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ORIGINAL PAPER

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Comparative AB-QTL analysis in barley using a single exotic donor of *Hordeum vulgare* ssp. *spontaneum*.

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Abstract This paper reports on the first comparative advanced backcross quantitative trait locus (AB-QTL) study in barley. The BC_2F_2 population H×101 was generated from crossing var. Harry [H; *Hordeum vulgare* ssp. *vulgare* (*Hv*)] with ISR101-23 [101; *H. v.* ssp. *spontaneum* (*Hsp*)]. The results of the AB-QTL analysis for 13 quantitative traits are presented and, subsequently, compared with the AB-QTL study of the barley cross *Apex* × ISR101-23 (A×101; Pillen et al., Theor Appl Genet 107:340–352). Both AB populations share the exotic *Hsp* donor accession ISR101-23. In H×101, 108 putative QTLs (17%) were identified among the 650 marker×trait combinations tested. Altogether 52 (48 %) favorable effects were identified from the exotic parent. At these marker loci, the homozygous *Hsp* genotype was associated with an improvement in the trait compared to the homozygous *Hv* genotype. The percentage of QTLs detected in H×101 was comparable to that in A×101 (17% vs. 15%), however more favorable exotic QTL alleles were located in H×101 than in A×101 (48% vs. 34%). In H×101, the *Hsp* QTL allele at $EBmac0679_{[4H]}$ was associated with a yield increase of 5.9% averaged across the six environments tested. A comparison of putative QTLs between H×101 and A×101 was based on 26 shared SSR markers. In total, 26% of the putative QTLs could be detected simultaneously in both AB populations. This finding indicates that only a portion of the QTL effects of the donor allele can be transferred from one elite recipient to the next.

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This work is dedicated to the 65th birthday of Prof. Dr. H.H. Geiger, Department of Plant Breeding, Seed Science and Population Genetics, University of Hohenheim, Germany.

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Introduction

The advanced backcross-quantitative trait locus (AB-QTL) strategy, introduced by Tanksley and Nelson (1996), combines the two breeding steps of (1) localizing exotic polygenes that exhibit effects on the expression of quantitative traits like yield and quality and (2) using the marker information to select new, improved breeding material. In order to achieve this goal, the authors utilized exotic germplasm as the genetic donor for the improvement of quantitative agronomic traits (Tanksley and McCouch 1997) and conducted the marker and phenotype analysis in advanced backcross generations like BC_2 or BC_3.

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. 1998a) and rice (Xiao et al. 1996, 1998; Moncada et al. 2001; Brondani et al. 2002). Reports have recently appeared on the first AB-QTL analyses in maize (Ho et al. 2002), wheat (Huang et al. 2003) and barley (Pillen et al. 2003). In most instances, significant improvements in yield and yield components could be associated with exotic donor segments. These effects were dramatic in tomato and rice, where yield increased up to 34% and 18%, respectively. The effects of wild-type QTL alleles on yield were less pronounced in maize, wheat and barley but still reached levels of 11%, 15% and 7%, respectively.

In barley, the AB-QTL analysis was conducted with a BC_2F_2 population from the cross *Apex* × ISR101-23 (A×101; Pillen et al. 2003). The genotype data were collected from SSR (simple sequence repeat) markers, and the phenotype data were compiled for 13 quantitative agronomic traits measured in a maximum of six environments. Altogether, 86 putative QTLs were identified by means of a two-factorial ANOVA. Favorable effects of

the exotic parent were identified at 29 putative QTLs (34%).

In order to verify QTL effects, two strategies have been applied. On one hand, a common parent between two backcrosses can assist in the validation of QTLs. In tomato, several backcross populations have been generated with the same recurrent parent. This rendered it possible to compare the effects of exotic QTL alleles from different tomato wild species in the genomic background of a single cultivar. Fulton et al. (1997) reported that 19% of the QTLs detected from a study with *Lycopersicon peruvianum* as the donor parent were also found in at least one of the crosses with *L. pimpinellifolium* or *L. hirsutum.* Thus, the authors concluded that most of the QTLs detected in *L. peruvianum* were unique. In rice, Xiao et al. (1998) and Moncada et al. (2001) used the same *Oryza rufipogon* accession as the exotic donor for their respective backcrosses. The latter authors reported that a yield-increasing exotic QTL allele was found in both studies in similar chromosomal regions, thus confirming its effect. The final proof of a QTL effect will be its confirmation in a pure nearly isogenic line (QTL-NIL) that contains a single donor segment in the background of the recipient genome. This concept has been successfully applied in order to validate favorable QTL effects of exotic tomato alleles (Bernacchi et al. 1998b; Monforte and Tanksley (2000) and Monforte et al. (2001). Until recently, the idea of a QTL as a genetic entity was solely a hypothesis. However, Frary et al. (2000) cloned the first QTL: the fruit weight regulator, *fw2.2*, in tomato. This example ultimately proved that the expression of quantitative traits can be traced back to the concerted action of single genes.

In this paper, we report on a second barley AB-QTL project which utilized the same *Hsp* (*Hordeum vulgare* ssp. *spontaneum*) donor accession (ISR101-23) as that used by Pillen et al. (2003) but with the variety Harry as the recurrent parent. Our goals were (1) to localize QTLs for the expression of quantitative traits in spring barley, (2) to identify favorable *Hsp* alleles that improve agronomic traits and (3) to compare the genetic effects of donor QTL alleles between the two related crosses H×101 and A×101.

Materials and methods

Plant material

For QTL analysis, the barley BC_2F_2 population H×101 was generated by crossing German spring var. Harry [H; *Hordeum vulgare* ssp. *vulgare* (abbreviated *Hv*)] as the female with the Israeli *Hsp* wild barley (*H. v.* ssp. *spontaneum*) accession ISR101-23 (101) as the pollinator followed by two cycles of backcrossing with Harry as the pollinator and one round of selfing. The H×101 population consisted of 164 randomly chosen individuals.

SSR markers

The SSR markers used and their map locations are explained in Pillen et al. (2003).

Genotyping BC_2F_2 individuals

The genotypes of 164 BC_2F_2 individuals of the H×101 population were determined by means of SSR analysis as explained in Pillen et al (2003).

Phenotyping BC_2F_2-derived H×101 families

The treatment of $BC_2F_{2:5}$ (1999) and $BC_2F_{2:6}$ (2000) plots and the phenotypic evaluation of up to 13 quantitative traits (Table 1) in a maximum of six environments (three locations × 2 years) was conducted as stated in Pillen et al. (2003).

