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ORIGINAL PAPER

H22, a major resistance gene to the Hessian fly (*Mayetiola destructor*), is mapped to the distal region of wheat chromosome 1DS

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Abstract *H22* is a major resistance gene conferring high-level of antibiosis to Hessian fly [*Mayetiola destructor* (Say)] larvae. It was previously assigned to wheat chromosome 1D through monosomic analysis (Raupp et al. in J Hered 84:142–145, 1993). The objective of this study was to identify molecular markers that can be used for marker-assisted selection for wheat breeding, and to further map this gene toward map-based cloning. Forty-five simple sequence repeat (SSR) and sequence-tagged site (STS) markers specific to chromosome 1D were evaluated for linkage to *H22* using a segregating population consisting of 192 $F_{2:3}$ families, which were derived from the cross Tugela-*Dn1* × KS85WGRC01(*H22*). The STS *Xhor2kv* and SSR *Xgdm33* are two flanking markers that are tightly linked to *H22* at genetic distances of 0.3 and 1.0 cM, respectively. Five other SSR markers including *Xgpw7082*, *Xwmc147*, *Xcfd15*, *Xwmc432* and *Xwmc336* were also linked to *H22* at the distance from 0.8 to 20.8 cM. Analysis of Chinese Spring (CS) deletion lines revealed that all the *H22*-linked markers are located distal to the breakpoint of del 1DS-5, indicating that the *H22* gene is located at the distal 30% region on the short arm of wheat chromosome 1D. Genomic comparison suggested that the *H22* gene is located in the same or similar chromosomal region as the leaf rust resistance genes *Lr21* and *Lr40* on 1DS, and orthologous to the *H9* gene cluster of 1AS.

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Introduction

The Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), is one of the major pests of wheat (*Triticum aestivum L.*) worldwide (Ratcliffe and Hatchett 1997). Historically, resistance genes in wheat have been the most effective and cost efficient means to control the damage caused by this insect pest. So far, 32 Hessian fly-resistance genes have been reported (Ratcliffe and Hatchett 1997; Dweikat et al. 2002; McIntosh et al. 2003; Martín-Sánchez 2003; Williams et al. 2003; Liu et al. 2005b; Sardesai et al. 2005). Many of these genes, including *H13, H22, H23, H24*, *H26, H32* and an unnamed *H* gene (*Hwgrc4)*, originated from *Aegilops tauschii* Coss., an important source for pest resistance (Gill and Raupp 1987; Ratcliffe and Hatchett 1997). Previously, *H13* and *H23* were mapped to wheat chromosome 6D, while *H22*, *H24* and *H26* were mapped to 1D, 3D and 4D, respectively, using monosomic analysis (Gill et al. 1987; Raupp et al. 1993; Cox and Hatchett 1994). Recently, *H13*, *H23* and the gene in *Hwgrc4* were mapped to the distal region of chromosome 6DS as a cluster of resistance genes (Liu et al. 2005a), *H32* and *H26* to the region of chromosome 3DL (Sardesai et al. 2005; Wang et al. 2006) using simple sequence repeat (SSR) markers.

The rapid development of molecular genetics and genomics has recently resulted in many molecular markers, which are being used to facilitate identification of new resistance genes (Yencho et al. 2000; Sourdille et al. 2004; Liu et al. 2005a). In addition, these markers are also used for marker-assisted selection (MAS) for plant breeding (Melchinger 1990; Gupta and Varshney 2000), and for map-based cloning (Huang et al. 2003). A variety of molecular markers have also been developed and used to map Hessian fly-resistance genes in wheat (Dweikat et al. 1997; Ma et al. 1993; Williams et al. 2003; Liu et al. 2005a, c).

H22 confers antibiosis to various biotypes including biotype GP and biotype L, which are widely prevalent in the USA (Gill et al. 1986). Utilization of *H22* in breeding programs is limited due to the lack of molecular markers that can be used for MAS. The objectives of the present study were to identify markers that are tightly linked to *H22* for MAS in breeding and for map-based cloning.

