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AB-QTL analysis in spring barley: III. Identification of exotic alleles for the improvement of malting quality in spring barley (*H. vulgare* ssp. *spontaneum*)

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Abstract Malting quality is genetically determined by the complex interaction of numerous traits which are expressed prior to and, in particular, during the malting process. Here, we applied the advanced backcross quantitative trait locus (AB-QTL) strategy (Tanksley and Nelson, Theor Appl Genet 92:191–203, 1996), to detect QTLs for malting quality traits and, in addition, to identify favourable exotic alleles for the improvement of malting quality. For this, the BC_2DH population S42 was generated from a cross between the spring barley cultivar Scarlett and the wild barley accession ISR42-8 (*Hordeum vulgare* ssp. *spontaneum*). A QTL analysis in S42 for seven malting parameters measured in two different environments yielded 48 QTLs. The exotic genotype improved the trait performance at 18 (37.5%) of 48 QTLs. These favourable exotic alleles were detected, in particular, on the chromosome arms 3HL, 4HS, 4HL and 6HL. The exotic allele on 4HL, for example, improved α-amylase activity by 16.3%, fermentability by 0.8% and reduced raw protein by 2.4%. On chromosome 6HL, the exotic allele increased α-amylase by 16.0%, fermentability by 1.3%, friability by 7.3% and reduced viscosity by 2.9%. Favourable transgressive segregation, i.e. S42 lines exhibiting significantly better performance than the recurrent parent Scarlett, was recorded for four traits. For α-amylase, fermentability, fine-grind extract and VZ45 20, 16, 2 and 26 S42 lines, respectively, surpassed the recurrent parent Scarlett. The present study hence demonstrates that wild barley does harbour valuable alleles, which can enrich the genetic basis of cultivated barley and improve malting quality traits.

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

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Introduction

The improvement of malting quality ranges among the most important breeding goals in spring barley. Malting quality is determined by the complex

interaction of several traits expressed during grain development, germination and the malting process. The development of molecular markers and genetic linkage maps has allowed to identify and map quantitative trait loci (QTL) for malting quality in a number of different crosses (Hayes et al. 1993, 2003; Han et al. 1995, 1997, 2004; Mather et al. 1997; Thomas et al. 1996; Marquez-Cedillo et al. 2000, Zale et al. 2000, Barr et al. 2003a, b; Fox et al. 2003; Karakousis et al. 2003; Read et al. 2003; Gao et al. 2004). So far, breeders and scientists have primarily targeted elite germplasm from different geographic regions to improve and analyse malting quality traits in barley. Modern plant breeding, however, has reduced the genetic variability among domesticated barley cultivars (Forster et al. 1997; Baek et al. 2003). In the wake of this development, the exploitation of natural variation in exotic germplasm for the improvement of cultivars has received increasing attention. Ahokas and Naskali (1990a, b) could show that *H. spontaneum* accessions from Israel and Jordan exhibit a wide variation for malting quality traits, such as α- and β-amylase, β-glucanase, and other hydrolases. Nevertheless, only few studies have attempted to use wild barley to improve malting quality, and these have primarily focused on single genes. Investigation of natural variation in the β-amylase gene *Bmy1*, for example, led to the identification of a new haplotype in wild barley encoding for a β-amylase isoform with increased thermostability (Eglington et al. 1998; Erkkilä et al. 1998). Only two QTL studies involving exotic germplasm have so far been conducted for malting quality (Pillen et al. 2003; Li et al. 2005). Pillen et al. (2003) analysed protein content, friability and water absorption in a cross between the feed barley Apex and the wild barley accession ISR101-23, and Li et al. (2005) examined protein content, malt extract and friability in the population Brenda/HS213. Although Pillen et al. (2003) and Li et al. (2005) reported that most exotic alleles had a negative influence on malting performance, a few exotic alleles clearly improved the analysed trait. These findings together with the large genetic diversity identified in wild barley, encourage further studies of the effect of exotic alleles on malting quality.

Therefore the aim of the present study was to detect favourable exotic alleles for malting quality using the AB-QTL strategy (Advanced backcross QTL) as proposed by Tanksley and Nelson (1996). The AB-QTL analysis was conducted with the BC_2DH population S42 derived from the cross of the malting barley cultivar Scarlett, a high quality malting variety, with the wild barley accession ISR42-8 from Israel. Favourable effects of the exotic donor accession ISR42-8 on disease resistances and agronomic traits have already been reported by von Korff et al. (2005, 2006).

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, made from the cross Amazone $\times$ St. 2730e $\times$ Kym at Saatzucht Breun, with the Israeli wild barley accession ISR42-8 is described in detail in von Korff et al. (2004). The BC_2DH lines are derived from 12 BC_1 families with a mean number of progenies per BC_1-family of 25.1 (STD = 19.1) and from 76 BC_2-families with a mean of 4 lines (STD = 5.8) per BC_2-family.

Molecular characterisation

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

Cultivation of the DH-population

The population S42 was grown at four different locations and in the two consecutive years 2003, 2004 to investigate agronomic performance (von Korff et al. 2006). Due to the high costs of micromalting, samples from only two different locations could be selected for the analysis of malting quality. The selected test locations were the Dikopshof Research Station (D03, University of Bonn, West Germany), and the experimental station of the breeding company Nordsaat Saatzucht (G03, Gudow, North Germany). The field experiment was designed in randomised plots without replications. As a control, the recurrent parent Scarlett was tested with 20 replications per test location. Net plot sizes were 6.0 (D03) and 8.0 m^2 (G03). Nitrogen fertilization was 60 kg N ha^{-1} in D03 and 40 kg N ha^{-1} in G03 taking into account the

N_{min} content in the soil. Sowing with 300 (D03) and 330 (G03) kernels/m^2, and the application of growth regulators (D03, G03) and fungicides (D03, G03) were in accordance with local practices. The grain was harvested with a plot harvester at maturity, and the cleaned grain samples were stored at 4°C before analysis.