QTL analysis

QTL analysis was performed as stated in Pillen et al. (2003). QTL detection from BC_2F_2 genetic data and field data from multiple environments was conducted using the procedure GLM of the SAS software (SAS Institute 1999). In each environment, field data from two to three replications were averaged by the least square means option of the GLM procedure. At each marker locus, only the homozygous genotypes (*Hv* or *Hsp*) were included in the calculation since the repeated selfing of heterozygous BC_2F_2 individuals lead to a mix of both homozygous genotypes in the derived $BC_2F_{2:5}$ and $BC_2F_{2:6}$ field plots, resulting in a false estimate of the performance of true heterozygotes. Like in Pillen et al. (2003), a mixed model was used to detect QTLs which included a fixed marker genotype (M) effect, a random environment (E) effect and the M×E interaction. The presence of a QTL in the vicinity of a marker locus was assumed, if the marker main effect or the M×E interaction was significant at $P<0.01$.

Results and discussion

Traits

The least square means of each trait across all environments was calculated for the H×101 backcross population and for the recurrent parent Harry (Table 1). The backcross significantly ($P<0.01$) excelled the recurrent parent Harry for the trait HEA. From a breeder's perspective, this result is highly regarded under the assumption that early flowering is independent of yield. The backcross was significantly ($P<0.001$) inferior to Harry with respect to traits HI, KER, MT and YLD. Both of these findings also applied to the A×101 population (Pillen et al. 2003). The altogether inferiority of the backcross was anticipated since no selection was exercised during the development of the AB population.

Correlations between the 13 aforementioned traits and the *Hsp* genome ratio per individual (P[*Hsp*]) were calculated across all environments (Table 1). In general, a high *Hsp* genome ratio exerted negative effects on the performance of the H×101 individuals. As in A×101, P[*Hsp*] showed significant negative correlations with YLD (r=-0.70), HI (r=-0.51), KER (r=-0.40) and MT (r=-0.36) and, on the other hand, a positive correlation with PRO (r=0.55). The negative correlations of the aforementioned traits with P[*Hsp*], in accordance with the significantly reduced trait mean values in the backcross population, confirm that the introgression of wild barley germplasm would not lead to an improvement in agro-

Table 1 Least square means for 13 traits and their correlation with P[*Hsp*][a]

Traits[d]	Least square means[b]		Correlation[c]
	H×101	LSD test[e] Harry	with P[*Hsp*][e]
EAR	492.90	482.60	0.17*
HEA	67.53	68.94**	–0.15*
HEI	83.21	82.56	0.08
HI	0.41	0.45***	–0.51***
KER	20.28	22.93***	–0.40***
LOF	2.56	2.10	0.11
LOH	4.77	4.94	0.14
MAS	43.03	42.66	0.16*
MT	62.81	72.84***	–0.36***
PRO	11.24	11.10	0.55***
TGW	50.47	50.42	–0.05
WA	45.87	45.73	–0.01
YLD	51.65	58.50***	–0.70***

[a] P[*Hsp*] is defined as the percentage of *Hsp* alleles present in a BC_2F_2 line (see Pillen et al. 2003)
[b] The least square means for the backcross H×101 and the recurrent parent Harry are calculated across all environments
[c] The trait performance of each BC_2F_2 line was averaged across all environments in order to compute the Pearson correlation coefficients
[d] The traits evaluated are: EAR, number of ears per square meter; HEA, days from sowing to heading; HEI, plant height (cm); HI, harvest index; KER, number of kernels per ear; LOF, lodging at flowering; LOH, lodging at harvest; MAS, above ground biomass (g/50 cm); MT, malt tenderness (%); PRO, grain protein content (%); TGW, thousand grain weight (g);, WA, grain water absorption (%); YLD, total yield (in 100 kg/ha). For details of trait evaluation see Pillen et al. (2003)
[e] The significance thresholds for the LSD test and for the correlations are: *P<0.05, **P<0.01, ***P<0.001

nomic traits without selection. Thus, the goal of the AB-QTL study was to identify those rare exotic QTL alleles that improve quantitative traits.

Marker data

More than 200 SSRs were tested for polymorphism between the parents Harry and ISR101-23; of these, 77 SSRs were polymorphic. The 164 BC_2F_2 lines of the H×101 population were successfully genotyped with 50 SSRs distributed over all seven barley chromosomes (Table 2). The remaining 27 (35%) SSRs failed to exhibit the *Hsp* allele in the BC_2F_2 population. The chromosomal location of the SSRs were inferred from Ramsay et al. (2000) and Pillen et al. (2003). In total, 72 SSRs could be placed in a map representing 850 cM of the barley genome. The mean SSR density is equal to 11.8 cM. Both the size and the density of the H×101 map are very similar to those of the A×101 map (Pillen et al. 2003) that covers 852 cM with an average marker density of 12.7 cM. The H×101 map contains seven gaps with marker distances of more than 30 cM. A similar observation was made in the A×101 map (Pillen et al. 2003), which included nine gaps.

From 50 informative SSRs, 45 (90%) could be scored co-dominantly. Two dominantly scored SSRs did not amplify an *Hsp* allele and three failed to amplify an *Hv* allele. A similar observation was made in the A×101 map (Pillen et al. 2003) where three dominantly scored SSRs did not amplify an *Hsp* allele and two failed to amplify an *Hv* allele. However, whereas *HvW1* was scored co-dominant in H×101 it was scored dominant in A×101 with a null allele in *Apex*. Presumably, at least one primer sequence of *HvW1* is absent in *Apex*, thereby preventing the amplification of this PCR fragment from *Apex*.

QTL detection

Like in Pillen et al. (2003), a single point-marker analysis by means of a two-factorial ANOVA rather than an interval mapping was preferred for QTL analysis because of the low marker coverage and the presence of gaps in the H×101 map. It should be noted that QTL effects simultaneously detected at two or more adjacent marker loci by ANOVA are presumably due to the existence of a single, linked genetic factor that exerts the QTL effect. However, because of two reasons we kept all putative QTLs in the records. First, the alternative hypothesis—that there are two or more QTL factors present on a single chromosomal segment—cannot be ruled out. Second, the ANOVA gives no clear indication which of the significant markers is located nearest to the true QTL factor.

