Theor Appl Genet (2000) 100:881–888

S. Kicherer · G. Backes · U. Walther · A. Jahoor

Localising QTLs for leaf rust resistance and agronomic traits in barley (*Hordeum vulgare* L.)

Received: 16 July 1999 / Accepted: 7 September 1999

Abstract The *Hordeum vulgare* accession 'HOR 1063' was crossed with the barley cultivar Krona, and 220 doubled haploid lines were produced based on this cross. A molecular map was constructed based on RFLP markers. Field trials were performed over 2 years and at two locations. In field trials, resistance to leaf rust by means of artificial infection, heading date, plant height and Kernel weight were assessed. For leaf rust resistance, 4 QTLs were localised, that explained 96.1% of the genetic variation. One QTL on chromosome 4H confirmed a position found in another genetic background and one mapped to the same position as *Rph16* on chromosome 2H. All digenic effects decreased the effects of the respective QTLs. In addition to the *denso*-locus and the *hex-v* locus, other QTLs influencing heading date, plant length and kernel weight were found in this cross.

Key words *Hordeum* · QTL · *Puccinia hordei* · Agronomic traits

Introduction

Leaf rust of barley (*Puccinia hordei* Otth) is an economically important disease in areas of moderate climate causing yield losses of up to 36% (Griffery et al. 1994) depending on the disease level. Two kinds of resistance against leaf rust have been described for barley: (1) qualitative resistance, expressed as a hypersensitive host response (chlorotic or necrotic spots), controlled by a single gene (Feuillet et al. 1997) and (2) quantitative or partial resistance, expressed as a reduced number of uredia, controlled by few to many genes and environmental conditions (Parleviet and Van Ommeren 1975). The main components of partial resistance against leaf rust – longer latency period, reduced infection frequency and low sporulation rate – are considered to be associated (Parlevliet and Kuiper 1977). Contrary to qualitative resistance, quantitative resistance maintains its effectiveness even after widespread agricultural use over an extended period (Clifford 1985).

Recently, in Europe nearly all of the major resistance genes (designated as *Pa* or *Rph* genes), have been completely overcome by adaption of the pathogene. This also includes *Rph3* and *Rph12*, which had been considered to be the most effective and were the most widely used in barley breeding programmes (Jin et al. 1993). The resistance gene *Rph7* from cv. Cebada Capa is still effective in Europe, but the occurence of virulence for this gene has been reported in the USA (Steffenson et al. 1993). This dramatic loss of sources for effective major resistance against barley leaf rust has increased the importance of quantitative resistances in breeding programmes. The application of molecular markers linked with quantitative trait loci (QTLs) offers an instrument for the accelerated use of quantitative traits in breeding (Thomas et al. 1995).

The construction of genetic maps of the barley genome (Graner et al. 1991; Heun et al. 1991; Kleinhofs et al. 1993) made it possible to map genome regions controlling the expression of quantitative traits. Recently, linkage maps of different barley offspring populations have been used for mapping QTLs affecting agronomic traits (Han and Ulrich 1994; Larson et al. 1996) and disease resistance (Heun 1992; Chen et al. 1994; Backes et al. 1995, 1996). Molecular markers for quantitative traits can increase the speed of backcross introgressions as an effective tool for selection (Dudley et al. 1993).

The investigation reported here analysed a population of doubled haploid lines (DHLs) derived from a cross between a spring barley cultivar ('Krona') and a barley landrace (HOR1063). These parental lines differ in

Communicated by G. Wenzel

S. Kicherer · U. Walther
Federal Centre for Breeding Research,
Institut for Epidemiology and Resistance, Theodor-Romor-Weg 4,
06449 Aschersleben, Germany

G. Backes · A. Jahoor (✉)
Risø National Laboratory, Plant Genetics and Epidemiology,
P.O. Box 49, 4000 Roskilde, Denmark
e-mail: A.Jahoor@risoe.dk

QTLs affecting leaf rust resistance, heading date and plant height.

Materials and methods

Plant material

A total of 220 DHLs from a cross between Krona and HOR 1063 were produced by anther culture from Dr. Jaeger-Gussen, Saaten-Union, Germany. Krona is a two-rowed spring barley cultivar, registered in 1989, with qualitative leaf rust resistance derived from Trumpf (=Triumph). HOR 1063 is a six-rowed barley landrace line from the Gatersleben world collection (collected 1928–1930 in Turkey) with high quantitative resistance based on several minor genes; it has been tested in different environments for 6 years (Walther, unpublished)

Field experiments

In 1994 and 1995 the DH-population was assessed for leaf rust resistance in the field. A highly virulent leaf rust isolate (I80) that overwhelms all recently known major resistance genes except *Rph7* was applied to spreader stripes in order to provide a uniform inoculation of DHLs. The qualitative resistance of Krona is completely overcome by this isolate. Whereas in 1994 the examination for leaf rust could be performed only at one site (Hadmersleben), in 1995 the experiments were carried out at two different locations (Hadmersleben and Aschersleben). The DHLs were planted in two-row plots in three or four replications and scored for resistance (in percentage attacked leaf area) up to six times during the vegetation period. The level of leaf rust attack was first determined by the Area under the Disease Progress Curve (AUDPC value) according to Wilcoxson (1974) and Moll et al. (1996). Subsequently, the date of heading (days after May 30th) and plant height (cm) after harvest were determined at the two locations in 1995.

