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G. Backes · A. Graner · B. Foroughi-Wehr
G. Fischbeck · G. Wenzel · A. Jahoor

Localization of quantitative trait loci (QTL) for agronomic important characters by the use of a RFLP map in barley (*Hordeum vulgare* L.)

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Abstract Two hundred and fifty doubled haploid lines were studied from a cross between two 2-row winter barley varieties. The lines were evaluated for several characters in a field experiment for 3 years on two locations with two replications. From a total of 431 RFLP probes 50 were found to be polymorphic and subsequently used to construct a linkage map. Quantitative trait loci (QTLs) were determined and localized for resistance against *Rhynchosporium secalis* and *Erysiphe graminis*, for lodging, stalk breaking and ear breaking tendency, for the physical state before harvest, plant height, heading date, several kernel parameters and kernel yield. The heritability of the traits ranged from 0.56 to 0.89. For each trait except for kernel thickness, QTLs have been localized that explain 5–52% of the genetic variance. Transgressive segregation occurred for all of the traits studied.

Key words Quantitative trait loci · *Hordeum vulgare* Agronomic characters · Resistance

Introduction

In the past, the localization of genes was largely restricted to the loci of qualitatively inherited traits. Only arduous attempts using wide linkages between morphological markers and some loci with large weights on the quantitative trait under examination (major genes) were successful. The number of genes affecting a trait was estimated by elaborated statistical methods based on simplified assumptions such as additive effects, no linkage between loci, equal effects of all loci and the loci from one parent affecting the trait in one direction (Wright 1968). The use of isozyme markers with their more frequent occurrence in breeding lines that compensated for some of the drawbacks of the morphological markers, enabled the localization of several loci responsible for quantitative traits (QTS) (Tanksley et al. 1982; Vallejos and Tanksley 1983; Edwards et al. 1982; Weller et al. 1988). Finally, the development of DNA markers such as restriction fragment length polymorphism (RFLP) markers (Botstein et al. 1980) and random amplified polymorphic DNA (RAPD) markers (Weber and May 1989) created the possibility of producing dense linkage maps. Such maps were subsequently generated for tomato (Tanksley and Rick 1980), potato (Gebhardt et al. 1991), sugar beet (Pillen et al. 1992), maize (Helentjaris 1987), barley (Graner et al. 1991), wheat (Liu 1991) and other agriculturally important crops and they are now being used for the mapping of quantitative trait loci (Knapp et al. 1990).

In addition to these analytical developments, much progress has been made in statistical treatment used in evaluation of the data output of QTL analysis (Geldermann 1975); specifically the maximum likelihood method (Lander and Botstein 1989) and the regression method (Haley and Knott 1992). Powerful computer programs for QTL analysis have become available (Paterson et al. 1988). Consequently, quantitative trait loci have been mapped, for example in tomato (Kinzer et al. 1990), maize (Melchinger et al. 1992), rice (Ahn et al. 1993) and barley (Hayes et al. 1993).

The purpose of the study presented here was the localization of loci for quantitative traits, including physiological, phenotypic and yield parameters as well as resistance against fungal diseases, and their integration into an existing RFLP map.

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G. Backes · G. Fischbeck · A. Jahoor (✉)
Lehrstuhl für Pflanzenbau und -züchtung der TU München, Weihenstephan, 85350 Freising, Germany

A. Graner · B. Foroughi-Wehr · G. Wenzel
Bundesanstalt für Züchtungsforschung an Kulturpflanzen, Institut für Resistenzgenetik, 84561 Grünbach, Germany

Materials and methods

Germplasm and field evaluation

Two hundred and fifty doubled haploid (DH) lines from the F_1 of the cross between two 2-row winter barley varieties 'Igri' and 'Danilo'

were developed by anther culture (Foroughi-Wehr and Wenzel 1990) and selfed for eight generations. These lines were evaluated in field experiments at two locations (Roggenstein and Grünbach) for 3 years (1989/1990, 1990/1991 and 1991/1992). The experimental plots of 10 m^2 (Roggenstein) or 5 m^2 (Grünbach) were arranged in a lattice design with two replications. The traits infection severity by *Rhynchosporium secalis*, infection severity by *Erysiphe graminis*, lodging, stalk breaking, ear breaking and physical state before harvest were scored on a scale of 1–9, where 1 denotes the most positive and 9 the most 'negative' expression of the character. Plant height, heading date (in days after the first of May), kernel weight, sieve fractions (22, 25 and 28 mm) and kernel yield were also determined. On the basis of the sieve fractions and the assumption of a normal distribution, the kernel thickness was calculated. The values calculated for thickness were used to compute kernel length based on the assumption of a regular ellipsoid, and kernel shape was determined as the quotient of kernel length and kernel thickness (see also Table 1).