Among 650 marker×trait combinations tested, 108 putative QTLs were detected: the marker main effect was significant at 71 putative QTLs (P<0.01), and the M×E interaction was significant at 41 putative QTLs (P<0.01) (Table 2). In four cases, both effects were significant. Altogether, 52 (48%) favorable QTL effects were detected in H×101. At these loci, the homozygous *Hsp* genotype was associated with an improvement in the trait compared to the homozygous *Hv* genotype (Table 2). The putative QTLs of H×101 were unevenly distributed over the chromosomes. Whereas at least 19 QTLs were located on chromosomes 2H, 3H, 4H and 5H, only three QTLs were detected on chromosomes 6H. However, on the latter chromosomes only three SSRs were genotyped. The majority of favorable QTLs were located on chromosomes 2H, 3H and 5H (23, 13 and 9, respectively). In contrast, only zero and one favorable QTL were detected on chromosome 1H and 7H, respectively. The distribution of putative QTLs among the 50 genotyped SSR markers in H×101 was also uneven. Six segregating SSRs were not associated with any QTL effect in H×101, whereas $HVM36_{[2H]}$, $GMS3_{[2H]}$, and $HvBKASI_{[2H]}$ revealed clusters of putative QTL effects for seven traits and $GMS27_{[5H]}$ showed a cluster of putative QTL effects for six traits. The QTLs detected in H×101 are summarized for each trait in Table 2 and presented in the following sections.

Table 2 List of 108 putative QTLs detected from the BC_2F_2 cross Harry×101-23

Trait[a]	Marker	Chromosome	Position [b]	S_M [c]	R^2_M [d] (%)	S_I [c]	R^2_I [d] (%)	QTL [e]	P/N [f]	LSM[g] [*Hsp*]	RP[*Hsp*] [h] (%)
EAR	HVM20	1H	58	**	0.7			M	–	449.42	–8.86
	EBmac0775	4H	42	**	0.6			M	–	462.52	–5.43
	HvBAMY	4H	88	***	1.5			M	+	522.22	6.70
HEA	*HvALAAT*	1H	57	***	0.9			M	–	70.34	4.92
	HVM20	1H	58	***	0.9			M	–	70.34	4.92
	Bmag0347	1H	70	***	1.0			M	–	70.34	4.99
	HVM36	2H	17	***	18.6	**	0.9	M+I	+	61.08	–11.31
	Bmag0378	2H	44	***	24.7			M	+	60.95	–12.59
	GMS3	2H	48	***	27.3	**	0.8	M+I	+	60.48	–12.53
	HvBKASI	2H	50	***	29.1	**	0.8	M+I	+	60.76	–12.40
	HVM54	2H	103	**	0.8			M	–	68.68	2.57
	EBmac0415	2H	105	***	0.4			M	–	68.23	1.81
	EBmac0705	3H	25	***	1.7			M	–	68.70	3.34
	Bmag0209	3H	55	***	4.7			M	+	62.25	–8.84
	HvES1A	3H	66	***	4.4			M	+	63.05	–7.58
	HVM33	3H	69	***	5.3			M	+	62.35	–8.48
	HVM60	3H	73	***	7.2			M	+	63.88	–6.10
	Bmag0225	3H	74	***	0.5			M	+	65.96	–2.71
	Bmag0013	3H	141	***	2.8			M	+	61.00	–10.06
	HVM40	4H	14	***	1.5			M	–	69.83	4.55
	HvOLE	4H	21	***	1.0			M	–	69.86	4.53
	HvB23D4	4H	26	***	1.4			M	–	69.83	4.55
	GMS89	4H	50	***	0.4			M	–	69.05	3.00
	EBmac0679	4H	83	**	2.0			M	–	69.80	4.48
	HVM67	4H	118	***	3.4			M	–	69.76	4.95
	Bmag0337	5H	35	***	4.8			M	–	70.68	6.38
	Bmac0113	5H	41	***	3.9			M	–	70.35	5.52
	Bmag0113	5H	61	***	1.0			M	+	65.27	–3.26
	HvUDPGPP	5H	91	**	0.7			M	+	65.72	–2.61
	HvLOXC	5H	114	***	2.1			M	+	64.04	–4.84
	GMS27	5H	148	***	16.8			M	+	62.45	–9.22
	HVM6	5H	200	**	1.0			M	+	64.25	–4.65
	HvW1	6H	17	**	0.3			M	–	68.17	1.73
	GMS6	6H	96	**	1.5			M	+	58.62	–13.41
	HvSS1	7H	45	***	0.4			M	–	69.17	3.07
	HvCMA	7H	85	***	0.5			M	–	69.17	3.13
	HvACL3	7H	125	**	0.7			M	–	69.15	3.18
	EBmac0755	7H	145	***	3.4			M	–	70.39	6.07
	HvPRP1B	7H	167	***	0.6			M	–	68.62	2.08
	HvCHI26A	7H	181	***	0.3			M	–	67.98	1.49
	HvGLB2	7H	205	**	0.2			M	+	67.96	–1.09
HEI	Bmag0378	2H	44	**	9.5			M	+	74.81	–12.63
	GMS3	2H	48	**	13.1	**	0.8	M+I	+	73.91	–13.00
	HvBKASI	2H	50	**	14.2	*		M	+	73.96	–13.15
	EBmac0705	3H	25	**	0.9			M	–	84.40	3.25
	HvOLE	4H	21	**	0.8			M	–	86.90	5.82
	HvBAMY	4H	88	**	2.5			M	+	77.99	–5.92
	GMS27	5H	148	**	7.2			M	+	77.85	–9.46
	GMS6	6H	96	**	1.6			M	+	66.83	–19.78
HI	HVM36	2H	17			**	2.4	I	+	0.42	5.00
	GMS3	2H	48			***	3.6	I	+	0.42	5.00
	HvBKASI	2H	50			***	3.2	I	+	0.42	5.00
	Bmag0209	3H	55			**	2.0	I	+	0.40	0.00
	HvES1A	3H	66			**	1.8	I	+	0.41	2.50
	HVM60	3H	73			**	1.9	I	+	0.42	5.00
	HvLOXC	5H	114	**	4.6			M	–	0.38	–7.32
KER	Bmag0113	5H	61	***	9.8			M	–	17.33	–16.04
LOF	*HvALAAT*	1H	57			**	1.0	I	–	3.70	48.00
	HVM20	1H	58			**	0.9	I	–	3.70	48.00
	Bmag0347	1H	70			**	0.9	I	–	3.70	48.59
	HVM36	2H	17			***	4.0	I	+	1.70	–39.72
	Bmag0378	2H	44			***	5.5	I	+	1.56	–45.83
	GMS3	2H	48			***	6.6	I	+	1.70	–39.07
	HvBKASI	2H	50			***	7.8	I	+	1.63	–42.61
	Bmag0337	5H	35			***	3.5	I	–	3.29	33.74
	Bmac0113	5H	41			***	3.4	I	–	3.29	33.20
	GMS27	5H	148			***	2.9	I	+	2.10	–27.08