Malting quality analysis

Micromalting was performed in the laboratory of the Nordsaat Saatzucht (Böhnshausen, Germany) with 100 g of grain of a sieving fraction of >2.5 mm. The malting process consisted of the following program. Steeping comprised of 2 cycles of 8 h immersion and 16 h air-rest both at 14°C. Ex-steep moisture was targeted to reach 45.5% for all the samples. Since the water absorption rate was variable among samples, samples with less than 45.5% moisture were further steeped to reach the desired moisture. Samples were germinated at 14°C and 95% air humidity for 5 days. Kilning was carried out for 16 h at 80°C. Rootlets were mechanically removed prior to analysis. Raw protein was measured from 20 g of ground sample using NIR (NIRSystems 5000, FOSS GmbH, Hamburg). α-amylase activity was determined as dextrination time of a standardized starch solution in the presence of excess ß-amylase (EBC, European Brewing Convention).

The remaining quality characters, fermentability (= final attenuation), fine-grind extract, friability, viscosity and Hartong 45°C (VZ45), were determined using the methods recommended by the EBC (European Brewing Convention) or the MEBAK (Mitteleuropäische Brautechnische Analysenkommission) as listed in Table 1.

Statistical analyses

Statistical analyses were carried out with SAS version 9.1 (SAS Institute 2003). Genetic correlations between trait values were calculated with the least square means of BC_2DH lines averaged across both environments. Significant favourable transgression of S42 lines, where the trait value is improved compared to the recurrent parent Scarlett, was accepted when the least square means of a BC_2DH line surpassed the least square means of the control Scarlett by more than two standard deviations.

The detection of QTLs was carried out using the following mixed hierarchical model in the SAS general linear model (GLM) procedure:

$$Y_{ijkmn} = \mu + M_i + BC1_j + BC2_k(BC1_j) + E_m + M_i{*}E_m + RP + Hea + \varepsilon_{n(jikm),}$$

where μ is the general mean, M_i is the fixed effect of the i-th marker genotype, $BC1_j$ is the random effect of the j-th BC_1-family, $BC2_k(BC1_j)$ is the random effect of the k-th BC_2-family nested in the j-th BC_1-family, E_m is the random effect of the m-th environment, $M_i{*}E_m$ is the random interaction effect of the i-th marker genotype with the m-th environment, $\varepsilon_{n(jikm)}$ is the error of Y_{ijkmn}. Two co-variates, protein content (RP) and heading date (Hea) were added to the model, as protein content and developmental stage have been shown to affect malting quality parameters. Marker main effects with an FDR of 0.05 (false discovery rate, Benjamini and Yekutieli 2005) were interpreted as putative QTLs. Linked significant markers with a distance of ≤ 20 cM and showing the same effect were interpreted as a single putative QTL, and only the marker with the highest *F*-value from each group of linked loci is recorded. The relative performance of the homozygous exotic genotype (RP[*Hsp*]) were calculated as described in von Korff et al. (2005). The genetic variance explained by a marker (R^2_M) was calculated as follows:

$$R^2_M = SQ_M \,/\, SQ_{G,}$$

SQ_M corresponds to the sum of squares of M. SQ_G was calculated as the sums of squares of the BC_2DH lines in the following ANOVA model:

$$Y_{ijkm} = \mu + L_i + BC1_j + BC2_k(BC1_j) + E_m + \varepsilon_{m(jik),}$$

where L_i is the fixed effect of the i-th BC_2DH line, $BC1_j$ is the random effect of the j-th BC_1-family, $BC2_k(BC1_j)$ is the random effect of the k-th BC_2-family nested in the j-th BC_1-family and E_m is the random effect of the m-th environment. SQ_G was calculated for every marker separately to account for the occurrence of missing genotype data.

Table 1 Least square means, standard deviations and number of favourable transgressive lines for seven malting traits calculated across two environments for the population S42 and the recurrent parent Scarlett

Abbr	Trait	Reference[a]	Lsmeans[b]		Standard deviation[c]		Number of transgressive S42 lines[d]
			S42	Scarlett	S42	Scarlett	
AA	α-amylase activity of malt	EBC 4.13	341.5	377.3*	86.8	35.7	20 (6.6%)
FER	Fermentability of wort (= Final attenuation)	EBC 4.11.2	85.1	85.2	2.6	1.5	16 (5.3%)
FGE	Fine-grind extract of malt	EBC 4.5.1	82.4	84.7**	2.2	0.8	2 (0.7%)
FRI	Friability of malt	EBC 4.15	74.1	89.7**	12.5	4.8	0
PRO	Grain protein content	EBC 3.3.1	10.1	9.1**	1.0	0.4	0
VIS	Viscosity of wort	EBC 4.8	1.6	1.5**	0.1	0.05	0
VZ45	Hartong 45°C, extract at 45°C	MEBAK	42.6	44.7*	6.3	2.5	26 (8.6%)

[a] EBC: European Brewery convention (2005), MEBAK, Mitteleuropäische Brautechnische Analysenkommission (1997)

[b] Significant differences of least square means were tested with $*P < 0.05$ and $**P < 0.01$

[c] Calculation of standard deviation of Scarlett was based on 20 replicates per environment (D03 and G03)

[d] Definition of favourable transgression: see materials and methods

Results

Comparison of the population S42 with the recurrent parent

In order to compare the performance of the BC_2DH population with that of the recurrent parent, the least square means of all traits for the population S42 and Scarlett were calculated (Table 1). The comparison of S42 and Scarlett revealed significant differences for the traits α-amylase, fine-grind extract, friability and VZ45, where the mean performance of S42 was below that of the recurrent parent. For protein content and viscosity the mean trait values of the population S42 were significantly above those of Scarlett.