RFLP assays

Genomic DNA was isolated according to the CTAB procedure (Saghai-Maroof et al. 1984, modified), digested with the restriction enzymes *Bam*HI, *Eco*RI, *Eco*RV, *Hin*dIII, *Sac*I and *Xba*I and separated electrophoretically in TAE buffer. The DNA was fixed by alkaline transfer (Reed and Mann 1985) to nylon membranes (Pall Biodyne B). A set of anonymous genomic barley DNA probes were developed as described elsewhere (Jahoor et al. 1991). The fragments were labeled with [^{32}P]dCTP by the random primed labeling method (Feinberg and Vogelstein 1983) and hybridized overnight with the DNA filters at 68°C using the Boehringer 'Blocking Reagent' (Boehringer Mannheim).

Data analysis

A linkage map was computed from the F_2 data of the polymorphic probes using the MAPMAKER 3.0 software (Lander et al. 1987). The genetical distances were calculated using the Haldane correction. The LOD threshold was fixed at 3.0 and the error detection was used. The heritabilities (h^2) of the traits were estimated from the formula:

$$h^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}^2 re + \hat{\sigma}_{ge}^2 e + \hat{\sigma}_g^2},$$

where $\hat{\sigma}_g^2$ is the genetic variance, $\hat{\sigma}_{ge}^2$ is the genetic-by environment interaction variance, $\hat{\sigma}^2$ is the error variance, r is the number of replications and e is the number of environments (Schön et al. 1993).

The traits mildew, stalk breaking, tiller breaking and physical state before harvest were transformed ($\log_{10}$) because of their significant deviation from a normal distribution. The correlations between the traits were computed based on the data from all environments using the computer program SPSS for Windows (SPSS). The effect of the RFLP locus on the QTLs was estimated by analysis of variance, taking into account the effect of the probe, the effect of the environment (location by year) and the interaction of the probe by environment (SPSS for Windows procedure MANOVA, SPSS). The QTLs were mapped to marker intervals by the MAPMAKER QTL 1.1 computer program (Paterson et al. 1988) using the means of the lines over all environments and replications. The formula for an appropriate threshold T under the assumption of a 'sparse-map' case (independent intervals) is given by Lander and Botstein (1989):

$$T = \frac{1}{2}(\log_{10} e)(Z_{\alpha_M})^2$$

where α is the probability of declaring a false QTL in a single interval and M is the number of intervals. In this case, a probability of 0.05 corresponds to LOD 2.0, a probability of 0.01 to LOD 2.56 and an error probability of 0.01 would coincide with LOD 3.59. The proportion of the variance explained by the RFLP locus is designated as the part of the genetic variance explained by the QTLs, as it based on the means of the lines. This calculation was carried out using the MAP function of MAPMAKER QTL following the definition of the actual sites of the QTLs as a sequence.

All computations were performed on an IBM compatible personal computer.

Results

RFLP analysis

A total of 50 out of 431 single- or low-copy probes showed different RFLP patterns for the two parental varieties. This indicates a degree of 11.6% polymorphism, which is very low in comparison to our previous studies (Graner et al. 1990). The map constructed with these probes consists of 54 RFLP loci. Therefore, former knowledge about the localization of the probes (Graner et al. 1991) was applied to assign a single marker to chromosome 1H and to arrange two linkage groups of probes on chromosomes 2H and 7H and four groups on chromosome 5H. The complete map with the probes and the map distance between them is presented in column 1 and 2 of of Table 3. All probes are designated by the prefix 'MWG', which is not added in the tables.