Table 2 (continued)

Trait[a]	Marker	Chromosome	Position [b]	S_M [c]	R^2_M [d] (%)	S_I [c]	R^2_I [d] (%)	QTL [e]	P/N [f]	LSM[g] [*Hsp*]	RP[*Hsp*] [h] (%)
LOH	HVM36	2H	17			***	3.0	I	+	3.27	–36.38
	Bmag0378	2H	44			***	4.7	I	+	3.98	–25.05
	GMS3	2H	48			***	2.6	I	+	3.29	–36.61
	HvBKASI	2H	50			***	3.3	I	+	3.42	–34.23
	GMS27	5H	148			***	5.7	I	+	4.27	–23.20
MAS	EBmac0679	4H	83	**	0.4			M	+	45.03	3.80
MT	*HvES1A*	3H	66	**	1.3			M	–	58.94	–7.11
TGW	*HvALAAT*	1H	57	**	1.4			M	–	48.69	–4.36
	HVM20	1H	58	**	1.3			M	–	48.69	–4.30
	Bmag0347	1H	70	**	1.4			M	–	48.69	–4.34
	HVM36	2H	17			***	6.2	I	+	51.15	1.15
	Bmag0378	2H	44			***	8.4	I	+	52.82	5.79
	GMS3	2H	48			***	8.3	I	+	52.34	4.06
	HvBKASI	2H	50			***	8.9	I	+	52.27	4.08
	HvITR1	3H	15	**	1.2			M	–	50.06	–2.05
	Bmag0209	3H	55			***	2.1	I	+	52.56	3.98
	HvES1A	3H	66			***	2.2	I	+	52.16	3.18
	HVM33	3H	69			**	1.6	I	+	51.61	2.02
	HVM60	3H	73			***	3.5	I	+	51.76	2.43
	HvBAMY	4H	88	**	0.4			M	–	50.47	–1.19
	Bmac0113	5H	41	*		**	1.3	I	–	49.09	–4.01
	GMS27	5H	148			***	7.8	I	+	52.54	4.20
WA	HVM36	2H	17			**	1.5	I	+	45.99	0.35
YLD	HVM36	2H	17			**	0.8	I	–	50.27	–1.66
	Bmag0378	2H	44	***	9.7			M	–	39.59	–22.60
	GMS3	2H	48	*		***	1.6	I	–	47.33	–8.66
	HvBKASI	2H	50	*		***	1.5	I	–	46.98	–9.67
	HvES1A	3H	66			**	0.7	I	–	48.47	–6.03
	HVM60	3H	73			**	0.7	I	–	50.88	–1.38
	HVM40	4H	14	**	1.1			M	–	47.18	–9.44
	HvB23D4	4H	26	**	1.1			M	–	47.18	–9.58
	EBmac0775	4H	42	**	1.4			M	–	47.25	–10.17
	Bmag0353	4H	45	**	2.7			M	–	44.49	–15.34
	HVM68	4H	45	**	2.0	*		M	–	47.41	–10.09
	EBmac0679	4H	83	**	0.6			M	+	53.91	5.85
	HvBAMY	4H	88	***	4.0			M	–	45.64	–12.28
	Bmag0113	5H	61	***	3.0			M	–	45.41	–13.34
	HvUDPGPP	5H	91	***	5.5			M	–	43.02	–17.60
	HvLOXC	5H	114	***	7.8			M	–	40.78	–22.37
	GMS27	5H	148	***	12.0			M	–	40.94	–20.46
	GMS1	5H	187	***	1.6			M	–	47.03	–9.99

[a] Trait abbreviations, see Table 1
[b] Chromosomal position of markers (in centiMorgans) are deduced from Ramsay et al. (2000) and Pillen et al. (2003)
[c] S_M and S_I, Level of significance of the marker main effect and the M×E interaction, respectively, at **P*<0.05, ***P*<0.01, ****P*<0.001
[d] R^2_M (%) and R^2_I (%), The portion of the phenotypic variance explained by the marker main effect and the M×E interaction, respectively, were calculated as in Pillen et al. (2003)
[e] QTL, A QTL was assumed within the vicinity of a marker locus if the marker main effect (M) or the M×E interaction (I) was significant in the two-factorial ANOVA at *P*<0.01
[f] P/N, Positive (+) or negative (-) effect of the *Hsp* allele at the QTL
[g] LSM[*Hsp*], The least square mean of the trait across all tested environments for homozygous *Hsp* genotypes at the given marker locus
[h] RP[*Hsp*], The relative performance of homozygous *Hsp* genotypes compared to homozygous *Hv* genotypes at a given marker locus

Days until heading (HEA)

Thirty-eight putative QTLs were located for HEA on all seven chromosomes. In all cases, the marker main effect was significant at *P*<0.01. In addition, three loci exhibited significant M×E interactions. For 17 QTLs, a favorable effect of the *Hsp* allele on HEA was observed. At these loci, which were located on chromosomes 2H, 3H, 5H, 6H and 7H, the presence of the *Hsp* allele was associated with a reduced heading time of up to 13.4% ($GMS6_{[6H]}$). At the remaining QTLs, the *Hsp* allele was associated with an increased heading time of up to 6.4% ($Bmag0337_{[5H]}$). The maximum explained phenotypic variance was found at $HvBKASI_{[2H]}$—29.1 %. The large number of QTLs detected for HEA might be partially explained by the occurrence of shared QTL effects of linked SSR loci, indicating that the associated effect could be caused by a single gene. This is, for instance, possible at the center of chromosome 3H where similar favorable QTL effects on HEA were located at markers $Bmag0209_{[3H]}$, $HvES1A_{[3H]}$, $HVM33_{[3H]}$, $HVM60_{[3H]}$ and $Bmag0225_{[3H]}$. These markers are spread across positions

55–74 cM, and the *Hsp* allele is associated with a decrease of HEA between 2.7% and 8.8%. In contrast, seven HEA QTLs were evenly distributed across the complete chromosome 7H, indicating that these partially unlinked SSRs are associated with independent or, at locus $HvGLB2_{[7H]}$, reciprocal QTL effects.

