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Genomic mapping of defense response genes in wheat

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Abstract Defense response (DR) genes are a broad class involved in plant defense. In this study we mapped 36 probes representing seven classes of defense response genes. This collection of probes represents genes involved in the hypersensitive response (HR), pathogenesis-related (PR) genes, genes for the flavonoid metabolic pathway, genes encoding proline/glycine-rich proteins, ion channel regulators, lipoxygenase, lectin, and others. Using nullisomic-tetrasomic lines of 'Chinese Spring', we were able to assign at least 167 loci to the 21 chromosomes of wheat. Homoeologous group 7 chromosomes possessed the most DR loci followed by group 2. Sixty-two loci were placed on existing genetic linkage maps of wheat. Map locations indicated that the DR gene loci are not randomly distributed throughout the wheat genome, but rather are located in clusters and/or in distal gene-rich regions of the chromosomes. Knowledge of the chromosomal locations and genome organization of DR genes will be useful for candidate gene analysis of quantitative trait loci.

Key words Molecular mapping · Wheat · Resistance · Defense response genes

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Introduction

Agricultural crops are constantly challenged by pathogens and insects. Utilization of host resistance is the most efficient and environment-friendly means of reducing losses to parasites. Resistance is usually recognized as being either monogenically or polygenically controlled. In most cases, monogenic resistance is race-specific and fits the "gene for gene" model (Flor 1971). Polygenic resistance involves quantitative variation at multiple loci.

Biochemical and molecular studies have demonstrated that two classes of genes contribute to the resistance reaction: resistance (R) genes involved in the recognition process and genes involved in the defense response (DR genes). Recently, the cloning of multiple R genes from various plant species has revealed conserved domains at the amino acid level (for review, see Bent 1996). In contrast, many DR genes have been isolated from various plant species, and these encode a diverse array of enzymes. Their structure, expression, and function have been thoroughly documented (Bowles 1990; Hammond-Kosack and Jones 1996; Yun et al. 1997). DR genes have become very important resources for crop improvement as potential target genes in resistance engineering. However, little is known about their organization in plant genomes.

Common wheat (*Triticum aestivum* L em. Thell., 2n = 6x = 42, AABBDD) is an important crop worldwide. Although the chromosome locations of many resistance genes have been determined (details at web site: http://greengenes.cit.cornell.edu/ggtabledefs.html) and a few resistance quantitative trait loci (QTLs) have been identified (Faris et al. 1997), their molecular identification is generally unknown. Only a few DR genes have been cloned (Lai et al. 1993) and mapped (Gale et al. 1995; Mingeot and Jacquemin 1997). This situation greatly limits our knowledge of both qualitative and quantitative resistance mechanisms in wheat, and

thus the full utilization of resistant resources. To understand the genomic organization of DR genes, we have determined the chromosomal locations of DR genes in wheat using clones from maize, barley, and rice as probes.

Materials and methods

Plant materials

Nullisomic-tetrasomic (NT) lines of 'Chinese Spring' (Sears 1966), where nullisomy for a specific chromosome is compensated by two extra copies of a homoeologue, were used to locate DR genes to specific wheat chromosomes. N2A T2B and N4B T4D were identified cytologically, as these plants are maintained as monosomic-tetrasomic lines.

A population of recombinant inbred lines (RILs) derived from a cross between a synthetic hexaploid wheat, W-7984, and the common wheat variety 'Opata 85' was provided by Dr. M.E. Sorrells, Cornell University, Ithaca, N.Y., and produced as described in Nelson et al. (1995c). Fifty-six F_2 plants from the cross of *Aegilops tauschii* Coss. [syn. *Ae. squarrosa* L., syn. *T. tauschii* (Coss.) Schmal. $2n = 14$, DD] accessions TA1691 and TA1704 were used when polymorphism was not detected between W-7984 and 'Opata 85'. The *Ae. tauschii* population and mapping have been described by Gill et al. (1991) and Kam-Morgan et al. (1989).