Materials and methods

Hessian fly

Biotype GP of Hessian fly originated from a laboratory colony collected in Ellis County, Kansas (Gagne and Hatchett 1989). The insects were maintained on wheat seedlings of the Hessian fly-susceptible cultivars (Karl 92 or Newton). Biotype L was supplied by S.E. Cambron, USDA-ARS, West Lafayette, Indiana, USA. The insects were maintained on seedlings of cultivars Ike (*H3*), Magnum (*H5*), Caldwell (*H6*), and Seneca (*H7H8*) sequentially. The pupae of both biotypes used in this study together with infested wheat plants were stored at 4°C until Hessian fly adults were needed.

Plant materials and DNA isolation

KS85WGRC01 is an *H22*-containing wheat germplasm with pedigrees of TA1644 (*T. tauschii* var.*strangulata*)/Newton//Wichita (Raupp et al. 1993). To map the *H22* gene in KS85WGRC01, a mapping population consisting of 192 $F_{2:3}$ families was developed from the cross Tugela-*Dn1* × KS85WGRC01. Tugela-*Dn1* is a Hessian fly-susceptible wheat germplasm containing *Dn1*, a gene conferring resistance to Russian wheat aphid, *Diuraphis noxia* (Mordvilko).

Wheat genetic stocks used for marker localization, including Chinese Spring (CS), CS ditelosomic line (Dt1DS, Dt1DL) (Sears 1954), and deletion lines (del1DS-1, del1DS-2, del1DS-3, del1DS-4, and del1DS-5) (Endo and Gill 1996), were kindly provided by the Wheat Genetics Research Center (WGRC) at Manhattan, KS, USA.

Wheat genomic DNA was extracted from leaf tissue of each F_2 plant according to the modified CTAB procedure as described by Gill et al. (1991). DNA concentration was quantified spectrophotometrically.

Evaluation of Hessian fly resistance

Parents Tugela-*Dn1* and KS85WGRC01 were evaluated with biotype GP and L, the F_1 plants were evaluated with biotype GP and the 192 $F_{2:3}$ families (about 20 individuals in each family) were evaluated with biotype L in growth chambers at 18 ± 1°C with a 14:10 h (light:dark) photoperiod as described previously with minor modifications (Maas et al. 1987; Liu et al. 2005a, b). Briefly, seedlings at the 1.5-leaf stage were infested by confining ~200 newly mated Hessian fly females in each flat with a cheesecloth tent. Three weeks after infestation, the seedlings were examined to identify susceptible and resistant phenotypes. Susceptible plants were stunted with dark green leaves and live larvae. Resistant plants grew normally (unstunted) with light green leaves and dead larvae. Chi-square (χ^2) test was conducted to determine the goodness of fit of plant segregation ratios to theoretical Mendelian segregation ratios.

Simple sequence repeat (SSR) and sequence-tagged site (STS) analysis

Because *H22* was previously assigned to wheat chromosome 1D, a total of 45 SSR and STS markers specific for wheat chromosome 1D were screened among selected progeny that consisted of four homozygous resistant, three susceptible and three heterozygous F_2 plants, and the parents Tugela-*Dn1* and KS85WGRC01 for polymorphisms. Polymorphic markers indicative of putative linkage with *H22* were further used to determine the genetic linkage between the gene and the markers using the $F_{2:3}$ mapping population.

The sequences of SSR and STS primers were obtained from the GrainGenes Database at http://www.wheat.pw.usda.gov/ggpages/ggtabledefs.html. Specific information on primers and PCR protocols with the prefixes listed herein can be found in the respective references: WMS (or GWM) (Röder et al. 1998), PSP (Devos et al. 1995; Stephenson et al. 1998), GDM (Pestsova et al. 2000), Hor2KV (Talbert et al. 1994), BARC (Ward et al.: http://www.scabusa.org/pdfs/BARC_SSRs_011101.html), WMC (Gupta et al. 2002), GPW (Nicot et al. 2004), and CFD (Guyomarc'h et al. 2002; Sourdille et al. 2004).

The PCR amplification was performed in a volume of 25 µl as described by Liu et al. (2005a, b). PCR-amplified fragments were separated on 2–3% agarose gels (Sigma, St Louis, MO, USA) under electrophoresis at 5 V/cm in 1× TAE buffer. DNA banding patterns were visualized under UV light with ethidium bromide staining.

