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Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.)

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Abstract A set of 114 recombinant inbred lines of the 'International Triticeae Mapping Initiative' mapping population was grown during the seasons 1997, 1998, 1999 and 2000 under several environments. Twenty morphological (glume colour, awn colour, waxiness, leaf erectness, peduncle length), agronomical (ear emergence time, flowering time, grain filling time, ear length, plant height, lodging, grain number, thousand-grain-weight, grain weight per ear, grain protein content, winter hardiness) and disease resistance (powdery mildew, yellow rust, leaf rust, fusarium) traits were studied. Not all traits were scored in each experiment. In total 210 QTLs with a LOD threshold of >2.0 (minor QTLs) were detected of which 64 reached a LOD score of >3.0 (major QTLs). Often QTLs were detected in comparable positions in different experiments. Homologous and homoeologous relationships of the detected QTLs, and already described major genes or QTLs determining the same traits in wheat or other Triticeae members, are discussed.

Keywords Agronomic traits · Genetic mapping · QTL · Disease resistance · Morphological traits · Wheat

Introduction

Genetic studies of agronomic important traits in cereals have revealed that most of them are inherited quantitatively and, therefore, they are difficult to detect within the genome. However, with the development of high-density linkage maps the discovery of such quantitative trait loci (QTLs) became possible in many species. In the Triticeae, QTLs for several characters, including grain yield, disease resistance, winter hardiness or tissue-culture ability, have been described in barley (Hayes et al. 1993; Backes et al. 1995; Mano et al. 1996; Steffenson et al. 1996; Bezant et al. 1997), wheat (Galiba et al. 1995; Nelson et al. 1995a, b, c; Ben Amer et al. 1997) or rye (Börner et al. 1999, 2000).

In hexaploid wheat the 'International Triticeae Mapping Initiative' (ITMI) was established in the early Nineties and used world-wide for joint mapping of RFLP (Nelson et al. 1995a, b, c; Van Deynze et al. 1995; Marino et al. 1996) or microsatellite markers (Röder et al. 1998). To-date about 800 RFLP loci and 600 microsatellite markers have been mapped (Röder et al. 1998; Röder, personal communication). Although molecular well-characterised recombinant inbred lines exist, only few data on using that population for trait mapping are described. For some major genes, determining red grain colour (*R1*, *R3*), red coleoptile colour (*Rc1*, *Rc3*), inhibition of epidermal waxiness ($W2^I$), kernel hardiness (*Ha*), vernalisation response (*Vrn1*, *Vrn3*) or leaf rust resistance (*Lr34*), the already known map positions have been confirmed (Nelson et al. 1995a, b, c; Sourdille et al. 1996; Khlestkina et al. 2001), whereas new QTLs were described for leaf and stem rust (Nelson et al. 1995a), *Pyrenophora tritici-repentis* resistance (Faris et al. 1996), Karnal bunt (Nelson et al. 1998) or stripe rust (Singh et al. 2000).

In the present study a set of 114 RILs of the ITMI mapping population was evaluated for morphological, agronomical and disease resistance traits during the seasons 1997, 1998, 1999 and 2000 under several environments. Homologous and homoeologous relationships of the detected QTLs, and comparable major genes or QTLs already described in wheat or other Triticeae members, are discussed.

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Table 1 Traits, experiments and detected QTLs in the ITMI mapping population. Bold = major QTLs (LOD > 3); normal = minor QTLs (LOD > 2; </= 3); for QTLs detected in more than one experiment the chomosome is given; remaining QTLs are only counted; empty cells: no observation for the trait in that experiment

Trait	Gene symbol	Experiments											
		Gatersleben 1997 growth chamber GC97	Gatersleben 1997 green-House GGH97	Gatersleben 1998 field spring GFS98	Hohenthurm 1998 field spring HFS98	Silstedt 1998 field spring SFS98	Gatersleben 1999 field spring GFS99	Hohenthurm 1999 field spring HFS99	Silstedt 1999 field spring SFS99	Gatersleben 1999 field autumn GFA99	Gaersleben 2000 field spring GFS00	Hohenthurm 2000 field autumn HFA00	Total
Morphological/colour traits													
Awn clolour	*Raw*	**0**+0	**0**+1	**1A**, 7B, **1**+1		**1D**	**0**+4		**1A, 1D**, 1D, 7B, **0**+1				**5**+10
Glume colour	*Rg*	**0**+0	**1D**	**0**+1		**0**+0	**1D, 0**+1		**1D, 1**+2				**4**+4
Waxiness	*Wax*	4A			2D, **0**+1			1D, 2D		4A	1D		0+7
Leaf erectness	*Ler*				**2A**		**0**+0				2A, **1**+3		2+4
Peduncle length	*Pdl*				**0**+2			**6A, 0**+2	**6A, 0**+2				2+6
Agronomic traits													
Ear emergence time	*Eet*			2D, 5D	**5D**, 7D, 1+1		**2D**, 5D, 7D	**5D**			**0**+2		**4**+8
Flowering time	*Flt*	**2D**		2B, 2D	**3A, 5D**		2B, 2D, **5D**	3A, **5D**			2B, 2D		5+7
Grain filling time	*Gft*										**1**+1		**1**+1
Ear length	*El*	4A	**1B**, 5A, **1**+1	**1B, 4A, 0**+1	1B, **4A**, 4A*, 5A, **0**+2	4A	**4A**, 5A, **0**+1	1B, **4A, 4A*, 5A**, 5D, **0**+2	1B, **4A**, 5A, 5D, **0**+2		**0**+0		**10**+21
Plant height	*Ht*	**0**+1		**4A**, 5D	6A, **0**+2	**1**+2		3B, 4A, **6A, 0**+1	3B, 4A, **6A, 0**+2	4A, 6A, **1**+1	**4A**, 6A**0**+3		**6**+21
Lodging	*Ld*			**0**+0				**1**+2					**1**+2
Grain number	*Gnu*			4A, 7D, **1**+0	7D, **0**+1	**0**+4	**0**+0	**4A**	**4A**				3+8
1000-grain-weight	*Tgw*	**0**+2	**0**+2	**0**+0	**0**+1	**0**+0	**5A, 0**+1	5A, **1**+0	**1**+3		**0**+1		**3**+11
Grain weight/ear	*Gwe*	**2D, 1**+2	**0**+2	**2D, 0**+2	**0+0**	**0+2**	**0+1**	4A	**4A, 2**+1				**6**+11
Grain protein	*Gpc*						7A, **0**+1	7A					**0**+3
Winter hardiness	*Win*									**6A, 0**+3		**6A**	**2**+3
Disease resistance traits													
Powdery mildew	*Pm*			**0**+0	**7D**	**0**+1		**1**+1	4B, 7D 0+**1**	**4B**, 7D	**0**+0		**3**+6
Yellow rust	*Yr*			**0**+0				**2B**	**2B**, 4A, 0+1	2B	**2B**	**2B**, 4A, **1**+0	5+4
Leaf rust	*Lr*			**0**+0	7D, **0**+2			**0**+3		**7D, 0**+2			**1**+8
Fusarium	*Fhs*								**1**+1				**1**+1
Total		**3**+7	**3**+7	7+13	7+20	**2**+10	**5**+15	**12**+21	**14**+26	**4**+11	**4**+15	**3**+1	**64**+146