Based on extreme values of the S42 progeny, favourable transgressive segregation, i.e. S42 lines exhibiting significant better performance than Scarlett, was recorded for four traits (Table 1). Favourable transgression was detected for the traits α-amylase with 20 S42 lines, fermentability with 16 S42 lines, fine-grind extract with 2 S42 lines and VZ45 with 26 S42 lines which surpassed the least square means of the recurrent parent Scarlett by more than two standard deviations (Table 1, Fig. 1).

Correlations

A total of 31 significant correlations were detected between seven malting traits, heading date and the

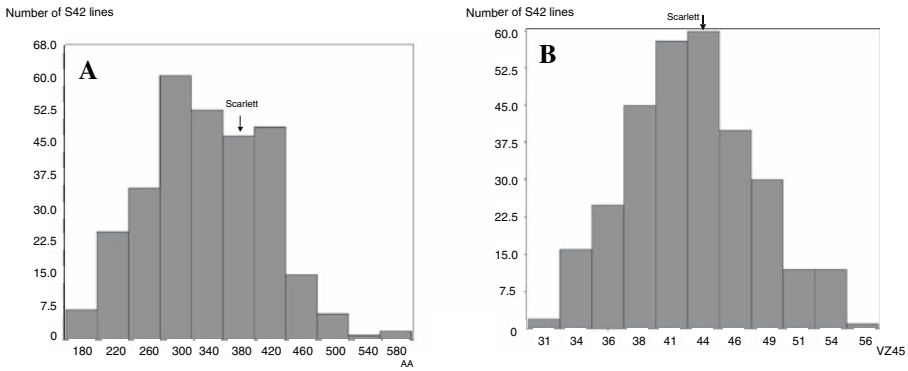

Fig. 1 Phenotypic distribution of the traits α-amylase (**A**) and VZ45 (**B**) in population S42. The distribution was calculated with least square means averaged across the two environments. Least square means and standard deviations are given in Table 1

percentage of exotic genome per line (P[*Hsp*], see Table 2). Higher correlations above 0.50 are as follows: α-amylase showed positive correlations with fermentability, friability and VZ45 of 0.55, 0.48 and 0.52, respectively, and a negative correlation of −0.59 with viscosity. In addition, fine-grind extract exhibited positive correlations with friability and VZ45 of 0.67 and 0.58, and negative correlations with raw protein and viscosity of −0.77 and −0.54, respectively. Finally, friability revealed negative correlations of −0.63 and −0.82 with protein and viscosity, respectively. In order to analyse the impact of developmental differences on malting quality, correlations between heading date (von Korff et al. 2006) and malting parameters were calculated. The parameters measuring enzyme activity, α-amylase and VZ45, showed no or low correlations with heading date. Heading date, however, was negatively correlated with protein content (−0.56), viscosity (−0.45) and positively correlated with fine-grind extract (0.46) and friability (0.64). In order to test the hypothesis that a high percentage of exotic germplasm P[*Hsp*] has a negative influence on malting quality, the proportion of exotic alleles in a BC_2DH lines was calculated. P[*Hsp*] revealed negative correlations with fine-grind extract and friability of −0.49 and −0.50, respectively, and positive correlations with protein content and viscosity of 0.28 and 0.47, respectively.

QTL analysis

The ANOVA revealed 103 significant marker trait associations. Due to linkage between markers, these effects were summarised to 48 putative QTLs for seven malting parameters (Table 3, Fig. 2). The exotic genotype improved the trait performance at 18 (37.5%) of 48 QTLs. In the following, the QTLs are presented for each trait separately.

α-amylase (AA)

For α-amylase, the analysis revealed eight QTLs on five chromosomes. The exotic alleles increased AA activity at four QTLs by a maximum of 16.3% at QAa.S42-4H.c. The latter QTL showed with 12.6% the strongest effect on the genetic variance. At four QTLs the exotic allele caused a decrease in enzyme activity by maximal 21.5% at QAa.S42-5H.b.

Fermentability (FER)

Three QTLs were detected for fermentability on chromosomes 4H and 6H. The exotic allele increased the trait value at all three QTLs by a maximum of 1.5% on the short arm of chromosome 4H. The maximum genetic variance was explained at QFer.S42-6H.a with 2.9%.

Fine-grind extract (FGE)

For fine-grind extract, altogether four QTLs were identified on the chromosomes 1H, 3H and 7H. Fine-grind extract was increased by the exotic allele at QFge.S42-3H.a. The exotic allele decreased fine-grind extract at three loci by a maximum of 2.2% at QFge.S42-1H.b. This locus explained 10.7% of genetic variance.