Clones

Genetic clones and their sources used in mapping experiments are listed in Table 1. Inserts were prepared by restriction enzyme digestion or polymerase chain reaction (PCR) amplification as suggested by suppliers.

Mapping analysis

The mapping population consists of 114 RILs and has been the subject of an extensive genome mapping effort by investigators of the International Triticeae Mapping Initiative (ITMI) (Marino et al. 1996; Nelson et al. 1995 a,b,c; Van Deynze et al. 1995). A subset of about 450 markers that map at an LOD > 2.0 was used as a base map for the placement of DR gene markers. At least RILs 1–60 were used for genetic mapping. Linkage relationships were evaluated with MAPMAKER (Lander et al. 1987) using a minimum LOD of 2.0 and the Kosambi mapping function (Kosambi 1944).

Genomic DNA was isolated from 'Chinese Spring' NT lines, W-7984, 'Opata 85' and their RILs, digested with restriction enzymes, separated by gel electrophoresis, and transferred to nylon membranes as described in Riede and Anderson (1996). Plasmid inserts containing DR genes were labeled and hybridized to membranes as described in Gill et al. (1993).

Results

Chromosome location of DR genes

Thirty-six clones were collected, and these represent seven classes of DR genes including genes involved in the hypersensitive response (HR), pathogenesis-related (PR) genes, genes for the flavonoid metabolic pathway, ion channel regulatory genes, genes encoding lipoxygenase and proline and/or glycine-rich proteins, and other unclassified DR genes. Upon hybridization to Southern blots of NT-lines using a single restriction enzyme, the 36 clones detected 322 fragments and at least 167 loci distributed on all of the 21 wheat chromosomes (Tables 2, 3). Only 17 fragments were not assigned to chromosomes, presumably due to comigration.

Group 7 chromosomes possessed the most DR genes (34 loci), followed by group 2 chromosomes (31 loci), and group 6 chromosomes had the least number of loci (12). Almost all clones detected 3 or more loci with the exception of *Rip* which detected only 1 locus on chromosome 6D. In some cases, not all homoeologous chromosomes of a particular group possessed the same DR genes. For example, in addition to groups 1 and 3, *Pld* hybridized to chromosomes 7B and 7D but not 7A. This suggests the existence of nonhomoeologous loci.

Peroxidase genes isolated from different species hybridized to different (nonhomoeologous) wheat chromosomes. *Per* from maize hybridized to group 7 chromosomes, but *Per2* from rice detected fragments on group 2 chromosomes. Chitinase and thaumatin/osmotin clones hybridized to many different chromosomes, and a similar situation was observed for a gene family encoding ion channel-regulating proteins (*1433a*, *1433b*, and *1433c*). This suggests that a high degree of variation in nucleotide sequences exists among the members of DR gene families.

Genomic mapping of DR genes

While aneuploid mapping allowed us to assign at least 167 loci to specific chromosomes, 58 loci were polymorphic in the ITMI population and were mapped genetically to specific regions of all common wheat chromosomes, except for chromosome 1A (Fig. 1). Four additional loci were mapped in the *Ae. tauschii* F_2 population (Fig. 2). Map locations of DR genes were not evenly distributed along the length of chromosomes. About 50% (32) of the 62 loci mapped within one of two types of clusters. One type of cluster is composed of different members of the same DR gene family. Four members of the glucanase family detected by *Glb3* on chromosome 3B were closely linked within a region of 5.9 cM. A similar situation was observed on the long arm of barley chromosome 3H where seven glucanase genes reside within 20 cM (Li et al. 1996). It was speculated that 7 loci of a gene cluster in barley correspond to seven isoforms of glucanase. A smaller cluster consisting of 2 loci detected by *Grp94* were closely linked on the long arm of chromosome 7A (Fig. 1).