Analysis of agronomic traits

As can be seen from a comparison of the mean value of the parents 'Igri' and 'Danilo' to the value of the DH lines with the lowest and the highest expression of the traits (all shown in Table 1), transgressive segregation has occurred for each of the traits. Lodging is an extreme example as it does not show any difference between the values of the parents but does show a difference of 4 scaling points between the values of the lowest and the highest DH line. Plant height is another striking case of transgression with a difference of about 3 cm between the parents and a range of 20 cm among the means of the DH lines.

The heritability of the different traits is shown in Table 1. For infection severity by powdery mildew, lodging' and kernel yield heritability was very low. For powdery mildew, this can be explained by the low mildew infection in 1990/1991. The highest heritability values were found for kernel parameters and heading date. Although large differences for heading date, existed between different years, low values for line-by-environment interaction variance together with low error variance (data not shown) explain the high heritability value obtained.

Correlations between traits

The correlation coefficients between the traits and their error probabilities are listed in Table 2. Very high correla-

Table 1 The traits examined, their codes and units, the mean of the parents, the minimum and maximum line (mean over environments), the heritabilities of the traits, the QTLs detected and the part of the genetic variance explained by these

Trait	Code	Units	Mean Igri	Mean Danilo	Minimum DH lines	Maximum DH lines	h^2	QTLs	$V_{g,\,expl}$
Infection by *Rhynchosporium*	RY	Scaling points (1–9)	4.5	6.6	2.9	7.7	0.76	5	52%
Infection by powdery mildew	PM	Scaling points (1–9)	4.4	3.0	1.9	5.8	0.56	1	9%
Lodging	LO	Scaling points (1–9)	2.2	2.1	1.0	5.1	0.67	3	26%
Stem breaking	SB	Scaling points (1–9)	2.6	3.3	1.2	6.0	0.74	4	33%
Ear breaking	EB	Scaling points (1–9)	2.1	1.6	1.0	4.3	0.70	3	44%
Physical state before harvest	SH	Scaling points (1–9)	5.1	5.8	3.7	8.0	0.72	3	23%
Plant height	PH	cm	81.5	84.3	73.3	93.0	0.72	3	29%
Heading date	HD	Days after first of May	14.7	17.4	8.0	20.25	0.89	3	48%
Kernel length	KL	mm	7.62	8.02	6.53	8.64	0.81	2	11%
Kernel thickness	KT	mm	2.96	2.90	2.67	3.32	0.88	–	–
Kernel shape	KS	mm/mm	2.59	2.78	1.99	3.18	0.86	1	5%
Kernel weight	KW	g/1000 kernel	44.0	44.5	37.8	48.5	0.86	2	15%
Kernel yield	KY	g/m^2	669	639	543	750	0.61	3	25%

Table 2 Correlation coefficients between the traits[a] (upper half) and their error probabilities α (lower half)

	RY	PM	LO	SB	EB	SH	PH	HD	KL	KT	KS	KW	KY
RY	–	+0.037	+0.027	+0.214	–0.073	+0.178	–0.128	+0.241	+0.106	–0.195	+0.167	–0.196	–0.048
PM	0.092	–	–0.226	+0.418	+0.363	+0.270	–0.260	+0.419	–0.140	+0.023	–0.097	–0.051	–0.090
LO	0.123	0.000	–	+0.354	+0.193	+0.523	+0.203	–0.023	+0.200	–0.331	+0.297	–0.318	+0.354
SB	0.000	0.000	0.000	–	+0.484	+0.649	–0.165	+0.110	+0.186	–0.516	+0.388	–0.575	+0.339
EB	0.000	0.000	0.000	0.000	–	+0.475	–0.157	–0.351	–0.129	–0.084	–0.024	–0.191	+0.243
SH	0.000	0.000	0.000	0.000	0.000	–	–0.573	+0.026	+0.123	–0.333	+0.258	–0.368	+0.168
PH	0.000	0.000	0.196	0.000	0.000	0.003	–	+0.143	+0.075	+0.194	–0.065	+0.311	+0.294
HD	0.000	0.000	0.000	0.000	0.000	0.170	0.000	–	+0.231	–0.279	+0.278	–0.234	–0.135
KL	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–0.711	+0.917	–0.303	+0.161
KT	0.000	0.285	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–0.926	+0.883	–0.197
KS	0.000	0.000	0.000	0.000	0.210	0.000	0.000	0.000	0.000	0.000	–	–0.653	+0.183
KW	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–	–0.162
KY	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	–