Genetic and physical mapping

A genetic linkage map was constructed by converting recombination frequencies to genetic map distance (centiMorgans, cM) using the Kosambi mapping function (Kosambi 1944) and MapMaker software (version 3.0) at LOD > 3.0 (Lander et al. 1987).

To determine the physical location of the *H22*-linked markers, DNA samples of CS, Dt1DS, Dt1DL, del1DS-1 [fraction length (FL) 0.59], del1DS-2 (FL0.57), del1DS-3 (FL0.48), del1DS-4 (FL0.66) and del1DS-5 (FL0.70) were amplified using the respective SSR and STS primer sets. The presence or absence of a specific fragment amplified from a deletion stock indicates that the corresponding marker is located proximal or distal to the breakpoint of the tested deletion stock. In this manner, the markers and linked genes were physically localized into chromosome interval regions (bins) within the chromosome arm.

Results

Inheritance and phenotypic expression of *H22*

The parents KS85WGRC01 (resistant) and Tugela-*Dn1* (susceptible) exhibited consistent resistance or susceptibility to both biotypes GP and L. All F_1 plants derived from the cross Tugela-*Dn1* × KS85WGRC01 exhibited complete resistance when tested with biotype GP. The phenotype of the F_2 plants was inferred from the $F_{2:3}$ using biotype L. The 192 $F_{2:3}$ families segregated into 50 homozygous resistant, 94 heterozygous, and 48 homozygous susceptible. The segregating data fit a major gene segregation ratio 1:2:1 ($\chi^2 = 0.125$, $df = 2$, $P = 0.940 > 0.05$), suggesting that the resistance gene in KS85WGRC01 is controlled by a single dominant gene which was consistent with the previous report (Raupp et al. 1993).

Molecular markers linked to *H22*

Of the 45 of 1D-specific SSR and STS primer pairs tested, STS primer pair Hor2KV1.2 and SSR primer pairs GPW7082, GDM33, CFD15, WMC147, WMC432, WMC336 and CFD61 from the short arm amplified DNA fragments (with the expected sizes similar to those from CS wheat) polymorphic between KS85WGRC01 and Tugela-*Dn1* as well as between the resistant and susceptible progenies (Table 1; Fig. 1). Evaluation of the entire $F_{2:3}$ mapping population indicated that six SSR and one STS markers from the short arm of chromosome 1D are linked to *H22*.

Six (1 STS and 5 SSR) of these markers are co-dominant and linked to *H22* at various distances. SSR markers *Xgdm33* and *Xwmc147* are distal to *H22* at 1.0 and 2.3 cM, respectively (Fig. 2). The GDM33 primer pair amplified a 175-bp DNA fragment that specifically associated with resistant plants and a 160-bp DNA fragment that cosegregated with susceptibility. Both the 175- and 160-bp fragments are present in the heterozygous progeny (Fig. 1). The primer pair WMC147 amplified a 165-bp DNA fragment from the resistant

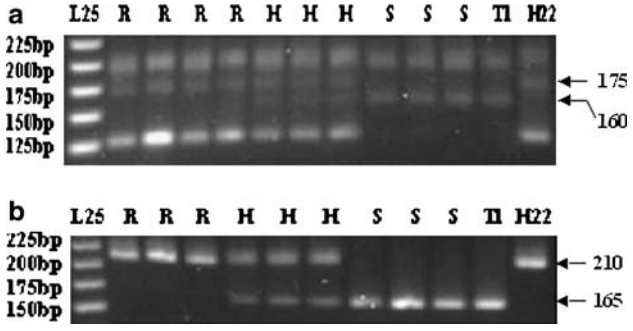

Fig. 1 DNA fragments amplified with primer pairs GDM33 (**a**) and CFD15 (**b**). The DNA samples were prepared from Tugela-*Dn1* (*T1*), KS85WGRC01 (*H22*) and F_2 plants from the cross Tugela-*Dn1* × KS85WGRC01. *R* resistant progeny, *S* susceptible progeny, and *H* heterozygous progeny. *L25* represents 25 bp DNA ladder. The *arrows* point to the polymorphic DNA fragments between the resistant and susceptible progeny

Table 1 Polymorphic DNA fragments (sizes in base pairs) amplified from the parents Tugela-*Dn1* and KS85WGRC01