A second type of cluster in wheat was composed of different types of DR genes. *Chs* and *Fmt* were found to be closely linked on the short arms of chromosomes 1B

Table 1 Proteins encoded by the defense response genes mapped in common wheat in this study. The clone designations, mapping symbols, source species, and suppliers are indicated

Gene product	Clone designation	Symbol	Source	Supplier
HR genes				
Peroxidase	po × 22.3	*Per2*	Rice	F. White
	6C02D10	*Per*	Maize	T. Musket
Catalase	5C05D01	*Cat*	Maize	T. Musket
Superoxide dismutase	CSU182	*Sod*	Maize	T. Musket
Oxalate oxidase	BH6-903	*Oxo1*	Barley	D. Collinge
	OXOXa	*Oxo2*	Barley	D. Collinge
PR genes				
Pr1	CR1	*Pr1*	Maize	S. Morris et al. (1998) MPMI
	HvPr1b	*Pr1b*	Barley	D. Collinge
β-(1-3) Glucanase	BH72-1l	*Glb3*	Barley	D. Collinge
Chitinase 1a	Chi-G11	*Cht1a*	Rice	S. Muthukrishnan
Chitinase 1b	Barchi3	*Cht1b*	Barley	S. Muthukrishnan
Chitinase 2	BH72-c4	*Cht21*	Barley	D. Collinge
	BH72-N12	*Cht22*	Barley	D. Collinge
Chitin binding protein	RRI 10	*Cbp1*	Maize	S. Hulbert
	BH72-B8	*Cbp2*	Barley	D. Collinge
Thaumatin	CR5	*Tha1*	Maize	S. Morris et al. (1998) MPMI
	BH72-C6	*Tha2*	Barley	D. Collinge
	BH72-K10	*Tha3*	Barley	D. Collinge
	Tlp-D34	*Tha4*	Rice	S. Muthukrishnan
Flavonoid metabolic pathway genes				
myb protein c1	c1	*Mpc1*	Maize	T. Musket
Chalcone isomerase	Fl19	*Chi*	Maize	E. Grotewold
Chalcone synthase	BH72-08	*Chs*	Barley	D. Collinge
Flavonol 7-*O*-methyl transferase	BH-72-F1	*Fmt*	Barley	D. Collinge
Phenylalanine ammonia lyase	CSU358	*Pal*	Maize	T. Musket
Proline-rich proteins				
Hydroxyproline-rich protein	p5C05D01	*Hrp*	Maize	T. Musket
Proline-rich protein	HvPRPb	*Prp*	Barley	D. Collinge
Ion channel regulators				
14-3-3 protein	pHv14-3-3a	*1433a*	Barley	D. Collinge
	pHv14-3-3b	*1433b*	Barley	D. Collinge
	pHv14-3-3c	*1433c*	Barley	D. Collinge
Grp94	HvGRP94	*Grp94*	Barley	D. Collinge
Others				
Lipoxygenase	6C02E12	*Lpx*	Maize	T. Musket
α-Phospholipase D	6αA	*Pld*	Rice	J. Leach
Ribosome inactivating protein	5C04F01	*Rip*	Maize	T. Musket
Polyphenol oxidase	7C02D02	*Ppo*	Maize	T. Musket
Wound-induced protein	5C05B11	*Wip*	Maize	T. Musket
Lectin	pNVR8	*Lec*	Wheat	J. Dvorak

and 1D. *Tha2* and *Cht21* were closely linked on 4AL, and *1433a* and *Oxo2* tightly linked near the centromere. *Oxo2*, *1433a*, and *Cht21* were all clustered in the distal region of 4BS. *Per2* and *Sod* were closely linked on chromosome 2BS, and *Tha1* and *Cbp1* were closely linked on 6BL. *Pr1b* hybridized to fragments on group 7 chromosomes and were found to be closely linked with *Cbp2* on 7BS and *Mpc1* on 7DS.

A more significant cluster of DR genes occurred in the long arm of group 7 chromosomes. The genetic linkage map of 7B revealed a cluster in the long arm where *Tha2*, *Cht1b*, *Tha1*, *Cat*, and *Grp94* all reside within a relatively small segment. It is interesting that most of the clusters were located in distal regions of the chromosome arms.