Height (HEI)

Eight putative QTLs for HEI were located on five chromosomes. All loci exhibited significant marker main effects. $GMS3_{[2H]}$ was, in addition, associated with a significant M×E interaction. For six QTLs, a favorable effect of the *Hsp* allele on HEI was observed. At these loci, the presence of the *Hsp* allele lead to a reduction in plant height of up to 19.8% ($GMS6_{[6H]}$). In contrast to A×101, only two loci were associated with an increased plant height of up to 5.8% ($HvOLE_{[4H]}$). The phenotypic variance explained by a QTL reached its maximum with 14.2% at $HvBKASI_{[2H]}$.

Lodging at flowering (LOF)

Compared with A×101, substantially more QTLs were located for LOF in H×101. Altogether ten QTLs for LOF were located on chromosomes 1H, 2H and 5H. All SSRs exhibited significant M×E interactions. At five QTLs, the *Hsp* allele was associated with a reduction of lodging of up to 45.8% ($Bmag0378_{[2H]}$). In contrast, at the remaining five QTLs the tendency to lodge increased up to 48.6% ($Bmag0347_{[1H]}$). The maximum explained phenotypic variance was reached at $HvBKASI_{[2H]}$—7.8%.

Lodging at harvest (LOH)

For LOH, five putative QTLs were located in close proximity on chromosome 2H or on chromosome 5H. All QTLs exhibited significant M×E interactions with favorable *Hsp* alleles. These five SSRs were already associated with the positive M×E interactions on LOF. The maximum effect on LOH was measured at locus $GMS3_{[2H]}$. Here, the *Hsp* allele resulted in a reduced lodging tendency of 36.6% relative to the *Hv* allele. The maximum explained phenotypic variance of the M×E interaction was measured at $GMS27_{[5H]}$—5.7%.

Ears per square meter (EAR)

Whereas no QTLs were detected for EAR in A×101, three putative QTLs for EAR were located in H×101 on chromosomes 1H and 4H. All loci exhibited significant marker main effects. At locus $HvBAMY_{[4H]}$, the *Hsp* allele was associated with a 6.7% increase in EAR. At the remaining two loci, EAR was maximally reduced by 8.9% ($HVM20_{[1H]}$). The maximum explained phenotypic variance was reached at $HvBAMY_{[4H]}$—6.7%.

Kernels per ear (KER)

As in A×101, only one QTL was detected for KER. Marker $Bmag0113_{[5H]}$ exhibited a significant main effect. The negative effect of the *Hsp* allele resulted in a 16.0% reduction in the number of kernels per ear. The explained phenotypic variance for $Bmag0113_{[5H]}$ amounted to 9.8%.

Thousand grain weight (TGW)

Fifteen putative QTLs were located for TGW on five chromosomes. While five loci exhibited significant marker main effects, the other ten loci showed significant M×E interactions. The *Hsp* alleles had favorable effects on TGW for nine QTLs on chromosomes 2H, 3H and 5H. At these loci, the presence of the *Hsp* allele resulted in a TGW increase of up to 5.8% ($Bmag0378_{[2H]}$). Contrasting negative effects of the *Hsp* allele were detected on chromosomes 1H, 3H, 4H and 5H which resulted in reduced TGW of up to 4.4% ($HvALAAT_{[1H]}$). The highest portion of the phenotypic variance was explained by $HvBKASI_{[2H]}$—8.9%.

Yield (YLD)

Altogether 18 putative QTLs for YLD were located on four barley chromosomes. Whereas 13 loci exhibited significant marker main effects, five loci showed significant M×E interactions. As in A×101, most QTL alleles from *Hsp* resulted in yield reductions, up to a maximum of 22.6% ($EBmac0378_{[2H]}$). However, a favorable wild species effect on yield could be detected at locus $EBmac0679_{[4H]}$, where the *Hsp* allele was associated with an average yield increase of 5.9%. The yield-increasing main effect of the *Hsp* allele was detected in all six environments and ranged from 1.8% to 10.5%. A maximum explained phenotypic variance was found at $GMS27_{[5H]}$—12.0%.

Above-ground biomass (MAS)

As in A×101, only one QTL was detected for MAS. Locus $EBmac0679_{[4H]}$ exhibited a significant main effect. The favorable effect of the *Hsp* allele resulted in a 3.8% increase in the above-ground biomass. The explained phenotypic variance for $EBmac0679_{[4H]}$ amounted to 0.4%.

Harvest index (HI)

Seven putative QTLs were located for HI on chromosomes 2H, 3H and 5H. Significant M×E interactions with favorable effects of the *Hsp* allele on HI were measured at six loci. A maximum favorable *Hsp* effect of 5.0% was reached at the three linked loci—HVM36$_{[2H]}$, GMS3$_{[2H]}$ and *HvBKASI*$_{[2H]}$. In contrast, *HvLOXC*$_{[5H]}$ showed a significant marker main effect where the *Hsp* allele was associated with a 7.3% reduction in HI. The highest portion of the phenotypic variance was explained by *HvLOXC*$_{[5H]}$—4.6%.

Protein content (PRO)

No QTLs regulating the expression of protein content were localized in H×101.

Water absorption (WA)

One putative QTL was located for the malting quality-related trait WA. HVM36$_{[2H]}$ exhibited a significant M×E interaction. The favorable effect of the *Hsp* allele was associated with an increase in WA by 0.4%. The phenotypic variance explained by HVM36$_{[2H]}$ was equal to 1.5%.

Malt tenderness (MT)

One putative QTL was located for the malting quality-related trait MT. *HvES1A*$_{[3H]}$ exhibited a significant main effect. The negative effect of the *Hsp* allele was associated with a MT reduced by 7.1%. The phenotypic variance explained by *HvES1A*$_{[3H]}$ was equal to 1.3%.

Comparison of the AB-QTL analyses between H×101 and A×101

In this section we compare the AB-QTL analysis of H×101 with our previous AB-QTL analysis of A×101. Both BC_2F_2 populations were investigated in adjacent fields and under identical field conditions during the 1999 and 2000 seasons (Pillen et al. 2003). The spring barley cultivars Harry and Apex are not related by descent since Harry originates from Arla M × Tellus, introduced in 1978 by Weibull, Sweden, and Apex originates from Aramir × (Ceb.6721 × Julia × Volla × L100), introduced in 1983 by Lochow-Petkus, Germany (Baumer and Cais 2000). Both populations share the wild barley accession ISR101-23 as the donor of new QTL alleles. A comparison of QTL effects will therefore reveal which effects of wild species alleles are conserved between the different elite barley recipients. The size of the two populations differs slightly. Whereas H×101 consists of 164 BC_2F_2 individuals, the number of A×101 individuals drops to 136. The number of informative markers was also slightly different. The H×101 population was genotyped with 50 informative SSRs, while 45 SSRs were used in the A×101 population. In both populations, the same 13 quantitative traits were phenotyped.