[a] Codes for the traits are given in Table 1

tion coefficients were found among the parameters kernel length (KL), kernel thickness (KT) and kernel shape (KS), which is due to the computation of the data as described in the method section. Poor correlation (–0.303) was detected between kernel weight (KW) and KL, while the correlation between KT and KW is high (+0.883). This is in agreement with the general findings that KL is independent from KW and vice versa. Furthermore, high positive correlations between stem breaking (SB), ear breaking (EB), lodging (LO) and physical state before harvest (SH) were found, since all of them depend on the stability of the stem tissue and are largely responsible for the trait physical state before harvest. A considerable positive correlation between infection severity of powdery mildew (PM) and SB as well as between PM and EB supports the hypothesis that tissue stability may be a main factor in the expression of quantitative resistance against powdery mildew in this cross. In addition, a positive correlation was found between heading date (HD) and PM, which possibly relates to adult resistance of the lines with the earlier heading date.

Detection and localization of QTLs

For the detection and localization of QTLs, both analysis of variance (ANOVA) and interval mapping were applied. The results are presented in Table 3. For every mapped RFLP probe, the significance of the mean sum of squares (MS) for the marker locus and for the marker locus-by-environment interaction is shown. For each interval between RFLP loci the LOD of 'one QTL in this interval' versus 'no QTL in this interval' and the effect of the QTL is listed, if the LOD is higher than 2. The sign attached to this value indicates differences in the expression contributed by the 'Igri' alleles. Positive and negative signs mark superior versus inferior contributions as compared to the respective 'Danilo' allele. It is striking that ANOVA detected many more markers influencing a given trait than QTLs have been found by interval mapping. Certainly, one explanation for this fact is the different database. ANOVA uses the full set of information about environmental effects including replications, while interval mapping is based upon the

Table 3 Results of the ANOVA and of the inverval mapping

		Traits[a]: significance of the marker locus (M) and marker locus by environment variance (ME), LOD (L) and weight (W)[b] of QTLs																							
		RY		PM		LO		SB		EB		SH		PH		HD		KL		KT		KS		KW		KY	
Chr	Marker distance	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W
1H	0954	–	–	–	–	***	–	–	–	–	–	**	–	–	–	–	–	***	–	***	–	***	–	–	–	–	–
2H	0557	–	–	–	–	–	–	***	–	***	**	–	–	***	–	***	–	–	–	–	–	***	–	–	–	***	–
	50 cM									5.0	+1.3					4.0	–1.3										
	0769	–	–	–	–	*	–	–	–	***	***	***	**	***	–	***	–	***	–	***	–	***	–	–	–	–	–
	14 cM							2.9	+1.0			2.3	+1.1														
	0581	*	–	–	–	–	–	***	–	***	**	***	–	***	–	***	–	–	–	***	–	***	–	***	–	–	–
	15 cM																										
	0882	–	–	–	–	*	–	*	–	***	**	***	–	**	–	***	–	*	–	***	–	***	–	***	–	–	–
	0866	***	–	–	–	**	**	***	–	–	–	–	–	–	–	***	–	–	–	***	–	***	–	***	–	***	***
	20 cM	16.9	1.1																					2.1	–1.0	7.4	–23
	0829	***	–	–	–	*	***	***	**	–	–	*	***	***	–	***	–	–	–	***	**	***	–	***	***	***	***
3H	0043	***	–	–	–	–	–	–	–	–	–	*	–	**	–	***	–	***	–	**	–	***	–	*	–	–	–
	30 cM																										
	0555a	–	–	–	–	–	–	–	–	–	–	*	–	–	–	**	–	–	–	–	–	–	–	*	–	–	–
	16 cM																										
	0555c	–	–	–	–	–	–	–	–	–	–	**	–	***	–	–	–	–	–	–	–	–	–	–	–	*	–
	43 cM																										
	0961	***	–	–	–	–	–	***	***	–	–	***	***	*	–	***	–	–	–	–	–	–	–	**	–	–	–
	24 cM																										
	0073	*	–	–	–	–	–	**	–	–	–	**	–	–	–	**	–	–	–	–	–	–	–	–	–	***	–
	13 cM																										
	0693	***	–	*	–	–	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–	**	–	–	–
	4 cM																										
	0542	–	–	**	–	*	–	–	–	***	–	–	*	–	–	***	–	–	–	–	–	–	–	–	–	–	–
	1 cM																										
	0103	*	–	***	–	–	–	–	–	*	–	–	**	–	***	–	–	–	–	–	–	–	*	**	**	–	–
	15 cM																										
	0041	–	–	*	–	*	–	–	–	***	–	**	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–
	4 cM																										
	0006	–	–	*	–	–	–	–	–	**	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	***	–
	27 cM	2.3	–0.5																								
	0838	***	–	–	–	***	*	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4H	2033	**	–	–	–	–	–	–	–	**	–	–	–	–	–	–	–	***	–	***	–	***	–	***	–	–	–
	38 cM																										
	0857	–	**	–	–	***	***	***	–	***	*	***	–	**	–	–	–	***	–	–	–	*	–	***	–	*	–
	12 cM																	2.4	+0.14								
	0611	–	–	*	–	***	***	***	***	***	***	***	*	***	–	**	–	***	–	–	**	***	–	***	*	***	–
	2 cM					7.2	–1.3			9.7	–1.3	6.4	–1.1														
	0921	–	–	*	–	***	***	***	***	***	***	***	*	**	–	*	–	***	–	***	–	–	–	***	**	***	–
	13 cM						5.4	–1.3															5.2	+1.5			