Due to the absence of polymorphism in the wheat RIL population, 4 loci were mapped in the *Ae. tauschii* population (Fig. 2). *Cht22* and *Chi2* both mapped to chromosome 5D, while *Pld* and *Chi1* mapped to chromosomes 3D and 7D, respectively. Segregation of *Chi1* significantly deviated from the expected 1 : 2 : 1 ratio in the F_2 population ($P < 0.05$). This agrees with the distorted segregation of this region observed by Faris et al. (1998).

Table 2 Chromosome locations of defense response genes using nullisomic-tetrasomic lines of 'Chinese Spring' wheat

Symbol	Enzyme	Total no. of bands	Uncharacter-ized bands	Chromosome	Minimum no. of loci
Per2	*Hind*III	13	2	Group 2	3
Per	*Hind*III	12	0	Group 7	3
Cat	*Eco*RI	8	0	2D, group 7	4
Sod	*Eco*RI	6	1	Group 2	3
Oxo1	*Eco*RI	18	2	4B, 4D, 5A	3
Oxo2	*Eco*RI	19	1	3B, group 4	4
Pr1	*Hind*III	17	0	Group 5	3
Pr1b	*Eco*RV	8	0	Groups 5, 7	6
Glb3	*Hind*III, *Eco*RI	14, 17	1, 2	Group 3	3
Cht1a	*Eco*RI	13	2	1B, 2B, 2D, 3A, 3D, 5D, 7B	7
Cht1b	*Eco*RI	12	1	3D, group 7	4
Cht21	*Eco*RI	3	0	Group 4	3
Cht22	*Hind*III, *Eco*RV	15, 12	3, 0	7B, 7D, groups 1, 2, 5	11
Cbp1	*Hind*III	11	2	2A, 2B, 3D, 6B, group 1	7
Cbp2	*Eco*RI	13	2	2A, 2B, 5A, 5D, 7B, 7D, group 3	9
Tha1	*Hind*III	8	0	4A, 6B, groups 2, 7	8
Tha2	*Hind*III	8	0	Groups 4, 7	6
Tha3	*Hind*III	7	0	7B, group 5	4
Tha4	*Eco*RI	6	0	Group 4	3
Mpc1	*Hind*III	9	0	4B, 4D, 5A, group 7	6
Chi	*Eco*RI	6	1	7D, group 5	4
Chs	*Eco*RI	14	1	Groups 1, 2	6
Fmt	*Hind*III	8	0	Group 1	3
Pal	*Eco*RV	5	1	3B, group 6	4
Lpx	*Eco*RI	11	0	Groups 4, 5	6
Hrp	*Eco*RI	6	0	Group 6	3
Prp	*Hind*III	3	0	Group 3	3
1433a	*Eco*RI	3	0	Group 4	3
1433b	*Eco*RI	8	0	Groups 2, 3	6
1433c	*Eco*RI	10	0	4B, 4D, groups 2, 3	8
Grp94	*Eco*RV	4	0	Group 7	3
Pld	*Eco*RI	8	0	7B, 7D, groups 1, 3	8
Rip	*Hind*III	1	0	6D	1
Ppo	*Hind*III	6	0	5B, 7D, group 6	5
Wip	*Eco*RV	5	0	4B, group 2	4
Lec	*Hind*III	7	0	3B, group 1	4
	Total	322	17		167

Table 3 Locations of defense response genes by chromosome according to hybridizations to 'Chinese Spring' nullisomic-tetrasomic lines