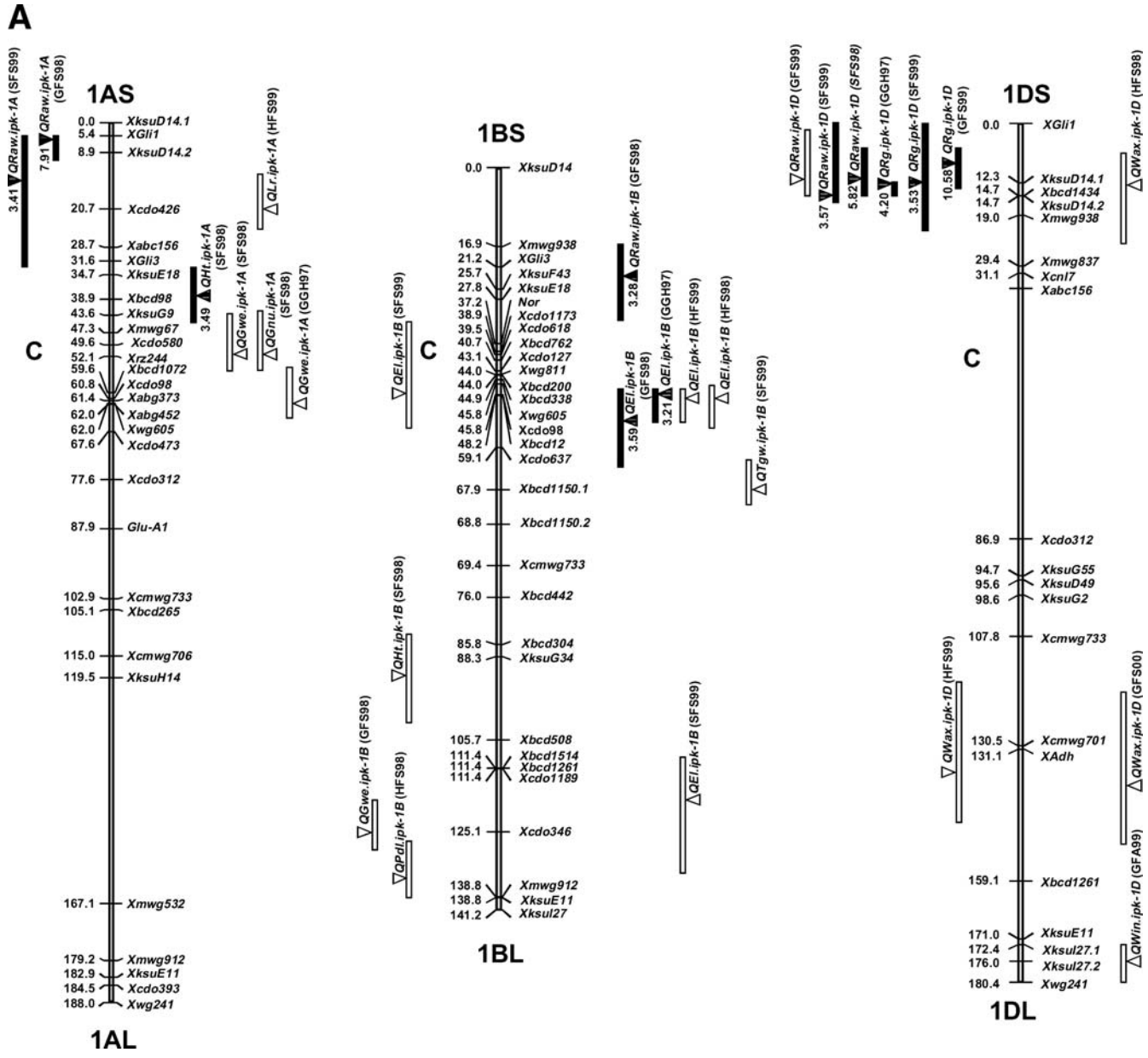

Fig. 1A–H Genetic linkage map of wheat showing 211 quantitative trait loci distributed over 20 chromosomes. The effects contributed by 'W7984' and 'Opata 85' are given on the left and right hand side of each chromosome, respectively. Supported intervals for QTLs are indicated by *vertical bars*. LOD max is pointed by a *triangle*. *Black bars and triangles* indicate QTLs with a LOD threshold of >3.0. The scores are given on the left. *Open bars and triangles* indicate QTLs with LOD scores between 2.0 and 3.0. The experiments and years in which the QTLs were detected are given in *brackets* (for explanation see Table 1). *c* = centromere position. Regions of chromosome arms 2AS, 3AL and 4AL which should move to distal parts of chromosome arms 2BS, 3DS and 7DS, respectively, are *hatched*

Materials and methods

Plant materials

The ITMI mapping population was created by crossing the spring wheat variety 'Opata 85' with the synthetic hexaploid wheat 'W7984', generated via a cross of the *Triticum tauschii* accession 'CIGM86.940' (DD) with the tetraploid wheat 'Altar 84' (AABB). The interspecific cross was carried out by Dr. A. Mujeeb-Kazi, International Maize and Wheat Improvement Center, Mexico. However, recent results of Singh et al. (2000) indicate that the pedigree of the synthetic wheat may not be correct. From a total of 150 RILs developed by single-seed descent to the F_8 or F_9 at Cornell University, Ithaca, USA, ten seeds of 114 randomly selected lines were obtained by Dr. Philippe Leroy, INRA, Clermont-Ferrand, France. The lines were bulked and divided for performing the experiments described below.

Target trait analyses

Ten seeds obtained were divided into two groups of five seeds, each which were grown under a short photoperiod (10 h light and 14 h darkness) in a growth chamber and under a long photoperiod (14 h light and 10 h darkness) in the green-house, respectively. Besides flowering time, further morphological and agronomical data were scored (see Table 1).

The multiplied stocks were divided and grown in plots during the 1998 season at three sites at the IPK in Gatersleben, at the