Restriction fragment length polymorphism (RFLP) analysis

The plant material for parental screening and analysis of the DHLs was obtained from greenhouse-grown plants harvested approximately 4 weeks after planting. Three grams of fresh leaf material was taken from each parental and DH line and frozen to –80°C until DNA isolation. DNA extraction was according to the CTAB procedure of Saghai-Maroof et al. (1984). Each DNA sample was digested with five restriction enzymes (*Bam*HI, *Eco*RI, *Eco*RV, *Hind*III, *Xba*I), separated by agarose gel electrophoresis and fixed to positively charged nylon membranes by an alkaline blotting procedure (Southern 1975).

Probes were selected from the MWG collection using the Igri×Franka map (Graner et al. 1991). Probes were prepared by first isolating the plasmids according to the method of Birnboim and Doley (1979), then digestion with the appropriate restriction enzyme (*Pst*I or *Eco*RI) and finally separation on a low-melting gel electrophoresis. The inserts were cut out of the gel, labeled with [^{32}P]-dCTP according to the method of Feinberg and Vogelstein (1983) and used for hybridisation.

Statistical analysis

The basic analyses, the analysis of variances and the analysis of covariances of the data were performed using the programmes MICROSOFT EXCEL® (v. 5.0, Microsoft Corp.) and SPSS® (v. 6.1, SPSS Inc). Only data for non-transformed data are shown because transformation of the data to obtain a normal distribution revealed approximately the same results as the analyses with the non-transformed data (data not shown). For the ANOVA, the model included environments, blocks within environments, genotypes and genotypes×environments. The heritabilities (h^2) of the traits were estimated according to Schön et al. (1993). The genetic correlation between environments was calculated as $V_G/(V_G+V_{GE})$ where V_G is the genetic variance and V_{GE} ist the part of the variance contributed by the genotype×environment effect (Pirchner 1983). For the analysis of covariances, the total covariance was separated into the (additive) genetic covariance and the covariance caused by environments, and the respective correlation coefficients were then calculated.

The QTL analysis was performed as a composite interval analysis (CIM) using PLABQTL (Utz and Melchinger 1996). The programme performs a multiple regression on evenly distributed positions of the linkage map. It calculates the test statistic (LOD) based on the sum of squares of the regression in a model with a putative QTL versus the sum of squares of the regression in a model without QTLs. The LOD threshold was set to 3.0, corresponding to an experiment-wise significance of 0.05 assuming a chi-square distribution for the test statistic. Markers as cofactors for the final regression were selected by the programme using stepwise regression. Digenic effects (QTL×QTL effects) were also calculated by this programme. The final model including all significant QTL- and QTL×QTL-effects was also determined by stepwise regression using this programme. Possible QTL×environment effects were analysed by a final ANOVA in PLABQTL.

Results

RFLP analysis

Parental screening revealed a degree of polymorphism of 77% where the probes were already tested for polymorphism in other crosses. There were 67 polymorphic RFLP probes and one morphological marker (*hex-v* for *hexastichon*) available for the analysis of DHLs, resulting in 73 loci. Based on the analysis of the DHLs we were able to construct a linkage map of the cross Krona×HOR 1063' containing 60 loci (Fig. 1). Seven loci were unlinked. A further 6 loci were omitted because they were very closely linked to other loci in the map and would therefore not contribute additional information in the QTL analysis. No significant distorted segregation was observed on the mapped loci.

Analysis of field experiments

The basic data and the results of the ANOVA are presented in Table 1. The analysis of leaf rust resistance measured as AUDPC values resulted in a quantitative distribution and significant differences between genotypes in all field tests. This table shows a relatively low mean for the leaf rust data in Hadmersleben 1995. In this case an accelerated ripening of barley, which is dependent on dry weather conditions, strongly decreased the development of leaf rust. The distribution of resistance data was skewed towards the resistant genotypes, which is very common for resistance traits (Backes et al. 1995; Spaner et al. 1998). ANOVA revealed significant genotype effects for all environments. The heritabilities ranged between 0.735 for leaf rust and 0.86 for kernel