Chromosome	Defense response genes
1A	*Cht22*, *Cbp1*, *Chs*, *Fmt*, *Pld*, *Lec*
1B	*Cht1a*, *Cht22*, *Cbp1*, *Chs*, *Fmt*, *Pld*, *Lec*
1D	*Cht22*, *Cbp1*, *Chs*, *Fmt*, *Pld*, *Lec*
2A	*Per2*, *Sod*, *Cht22*, *Cbp1*, *Cbp2*, *Tha1*, *Chs*, *1433b*, *1433c*, *Wip*
2B	*Per2*, *Sod*, *Cht1a*, *Cht22*, *Cbp1*, *Cbp2*, *Tha1*, *Chs*, *1433b*, *1433c*, *Wip*
2D	*Per2*, *Cat*, *Sod*, *Cht1a*, *Cht22*, *Tha1*, *Chs*, *1433b*, *1433c*, *Wip*
3A	*Glb3*, *Cht1a*, *Cbp2*, *Prp*, *1433b*, *1433c*, *Pld*
3B	*Oxo2*, *Glb3*, *Cbp2*, *Pal*, *Prp*, *1433b*, *1433c*, *Pld*, *Lec*
3D	*Glb3*, *Cht1a*, *Cht1b*, *Cbp1*, *Cbp2*, *Prp*, *1433b*, *1433c*, *Pld*
4A	*Oxo2*, *Cht21*, *Tha1*, *Tha2*, *Tha4*, *Lpx*, *1433a*
4B	*Oxo1*, *Oxo2*, *Cht21*, *Tha2*, *Tha4*, *Mpc1*, *Lpx*, *1433a*, *1433c*, *Wip*
4D	*Oxo1*, *Oxo2*, *Cht21*, *Tha2*, *Tha4*, *Mpc1*, *Lpx*, *1433a*, *1433c*
5A	*Oxo1*, *Pr1*, *Pr1b*, *Cht22*, *Cbp2*, *Tha3*, *Mpc1*, *Chi*, *Lpx*
5B	*Pr1*, *Pr1b*, *Cht22*, *Tha3*, *Chi*, *Lpx*, *Ppo*
5D	*Pr1*, *Pr1b*, *Cht1a*, *Cht22*, *Cbp2*, *Tha3*, *Chi*, *Lpx*
6A	*Pal*, *Hrp*, *Ppo*
6B	*Cbp1*, *Tha1*, *Pal*, *Hrp*, *Ppo*
6D	*Pal*, *Hrp*, *Rip*, *Ppo*
7A	*Per*, *Cat*, *Pr1b*, *Cht1b*, *Tha1*, *Tha2*, *Mpc1*, *Grp94*
7B	*Per*, *Cat*, *Pr1b*, *Cht1a*, *Cht1b*, *Cht22*, *Cbp2*, *Tha1*, *Tha2*, *Tha3*, *Mpc1*, *Grp94*, *Pld*
7D	*Per*, *Cat*, *Pr1b*, *Cht1b*, *Cht22*, *Cbp2*, *Tha1*, *Tha2*, *Mpc1*, *Chi*, *Grp94*, *Pld*, *Ppo*