Table 3 (continued)

Chr	Marker distance	Traits[a]: significance of the marker locus (M) and marker locus by environment variance (ME), LOD (L) and weight (W)[b] of QTLs																							
		RY		PM		LO		SB		EB		SH		PH		HD		KL		KT		KS		KW		KY	
		M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W
	0880	***	–	–	–	***	***	***	***	***	***	***	***	***	–	**	–	*	–	***	–	*	–	***	*	***	–
	39 cM													2.5	+2.1												
	0842	–	–	***	–	*	–	***	–	*	–	***	*	***	–	**	–	*	–	–	–	–	–	***	*	***	***
	28 cM																										
	0042	–	–	–	–	*	–	*	–	–	–	**	–	–	–	***	–	**	–	***	–	***	–	***	–	***	*
5H	0770	***	–	–	–	–	–	–	–	**	–	–	–	***	–	***	–	***	–	***	***	***	–	***	–	–	–
	35 cM																										
	0526	–	–	–	–	–	–	–	–	–	–	–	–	**	–	***	–	–	–	**	–	–	–	***	–	–	–
	0946	***	–	–	–	–	–	***	–	–	–	–	–	**	–	***	–	–	–	*	–	–	–	**	–	*	–
	18 cM							2.2	+1.3																		
	0550	–	–	–	–	**	–	***	–	–	–	**	–	–	–	***	–	–	–	–	–	–	–	–	–	**	–
	0900			–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
	47 cM																										
	0650	***	–	*	–	***	–	–	–	–	–	*	–	***	–	***	–	*	–	*	–	*	–	–	–	**	–
	0034	**	–	*	–	***	***	–	–	–	–	–	–	***	–	***	–	*	–	*	–	*	–	–	–	–	–
	19 cM					2.9	–1.2																				
	0002	***	–	*	**	***	*	–	–	–	–	*	–	***	–	***	–	–	–	***	–	–	–	**	–	–	–
	14 cM													7.0	+2.9												
	0851a	–	–	***	–	*	–	–	–	–	–	–	–	***	–	–	–	*	–	***	–	***	–	***	–	–	–
6H	0966	–	–	***	***	–	–	–	–	–	***	–	–	–	–	***	–	–	–	*	–	*	–	–	–	–	–
	27 cM																										
	0916	–	–	***	*	***	–	**	–	***	***	***	–	–	–	–	–	*	–	–	–	*	–	–	–	***	–
	41 cM																										
	0617	***	–	–	–	–	–	–	–	*	–	–	**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	12 cM																										
	0715	***	–	–	–	–	*	**	–	–	–	*	–	–	–	***	–	–	–	**	–	*	–	***	–	*	–
	18 cM	2.3	–0.6																								
	0820a		**	–	–	–	***	**	***	–	***	**	–	–	–	***	–	–	–	–	–	–	–	–	–	–	–
	20 cM					2.9	–1.2																				
	0820c	–	–	–	–	***	***	***	***	***	***	***	*	–	–	–	–	**	–	–	–	*	–	–	–	***	–
	13 cM							2.5	–1.2	3.6	–1.2	2.9	–1.1													2.4	+15
	0820b	*	–	*	–	***	*	***	***	***	**	***	**	–	–	***	–	–	–	–	–	–	–	***	–	***	***
	50 cM																										
	0549	**	–	–	–	–	–	–	–	–	–	*	–	**	–	***	–	***	–	***	–	***	–	***	–	–	–
	20 cM																										
	0911	***	–	–	–	***	***	***	–	***	*	***	**	***	–	*	–	***	–	–	–	**	–	*	*	***	***
	16 cM	2.3	0.4											2.8	+1.7												
	0514	***	–	–	–	***	**	***	–	–	–	**	–	***	–	*	–	**	–	–	–	–	–	–	–	–	–