Table 2 Pearson correlation coefficients (*r*) between seven malting traits, heading date and the percentage of exotic genome per line (P[*Hsp*])

	FER	FGE	FRI	PRO	VIS	VZ45	HEA	P[*Hsp*]
AA	0.55***	0.25***	0.48***	−0.14*	−0.59***	0.52***	−0.09 n.s.	−0.16*
FER		0.13*	0.49***	−0.21***	−0.49***	0.07 n.s.	0.04 n.s.	−0.12*
FGE			0.67***	−0.77***	−0.54***	0.58***	0.46***	−0.49***
FRI				−0.63***	−0.82***	0.33***	0.64***	−0.50***
PRO					0.42***	−0.27***	−0.56***	0.28***
VIS						−0.46***	−0.45***	0.47***
VZ45							−0.04 n.s.	−0.25***

For calculating correlations, the least square means of the trait performance of each BC_2DH line averaged across environments were used. The significance thresholds for *r* values are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, n.s. not significant. P[*Hsp*] is the percentage of exotic genome per S42 line calculated according to von Korff et al. (2004). Heading date was analysed as reported in von Korff et al. (2006)

Table 3 List of 48 putative QTLs for seven malting traits detected in S42*

QTL name	SSR	Chr[a]	Pos[b](cM)	Bin range[c]	*F*-value[d]	R^2_M[e]	[Hv][f]	[Hsp][f]	RP[Hsp][g]	RP [HspD03][g]	RP [HspG03][g]
α-amylase (AA)											
QAa.S42-1H.a	S53707	1H	20	3–4	11.1	2.2	344.0	294.6	−14.4	−15.9	−12.8
QAa.S42-2H.a	BMAG125	2H	122	10	16.8	3.2	347.8	310.8	−10.6	−10.1	−11.2
QAa.S42-4H.a	*HVM40*	*4H*	*14*	*2*	*12.7*	*2.6*	*331.6*	*377.6*	*13.9*	*14.5*	*13.2*
QAa.S42-4H.b	*HVPAZXG*	*4H*	*44*	*5*	*14.2*	*3.0*	*334.1*	*366.2*	*9.6*	*10.7*	*8.5*
QAa.S42-4H.c	*HDAMYB*	*4H*	*190*	*12–13*	*92.0*	*12.6*	*330.9*	*385.0*	*16.3*	*16.8*	*15.8*
QAa.S42-5H.a	MGB384	5H	0	2	11.5	2.3	347.1	308.6	−11.1	−11.0	−11.2
QAa.S42-5H.b	BMAG337	5H	43	5–8	71.2	12.3	352.5	276.8	−21.5	−21.4	−21.5
QAa.S42-6H.a	*EBMAC624*	*6H*	*107*	*6–9*	*22.5*	*5.0*	*329.5*	*382.1*	*16.0*	*15.4*	*16.6*
Fermentability (FER)											
QFer.S42-4H.a	*HVM40*	*4H*	*14*	*2*	*8.3*	*2.2*	*84.9*	*86.2*	*1.5*	*1.6*	*1.4*
QFer.S42-4H.b	*GBM1015*	4H	*170*	*12*	*10.5*	*2.0*	*85.0*	*85.7*	*0.8*	*0.7*	*0.8*
QFer.S42-6H.a	*HVM74*	*6H*	*103*	*6–7*	*10.9*	*2.9*	*84.9*	*86.0*	1.3	*1.3*	*1.3*
Fine-grind extract (malt extract, FGE)											
QFge.S42-1H.a	GBM1007	1H	28	4	16.3	2.8	82.5	81.3	−1.6	−1.5	−1.6
QFge.S42-1H.b	BMAG149	1H	70	7	44.9	10.7	82.5	80.7	−2.2	−1.9	−2.4
QFge.S42-3H.a	*GBM1043*	*3H*	*130*	*10*	*12.6*	*2.6*	*82.3*	*82.9*	*0.7*	*0.8*	*0.6*
QFge.S42-7H.a	EBMAC603	7H	50	3	14.0	1.5	82.5	81.7	−1.1	−1.1	−1.1
Friability (FRI)											
QFri.S42-1H.a	BMAG149	1H	70	6–8	152.9	16.0	76.9	62.0	−19.4	−18.8	−20.0
QFri.S42-1H.b	BMAC32	1H	105	10	23.3	2.6	76.0	71.9	−5.4	−5.2	−5.8
QFri.S42-2H.a	BMAG381	2H	107	9	18.8	2.4	76.3	72.0	−5.5	−5.3	−5.7
QFri.S42-3H.a	*GBM1043*	*3H*	*130*	*10*	*14.7*	*1.9*	*74.9*	*78.3*	*4.6*	*4.6*	*4.5*
QFri.S42-4H.a	EBMAC775	4H	80	7	18.0	3.1	76.4	70.8	−7.3	−6.2	−8.4
QFri.S42-5H.a	BMAG337	5H	43	3–5	29.2	4.2	76.4	69.9	−8.5	−7.9	−9.2
QFri.S42-6H.a	*BMAG613*	*6H*	*112*	*9*	*17.5*	*3.9*	*74.2*	*79.6*	*7.3*	*8.0*	*6.5*
QFri.S42-7H.a	*BMAG7*	*7H*	*27*	*2*	*18.5*	*2.3*	*73.6*	*80.7*	*9.7*	*9.7*	*9.7*
QFri.S42-7H.b	BMAG11	7H	93	6–7	13.6	1.4	75.8	72.6	−4.3	−4.2	−4.3
QFri.S42-7H.c	EBMAC755	7H	166	11	19.8	3.0	75.8	69.3	−8.6	−8.8	−8.3
Protein content (PRO)											
QPro.S42-1H.a	S53707	1H	20	3	13.3	2.2	10.2	10.7	4.6	4.8	4.4
QPro.S42-1H.b	BMAG211	1H	68	6–8	59.1	7.9	10.2	10.9	6.7	6.5	7.0
QPro.S42-1H.c	*HVABAIP*	*1H*	*144*	*13*	*22.4*	*3.5*	*10.3*	*10.0*	*−3.3*	*−3.0*	*−3.6*