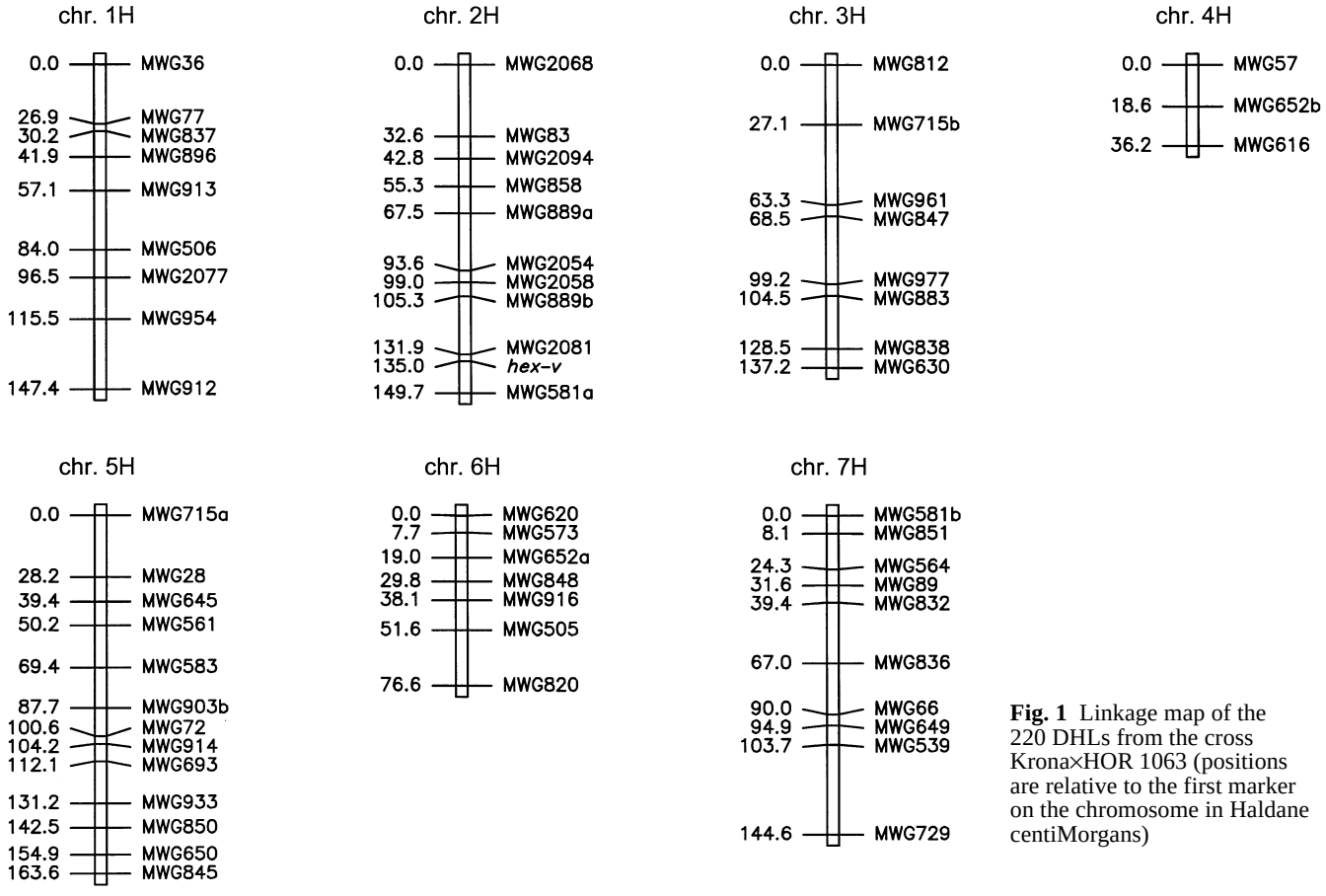

Fig. 1 Linkage map of the 220 DHLs from the cross Krona×HOR 1063 (positions are relative to the first marker on the chromosome in Haldane centiMorgans)

weight. The genetic correlation between the environments was much lower for leaf rust resistance than for the other traits, which was mainly due to the poor infection level at Hadmersleben in 1995.

The results of the covariance analysis between the traits (Table 2) revealed the highest phenotypic correlation with a high contribution of genetic correlation between leaf rust resistance and heading date.

Detection and localization of QTLs

The individual QTLs as detected by the CIM analysis are presented in Table 3. The corresponding LOD scans over the chromosomes are presented in Fig. 2. For leaf rust resistance, 4 QTLs were detected, where the 1 QTL on chromosome 2H (LR-1) explained 22.5% of the phenotypic variation. All resistance loci originated from the landrace parent. Two QTLs were detected for heading date; the one on chromosome 2H near the QTL for leaf rust (HD-1) explained 20.8% of the phenotypic variation of this trait. The loci for later heading originated from Krona. For plant height, 2 QTLs with similar effect but of different origins were detected. For kernel weight, 1 main QTL was detected at the position of the *hex-v* locus on chromosome 2H (KW-1). Two minor QTLs were localised on chromosome 5H (KW-2) and 6H (KW-3). The alleles from Krona caused higher kernel weight for KW-1 and KW-3, whereas the barley landrace contributed the allele with the higher kernel weight at the KW-2 locus.