Table 3 (continued)

Chr	Marker distance	Traits[a]: significance of the marker locus (M) and marker locus by environment variance (ME), LOD (L) and weight (W)[b] of QTLs																							
		RY		PM		LO		SB		EB		SH		PH		HD		KL		KT		KS		KW		KY	
		M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W	M L	ME W
7H	0851b	***	–	***	**	**	–	–	–	–	–	–	–	***	–	***	–	**	–	***	–	***	–	***	*	**	***
	11cM																										
	0555b	***	–	***	**	***	*	**	*	–	–	–	–	***	–	***	–	***	–	***	–	***	–	***	–	***	–
	10 cM			3.8	–1.1																						
	0530	***	–	***	***	**	*	–	–	–	–	–	**	***	–	***	–	**	–	–	–	–	–	–	*	***	**
	13 cM																									2.4	+13
	0635	***	–	***	***	**	**	–	–	–	–	–	*	**	*	***	–	***	*	***	*	–	***	–	*	***	**
	11 cM	3.5	–0.5													16.6	+1.7										
	0527	***	–	***	**	***	***	–	–	–	–	–	***	***	**	***	–	***	**	***	**	***	*	–	***	***	*
	6 cM																	2.8	+0.17				2.3	+0.09			
	0104	***	–	–	–	***	***	–	–	–	–	*	***	***	***	***	–	***	**	***	**	***	*		***	**	***	***
	0539	–	–	–	–	**	*	**	–	–	–	**	–	–	***	–	***	–	***	–	***	–	***	–	***	**	***
	36 cM															2.6	+0.7										
	0929	–	–	–	–	***	–	**	–	**	–	***	–	**	–	***	–	–	–	–	–	–	–	–	–	–	–

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; –, not significant

[a] See Table 1 for codes

[b] QLT effect: + value, 'Igri' allele has the greater value; – value, 'Danilo' allele has the greater value

mean of the lines over all environments and replications. Furthermore, significant results of ANOVA relate to single markers, which includes the possibility of chance associations when applied to a large number of markers. In Table 1, the number of QTLs detected for the respective traits are listed and their contribution to the variance of the means of the DHs is indicated

For the trait infection by *Rhynchosporium* (RY) 5 QTLs on four chromosomes were been determined, the one with the highest effect (1.1 scaling points) on chromosome 1H with an effect in the opposite direction as compared to the other 3 QTLs on the chromosomes 3H, 6H and 7H with relatively smaller effects. Therefore, lines combining all 4 positive QTLs showed a lower degree of infection by *Rhynchosporium* than the better parent 'Igri'(data not shown). Fifty-two percent of the genetical variance can be explained by recombinations between these 4 QTLs.