Fig. 1 (continued)
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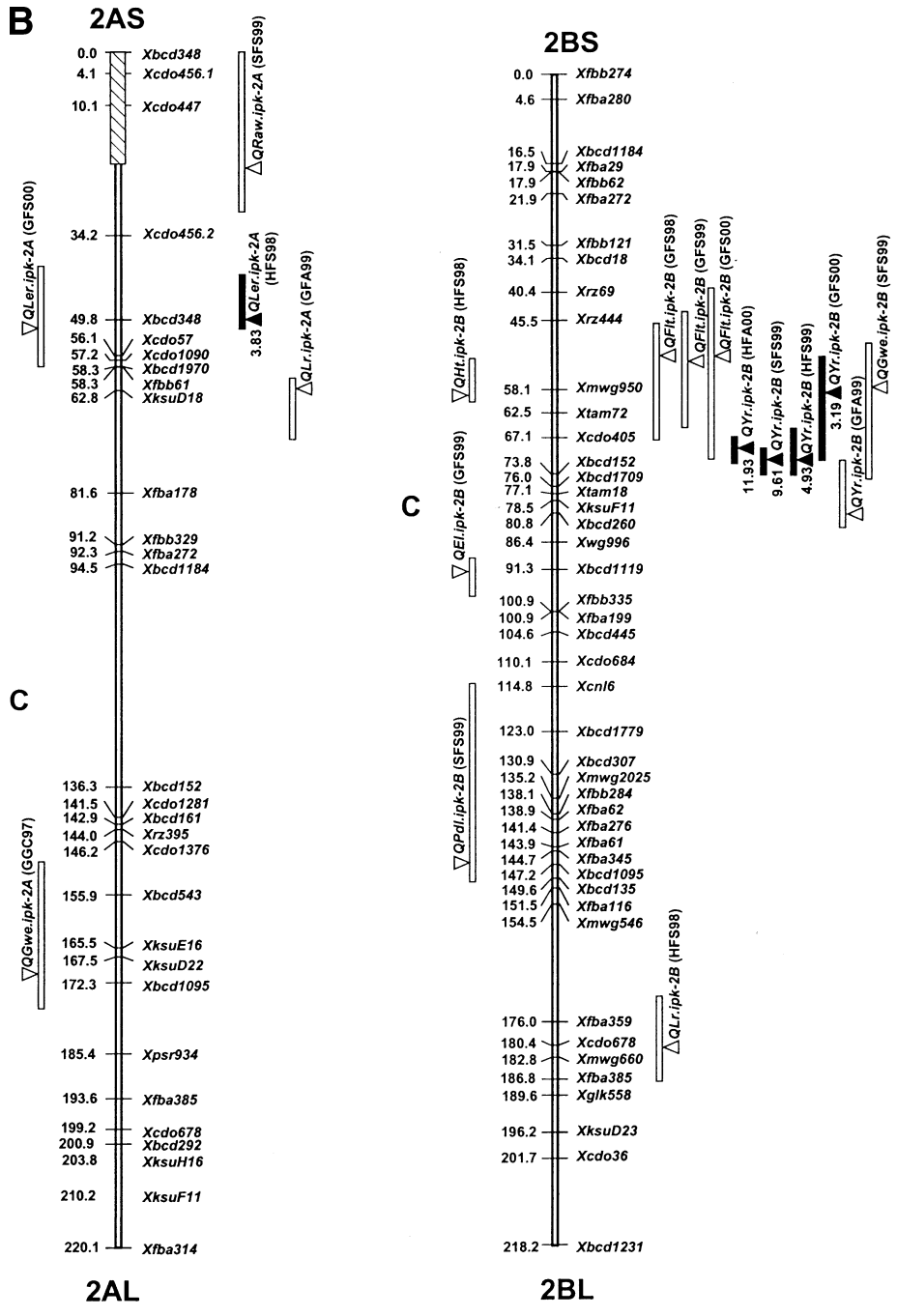
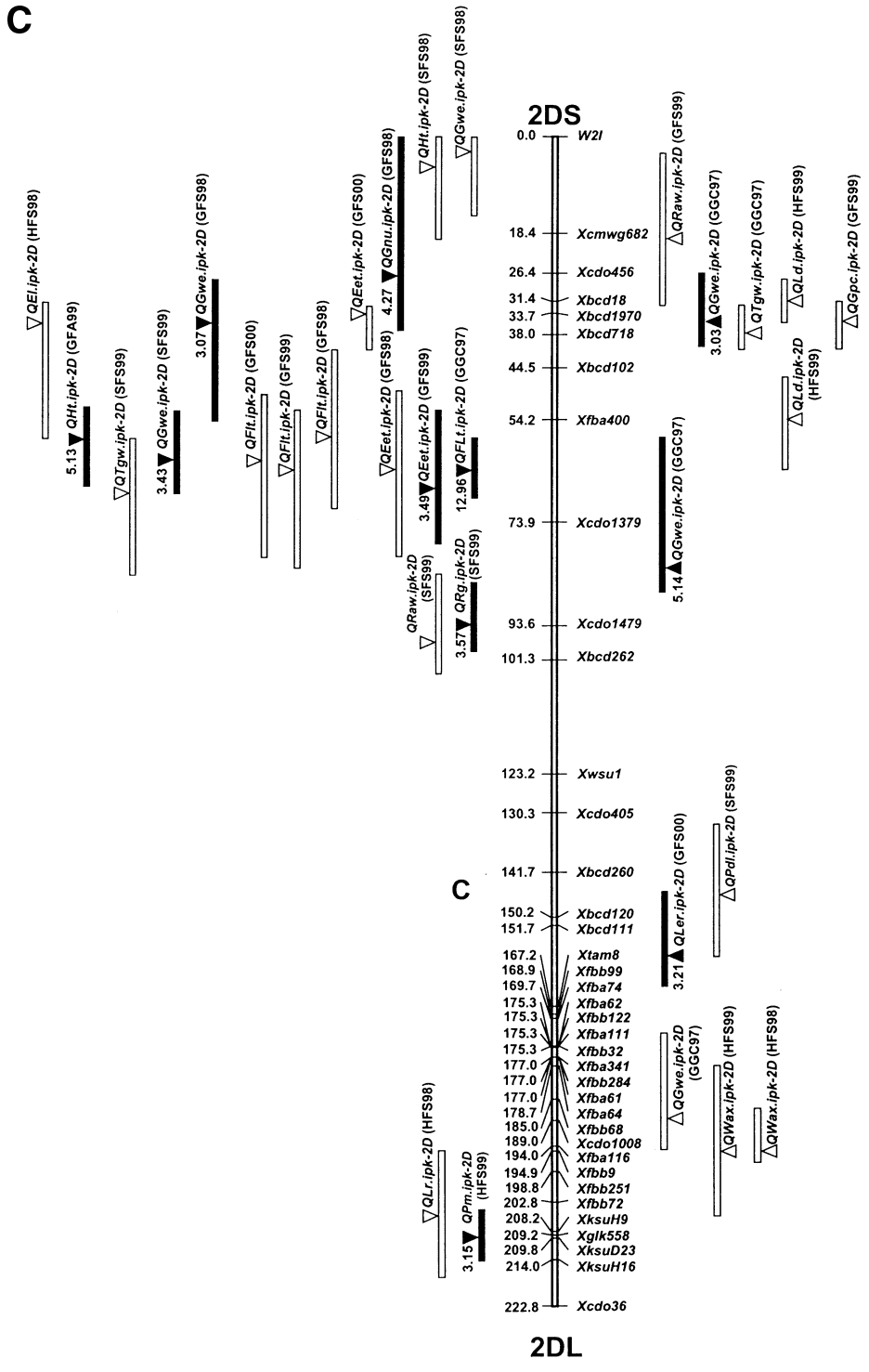


Institut für Pflanzenzüchtung und Pflanzenschutz, Martin-Luther-Universität Halle-Wittenberg, in Hohenthurm, and at Monsanto Agrar Deutschland GmbH in Silstedt. Using the seeds of the 1998 harvest the RILs were grown again at all three sites in 1999, and at Gatersleben and Hohenthurm in 2000. The sizes of the plots were 3 m^2, 4.5 m^2 and 9 m^2 at Gatersleben, Hohenthurm and Silstedt, respectively. For evaluating winter hardiness, the population was sown in autumn 1999 at IPK. Winter hardiness and yellow rust could also be scored in an additional experiment at Hohenthurm sown in autumn 2000. In total 20 characters were scored in the different experiments, and divided into morphological, agronomical and disease resistance traits. Not all characters were recorded in each experiment (see Table 1).

For determining winter hardiness, awn and glume colours, waxiness, leaf erectness and lodging, the intensity of phenotypic expression was scored on scales of 1–3, 1–5 or 1–9. Days to ear emergence and flowering time were recorded when >50% of the ears of each RIL had left the flag leaf or flowered. Grain-filling time was measured as the time between flowering and maturity (DC92). Plant heights and peduncle lengths were recorded just before harvest. After harvest, ear length, grain weight per ear, grain number and thousand-grain-weight were determined from three to five main spikes per line. For assessing grain protein content, near-infrared spectroscopy with the Infratec 1255 Food and Feed Analyser of Persdorp was used. The method had been calibrated on a sample set of 80 wheat genotypes assayed in parallel with the Kjeldahl method.

The RILs were scored for the three leaf diseases, powdery mildew (*Erysiphe graminis*), yellow rust (*Puccinia striiformis*) and leaf rust (*Puccinia graminis*), as well as for the ear disease fu-

Fig. 1 (continued)



sarium (*Fusarium graminearum*). The severity of natural (mildew and rusts) or artificial infections (fusarium) on a scale of 1–9 was recorded at the adult-plant stage in the field.

Statistical analysis

QTL analysis was performed with MAPMAKER/QTL 1.1 (Paterson et al. 1988). This program uses the Haldane mapping function (Haldane 1919). Therefore, the mapping data published in the GrainGenes database (gopher:http: //www.greengenes.cit.cornell.edu) had to be used to re-calculate the map with MAPMAKER/EXP 3.0 (Lander et al. 1987) employing the Haldane mapping function. Only those markers mapped before with the Kosambi mapping function (Kosambi 1944) were used.

In contrast to the mapping data published in the GrainGenes database three changes were described by Röder et al. (1998) and Pestsova et al. (2000), suggested by the results of nulli-tetrasomic or di-telosomic analyses. Based on these results the distal parts of chromosomes 2AS, 3AL and 4AL should move to the ends of chromosomes 2BS, 3DS and 7DS, as indicated in Fig. 1. In the present study we use the published GrainGenes framework maps.