Table 4 shows the results of the multiple regression of the most significant genetic effects performed by PLABQTL. The model for leaf rust resistance explained 70.6% of the phenotypic variance and 96.1% of the genetic variance. For this model, three digenic epistatic interactions were included. Their effect is always opposite to the main effects of the QTLs. No epistatic interactions could be included in the models for the remaining traits. All QTL and QTL × QTL effects for this trait showed significant interactions with the environment. The QTLs conferring heading date explained 30.2% of the total phenotypic and 35.7% of the total genetic variance. The QTL with the highest effect showed significant interaction with the environment. The 2 QTLs localised for plant height explained 26.1% of the phenotypic and 33.8% of the genetic variance. Here, no interaction with environments was observed. Finally, the QTLs detected for kernel weight could explain 26.8% of the phenotypic and 31.2% of the genetic variance. All QTLs for this trait showed significant environment interaction.

Table 1 Means, standard deviations and results of the ANOVA

Units		Leaf rust (AUDPC-units)	Heading date (days after 30th of May)	Plant height (cm)	Kernel weight (g per 1000 kernels)
– Means and standard deviations –					
Hadmersleben	Mean	3.60	–	–	–
1994	SD	5.04	–	–	–
Aschersleben	Mean	7.25	7.25	106.3	40.75
1995	SD	10.33	4.40	12.6	6.69
Hadmersleben	Mean	1.47	4.33	83.3	38.94
1995	SD	3.10	3.81	12.9	6.48
Total	Mean	4.42	6.00	96.4	39.98
mean	SD	7.70	4.40	17.1	6.66
– Results of the ANOVA –					
SS_{total}[a]	(*df*=1979)	109551	29853	406098	68173
$SS_{Genotypes}$	(*df*=219)	56468	23210	193225	58855
$SS_{Environment}$	(*df*=2)	11496	3211	200232	1243
$SS_{Genotype\ x\ Env.}$	(*df*=438)	24435	1071	12444	2158
$SS_{Block\ within\ Env.}$	(*df*=6)	1346	13	196	78
F Genotypes[b]		21	49**	23**	50**
$F_{Environment}$		478**	1498**	5199**	233**
$F_{Genotypes \times Environment}$		5**	2**	1**	2**
$F_{Block\ within\ Environment}$		19**	1	1	3+
h^2[c]		0.735	0.845	0.772	0.860
r_G[d]		0.698	0.956	0.939	0.965

[a] SS, sums of squares,
[b] *F*, F-values
[c] h^2, Heritability
[d] r_G, Genetical correlation between environments
* $P<0.01$, ** $P<0.001$, + <0.05

Table 2 Results of the covariance analysis (genetic correlations between the traits in the upper right part and phenotypic correlations between the traits in the lower left part of the table)

	Leaf rust	Heading date	Plant height	Kernel weight
Leaf rust	–	0.427**	0.132**	0.112**
Heading date	0.557**	–	0.050	0.114**
Plant height	0.381**	0.321**	–	0.184**
Kernel weight	0.139**	0.148**	0.281**	–

** Significant at $P<0.001$

Table 3 Results of the CIM-Analysis (individual QTLs) based on means over environments

QTLs	Chromosome	Pos[a]	Support interval[b]	LOD	r^2 [c]	Effect[d]
– Leaf rust –						
LR-1	2H	44	38–48	10.88	22.5%	+2.330
LR-2	2H	80	70–94	4.40	9.8%	+1.633
LR-3	2H	134	130–136	3.49	7.8%	+1.081
LR-4	4H	10	2–20	4.89	13.8%	+1.588
– Heading date –						
HD-1	2H	46	34–52	9.98	20.8%	+0.999
HD-2	2H	116	100–132	3.01	6.8%	+0.633
– Plant height –						
PH-1	2H	60	48–66	7.81	16.7%	+2.985
PH-2	3H	82	70–94	6.69	14.5%	–2.922
– Kernel weight –						
KW-1	2H	134	132–136	13.65	25.3%	+2.124
KW-2	5H	104	100–110	3.12	6.4%	–0.776
KW-3	6H	14	6–28	3.14	7.1%	+0.846

[a] Putative QTL position
[b] Interval with a LOD decrease of 1.0 from the maximum
[c] Coefficient of determination of the phenotypic variance
[d] Estimated additive effect of substituting one allele of HOR1063 by one allele of Krona (units as described in Table 1)