For infection by powdery mildew only 1 QTL was detected on 7H, explaining 9% of the genetic variance. As mentioned before, the infection rate of powdery mildew was low in 1990/1991. In 1991/1992 no infection occurred at all and due to this fact the PM data of these years are excluded from the analysis of this trait. Taking into account the data of 1992/1993, the QTLs on chromosome 7H reached an LOD of 5.5 and an additional QTL with an LOD of 2.2 appeared on chromosome 6H between *MWG966* and *MWG916*.

For the traits lodging, stalk breaking, ear breaking and physical state before harvest similar QTL patterns were found, as would be expected from the close correlations between these traits (Table 2). A QTL was found for SB, EB and SH on chromosome 2H, although its position on the chromosome is slightly different for EB. The shape of the LOD curve suggests the presence of 2 different QTLs in all of the 3 traits, with different values of the peaks in EB as compared to SO and SH. On chromosome 4H, another QTL for LO, SB, EB and SH was detected. All these traits are influenced in the same direction and the shape of the LOD line is similar. On chromosome 5H a QTL for LO and one for SB was discovered. The QTL detected for SB, EB and SH on chromosome 6H seemed to be the same as the one detected for LO in the neighboring interval. The parts of the variance explained for these traits ranged from 23% (SH) to 44% (EB).

For plant height 3 QTLs with positive weight on the chromosomes 4H, 5H and 7H were detected, explaining 29% of the genetic variance. QTLs with negative effects were not detected.

The trait heading date is remarkable by the fact that 1 QTL was mapped with a very high LOD of 16.6 (on chromosome 7H). Two additional QTLs of minor reliability and effect were detected on chromosome 2H and 7H. These QTLs explained 48% of the genetic variance.

For kernel length, 2 QTLs were localized on chromosome 4H and 7H. In addition, the QTL detected on chromosome 7H also affected kernel shape. No QTLs were found for kernel thickness. For kernel weight, 2 QTLs on chromosome 2H and 3H were detected, but the explanation of genetic variance for these kernel parameters is low.

Remarkably, for kernel yield 3 QTLs were localized explaining 25% of the genetic variance although the heritability of this trait was lower than for other characters. However, the QTL with the largest influence on chromosome 2H coincides with the one influencing the trait infection by *Rhynchosporium*. When the kernel yield was adjusted for *Rhynchosporium* infection by linear regression, this QTL disappeared. Even though the association between KY and RY is low over the mean of the years, the correlation obtained in the Roggenstein trials exceeded 0.5 in 1990/1991 and 1991/1992.

Discussion

Some of the traits examined in this work had been explored in barley by other scientists. Where possible, additional data of barley maps (Kleinhofs et al. 1993; Graner et al. 1991; and unpublished results) were taken into account to discuss the parallelism of different localizations of the subsequent comparisons.

For lodging, the NABGM group (Hayes et al. 1993) localized QTLs on chromosomes 1H, 2HS, 2HL, 3HL, 4HL, 7HS and 6HL. When we compose the positions of the QTLs on chromosome 4HL and 6HL with the QTL assigned to the same chromosome arms in this study, these QTLs are situated at least in neighboring regions. No QTL was detected in the NABMG analysis that corresponded to the QTL on chromosome 5H localized in this investigation.

For plant height, in the NABGM group found QTLs on chromosome 1H, 2HS, 2HL, 3HL, 4HS, 5HL, 4HL, 6HL and 7HS (2). Barua et al. (1993) localized the *denso* dwarfing gene to chromosome 3HL and a further QTL for plant height on chromosome 7H. The QTL detected on chromosome 4H(L) in this experiment is located slightly more distally than the corresponding QTL from the NABGM group. The same situation applies to the QTL detected on chromosome 6H(L). The QTL on 5H found in this investigation seems to be located much more distally than that localized in the NABGM project.

QTLs for the trait heading date were assigned to barley chromosomes 2HS, 2HL, 3HL (2), 4HS, 4HL, 6HS, 7HS and 7HL by Hayes et al. (1993) and to chromosomes 5H and 6H by Barua et al. (1993). Thomas et al. (1991) found linkage between the *denso* locus on chromosome 3HL and the date of heading. The QTL mapped in this investigation on 2HS is more proximal than the one found in the NABGM analysis, whereas the QTL mapped on 7H(S) is more distal. The QTL with a minor effect mapped on 7H(L) in this investigation seems to be the same as the one found in the NABGM investigation.