Whereas 108 putative QTLs (Table 2) were detected among 650 marker×trait combinations (17%) in H×101, 86 putative QTLs were located among 585 marker×trait combinations (15%) in A×101. Thus, no clear difference between the two populations exists with respect to the QTL detection rate. However, a notable difference was measurable in regard to the percentage of favorable QTL alleles. The QTL alleles of ISR101-23 revealed much more positive effects in H×101, where 52 favorable alleles of the wild species (48%) were located, than in A×101, where 29 favorable alleles (34%) were detected. This discrepancy can be primarily explained by the higher number of significant M×E interactions in H×101 (41 vs. 27 in A×101), giving rise to favorable QTLs effects on HI, LOF, LOH and TGW. While 25 favorable M×E interactions were localized for these traits in H×101, only one favorable interaction was found in A×101.

In order to compare the two backcross populations further, the amount of potentially identical effects of the *Hsp* allele in both populations was investigated. For this, the set of markers was reduced to those markers that were polymorphic in both populations. Table 3 presents the QTL data for 26 SSRs that were informative in both populations. At these SSRs, 338 marker×trait combinations were tested for significant deviations between the *Hv* and the *Hsp* alleles. In total, 55 (16%) and 45 (13%) putative QTLs were located in H×101 and A×101, respectively. Both values are in good agreement with the overall QTL detection rates of 17% and 15%. Seventeen putative QTLs were simultaneously detected in H×101 and in A×101. The majority of reproducible QTLs were found for HEA (11) and the remaining for HEI, TGW and YLD (two each). This finding indicates that most of the heading QTL alleles from Apex and Harry exhibit similar effects and that these effects are significantly different in their ISR101-23 counterpart. In four cases (*HvALAAT*$_{[1H]}$×HEA, HVM40$_{[4H]}$×YLD, GMS27$_{[5H]}$×HEA and GMS27$_{[5H]}$×HEI), the *Hsp* allele was associated with contrary QTL effects between the two populations. The highest number of QTLs detected in both populations were found at GMS27$_{[5H]}$ (three), however in two cases (HEA and HEI) the ISR101-23 allele had opposite effects in H×101 and A×101. In summary, 26% of the putative QTL effects of the ISR101-23 alleles (i.e. 13 common QTLs × 2/100 QTLs investigated in H×101 and A×101) were reproducible between the two genetic backgrounds of Harry and Apex. For 8% of the QTLs investigated, the ISR101-23 allele was associated with significant but opposite QTL effects in H×101 and A×101. The vast majority of the putative QTL effects (66%) were not reproducible between the two populations. Consequently, it remains difficult for breeders to predict the performance of a favorable exotic QTL allele in a new genomic background. The preponderance of

Table 3 Comparison of putative QTL effects between the A×101 and H×101 populations[a]

Chromosome	1H				2H								3H				4H									
Position (cM)	17		57		48		50		103		105		25		74		14		26		45		50		62	
Marker	GMS21		HvALAAT		GMS3		HvBKASI		HVM54		EBmac-0415		EBmac-0705		Bmag-0225		HVM40		HvB23D4		Bmag-0353		GMS89		EBmac-0658	
Population[b]	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H
EAR[c]																										
HEA	–		(–)	(+)	[–]	[–]	[–]	[–]	[+]	[+]		+		+		–		+	[+]	[+]				+	+	
HEI			–			–		–						+					+		+				–	
HI						+		+											–							
KER	–																									
LOF				+		–		–																		
LOH			–			–		–																		
PRO																			+							
TGW				–	[+]	[+]	[+]	[+]											–		–					
WA																			+							
YLD	–					–		–	–		–				–		(+)	(–)		–		–	+			

[a] Putative QTL effects of the *Hsp* allele are either trait-increasing (+) or trait-decreasing (–). QTLs which are common in both populations are in bold and enclosed by square brackets. Those *Hsp* alleles which exhibit opposite QTLs effects in both populations are enclosed by parenthesis

non-reproducible QTLs between the two related backcross populations presumably indicates a high degree of epistatic genetic interaction between the detected QTLs and the genomic background. A similar result was reported for tomato by Fulton et al. (1997) when they compared AB-QTL results from three different wild species accessions which were backcrossed with a single tomato cultivar—only 19% of the QTLs found in the *Lycopersicon peruvianum* cross could be confirmed in at least one of the two additional crosses. The authors interpreted this result as an indication that further investigation of additional donor accessions would be promising in order to identify addition favorable QTL alleles from wild species. Our finding, that roughly one-quarter of the *Hsp* effects are uniform between H×101 and A×101, suggests that only a portion of the QTL effects of a donor can be transferred from one recipient to the next. The same conclusion was drawn by Thomas et al. (1995) and Mather et al. (1997) from classical QTL analyses in barley. Both studies emphasized that only a few QTLs were conserved between the barley crosses Blenheim×E224/3, Harrington×TR306 and Steptoe×Morex.

Comparison of the AB-QTL analyses in A×101 and H×101 with classical QTL analyses in barley

We compared our AB-QTL analysis with classical QTL analyses conducted in doubled haploid (DH) and F_2 generations with respect to common QTL effects. The QTL comparison was carried out by means of a compilation of mapped barley QTLs from P. Hayes (http://barleyworld.org/NABGMP/qtlsum.htm), which is based on the Steptoe×Morex BIN classification published by A. Kleinhofs (http://barleygenomics.wsu.edu/databases/databases.html). The BIN map integrates RFLP, AFLP and SSR markers by allocating them to 99 evenly spaced BIN groups. Based on the BIN map, 14 SSRs of our AB-QTL analyses could be compared with classical barley QTL analyses. These markers are: $HVM4_{[7H]}$, $HVM6_{[5H]}$, $HVM20_{[1H]}$, $HVM33_{[3H]}$, $HVM40_{[4H]}$, $HVM54_{[2H]}$, $HVM60_{[3H]}$, $HVM67_{[4H]}$, $HVM68_{[4H]}$, $WMS6_{[4H]}$, $HvBKASI_{[2H]}$, $HvCMA_{[7H]}$, $HvOLE_{[4H]}$ and $HvPRP1B_{[7H]}$. A possible common QTL was assumed if the BIN groups of two independently detected QTLs were identical or at least overlapped.