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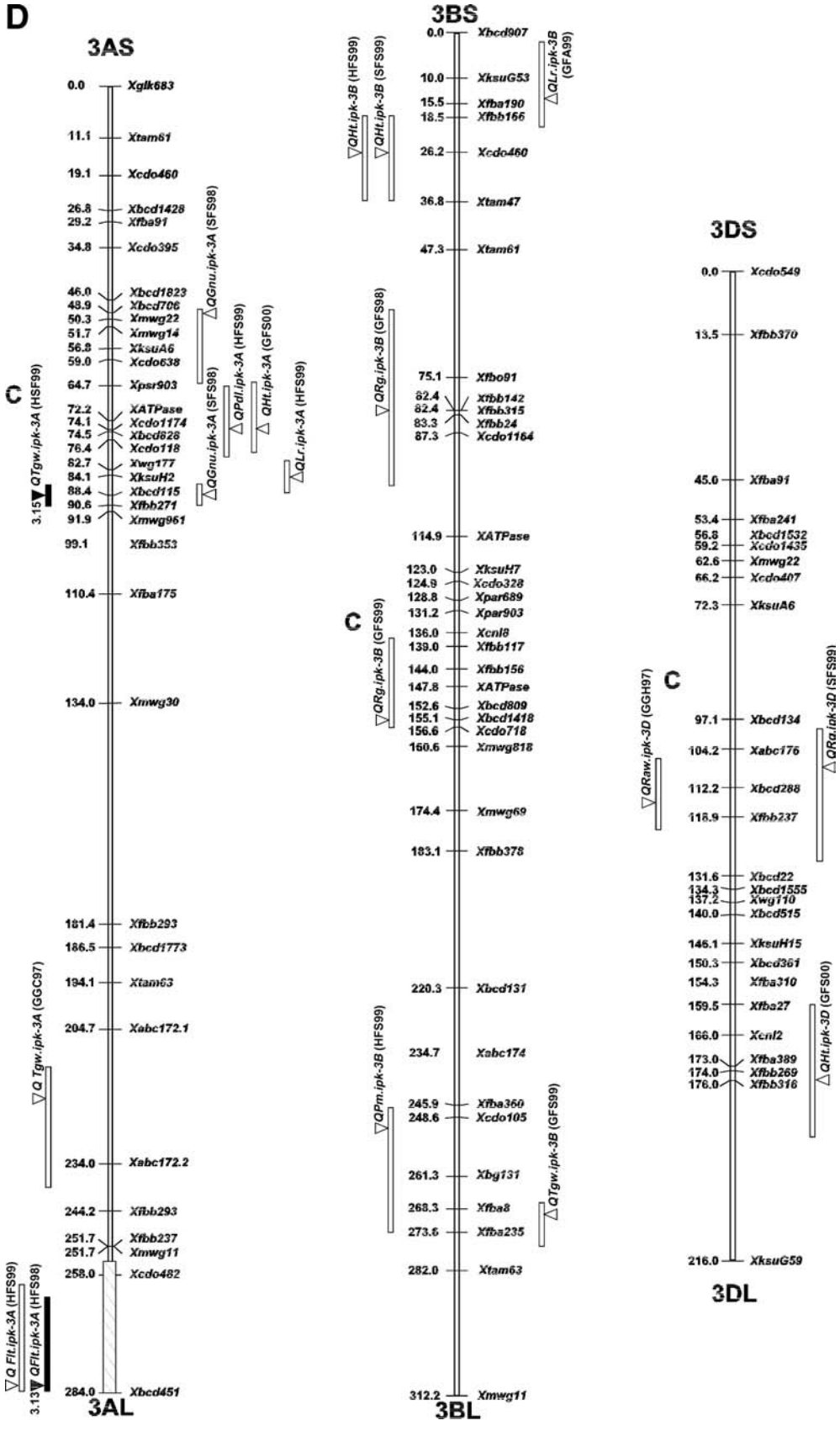

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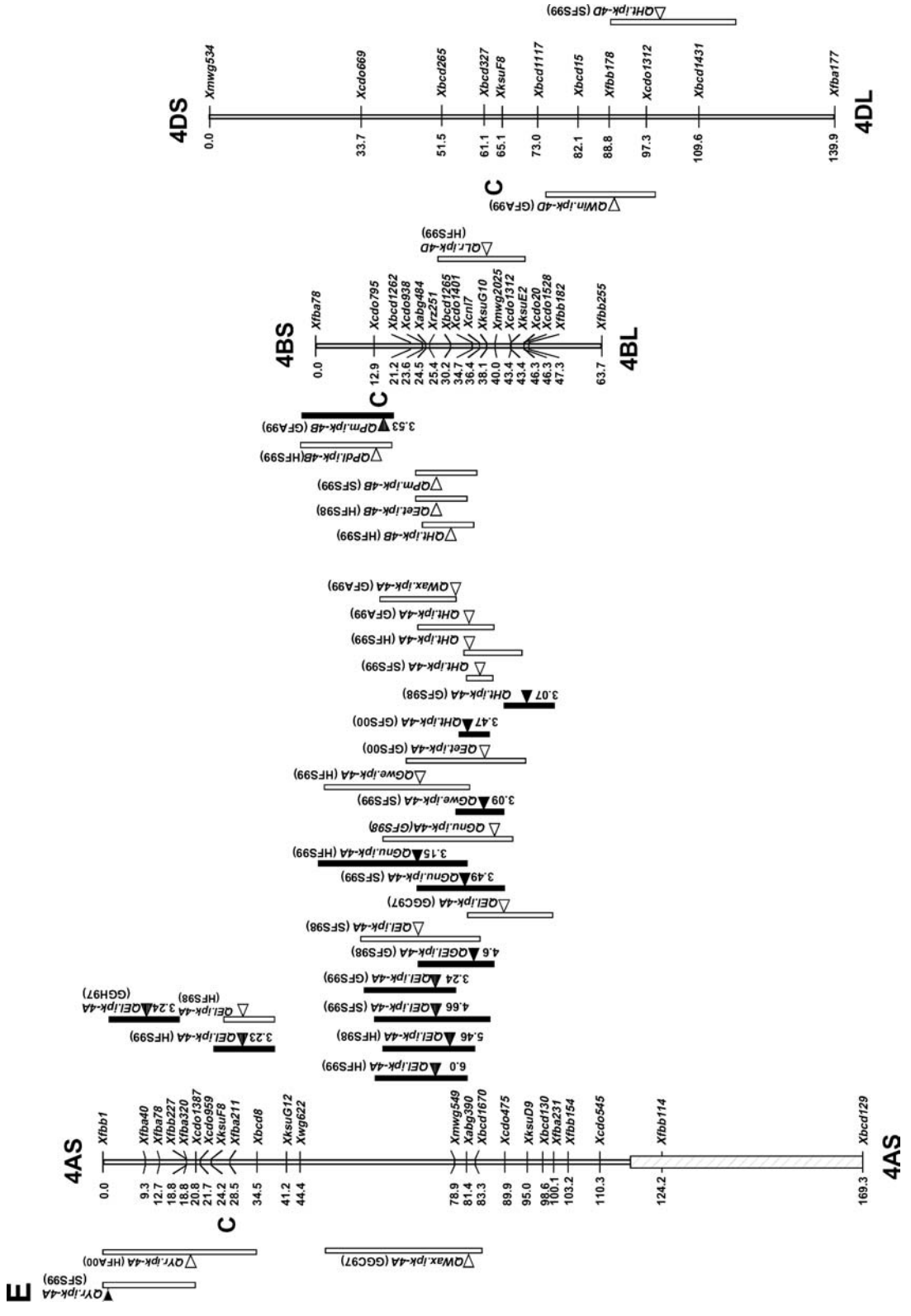