Table 3 continued

QTL name	SSR	Chr[a]	Pos[b](cM)	Bin range[c]	*F*-value[d]	R^2_M[e]	[Hv][f]	[Hsp][f]	RP[Hsp][g]	RP [HspD03][g]	RP [HspG03][g]
QPro.S42-2H.a	*EBMAC684*	*2H*	*80*	*7–8*	*12.2*	*3.3*	*10.3*	*10.2*	*−0.8*	*−2.7*	*1.3*
QPro.S42-4H.a	HVOLE	4H	21	3	25.5	5.5	10.1	10.7	6.2	5.4	7.0
QPro.S42-4H.b	*EBMAC775*	*4H*	*80*	*7–8*	*15.4*	*2.5*	*10.3*	*10.0*	*−3.1*	*−2.7*	*−3.6*
QPro.S42-4H.c	*EBMAC679*	*4H*	*132*	*9–10*	*19.9*	*4.6*	*10.3*	*9.9*	*−3.6*	*−3.9*	*−3.2*
QPro.S42-4H.d	*HDAMYB*	*4H*	*190*	*13*	*26.5*	*2.9*	*10.3*	*10.0*	*−2.4*	*−2.2*	*−2.6*
QPro.S42-6H.a	GBM1049	6H	40	3	22.8	4.1	10.2	10.6	4.4	4.5	4.3
QPro.S42-6H.b	GMS6	6H	96	5	10.5	2.8	10.1	10.5	3.7	4.1	3.2
Viscosity (VIS)											
QVis.S42-1H.a	BMAG211	1H	68	6–9	163.9	19.1	1.6	1.8	10.8	10.8	10.8
QVis.S42-1H.b	BMAC32	1H	105	10	15.0	2.2	1.6	1.6	2.5	2.2	2.8
QVis.S42-2H.a	GBM1052	2H	42	4	13.2	2.7	1.6	1.7	9.0	9.4	8.6
QVis.S42-2H.b	GMS3	2H	86	7–8	19.6	3.2	1.6	1.7	3.0	2.7	3.2
QVis.S42-3H.a	MGB410	3H	65	5–6	24.5	2.9	1.6	1.7	4.5	4.4	4.6
QVis.S42-3H.b	*GBM1043*	*3H*	*130*	*10*	*15.6*	*2.0*	*1.6*	*1.6*	*−2.3*	*−2.3*	*−2.3*
QVis.S42-5H.a	BMAG337	5H	43	3–8	45.2	7.4	1.6	1.7	5.6	5.9	5.2
QVis.S42-6H.a	*BMAG613*	*6H*	*112*	*7–10*	*16.4*	*2.6*	*1.6*	*1.6*	*−2.9*	*−2.8*	*−2.9*
Hartong 45°C (VZ45)											
QVZ45.S42-1H.a	BMAG149	1H	70	7	22.1	6.5	42.3	38.5	−9.1	−7.2	−11.2
QVZ45.S42-2H.a	EBMAC415	2H	146	13	14.9	2.5	42.2	39.1	−7.2	−6.9	−7.7
QVZ45.S42-5H.a	BMS2	5H	12	3	10.8	2.1	42.5	40.1	−5.6	−5.4	−5.8
QVZ45.S42-5H.b	BMAG337	5H	43	5–8	37.5	6.9	42.6	39.3	−7.7	−6.9	−8.7
QVZ45.S42-7H.a	BMAG321	7H	100	6–7	20.1	2.5	42.3	40.5	−4.1	−3.7	−4.5

*A putative QTL was assumed in the vicinity of a marker locus, if the marker main effect (M) was significant in the 4-factorial ANOVA with an FDR of 0.05 (Benjamini and Yekutieli 2005). QTLs with a favourable effect of the exotic allele are marked in italics

[a] Chromosomal localisation of the QTL-linked marker showing the highest *F*-value

[b] Position of the listed marker in cM, based on von Korff et al. (2004)

[c] Bin range of all significant QTL markers according to information by Kleinhofs and Graner (2001) and by the OWB population (Costa et al. 2001, http://barleyworld.org)

[d] *F*-value of the given marker in the 4-factorial ANOVA

[e] Proportion of the genetic variance, which is explained by the marker main effect

[f] Least square means of trait values across all tested environments for BC_2DH lines carrying the elite genotype [*Hv*] or the exotic genotype [*Hsp*] at the given marker locus

[g] Relative performance: $((Hsp-Hv) \times 100/Hv)$, where *Hv* and *Hsp* are the least square means of lines with the elite and exotic genotype, respectively, at a given marker locus. The relative performance is calculated across both environments (RP[Hsp]) and, in addition, separately for environment D03 (RP[HspD03]) and G03 (RP[HspG03])

Friability (FRI)

Ten QTLs were identified for friability on all seven chromosomes. The exotic allele improved friability at three QTLs by a maximum of 9.7% at QFri.S42-7H.a. At seven QTLs the exotic allele decreased friability by maximal 19.4% at QFri.S42-1H.a. This locus explained 16.0% of the genetic variance.