Altogether, the 14 selected SSRs could be associated with 33 putative QTLs in the H×101 (Table 2) and A×101 backcrosses (Pillen et al. 2003). By comparing BIN groups, we were able to verify 15 QTL effects (45%) in at least one classical barley QTL analysis (Table 4). Eleven verified QTLs were detected in H×101, four in A×101 and three in both AB populations. The highest number of matching QTLs was found for trait HEA. Here, seven putative QTLs, two of them common to A×101 and H×101, could be verified in classical barley QTL studies. The putative QTL effect for HEA which was associated with $HVM67_{[4H]}$ in A×101 and H×101 was also detected in the same or in overlapping BIN groups in three classical barley QTL studies. The putative HEA QTLs at $HvCMA_{[7H]}$ and $HvPRP1B_{[7H]}$ as well as the HEI QTL at $HvOLE_{[4H]}$ and the LOF QTL at $HvBKASI_{[2H]}$ were also detected in two classical barley QTL studies. In the case of the putative QTLs for HEI and TGW at $HvBKASI_{[2H]}$, the same SSR was found to be associated with two QTL effects in Marquez-Cedillo et al. (2001). A maximum of matching QTLs was found with the Steptoe×Morex population (Hayes et al. 1993, 1996) and with the Harrington×Morex population (Marquez-Cedillo et al. 2000, 2001). In both cases, five putative QTLs could be verified (Table 4). The correspondence of QTLs in A×101 and H×101 with those in the latter two crosses might be reflected by the relatively close genetic distance between the barley wild form ISR101×23 and barley variety Morex. We found a genetic similarity of GS=0.52 between ISR101-23 and Morex based on a fingerprint

Table 3 (continued)

				5H												6H		7H					
88		118		35		41		61		91		148		187		200		17		85		145		167	
HvBAMY		HVM67		Bmag-0337		Bmac-0113		Bmag-0113		HvUDPGPP		GMS27		GMS1		HVM6		HvW1		HvCMA		EBmac-0755		HvPRP1B	
A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H	A	H
	+																								
[–]	[–]	[+]	[+]		+	[+]	[+]		–	[–]	[–]	(+)	(–)	+			–		+		+	[+]	[+]	[+]	[+]
												(+)	(–)									+			
									–																
					+		+						–			–									
													–												
												+													
	–			–			–			+			+	–											
	–					–			–		–	[–]	[–]		–	–						–			

[b] A, A×101; H, H×101
[c] Trait abbreviations: see Table 1

Table 4 Alignment of common QTL between H×101, A×101 and classical QTL analyses in barley based on 14 SSR markers[a]

QTL location in AB-QTL analyses with A×101 or H×101					QTL location in classical QTL analyses of barley		
Trait[b]	Population[c]	Marker	Chromosome	$BIN_{[M]}$[d]	Marker or interval	$BIN_{[R]}$[e]	Reference
HEA	H	HVM60	3H	8	ABG377-ABC307B	8–9	Hayes et al. (1993)
	H	HVM40	4H	2	CDO669-*TubA1*	2–5	Hayes et al. (1993)
	A+H	HVM67	4H	13	*Bmy1*	13	Hackett et al. (1992)
					ABG397-ksuH11	11–13	Hayes et al. (1993)
					ABG397-*Bmy1*	11–13	Hayes et al. (1996)
	H	*HvCMA*	7H	6	ABG380-VAtp57A	4–7	Tinker et al. (1996)
					MWG836-ABG476	5–7	Pena et al. (1999)
	A+H	*HvPRP1B*	7H	12	MWG539-MWG929	11–12	Backes et al. (1995)
					BCD512A	12	Laurie et al. (1995)
HEI	H	*HvBKASI*	2H	8	*HvBKASI-vrs1*	8–10	Marquez-Cedillo et al. (2001)
	H	*HvOLE*	4H	3	CDO542	3	Zhu et al. (1999)
					int c-Phy2	2–4	Marquez-Cedillo et al. (2001)
LOF	H	*HvBKASI*	2H	8	*Adh8*-ABC162	6–8	Hayes et al. (1993)
					ABG716-MWG865	7–10	Tinker et al. (1996)
	A	HVM6	5H	15	MWG650-MWG002	13–15	Backes et al. (1995)
TGW	H	HVM20	1H	7	*Ica1*/ABG452	6–7	Marquez-Cedillo et al. (2000)
	A+H	*HvBKASI*	2H	8	*HvBKASI-vrs1*	8–10	Marquez-Cedillo et al. (2001)
YLD	H	HVM60	3H	8	PSR156A-ABG453	7–9	Marquez-Cedillo et al. (2001)

[a] The alignment of QTL data is based on the barley QTL database curated by Dr. P. Hayes (http://barleyworld.org/NABGMP/qtlsum.htm)
[b] Trait abbreviations: see Table 1
[c] The QTL effect was detected either in A×101 (A), in H×101 (H) or in both AB-QTL populations (A+H)
[d] $BIN_{[M]}$,The assignment of SSR markers to BIN groups is based on mapping results of Dr. A. Kleinhofs in Steptoe×Morex (http://barleygenomics.wsu.edu/databases/databases.html)
[d] $BIN_{[R]}$,The BIN group of a reference marker or interval which is identical or, at least, overlapping with $BIN_{[M]}$

analysis with 22 SSR markers (Pillen et al. 2000 and unpublished results). It should be noted that a corresponding localization of a QTL in two independent studies does not necessarily verify that the same gene is responsible for the phenotypic variation of the trait. It is also possible that two linked loci are the cause of the phenotypic variation in both QTL studies. However, the corresponding location of a QTL in independent studies confirms that a chromosomal sub-region might be important for the expression of the trait under investigation.