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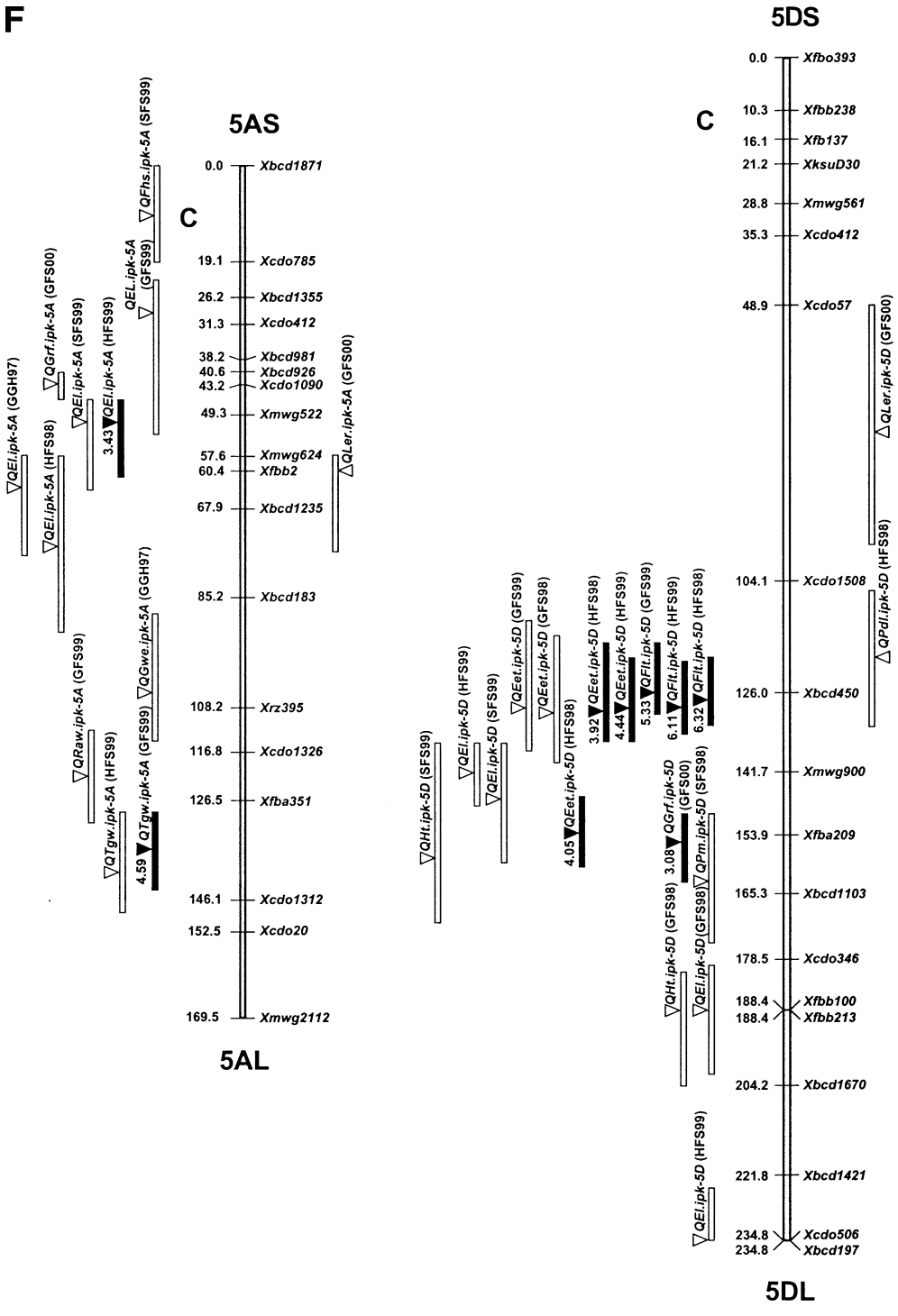


For each trait a separate QTL analysis was performed. Only loci with a LOD > 2 were taken into account. Several traits were observed at two or three sites in 2 or 3 years. For ear emergence time, flowering time, ear length, grain number, thousand-kernel-weight and grain weight per ear, a three-factorial analysis of variance with the procedure GLM of SAS (SAS Institute 2000) could be performed with genotypes, sites and years. Correlation coefficients were calculated with the procedure CORR for each quantitative trait separately between pairs of environments and between traits of the same experiment.

Results

In total 99 records covering the 20 characters considered were analysed. Out of this 84 and 50 were found to be determined by at least one QTL having a LOD score higher than 2 and 3, respectively, resulting in totals of 210 and 64 QTLs with LODs > 2 and >3, respectively (Table 1). Twentysix loci were found having LOD scores > 4. The loci with a LOD score between 2 and 3 will be designated