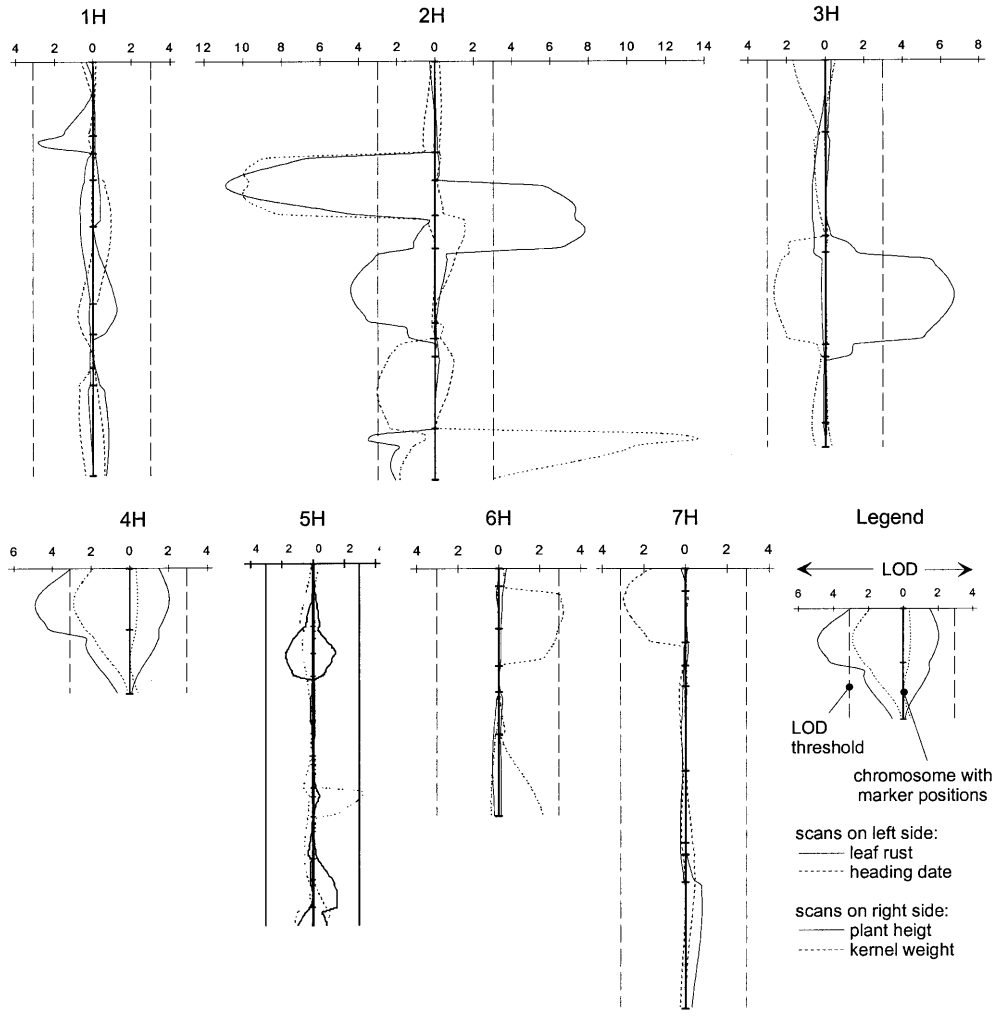

Fig. 2 LOD scans over the linkage map for the cross Krona×HOR 1063 for the traits resistance to leaf rust, heading date, plant height and kernel weight

Discussion

The population consisting of 220 DHLs from the cross of a two–rowed barley cultivar and a six–rowed barley landrace proved to be a suitable instrument to study the quantitative resistance of barley to leaf rust. The large genetic distance between the parental lines provided a high degree of polymorphism and a sufficient number of offspring genotypes differing in leaf rust resistance.

The calculation of QTLs based on field tests at two environments over 2 years resulted in an accumulation of QTLs on the short arm of chromosome 2H that affected leaf rust resistance, heading date, plant height as well as kernel weight. This accumulation may support the hypothesis of the occurrence of multilocus clusters in the barley genome (Hayes et al. 1993, Oziel et al. 1996).

As for leaf rust resistance, chromosome 2H is known to carry the major resistance genes *Rph1* (Tuleen and Daniel 1971) and *Rph16* (Ivandic et al. 1998). *Rph1* has not yet been localised with molecular markers. Previous tests of the parental lines using leaf rust pathotypes avirulent for *Rph1* showed clearly that neither Krona nor HOR 1063 possess this major gene (data not shown). Subsequently, the leaf rust races used for field inoculation were proved to be virulent against *Rph1*.

Rph16 is proximal to the marker locus MWG858, whereas LR1, the major QTL on 2H, is distal to this locus. However, the confidence interval of the QTL LR2 in this analysis includes the mapped position of *Rph16*. The same isolate (I80) was used in both experiments. Therefore, it is very likely that LR2 and *Rph16* could describe the same locus while probably representing different alleles. This is in contradiction with the results of Qi et al. (1998), who found no shared positions between *Rph* loci and partial resistance in their analysis. They concluded, in agreement with Niks (1986), that *Rph* resistance acts post-haustorially with hypersensitivity, whereas partial resistance is based on pre-haustorial mechanisms associated with the formation of papillae. On the other hand, in the present experiments infection was accomplished done with one specific isolate. Therefore, the QTL LR2 could be race-specific. QTLs for resistance in barley, which mapped approximately on the same position as earlier localised qualitative resistance genes, have been found for powdery mildew (Backes et al. 1996), net blotch disease (Richter et al. 1998), yellow rust and also for leaf rust (Thomas et al. 1995).