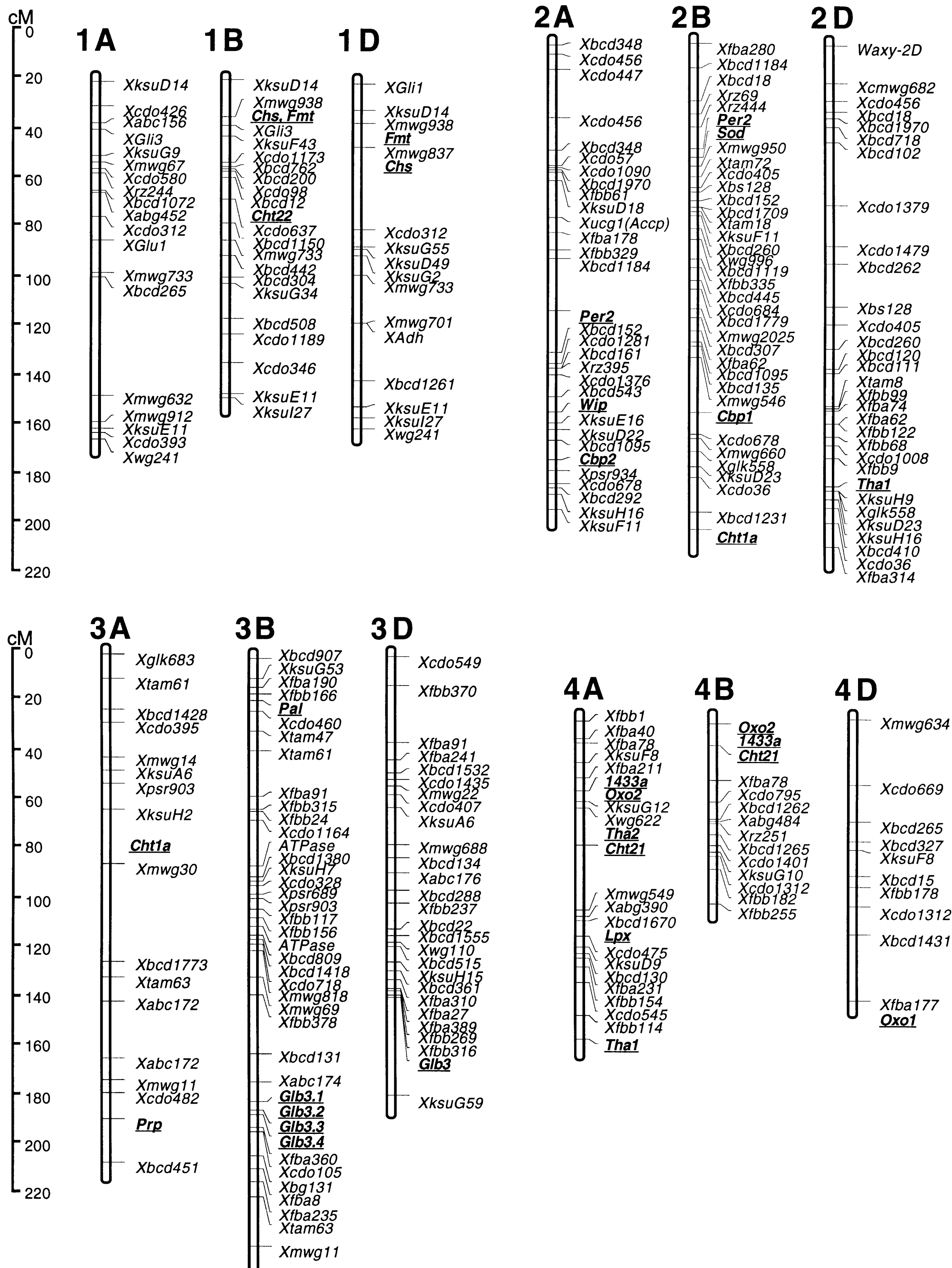

Fig. 1 Continued

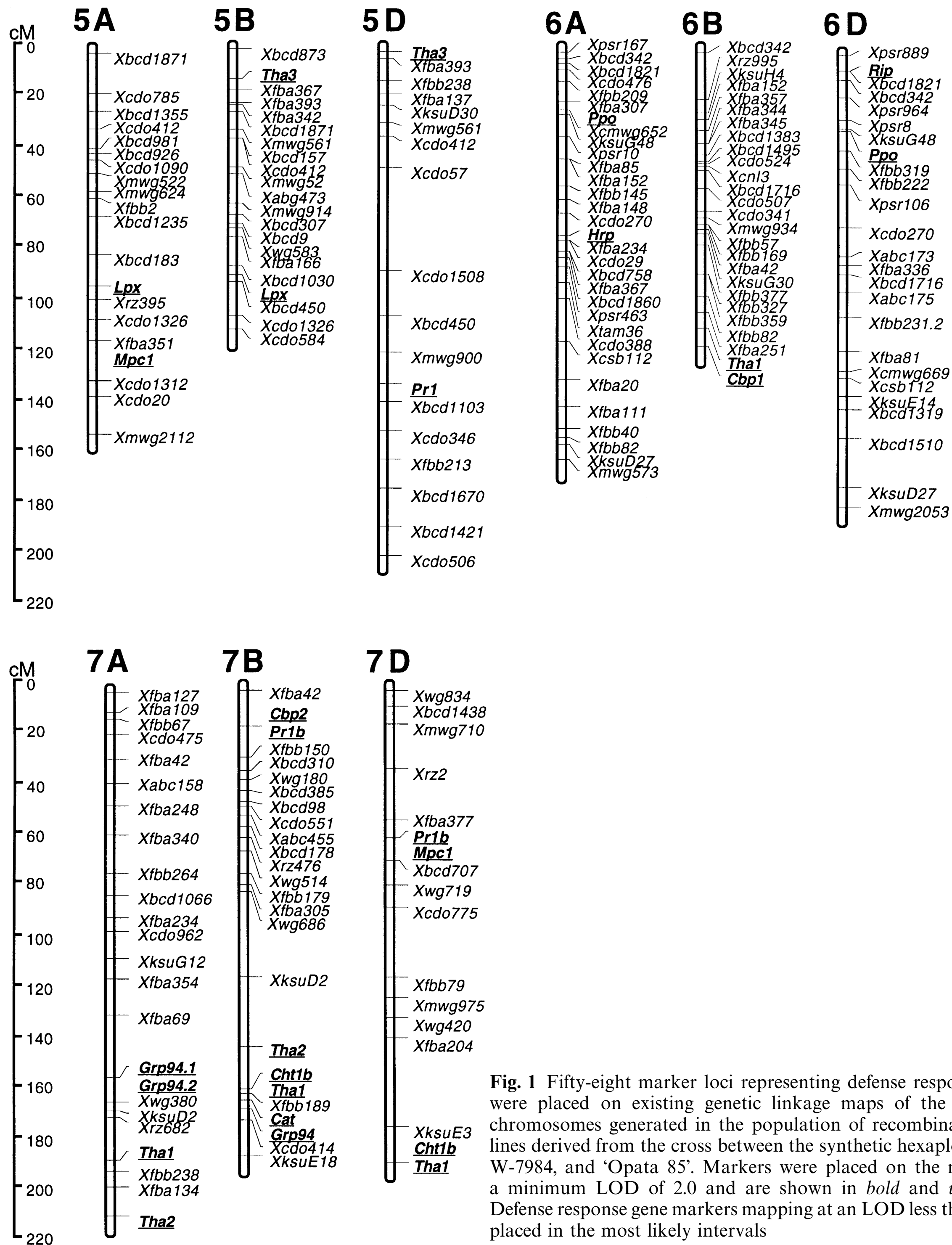

Fig. 1 Fifty-eight marker loci representing defense response genes were placed on existing genetic linkage maps of the 21 wheat chromosomes generated in the population of recombinant inbred lines derived from the cross between the synthetic hexaploid wheat, W-7984, and 'Opata 85'. Markers were placed on the map using a minimum LOD of 2.0 and are shown in **bold** and *underlined*. Defense response gene markers mapping at an LOD less than 2.0 are placed in the most likely intervals

Discussion

DR genes are a broad class of genes involved in the plant defense response process. Where the functions are known, they encode diverse enzyme activities. The common feature is that their expression is induced by a range of