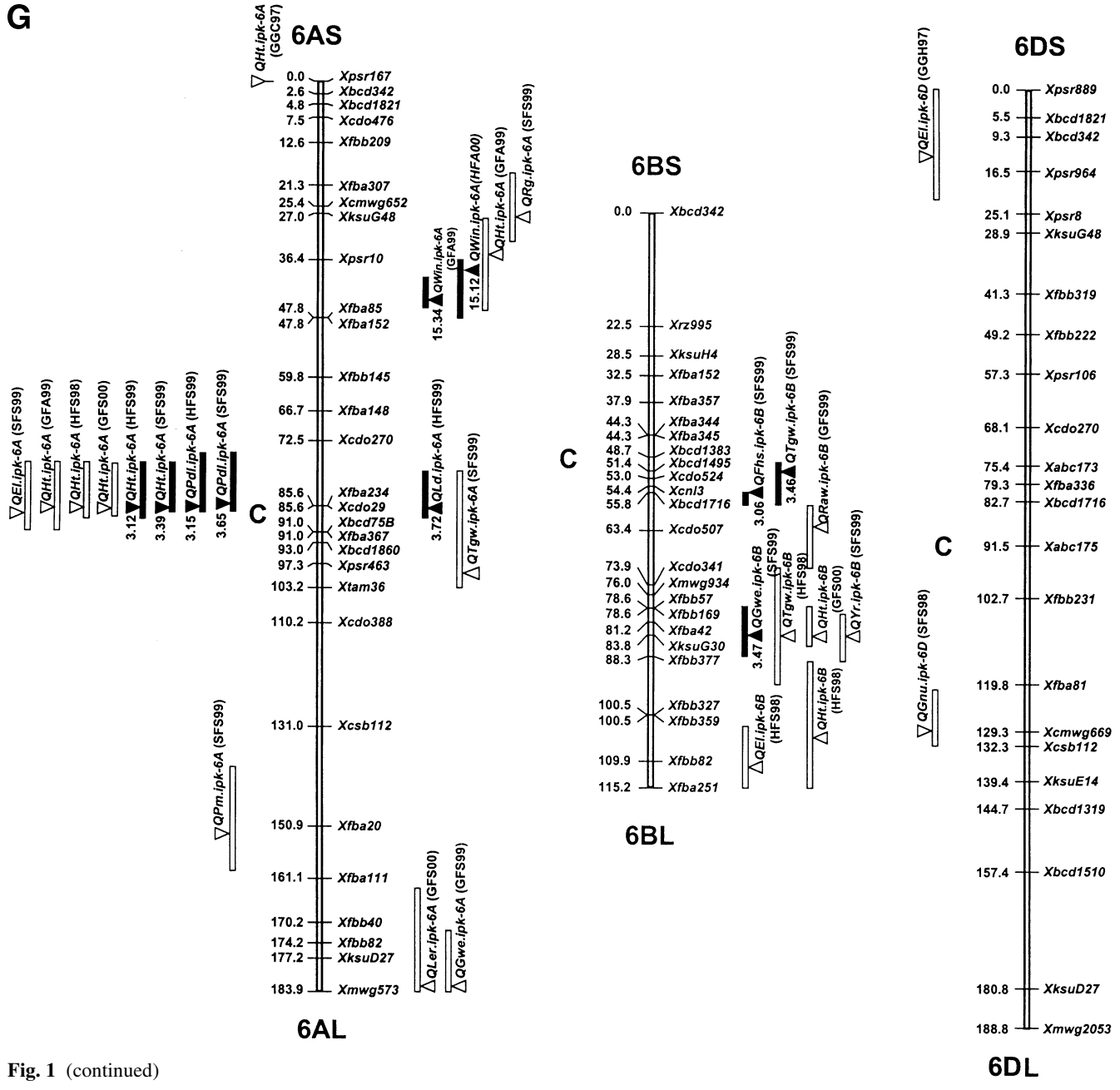
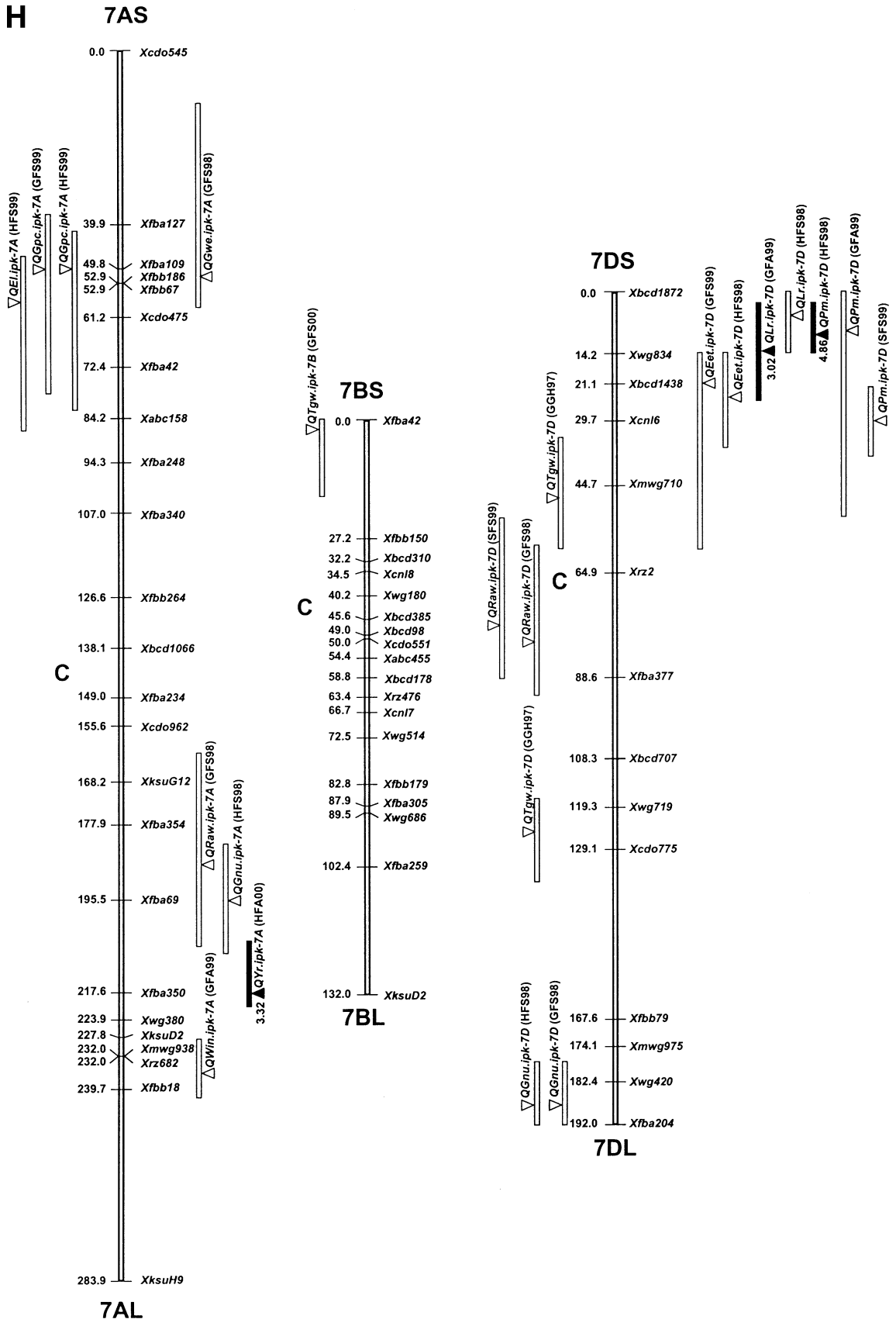


Fig. 1 (continued)

as minor QTLs, the ones with LOD scores > 3 as major QTLs. The symbolisation of the QTLs follows the rules of McIntosh et al. (1998). The trait designators (symbols) used are given in Table 1. The map positions of the QTLs together with their supported intervals are presented in Fig. 1. The loci are distributed over all chromosomes except 5B. The experiments and years in which the QTLs were detected are given in brackets behind each QTL. The effects contributed by 'W7984' and 'Opata 85' are given on the left and right hand side of each chromosome, respectively. Discussed in the following are mainly major QTLs. Minor QTLs were included only if they were in the same position as major QTLs or as in other experiments.

Morphological/colour traits

For awn and glume colour both major and minor QTLs were discovered, mainly contributed by 'W7984'. Whereas the major QTLs for awn colour were detected in the distal regions of chromosomes 1A (two experiments), 1B (one experiment) and 1D (two experiments together with one minor QTL), major loci for glume colour were found on chromosome arm 1DS (three experiments), again in the distal region and on chromosome arm 2DS (one experiment). In two experiments QTLs with a LOD score between 2 and 3 were associated with one region on chromosome arm 7BL.



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Leaf erectness was scored in two experiments only, and two major QTLs were discovered on chromosome arms 2AS and 2DL, both transmitted by 'Opata 85'. Also two major QTLs were found in different experiments for peduncle length at the same position on chromosome arm 6AS close to the centromere. The extended peduncle is contributed by synthetic wheat. Only QTLs with LOD scores between 2 and 3 were identified for waxiness. Loci of repeated experiments are located on chromosome arms 1DL (two experiments), 2DL (two experiments) and 4AL (two experiments).

Agronomic traits

For the two related traits, ear emergence time and flowering time, major and/or minor QTLs were detected in comparable regions of the genome. For ear emergence time major loci were found to map on chromosome arm 2DS (together with one minor QTL) and on chromosome arm 5DL (detected in three experiments, together with two minor QTLs). In two experiments minor QTLs were detected in the distal region of chromosome arm 7DS. Growing the RILs under a short photoperiod, one major QTL was found for the trait flowering time on chromosome arm 2DS. In the field studies, minor loci determining flowering time were mapped in the same position (three experiments). Minor loci were also found in the homoeologous region on chromosome arm 2BS (three experiments). Further QTLs were found again on chromosome arm 5DS (major loci detected in three experiments) and on chromosome arm 3AL (one major QTL together with one minor QTL). For most of the loci the 'Opata 85' alleles determined earliness. Exceptions are the QTLs detected on chromosomes 3A and 7D.

Four major QTLs were detected for plant height on chromosome arms 1AS, 2DS, 4AL (detected in two experiments together with minor QTLs detected in three experiments) and 6AS (detected in two experiments together with minor QTLs detected in three experiments). The trait is contributed by alleles of both parents. Correlated with plant height, but scored in only two experiments, lodging was found having one major QTL on chromosome arm 6AS and two minor QTLs on 2D.

The highest number of QTLs was detected for the trait ear length, measured in 9 of the 11 experiments. The main loci were mapped on chromosome arms 1BS (major and minor loci from two and three experiments, respectively), 4AS (one major QTL), 4AL (major and minor loci from four and three experiments, respectively) and 5AL (one major locus and three minor loci). The increase in ear length was again transmitted by alleles of both parents.

The traits winter hardiness and grain-filling time were scored in only two and one experiments, respectively. For winter hardiness, contributed by 'Opata 85', one major QTL was mapped on chromosome arm 6AS (in two experiments with LOD scores of 15.34 and 15.12, respectively). The grain-filling time was determined by one major QTL on chromosome arm 5AL and one minor QTL on chromosome 5B. The extension of that period was due to the 'W7984' alleles.

Two and three major QTLs together with several minor QTLs were detected for the yield components grain number and thousand-grain-weight, respectively. The number of grains per ear is determined by major QTLs on chromosome arms 2DS and 4AL (detected in two experiments together with one minor QTL). Major QTLs for grain weight map on chromosome arms 3AS, 5AL (together with one minor QTL) and 6BS. For the trait grain weight per ear, the product of the two components, grain number and grain weight, three major QTLs could be mapped on chromosome arms 2DS (detected in four experiments), 4AL (together with one minor QTL) and 6BL. Both alleles of 'Opata 85' and 'W7984' contributed to the yield and its components. Only minor QTLs were discovered for the grain protein content on the short arms of chromosomes 7A (two experiments) and 2D.