Table 4 Results of the CIM analysis (multiple regression based on the final model)

Leaf rust:	$r^2_{phenot.}$[a]=70.6%		$r^2_{genet.}$[b]=96.1%
Factor	Regr. coeff[c]	Partial r^2 [d]	Factor×env.[e]
LR-1	+2.130	24.4%	**
LR-2	+1.611	10.8%	**
LR-3	+0.524	2.2%	**
LR-4	+2.119	19.3%	**
LR-1×LR-2	–1.810	13.7%	**
LR1×LR-4	–1.380	11.1%	**
LR-3×LR-4	–0.591	1.8%	*
Heading date:	$r^2_{phenot.}$=30.2%		$r^2_{genet.}$=35.7%
Factor	Regr. coeff.	Partial r^2	Factor×env.
HD-1	+1.030	19.2%	**
HD-2	+0.672	7.1%	
Plant height:	$r^2_{phenot.}$=26.1%		$r^2_{genet.}$=33.8%
Factor	Regr. coeff.	Partial r^2	Factor×env.
PH-1	+3.157	18.8%	
PH-2	–2.978	14.7%	
Kernel weight:	$r^2_{phenot.}$=26.8%		$r^2_{genet.}$=31.2%
Factor	Regr. coeff.	Partial r^2	Factor×env.
KW-1	+1.490	20.0%	**
KW-2	–0.962	9.0%	*
KW-3	+0.544	2.6%	+

[a] $r^2_{phenot.}$, Phenotypical variance explained by the model
[b] $r^2_{genet.}$, Genetical variance explained by the model
[c] Regr. coeff., Regression coefficient as estimated additive effect of one allele of Krona (for units see Table 1)
[d] Part. r^2, Squared partial correlation coefficient
[e] Factor×env., Significance of the factor×environment-effect (*=P<0.01, ** P<0.001, + P<0.05)

Quantitative trait loci for leaf rust resistance on chromosome 2H were localised by Qi et al. (1998). None of these QTLs on 2H could be found at the same position in this population. On the other hand Qi et al. (1998) found the quantitative resistance locus *Rphq5* to be at the same chromosomal site near the centromere on chromosome 4H as that of LR-4 mapped in the present cross. Therefore, it is very likely that the same QTL was found in two completely different genetic backgrounds. Apart from that, there are no previous reports about loci coding for qualitative leaf rust resistance on chromosome 4H. Chromosome 4H is considered to be characterised by a lack of variation due to an accumulation of genes conferring adaptation to agricultural conditions (Forster 1994). However, loci have been reported coding for ear emergence and plant height near the *mlo* locus for mildew resistance (Sogaard and von Wettstein-Knowles 1987; Hacket et al. 1992).

Including digenic epistatic effects in a model for leaf rust resistance increased substantially the variance explained by this model (Table 4). It is striking that each significant combination has a negative effect on the expression of the resistance. Therefore, the effect of an accumulation of QTLs, which can be calculated by adding up the different regression coffefficients, is not a summarisation of the single effects. In this way, a plant with resistant alleles at all 4 loci would be 5.2 AUDP units more resistant than a plant with the susceptible alleles. If the QTL effects could by added simply, the difference would be 12.8 AUDP units. This is important for the breeder who would like to combine these QTLs. A selection based on only morphologic observations would not lead to the desired success. Therefore, marker-assisted selection would facilitate to isolate genotypes with the appropriate combination of resistant alleles.

As for heading date, plant height and kernel weight there are several reports about QTLs on chromosome 2H affecting these traits (see Han and Ullrich 1994; Pan et al. 1994). Hayes and Ivambo (1994) found a very stable QTL for heading date on chromosome 2 in 16 out of 17 environments. On the same position, near the marker MWG858, Laurie et al. (1995) found the major gene *Ppd-H1* controlling flowering time under long days in the cross Igri×Triumph. This marker is also present in this study. As mentioned above, Triumph (or Trumpf) is one of the ancestors of Krona. Furthermore, the late allele in the cross Igri×Triumph originates from Triumph. In this cross, the late allele and the allele for higher plants is derived from Krona at the respective QTLs on 2H. Therefore, at least some of the peaks for heading day and plant height can be explained by the presence of *Ppd-H1*. At the same chromosomal region, the LR-2-locus for leaf rust was found in this analysis. Therefore, it could be considered that the leaf rust effect at this site is a pleiotropic effect of the earliness. The earlier plants could avoid the infection, and this would result in a better resistance. On the other hand, the difference between the Krona QTL genotype and the landrace genotype is only 2 days, and the difference in the leaf rust scoring is quite high compared to that. In addition, the shape of the LOD peaks is different for leaf rust and heading date at this part of the chromosome. Therefore, it is more likely that there are 2 linked QTLs at this location, one for heading date and one for leaf rust.