Protein content (PRO)

For protein content, ten QTLs were detected on chromosomes 1H, 2H, 4H and 6H. The exotic genotype reduced protein content at five QTLs by a maximum of 3.6% at QPro.S42-4Hc. At five loci the exotic allele increased PRO where the strongest effect was measured at QPro.S42-1H.b, which explained 7.9% of the genetic variance and increased PRO by on average 6.7%.

Viscosity (VIS)

Eight QTLs were found for viscosity on chromosomes 1H, 2H, 3H, 5H and 6H. The exotic allele decreased viscosity at two QTLs by maximal 2.9% at QVis.S42-6H.a. At six loci the exotic genotype increased VIS by a maximum of 10.8% at QVis.S42-1H.a. This locus explained 19.1% of the genetic variance.

Hartong 45°C (VZ45)

For VZ45, five QTLs were discovered on chromosomes 1H, 2H, 5H and 7H. At all loci the exotic allele decreased VZ45 by up to 9.1% at QVZ45.S42-1H.a. The maximum genetic variance was explained at QVZ45.S42-5H.b with 6.9%.

Discussion

Malting quality is often viewed as one of the most complex and sensitive traits, which needs fine-tuning of a high number of interacting genes over many decades of selection. Breeding for malting quality has therefore concentrated on a restricted gene pool with high malting quality donors and avoided the use of exotic germplasm. The present study, however, indicated, that wild barley does harbour genes which have the potential to improve malting quality parameters. The exotic donor improved malting quality at 37.5% of all QTLs. Only for VZ45 no favourable exotic alleles could be detected. Most favourable exotic alleles were found for improved protein content (5) and α-amylase (4). It has been shown that wild barley harbours a wealth of diverse alleles for resistance against abiotic stresses, e.g. for drought tolerance (Grando and Ceccarelli 1995), and for cold tolerance (Crosatti et al. 1996). Consequently, the exotic alleles may be a source for α-amylases with increased activity, possibly due to better thermostability. Indeed, a more thermostable β-amylase form of the *Bmy1* gene has already been identified in wild barley (Erkkilä et al. 1998; Paris et al. 2002). Sequencing of the *Bmy1* locus in ISR42-8 revealed the *Bmy1*-Sd3 allele which is associated with increased β-amylase thermostability (data not shown).

Figure 2 shows that some genomic regions, in particular on 1H and 5H, affected several different malting quality traits and simultaneously, showing the strongest effects on the genetic variance. The interspecific cross showed a wide variation for protein content and heading date (von Korff et al. 2006) and these traits are known to affect malting quality parameters. Consequently, these two characteristics were added as covariates to the analysis model, to exclude confounding effects of protein content and development on the malting quality parameters. Transgressive lines surpassing the recurrent parent Scarlett were detected for four malting parameters (Table 1). After validation of the superior performance in further field testings, these lines will be promising candidates for introgression of favourable alleles into elite material. In the following the studied traits will be discussed.

α-amylase and fermentability

α-amylase and fermentability showed a correlation of 0.55 (Table 2) and the three QTLs for fermentability coincided with QTLs for α-amylase. Indeed, Evans et al. (2005) demonstrated that fermentability is primarily determined by the level and thermostability of α- and β-amylase and limit dextrinase. The exotic allele increased α-amylase activity by 13.9% at QAa.S42-4H.a, by 16.3% at QAa.S42-4H.c and by 16.0% at QAa.S42-6H.a At these loci the exotic allele