Disease resistance

For all four diseases considered, at least one major QTL was detected. For fusarium resistance a major QTL was detected on the long arm of chromosome 6B, together with one minor QTL on 5A. Three major QTLs were mapped for mildew resistance. They are located on chromosome arms 2DL and 7DS (together with two minor QTLs) and on chromosome 4B (centromere). Rust resistance major QTLs were detected on chromosome arms 2BS (detected in four from six experiments) and 7AL for yellow rust and 7DS (one major and one minor QTL) for leaf rust, respectively. Whereas rust resistance was mainly contributed by 'Opata 85' several alleles for mildew resistance originated from 'W7984'.

Correlations between experiments and traits

The analysis of variance showed that strong differences exist between genotypes for all seven analysed quantitative traits (Table 2). The interaction with sites and with years was much smaller. Nevertheless, the experiments showed that the interaction with years was significant for the agronomic traits and with sites for the yield components thousand-grain-weight and grain number.

The correlation coefficients for the single traits between pairs of experiments were in the range between 0.58 and 0.76 for the agronomic characters (Table 3). These correlation coefficients can serve as rough estimates of heritability in these experiments. There was some variation in size between pairs of experiments. The corresponding correlation coefficients for yield components were lower and ranged between 0.31 and 0.54.

The quantitative traits formed two distinct groups (Table 4). Flowering time was highly correlated with ear emergence, as expected. Ear length, plant hight, pe-

Table 2 Analysis of variance for quantitative traits tested over sites (G = Gatersleben, H = Hohenthurm, S = Silstedt) and years (1998 and 1999)

Trait	Sites	Genotypes		Genotypes × sites		Genotypes × years		Error	
		df	m.s.	*df*	m.s.	*df*	m.s.	*df*	m.s.
Ear emergence time	G, H	114	26.58	104	1.84	114	2.43	101	1.70
Flowering time	G, H	114	30.10	105	2.96	114	3.86	100	2.31
Ear length	G, H, S	114	5.29	205	0.70	113	0.73	170	0.52
Plant height	H, S	106	180.51	94	32.67	93	49.08	77	27.29
Grain number	G, H, S	113	299.42	201	53.43	107	43.72	167	39.83
1000-grain-weight	G, H, S	113	130.70	205	49.89	113	45.29	173	34.48
Grain weight/ear	G, H, S	114	0.86	205	0.25	113	0.25	169	0.21

Table 3 Correlation coefficients between experiments

Trait	Minimum	Mean	Maximum
Ear emergence time	0.69	0.76	0.84
Flowering time	0.60	0.73	0.84
Ear length	0.32	0.61	0.82
Peduncle length	0.53	0.69	0.75
Plant height	0.29	0.58	0.77
Grain number	0.39	0.54	0.67
1,000-grain-weight	–0.05	0.31	0.58
Grain weight/ear	0.16	0.37	0.52

Table 4 Correlation coefficients between traits of the same experiment

Trait	Flowering time	Peduncle length	Ear length	Plant height	Grain number	1000-grain-weight	Grain weight/ear
Ear emergence time	0.83	0.01	0.07	0.10	0.08	–0.08	0.05
Flowering time		–0.04	0.05	0.08	0.06	–0.10	0.03
Peduncle length			0.30	0.66	0.21	0.23	0.37
Ear length				0.46	0.48	0.21	0.51
Plant height					0.33	0.30	0.47
Grain number						–0.04	0.83
1000-grain-weight							0.48

duncle length, grain weight per ear and kernel number formed the other group of positively correlated traits. No correlation was found between these groups.

Discussion

Relationships between detected QTLs and major genes, or QTLs mapped in other experiments

Genes determining the coloration of the glumes and awns are described as being located on the short arms of the homoeologous group-1 chromosomes (McIntosh et al. 1998) as are most of the major QTLs detected here. It is very likely that the glume colour QTLs found on chromosome arm 1DS belong to the major gene *Rg2* (red glume). Also at the distal end of chromosome arm, 1DS closely linked to *Gli-D1* the gene *Brg* (brown glume) was localised by Koval (1994). It was assumed that *Brg* and *Rg2* may be allelic. As shown in Fig. 1 the *QRg.ipk-1D* loci were also linked to *XGli1*. No glume colour genes have been described in the region of *QRg.ipk-2D*.

In general, awn colour is described to be associated with glume colour. According to Panin and Netsvetaev (1986) black awns are determined by three complementary genes designated *Bla1*, *Bla2* and *Bla3*. *Bla1* was located on chromosome 1AS linked to *Gli-A1*. All the major QTLs mapped in the ITMI population were found to be closely linked to the *XGli* loci on chromosome arms 1AS, 1BS and 1DS and, thus, may correspond with the *Bla* genes.

The morphological trait-leaf erectness has not previously been considered in genetic studies so far, except for mutants lacking the ligules which are known to have erect leaves. In wheat two *liguless* mutants designated *lg1* and *lg2* are located on chromosomes 2B and 2D, respectively (McIntosh et al. 1998). Homoeologous loci are also known in barley, rye, maize and rice (Korzun et al. 1997). It should be mentioned here that plant breeders recently recognised that a certain architecture of the plants may provide the possibility to escape from diseases. So could more-erect leaves decrease the infection of plants with spores from the straw retained in the soil after the harvest of the year before. Two major loci

determining leaf erectness were detected on chromosome arms 2AS and 2DL, respectively. Although the latter was mapped in the region most probably carrying *lg2* (Korzun et al. 1997) it is not related to that mutant. All RILs of the ITMI population carry ligules.

Another trait that may be important for disease escape is peduncle length. In general it is known that plants having short peduncles are more susceptible to ear diseases because of micro-climatical conditions. The mapping studies presented here give clear indication that there exists at least one major QTL, detected in two experiments in the centromere region of chromosome 6A, which could be exploited in the future.

For the trait waxiness the ITMI population was already screened by Nelson et al. (1995a). The authors detected one locus determining waxiness on chromosome arm 2DS distally, and suggested that the mapping population is segregating for the gene *W2[1]* which is known to be located in that position. In our studies this result could not be confirmed. Instead of one major locus on 2DS minor QTLs were detected in repeated experiments on chromosome arms 1DL, 2DL and 4AL suggesting that the inheritance of that character is more complex than expected.

By scoring the traits ear-emergence time and flowering time major QTLs were detected in regions of the genome known to carry major genes for photoperiod and vernalisation response in wheat (McIntosh et al. 1998) and other Triticeae (Börner 1999). On chromosomes 2BS and 2DS the major genes *Ppd2* and *Ppd1*, respectively, are located, whereas the detected QTLs on 5DL correspond with *Vrn-D1*. This vernalisation response locus was already discovered by Nelson et al. (1995c) in the same mapping population.

In two experiments minor QTLs for ear-emergence time (*QEet.ipk-7D*) were detected in the distal region of chromosome arm 7DS. A homoeology to a vernalisation response gene in the distal region of chromosome 7DS described by Law (1966) and Law and Wolfe (1966) and designated *Vrn-B4* (McIntosh et al. 1998) may be suggested. *QEet.ipk-7D* is located on the segment of the 7DS chromosome which is homoeologous to 4AL (Nelson et al. 1995c) carrying the *Wx* locus determining the amylose content of the starch. Araki et al. (1999) described a QTL for flowering time closely linked to *Wx* on chromosome arm 4AL, which may also be related to the minor QTL on chromosome arm 4AL detected here.