Hayes et al. (1993) localized QTLs for kernel yield on chromosomes 2HS and 2HL, 3HL (2) and 7HS. The QTL for kernel yield found on 2H(L) in this investigation is located more distally than the one detected by the NABGM study, whereas the QTL on 7H(S) may be identical to that detected in the NABGM project.

Heun (1992) found 2 QTLs for quantitative powdery mildew resistance, on the short arm of chromosome 5H and on 7H; together they explained 19.8% of the variance. The QTL for the same trait found in the present study is also located on the short arm of chromosome 7H. It is reasonable to assume that these QTLs identified in different crosses trace back to the same position on the chromosome 7H.

When all these comparisons are taken into consideration, it appears that when maps from different populations are compared the collinear arrangement of the markers on the chromosome is consistent, but the recombination fractions between them is not (Graner et al. 1991). That is why small deviations between QTL positions in different crosses should not be overrated. Although only a few QTLs can be detected to be in common in different investigations, it is encouraging that at least some QTLs likely match. In our view, some of the reasons for diverging QTLs in different crosses may be on differences in measuring the respective trait and in the analytical procedures, and in the existence of QTLs with a more general and QTLs with a more specific influence on a specific trait.

Boppenmaier et al. (1992) tried to find correlations between the genetic distance of maize inbred lines and the performance of the resulting F_1 hybrids for several forage traits. As they failed to find any significant correlation, they concluded that instead of using a general measure like genetic distance, it would be necessary to find specific markers for quantitative traits to predict differences in combining ability between parents in a cross.

Many quantitative traits can be segmented into smaller components of a quantitative and/or qualitative nature. For example kernel yield can be subdivided into kernel weight, number of kernels per ear, number of ears per plant and number of plants per area. Another example is heading date, in which inter alia dormancy, cold tolerance, vernalization requirement and photoperiodic response are cumulated (Fujita 1992). Edwards et al. (1992) successfully dissected plant height into node numbers and internode length in maize. They localized QTLs responsible for plant height, internode length and node numbers. Furthermore, they detected QTLs contributing to the growth of the plants in different developmental stages. Therefore, instead of looking for QTLs for yield, QTLs for yield components should be determined; instead of QTLs for height, QTLs for height components; or instead of QTLs for heading date, QTLs for the components of this trait. These may give more useful information and could be detected in distinct crosses.

Nevertheless, QTLs have already been described that are common in different crosses, even for complex traits like kernel yield. One possible explanation of this fact may be the parallel existence of QTLs with a more broad effect on a trait and of other QTLs with a specific effect on a trait component. In the examination mentioned above (Edwards et al. 1992), the QTLs for plant height could be assigned either specifically to internode length or node numbers, or in a more common mode, to both of them. The QTLs with a more general control of the trait were identical with QTLs that affected growth over the complete developmental cy-

cle of the plants. On the other hand, QTLs with a more specific effect influenced plant growth only during early or late development. If QTLs with a more specific effect on the trait were linked in repulsion, overdominance occurred.

A similar phenomenon can probably be found in other crops and other traits. On the one hand, QTLs responsible for the trait in a more general manner may be determined, for instance tracing back to loci for broad-sense fitness. These QTLs most likely will have additive effects. On the other hand, specific QTLs may be assigned to trait components exhibiting nonadditive effects, on the basis of recombinations in individual plants. This could give a lead to the genetic background for general and specific combining ability.

With more detailed QTL localization studies, it should be possible to detect parallelism between QTLs commonly found in many crosses and even in related species. Such QTLs with general influence have to be separated from other QTLs with a more specific influence on a given trait and characterized more exactly. In this way, it might be possible to determine the breeding value of the genetic constitution of particular genotypes. On the basis of corresponding QTL composition in parental lines, the breeder eventually should be able to create specific transgressions by choosing the appropriate parents before the cross is made and by selecting for the desired QTL arrangements among progenies even in early generations.

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