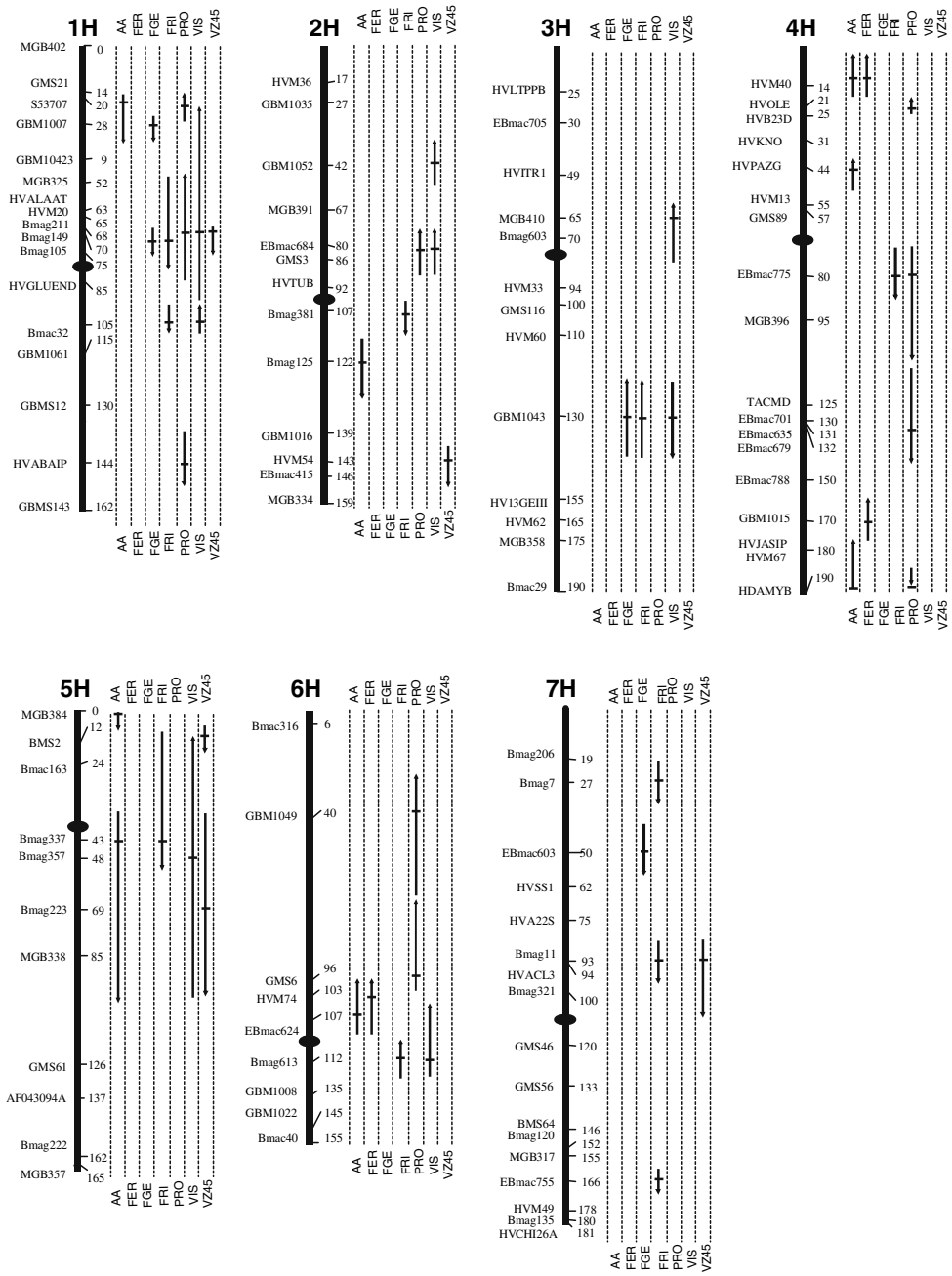

Fig. 2 QTL map of the population S42 containing 48 putative QTLs detected for seven malting traits. QTLs are indicated by black arrows along the chromosomes. Linked significant markers (≤ 20 cM) showing the same effect are interpreted as one QTL extending from the half-intervals flanking the first and the last marker in that linkage group. The horizontal dashes in the arrows indicate the marker with the highest *F*-value in the ANOVA. The direction of the arrows indicates the *Hsp* effect: upward, the *Hsp* allele is increasing the trait value, downward; the *Hsp* allele is decreasing the trait value

also improved fermentability. Improved fermentability of lines carrying the exotic genotype at these QTLs may thus be caused by increased α-amylase activity. At QAa.S42-4H.c the exotic allele had also favourable effects on protein level. This region of the chromosome 4H corresponds to the map position of *Bmy1*, coding for *β*-amylase. The favourable effect on several malting parameters could be due to a

pleiotropic effect of a single gene (*Bmy1*) on α–amylase and fermentability as the traits are biochemically correlated. The *Bmy1* gene, however, has also been associated with QTLs for height, flowering time and yield in S42 (von Korff et al. 2006) and is tightly linked to a major vernalisation gene, *Vrn-H2* (Laurie et al. 1995). Therefore, the association of *Bmy1* with malting parameters in wild barley may be due to linkage with variation at the *Vrn-H2* locus. However, as the analysis model included heading data as a covariate, the QTL-effect for AA and FER may also be independent of the *Vrn-H2* locus. Alternatively, the measurement of α-amylase may have been confounded with β-amylase activity. With a suboptimal amount or activity of β-amylase added to the α-amylase assay (as stated in the EBC 4.13 section 5.2) the amount of dextrinized soluble starch may have been limited not only by α-amylase activity alone but also β-amylase activity in the sample.

There are two known forms of α-amylase encoded by the *Amy1* locus on chromosome 6H, bin 9, and the *Amy2* locus on chromosome 7H, bin 7 (Kleinhofs and Graner 2001). Significant α-amylase QTLs have been located at the *Amy1* locus in two QTL studies involving the populations Harrington/TR306 and Chebec/Harrington (Mather et al. 1997; Marquez-Cedillo et al. 2000). In this study, the QTL QAa.S42-6H.a mapped close to the *Amy1* locus. At this locus the exotic allele encoded an enzyme with higher activity than the elite allele. Han et al. (1997) mapped QTLs with effects on diastatic power, α-amylase, malt extract and β-glucan to the interval Brz-*Amy2* in the Steptoe/Morex population. However, no significant effect for α-amylase was detected at the *Amy2* locus in this study.

QAa.S42-5H.b explained 12.3% of the genetic variance, and the exotic allele reduced enzyme activity by 21.5%. Significant QTLs for α-amylase activity have been detected in the vicinity of this locus in several mapping populations by Coventry et al. (2003). The locus revealed pleiotropic effects on friability, viscosity and VZ45 in this study and has been associated with various malting parameters in previous studies (Zale et al. 2000). A number of stress related genes have been mapped to the same region on chromosome 5H, including *Dhn1/Dhn2* (Choi et al. 2000), *Vrn1* (Laurie et al. 1995), the *Cbf3* gene, a putative regulator of cold and drought response (Choi et al. 2002), and a gene encoding low molecular weight heat shock proteins (Maestri et al. 2002). These genes may also play a role in preserving enzyme activity at elevated temperatures during the malting process.