In addition, Triumph has passed the *denso* locus to 'Krona'. This locus is localised on chromosome 3H (Laurie et al. 1995), and the Triumph-allele causes shorter plants. At the position of the *denso* locus, a QTL for plant height has been found (PH-2) that can be completely explained by this major gene. Consequently, shorter plants can be observed with the Krona-allele, in this cross.

In the region of the *hex-v* locus (the morphological marker associated with two-rowed and six-rowed spikes, respectively), QTLs affecting leaf rust resistance (LR-3), heading date (HD-2) and kernel weight (KW-1) were found. This locus has been described to affect the developmental process with strong influences on numerous

quantitative traits (Allard 1988). The effect of this locus on heading date, plant height and kernel characters has been frequently reported (Powell et al. 1990, Frégeaud-Reid et al 1996; Jui et al. 1997). The alleles from Krona at this locus contribute to later heading and higher kernel weight, thereby confirming the observation, that two-rowed spikes are associated with higher kernel weight (Jui et al. 1997). It is also interesting that for one of the other QTLs for this trait, KW-2, the landrace has the allele with the higher kernel weight. This illustrates the potential of old landraces of the modern crops as an easily accessible genetic pool that can contribute to competitive varieties in the future.

Acknowledgements All experiments comply with the current laws of the Germany and Denmark, respectively.The authors acknowledge the financial support of German Research Foundation to Sonja Kicherer and of the Danish Ministry of Food, Agriculture and Fisheries (Cereal Network) to Gunter Backes. The authors would like to thank Hanne Østergård for her reading and comments.

References

Allard RW (1988) Genetic changes associated with the evolution of adaptedness in cultivated plants and their wild progenitors. J Hered 79:225–238

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

Backes G, Schwarz G, Wenzel G, Jahoor A (1996) Comparison between QTL analysis on powdery mildew resistance in barley based on detached primary leaves and on field data. Plant Breed 115:419–421

Birnboim HC, Doley J (1979) A rapid alkaline extraction procedure for screening recombinant plasmid DNA. Nucleic Acids Res 7:1513–1523

Chen FQ, Prehn D, Hayes PM, Mulrooney D, Corey A, Vivar H (1994) Mapping genes for resistance to barley stripe rust (*Puccinia striiformis* f. sp. *hordei*). Theor Appl Genet 88: 215–219

Clifford BC (1985) Barley leaf rust. In: Roelfs AP, Bushnell WR (eds) The cereal rusts II. Academic Press, Orlando, FL, 173–205

Dudley JW (1993) Molecular markers in plant improvement: manipulation of genes affecting quantitative traits. Crop Sci 33: 660–668

Feinberg AP, Vogelstein B (1983) A technique for radiolabeling DNA restriction endonuclease fragments to high specific activity. Anal Biochem 132:6–13

Feuillet C, Schachermayr G, Keller B (1997) Molecular cloning of a new receptor-like kinase gene encoded at the *Lr10* disease resistance locus in wheat. Plant J 11:45–52

Forster BP, Russell JR, Ellis RP, Handley LL, Robinson D, Hackett CA, Nevo E, Waugh R, Gordon DC, Keith R, Powell W (1997) Locating genotypes and genes for abiotic stress tolerance in barley: a strategy using maps, markers and the wild species. New Phytol 1:141–147

Frégeau-Reid J, Choo TM, Jui P, Ho KM (1996) Inheritance of kernel size and shape of barley. SABRAO J 28:47–55

Graner A, Jahoor A, Schondelmaier J, Siedler H, Pillen K, Fischbeck G, Wenzel G, Herrmann RG (1991) Construction of an RFLP map of barley. Theor Appl Genet 83:250–256

Griffery CA, Das MK, Baldwin RE, Waldenmaier CM (1994) Yield loss in winter barley resulting from a new race of *Puccinia hordei* in North America. Plant Dis 78:256–260

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

Han F, Ulrich SE (1994) Mapping quantitative trait loci associated with malting quality in barley. Barley Genet Newsl 23:84–97

Hayes PM, Iyambo OE (1994) Summary of QTL effects in the Steptoe×Morex population. Barley Genet Newsl 23:98–143

Hayes PM, Blake T, Chen THH, Tragoonrung S, Chen F, Pan A, Liu B (1993) Quantitative trait loci on barley (*Hordeum vulgare* L.) chromosome 7 associated with components of winterhardiness. Genome 36:66–71

Heun M, Kennedy AE, Anderson JA, Lapitan NLV, Sorrels ME, Tanksley SD (1991) Construction of a restriction fragment length polymorphism map for barley (*Hordeum vulgare*). Genome 34:437–447

Ivandic V, Walther U, Graner A (1998) Molecular mapping of a new gene in wild barley conferring complete resistance to leaf rust (*Puccinia hordei* Otth). Theor Appl Genet 97:1235–1239