offensive stimuli, e.g. pathogen challenge, insect attack, wounding, etc. (Bowles 1990). Mapping this special class of genes provides insights to the genome organization of functionally related genes. In this study, 36 DR gene clones were assigned to all 21

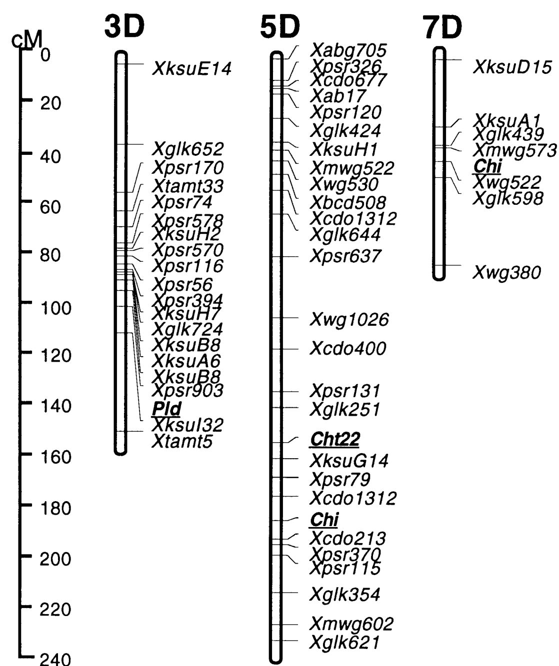

Fig. 2 Four defense response gene probes were nonpolymorphic in the recombinant inbred population and were subsequently mapped in the *Aegilops tauschii* F_2 population derived from the cross of accessions TA1691 and TA1704. Markers representing defense response genes are shown in *bold* and *underlined* and were placed using an LOD threshold of 2.0. Those mapping at an LOD < 2.0 were placed in the most likely interval

chromosomes of wheat. The number of chromosomes that each clone hybridized to varied from 1 to 11.