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References

Backes G, Graner A, Foroughi Wehr B, Fischbeck G, Wenzel G, Jahoor A (1995) Localization of quantitative trait loci (QTL) for agronomic important characters by the use of a RFLP map in barley *(Hordeum vulgare* L.). Theor Appl Genet 90:294–302

Baumer M, Cais R (2000) Abstammung der Gerstensorten. Bayerische Landesanstalt für Bodenkultur und Pflanzenbau

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

Bernacchi D, Beck Bunn T, Emmatty D, Eshed Y, Inai S, Lopez J, Petiard V, Sayama H, Uhlig J, Zamir D, Tanksley S (1998b) Advanced backcross QTL analysis of tomato. II. Evaluation of near-isogenic lines carrying single-donor introgressions for desirable wild QTL-alleles derived from *Lycopersicon hirsutum* and *L. pimpinellifolium*. Theor Appl Genet 97:170–180

Brondani C, Rangel PHN, Brondani RPV, Ferreira ME (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

Frary A, Nesbitt TC, Frary A, Grandillo S, van der Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert KB, Tanksley SD (2000) *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. Science 289:85–88

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 parviflorum* cross. Theor Appl Genet 100:1025–1042

Fulton TM, Bucheli P, Voirol E, Lopez J, Petiard V, Tanksley SD (2002) Quantitative trait loci (QTL) affecting sugars, organic acids and other biochemical properties possibly contributing to flavor, identified in four advanced backcross populations of tomato. Euphytica 127:163–177

Hackett CA, Ellis RP, Forster BP, McNicol JW, Macaulay M (1992) Statistical analysis of a linkage experiment in barley involving quantitative trait loci for height and ear-emergence time and two genetic markers on chromosome 4. Theor Appl Genet 85:120–126

Hayes PM, Liu BH, Knapp SJ, Chen F, Jones B, Blake T, Franckowiak J, Rasmusson D, Sorrells M, Ullrich SE, Wesenberg D, Kleinhofs A (1993) Quantitative trait locus effects and environmental interaction in a sample of North American barley germplasm. Theor Appl Genet 87:392–401

Hayes P, Prehn D, Vivar H, Blake T, Comeau A, Henry I, Johnston M, Jones B, Steffenson B, St. Pierre CA, Chen F (1996) Multiple disease resistance loci and their relationship to agronomic and quality loci in a spring barley population. J Agric Genomics (http://www.ncgr.org/research/jag/papers96/paper296/ indexp296.html)

Ho JC, McCouch SR, Smith ME (2002) Improvement of hybrid yield by advanced backcross QTL analysis in elite maize. Theor Appl Genet 105:440–448

Huang XQ, Cöster H, Ganal MW, Röder MS (2003) 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

Laurie DA, Pratchett N, Bezant JH, Snape JW (1995) RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter × spring barley *(Hordeum vulgare* L.) cross. Genome 38:575–585

Marquez-Cedillo LA, Hayes PM, Jones BL, Kleinhofs A, Legge WG, Rossnagel BG, Sato K, Ullrich SE, Wesenberg DM (2000) QTL analysis of malting quality in barley based on the doubled-haploid progeny of two elite North American varieties representing different germplasm groups. Theor Appl Genet 101:173–184

Marquez-Cedillo LA, Hayes PM, Kleinhofs A, Legge WG, Rossnagel BG, Sato K, Ullrich SE, Wesenberg DM (2001) QTL analysis of agronomic traits in barley based on the doubled-haploid progeny of two elite North American varieties representing different germplasm groups. Theor Appl Genet 103:625–637

Mather DE, Tinker NA, LaBerge DE, Edney M, Jones BL, Rossnagel BG, Legge WG, Briggs KG, Irvine RB, Falk DE, Kasha KJ (1997) Regions of the genome that affect grain and malt quality in a North American two-row barley cross. Crop Sci 37:544–554

Moncada PP, 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* BC2F2 population evaluated in an upland environment Theor Appl Genet 102:41–52

Monforte AJ, Tanksley SD (2000) Fine mapping of a quantitative trait locus (QTL) from *Lycopersicon hirsutum* chromosome 1 affecting fruit characteristics and agronomic traits: Breaking linkage among QTLs affecting different traits and dissection of heterosis for yield. Theor Appl Genet 100:471–479

Monforte AJ, Friedman E, Zamir D, Tanksley SD (2001) Comparison of a set of allelic QTL-NILs for chromosome 4 of tomato: Deductions about natural variation and implications for germplasm utilization. Theor Appl Genet 102:572–590

Pena de la RC, Smith KP, Capettini F, Muehlbauer GJ, Gallo Meagher M, Dill Macky R, Somers DA, Rasmusson DC (1999) Quantitative trait loci associated with resistance to *Fusarium* head blight and kernel discoloration in barley. Theor Appl Genet 99:561–569

Pillen K, Binder A, Kreuzkam B, Ramsay L, Waugh R, Förster J, Léon J (2000) Mapping new EMBL-derived barley microsatellites and their use to differentiate German barley cultivars. Theor Appl Genet 101:652–660

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

Ramsay L, Macaulay M, degli Ivanissevich S, MacLean K, Cardle L, Fuller J, Edwards KJ, Tuvesson S, Morgante M, Massari A, Maestri E, Marmiroli N, Sjakste T, Ganal M, Powell W, Waugh R (2000) A simple sequence repeat-based linkage map of barley. Genetics 156:1997–2005

SAS Institute (1999) The SAS system for Windows, release 8.00. SAS Institute, Cary, N.C.

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: Unlocking genetic potential from the wild. Science 277:1063–1066

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 Y, 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

Thomas WTB, Powell W, Waugh R, Chalmers KJ, Barua UM, Jack P, Lea V, Forster BP, Swanston JS, Ellis RP, Hanson PR, Lance RCM (1995) Detection of quantitative trait loci for agronomic, yield, grain and disease characters in spring barley *(Hordeum vulgare* L.). Theor Appl Genet 91:1037–1047

Tinker NA, Mather DE, Rossnagel BG, Kasha KJ, Kleinhofs A, Hayes PM, Falk DE, Ferguson T, Shugar LP, Legge WG, Irvine RB, Choo TM, Briggs KG, Ullrich SE, Franckowiak JD, Blake TK, Graf RJ, Dofing SM, Saghai Maroof MA, Scoles GJ, Hoffman D, Dahleen LS, Kilian A, Chen F, Biyashev RM, Kudrna DA, Steffenson BJ (1996) Regions of the genome that affect agronomic performance in two-row barley. Crop Sci 36:1053–1062

Xiao J, Grandillo S, Ahn SN, McCouch SR, Tanksley SD, Li J, Yuan L (1996) Genes from wild rice improve yield. Nature 384:223–224

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

Zhu H, Gilchrist L, Hayes P, Kleinhofs A, Kudrna D, Liu Z, Prom L, Steffenson B, Toojinda T, Vivar H (1999) Does function follow form? Principal QTLs for *Fusarium* head blight (FHB) resistance are coincident with QTLs for inflorescence traits and plant height in a doubled-haploid population of barley. Theor Appl Genet 99:1221–1232