The flowering-time locus on chromosome arm 3AL may correspond with an earliness *per se* gene (*Eps-A1*) affecting the plant development, independent of the response to vernalisation and photoperiod (Miura et al. 1999; McIntosh et al. 2000). However, taking into consideration the suggested changes of the RFLP maps described by Pestsova et al. (2000), the QTL for earliness *per se* may be located on chromosome arm 3DL instead of 3AL. It should be mentioned here that, in barley, QTLs determining flowering time were also detected in the distal region of chromosome arm 3HL (Laurie et al. 1995; Noli et al. 2000).

Besides flowering time the time for grain filling influences the time of harvest and, to some extent, the final grain yield. Plants having a lengthened grain-filling time may have higher grain weights. Loci determining the trait were detected on the long arms of chromosomes 5A and 5B. No data have been described in the literature.

Final plant height is known to be determined by many genes (Börner et al. 1996). Therefore, it was not surprising that in the present study many QTLs were detected. Only one locus was found to be in the position of a known major dwarfing gene (*Rht8*) on the short arm of chromosome 2D (Korzun et al. 1998), although the effect on height may be also caused by pleiotropy of the detected *Ppd* locus, as described by Börner et al. (1993). QTLs for plant height were already detected by Cadalen et al. (1998), of which three were in comparable positions on chromosome arms 1AS, 1BL and 4BL, as discovered here. Of further interest may be the two loci on chromosome arms 4AL and 6AS, where major and minor QTLs were detected in several experiments.

The former locus was also found to affect ear length as shown by the presence of four major and four minor QTLs. In the literature only one locus determining ear length (*Qel.ocs-5A.1*) was described to be mapped on chromosome arm 5AL (Kato et al. 1999), in a region comparable to the map position of the QTLs shown in Fig. 1.

The two loci detected for lodging correspond with the plant height QTLs on chromosomes 6A and 2D, and are most probably pleiotropic effects. Keller et al. (1999a) detected 29 QTLs for lodging in three experiments of which none were found to map on chromosomes 2DS and 6A.

Genes determining winter hardiness or frost resistance are known to be located chromosome arms 5AL (*Fr1*) and 5DL (*Fr2*) of wheat, closely linked to the *Vrn* genes (Galiba et al. 1995; Snape et al. 1997). QTLs associated with low-temperature tolerance were also described in a comparable region of chromosome 5H (Hayes et al. 1993; Pan et al. 1994). In the present investigation no homoeologous group-5 locus was detected; however, strong effects were associated with chromosome arm 6AS. It should be noted that the QTLs for winter hardiness described here were detected in a spring wheat mapping population contributed by 'Opata 85'. Whether they will be expressed in a winter wheat background can only be speculated.

The inheritance of the character grain yield and its components is known to be complex. The study of the genetics of such multiple traits becomes possible only by performing QTL analyses. First experiments on mapping QTLs for yield and yield components in wheat considering chromosome 4A only, were described by Araki et al. (1999). Interestingly, the authors describe a QTL for grain weight per ear in the centromere region of chromosome 4A, which may correspond to the locus detected in the ITMI population. However, whereas Araki et al. (1999) found the QTL for grain yield to be associated with a QTL for grain weight, in the present study it

aligns with loci for grain number and spike length. The major QTLs discovered on chromosome arm 2DS are most probably caused by pleiotropy of *Ppd-D1*, known to affect yield (Börner et al. 1993).

QTL mapping studies for grain protein content were performed by several authors considering tetraploid (Blanco et al. 1996; Joppa et al. 1997; Mesfin et al. 1999) and hexaploid (Prasad et al. 1999) wheats. Loci were described to map on chromosome arms 4BS, 5AL, 6AS, 6BS, 7BS or 2DL. None of these loci were detected in the ITMI population. Here the distal parts of chromosome arms 7AS and 2DS were found to carry loci for grain protein content detected by using near-infrared spectroscopy.

From the four diseases scored in the present study leaf rust and yellow rust were already studied by Nelson et al. (1995a, c, 1997) and Sing et al. (2000), respectively, investigating the ITMI population. The presence of a major QTL on chromosome 7DS corresponding to *Lr34* was confirmed. Whether the minor QTLs detected on chromosome arms 1AS and 3BS correspond to the seedling resistance genes *Lr10* and *Lr27*, respectively, can only be speculated.

About 50 major genes were described for yellow rust (McIntosh et al. 1998). Two of them, *Yr27* and *YrCv*, were located on chromosome arm 2BS; however they have not been mapped. The major QTL detected in four of six experiments in our studies may be one of these loci. To clarify this allelic test, crosses will become necessary. No major genes are known on chromosome arm 7AL. Interestingly, none of the yellow rust QTLs detected by Sing et al. (2000) on chromosome arms 3BS, 3DS, 4DS and 5DS were confirmed in the present investigation.

All three major QTLs discovered for mildew resistance can be discussed in relation to literature data. The locus on chromosome arm 7DS may be associated with *Pm15* described by Tosa and Sakai (1990), whereas *QPm.ipk-2D* was found to map in a region comparable to that of *QPm.sfr-2D*, mapped in a wheat × spelt population (Keller et al. 1999b). The third locus was mapped in the centromere region of chromosome 4B and may correspond to *Mld* located, but not mapped, on that chromosome (Bennett 1984).

Most cultivars of common wheat are susceptible to the ear disease fusarium head blight (Mesterhazy et al. 1999), and only a few sources for resistance are known, mainly originating from China. QTL mapping studies were performed by Bai et al. (1999) and Waldron (1999). The latter detected two significant QTLs (LOD > 3.0) on chromosome arms 3BS and 2AL whereas loci on chromosome arms 4BL and 6BS did not reach the LOD threshold of 3.0. The QTLs detected by Bai et al. (1999) were associated with AFLP markers without chromosomal location. No QTLs were mapped on chromosome arms 5AS or 6BL. However, chromosomes 5A and 6B were found to be associated with fusarium resistance by Grausgruber et al. (1998) and Buerstmayr et al. (1999) analysing cytogenetic tester stocks.

It must be noted that not in every experiment were all diseases scored. For the rusts and for mildew, only naturally occurring infection was tested. Fusarium was scored only once, powdery mildew in seven experiments, leaf rust in five and yellow rust in six experiments.

Relationships between experiments

With the analysis of QTLs, critical chromosomal regions can be identified. This is the main goal of the so called AB-QTL approach (Tanksley and Nelson 1996). With this method regions in exotic materials can be searched for, which could be of interest for transfer into breeding material. The situation in this study is quite similar. Both parents of the mapping population are exotic and not adapted to middle-European conditions. Plant breeders can use information from QTL analysis only if the results can be reproduced. This was done here with the same material, changing only the environment. However, even in this case the QTLs could not be detected in all experiments. The main reasons are the interaction between genotypes and environments, and the experimental error.

The major QTL for yellow rust on 2BS could be detected in four out of six experiments, indicating a very low degree of interaction. This may be explained by assuming a very stable yellow rust population. The resistance was transmitted from ‘Opata 85’. On 7D a locus for resistance against powdery mildew was found in two experiments, and in the same region for the same two experiments, for leaf rust, though both diseases were recorded in seven and five experiments, respectively.

QTLs can be detected only if the parents carry different alleles. The favourable allele may be very specific for one of the parents and can not be found in other genotypes. Nevertheless, the detected QTLs indicate that an improvement is possible if chromosomal regions with positive effects are combined.

As indicated, the quantitative traits were correlated. This resulted in QTLs for more than one trait at the same position. The data do not allow one to separate closely linked loci and pleiotropy.

In the literature a LOD of <3 is often considered as a lower value, since the QTL analysis is faced with multiple testing (Lander and Botstein 1989). However, major and minor QTLs were detected at the same position in different experiments for several traits. Therefore LOD values <3 should also be taken into account in repeated experiments.

In this study, no QTLs for main effects over experiments have been estimated. This has two reasons. First, not all traits could be evaluated in all experiments so that the results for different traits could be compared only on the basis of single experiments. Second, the experiments focused on the interaction between genotypes and environments to check if results from one experiment allows conclusions for other experiments. To do this, experiments must be analysed separately. The main conclusion

of the results is that there is no way to circumvent repeated experiments, but some QTLs could also be detected in independent trials.

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