-QTL analyses revealed that the QTLs with the strongest favourable effect of the exotic allele detected in the populations A101 and H101 (Pillen et al. 2003, 2004) also mapped to chromosome 4H. Here, it is worthwhile to point out that the exotic accession ISR101-23 used by the above mentioned studies was also collected from Israel. Pillen et al. (2000), however, demonstrated that ISR101-23 was genetically different from ISR42-8 based on SSR marker

data. In addition, fragment lengths scored for all SSR markers on 4H differed between ISR42-8 and ISR101-23 (data not shown). Further concordances of QTL positions with yield QTLs detected by Li et al. (2004) and Pillen et al. (2003, 2004) were found on chromosome arms 1HS, 2HL, 5HL and 7HL. In all cases, negative effects of the exotic allele were recorded. In addition, Li et al. (2004) detected a yield QTL on chromosome 3H coinciding with the QTL QYld.S42-3H.b.

Yield components

In this study, the yield components ears per m^2 and thousand grain weight were analysed next to harvest index and vegetative biomass. Yield components generally show negative correlations, as it was also detected in this study, where EAR and TGW exhibited a negative correlation of −0.21 (Table 2). For the manipulation of yield it is particularly interesting to find alleles, which break these genetic correlations. Indeed, the exotic alleles on the short arm of chromosome 2H revealed positive effects on EAR (QEar.S42-2H.a and QEar.S42-2H.b) and TGW (QTgw.S42-2H.a) which also resulted in a significant yield increase (QYld.S42-2H.a and QYld.S42-2H.b). A second coincidence of QTLs can be found on chromosome 4H. Here, the favourable effect of the exotic alleles on EAR (QEar.S42-4H.c) and YLD (QYld.S42-4H.a) was coupled with a negative effect on TGW (QTgw.S42-4H.b). Reciprocal effects, however, may also arise when trait values are indirectly inferred. This holds true for the trait HI, which was inferred from the traits MAS and single plant yield. Accordingly, QTLs detected for MAS on chromosomes 2H, 3H, 4H and 7H were also significant for HI but exhibited opposing effects on both traits.

The present study has demonstrated that wild barley does harbour favourable alleles, which have the potential to improve quantitative agronomic traits and can enrich the genetic basis of cultivated barley. In this study, exotic alleles with a favourable effect on yield and yield component traits were detected, in particular on the short arm of chromosome 2H and the long arm of chromosome 4H. Exotic alleles on chromosome 2H improved the performance of the traits EAR, HEA, HEI, HI, LOF, TGW and YLD. Similarly, exotic alleles on chromosome 4H exhibited favourable effects on EAR, HEI, HI, LOF and YLD. In future, the effects of the favourable exotic alleles at the two genomic regions on 2H and 4H are of particular interest and will be verified (1) in a second AB population derived from the same donor accession and (2) in near-isogenic lines (NILs). The identification of markers linked to the favourable QTL alleles as well as the advanced backcross population structure employed in this study will allow us to rapidly isolate these QTLs in NILs. Markers closely linked to the QTLs can be used to select against deleterious wild characters, like brittleness, and to select lines carrying the favourable alleles using marker assisted selection. In addition, pure introgression lines (ILs) are currently generated from pre-selected candidate lines of the population S42 (von Korff et al. 2004). In future, these ILs will be exploited in order to verify the QTL effects and to systematically study the molecular basis of these QTLs.

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