Jin Y, Statler GD, Franckowiak JD, Steffenson BJ (1993) Linkage between leaf rust resistance genes and morphological markers in barley. Phytopathology 83:230–233

Jui PY, Choo TM, Ho KM, Konishi T, Martin RA (1997) Genetic analysis of a two-row x six-row cross of barley using doubled-haploid lines. Theor Appl Genet 94: 549–556

Kleinhofs A, Kilian A, Saghai-Maroof MA, Biyashev RM, Hayes P, Chen FQ, Lapitan N, Fenwick A, Blake TK, Kanazin V, Ananiev E, Dahleen L, Kudrna D, Bollinger J, Knapp SJ, Liu B, Sorrels M, Heun M, Franckowiak DJ, Hoffman D, Skadsen R, Steffenson BJ (1993) A molecular, isozyme and morphological map of the barley (*Hordeum vulgare*) genome. Theor Appl Genet 86:705–712

Larson SR, Kadyrzhanova D, McDonald C, Sorrells M, Blake TK (1996) Evaluation of barley chromosome-3 yield QTLs in a backcross F_2 population using STS-PCR. Theor Appl Genet 93:618–625

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

Moll E, Walther U, Flath K, Prochnow J, Sachs E (1996) Methodical guidelines for the assessment of partial resistance and the SAS application RESI. Reports from the BBA 12, Saphir Druck+Verlag, Ribbesbüttel

Niks RE (1986) Failure of haustorial development as a factor in slow growth and development of *Puccinia hordei* in partially resistant barley seedlings. Physiol Mol Plant Pathol 28:309–322

Oziel A, Hayes PM, Chen FQ, Jones B (1996) Application of quantitative trait locus mapping to the development of winter-habit malting barley. Plant Breed 115:43–51

Pan A, Hayes PM, Chen F, Chen THH, Blake T, Wright S, Karsai I, Bedö Z (1994) Genetic analysis of the components of winterhardiness in barley (*Hordeum vulgare* L.). Theor Appl Genet 89:900–910

Parlevliet JE, Kuiper HJ (1977) Partial resistance of barley to leaf rust, *Puccinia hordei*. IV. Effect of cultivar and development stage on infection frequency. Euphytica 26:249–255

Parleviet JE, Van Ommeren A (1975) Partial resistance of barley to leaf rust, *Puccina hordei*. II. Relationship between field trials, micro plot test and latent period. Euphytica 35:267–272

Pirchner F (1983) Population genetics in animal breeding, 2nd edn. Plenum Press, New York

Powell W, Ellis RP, Thomas WTB (1990) The effect of major genes on quantitatively varying characters in barley. III. The two row/six row locus (V-*v*). Heredity 65:259–264

Qi X, Niks RE, Stam P, Lindhout P (1998) Identification of QTLs for partial resistance to leaf rust (*Puccinia hordei*) in barley. Theor Appl Genet 96:1205–1215

Richter K, Schondelmaier J, Jung C (1998) Mapping of quantitative loci affecting *Drechslera teres* resistance in barley with molecular markers. Theor Appl Genet 97:1225–1234

Saghai-Maroof MA, Soliman KM, Jorgensen RA, Allard RW (1984) Ribosomal spacer length polymorphisms in barley: Medelian inheritance, chromosomal location and population dynamics. Proc Natl Acad Sci USA 81:8014–8018

Schön CS, Lee M, Melchinger AE, Guthrie WD, Woodman WL (1993) Mapping and characterization of quantitative trait loci affecting resistance against second-generation European corn borer in maize with the aid of RFLPs. Heridity 70:648–659

Sogaard B, von Wettstein-Knowles P (1987) Barley – genes and chromosomes. Carlsberg Res Commun 52:123–196

Southern EM (1975) Detection of specific sequences among DNA fragments seperated by gel electrophoresis. J Mol Biol 98: 503–517

Spaner D, Shugar LP, Choo TM, Falak I, Briggs KG, Legge WG, Falk DE, Ullrich SE, Tinker NA, Steffenson BJ, Mather DE (1998) Mapping of disease resistance loci in barley on the basis of visual assessment of naturally occurring symptoms. Crop Sci 38:843–850

Steffenson BJ, Jin Y, Griffey CA (1993) Pathotypes of *Puccinia hordei* with virulence for the barley leaf rust resistance gene *Rph7* in the United-States. Plant Dis 77:867–869

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

Tuleen NA, McDaniel ME (1971) Location of genes *Pa* and *Pa5*. Barley Newsl 15:106–107

Utz HF, Melchinger AE (1996) PLABQTL: A program for composite interval mapping of QTL. J Quant Trait Loci 2 : http://probe.nalusda.gov:8000/otherdocs/jqtl/jqtl1996–01/utz.html

Wilcoxson RD, Atif AH, Skovmand B (1974) Slow rusting of wheat varieties in the field correlated with stem rust severity on detached leaves in the greenhouse. Plant Dis Rep 58: 1085–1087