Fine-grind extract and VZ45

Fine-grind extract and VZ45 revealed high positive correlations of above 58%. The VZ45 measures low-temperature extraction and characterises cytolytic and proteolytic activity of malt enzymes. Cytolytic and proteolytic enzymes are involved in the breakdown of cell wall and degradation of starch into fermentable sugars, which results in the development of malt extract. Fine-grind extract was most strongly influenced by the QTL QFge.S42-1H.b which explained 10.7% of the genetic variance. This QTL coincides with the major QTL for VZ45, QVZ45.S42-1H.a. The same locus on 1H also showed an effect on friability, protein content and viscosity in this study. At the same region on 1H, Collins et al. (2003) identified a QTL for hot water extract in the populations Sloop/Alexis. In addition, Marquez-Cedillo et al. (2000) mapped a QTL for malt extract to the long arm of 1H in the Harrington/Morex population.

As 26 lines showed transgressive segregation for VZ45 as compared to the elite parent, it was surprising that no QTLs with favourable effects of the exotic allele were recorded. This could be due to epistatic interactions between elite and exotic germplasm. On the other hand, a number of marker*environment interactions with favourable effects of the exotic allele were detected (data not shown). Due to differences in magnitude of the effects and cross over interactions, these loci were not significant as a marker main effect. The major QTL for VZ45 mapped to the long arm of chromosome 5H (QVZ45.S42-5H.b) and coincides with a QTL for height in S42 (von Korff et al. 2006) and with QTLs for α-amylase and diastatic power mapped in Dicktoo × Morex (Oziel et al. 1996) and Steptoe × Morex (Hayes et al. 1993).

PRO

In breeding for malting quality moderate protein levels are desirable. A sufficient protein quantity is necessary to provide starch-degrading enzymes, whereas high protein contents reduce malt extract.

In this study, however, protein content showed a low negative correlation with enzyme activity. The amount of grain protein was thus no limiting factor for enzyme activity. Protein content showed a strong negative correlation with malt extract of −77% and with friability of −63%. Although the model corrected for protein content, two QTLs were overlapping between PRO and FGE and two QTLs between PRO and FRI. At these QTLs, common between PRO, FGE and FRI, the exotic allele increased protein content and reduced fine-grind extract and friability. Attempts to describe the negative relationship between protein and malt extract have been reviewed by Tatham and Shewry (1995) who showed that different hordein groups had some relationship to malt extract or final beer quality. In this study, the QTL QPro.S42-1H.a mapped to bin 3 where also the *Hor* loci have been located. Variation at this locus may thus be explained by differences in the structural composition of the exotic and elite *Hor* alleles.

Viscosity and friability

The cytolytic parameters viscosity and friability showed a correlation of −82% in S42. QTLs with opposing effects of the exotic allele for FRI and VIS coincided at 1H, 3H, 5H and 6H. The locus at the centromeric region of chromosome 1H had the strongest effect on both traits, explaining 16.0% (FRI) and 19.1% (VIS) of the genetic variance. As viscosity and friability are mainly affected by the breakdown of β-glucan and other cell wall polysaccharides, genes affecting β-glucan or β-glucanase activity may underlie the QTLs detected for viscosity and friability. Indeed, the strongest QTLs for viscosity and friability, QVis.S42-1H.a and QFri.S42-1H.a, coincided with QTLs for β-glucan and β-glucanase activity detected in the Steptoe/Morex population (Han et al. 1995). The exotic allele at the QTL on 3H, bin 10 improved friability and viscosity and had also a favourable effect on fine-grind extract. Thomas et al. (1996) detected QTLs for α-amylase, diastatic power and grain protein at the same location in the cross Blenheim × E224/3. This locus maps also close to a gene for α-amylase, *amyb*, which may be at the basis of these QTLs. QFri.S42-6H.a and QVis.s42-6H.a map to the location of the *Amy1* locus, and the favourable effect of the exotic allele on these two parameters may be explained by improved α-amylase activity at this locus. QFri.S42-6H.a and QVis.s42-6H.a do also partially overlap with QTLs for yield, heading date and a minor QTL for brittleness (von Korff et al. 2006) and may reflect differences in grain maturity. As brittle spikes were not collected prior to harvest, the remaining grain may have been later maturing and thus affected malting quality.

Conclusion

In this study, transgressive S42 lines with improved performance were detected for four out of seven analysed malting parameters, despite the overall inferior impact of the ISR42-8 germplasm on malting quality. The highest numbers of transgressive lines were detected for the traits VZ45 (26 S42 lines) and α-amylase (20 S42 lines). Exotic alleles with a favourable effect on malting quality were identified at 18 out of 48 QTLs. Favourable exotic QTL alleles were detected on the chromosomes 3H, 4H, 6H and 7H. For example, three favourable exotic QTL-alleles for α-amylase and protein content each, and one favourable exotic QTL-allele for friability were identified on chromosome 4H. In addition, on chromosome arm 6HL the exotic allele increased α-amylase by 16.0%, fermentability by 1.3%, friability by 7.3% and reduced viscosity by 2.9%. In future, the favourable effects of the exotic alleles will be verified in a second AB-population derived from the same donor germplasm and in near-isogenic lines. Pure introgression lines are currently generated (von Korff et al. 2004). These will be used to verify and fine-map the malt QTLs and to introgress the exotic QTL alleles into adapted germplasm.

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