In some cases, only 1 or 2 chromosomes of a homoeologous group possessed the DR gene. This may reflect the evolutionary phenomenon of diploidization where it has been suggested that speciation through allopolyploidy may be accompanied by a rapid, nonrandom elimination of specific, low-copy DNA sequences at the early stages of allopolyploidization (Feldman et al. 1997).

The marker *Rip* (ribosome-inactivating protein) was present as a single copy in the short arm of chromosome 6D. Analysis of various wheat relatives indicated that *Rip* exists only in species possessing the D-genome, i.e., *Ae. tauschii* and common wheat, but not in *T. monococcum* (AA), *T. turgidum* (AABB), and *T. dicoccoides* (AABB) (data not shown). It is possible that *Rip* sequences underwent extensive divergence or exclusion in A-and B-genome-containing species.

Another variation is that different members of a DR gene family were sometimes located in chromosomes belonging to different homoeologous groups. The most significant data came from chitinase and thaumatin (Table 2). This reflects the sequence modification among the individual loci. Different expression patterns have been found among members of some DR gene families (Chittoor et al. 1997). Correspondence between locus variation and expression activities need to be confirmed using specific probes and sequence data.

A significant feature in the genome organization of DR genes is that many are present in clusters along the chromosome. Most of the DR gene clusters are located in distal regions of wheat chromosomes. The cluster of DR genes in the distal region of 4B appears to have been involved in the pericentric inversion that occurred on chromosome 4A during the evolution of polyploid wheat (Devos et al. 1995; Mickelson-Young et al. 1995; Nelson et al. 1995a). Indeed, analysis using ditelosomic lines of 'Chinese Spring' indicated that the homoeologous group 4 genes detected by *Cht21*, *Oxo2*, *Tha2*, and *1433a* reside on the short arms of 4B and 4D, and on the long arm of 4A (data not shown).

The map order of the DR genes within the clusters on chromosomes 7AL and 7BL suggests that an inversion may have occurred on these chromosomes. Comparison with physical maps of wheat (Delaney et al. 1995a,b; Gill et al. 1993, 1996a,b; Hohmann et al. 1994; Mickelson-Young et al. 1995) indicates the regions in which they reside have higher gene densities and recombination frequencies than other regions of the wheat genome. Genes within these regions are more closely linked physically than those in other regions with similar genetic distances.

These clusters have probably been maintained through the history of evolution because of the association of their functions. This deduction is supported by evidence from DR gene expression studies and transgenic experiments. Host-pathogen interaction studies indicated that the expression of DR genes are highly coordinated among families, synergistic or sequential (Hahlbrock et al. 1995; Jabs et al. 1997), especially the subsets of DR genes whose expression is regulated by signaling molecules such as ethylene, salicylic acid, or jasmonic acid (Ryals et al. 1996; Xu et al. 1994). Transgenic plants coexpressing multiple DR genes enhanced fungus resistance quantitatively compared with the transgenic plants in which only one DR gene was expressed constitutively (Jach et al. 1995; Zhu et al. 1994). Characterization of the specificities of DR gene combination in each cluster would provide more information about the interaction between DR gene products.

Knowledge of the chromosomal locations and genome organization of DR genes will aid geneticists in conducting candidate gene analysis studies of quantitative trait loci associated with disease resistance (Faris et al. 1999). Plant breeders will then be able to use this information to develop marker-assisted selection schemes that allow them to efficiently select and combine the most desirable DR gene alleles.

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