Primers	Tugela -*Dn1*	KS85WGRC01
Hor2KV1.2	400	Null
	Null	410
	Null	530
GPW7082	Null	210
	Null	225
GDM33	160	Null
	Null	175
CFD15	165	Null
	Null	210
CFD61	Null	180
WMC147	160	Null
	Null	165
WMC432	185	Null
	205	Null
	Null	230
WMC336	Null	100
	115	Null

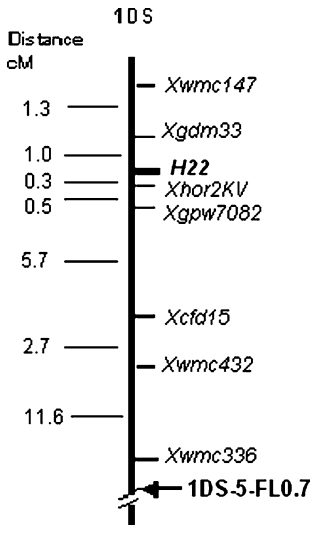

Fig. 2 Linkage map of *H22* on wheat chromosome 1DS. The breakpoint in the shortest CS deletion line 1DS-5 is indicated with an *arrow*

parent KS85WGRC01 as well as resistant progeny, and a 160-bp DNA fragment from the susceptible parent Tugela-*Dn1* as well as susceptible progeny (Table 1). Both the 165 and 160-bp fragments are present in the heterozygous progeny. STS marker *Xhor2kv1.2* and SSR markers *Xgpw*7082, *Xcfd*15 and *Xwmc*432 are proximal to *H22* at 0.3, 0.8, 6.5 and 9.2 cM, respectively (Fig. 2). In addition to these co-dominant markers, SSR *Xwmc336* is a dominant marker that linked to *H22* at a distance of 20.8 cM (Table 1; Fig. 2).

Physical mapping of the *H22*-linked markers

DNA samples of CS Dt1DS, Dt1DL, and its derived deletion lines including del1DS-1, del1DS-2, del1DS-3, del1DS-4 and del1DS-5 were amplified using STS primer pair Hor2KV1.2 and SSR primer pairs GDM33, WMC147, GPW7082, CFD15, WMC432 and WMC336. Each primer pair amplified DNA fragments of the expected size(s) from CS and CS ditelosomic line Dt1DS, but no corresponding fragments were amplified from Dt1DL and deletion lines del1DS-1, del1DS-2, del1DS-3, del1DS-4 and del1DS-5. This observation indicated that all of these *H22*-linked markers are located distal to the breakpoint of 1DS-5(FL0.7), and the *H22* gene is located in the distal 30% region on the short arm of wheat chromosome 1D (Fig. 2).

Discussion

Using a segregating population consisting of 192 $F_{2:3}$ families, which were derived from the cross Tugela-*Dn1* × KS85WGRC01, we mapped the *H22* gene to the distal region of wheat chromosome 1DS. Interestingly, another cluster of Hessian fly-resistance genes containing *H9*, *H10*, *H11* and *Hdic* was also mapped to a similar region of chromosome 1AS (Liu et al. 2005a, b, c). This observation could indicate that the resistance genes on these two chromosomes might have common origin. This postulation is consistent with the fact that they also have similar resistance mechanisms with antibiosis against Hessian fly larvae. Paillard et al. (2003) established an integrative wheat genetic linkage map and showed that SSR marker *Xgdm33* has a locus at the distal end of wheat chromosome 1AS. More recent studies showed that *Xgdm33* is distally linked to *H9* and *Hdic* at the distance of 2.2 cM on 1AS (Liu et al. 2005b; Kong et al. 2005). The result of this study indicated that *Xgdm33* is also distal to *H22* at 1 cM on 1DS. The presence of the same SSR marker on the two gene clusters located on different chromsomes suggested that the *H22* locus on 1DS is most likely orthologous (or homoeologous) to the *H9* gene cluster on 1AS.

It has been known that the wheat genome can be divided into gene-rich and gene-poor regions with recombination restricted mainly to gene-rich regions (Werner et al. 1992; Feuillet and Keller 1999). Gill et al. (1996) demonstrated that the genes are present in cluster, four to six per chromosome, usually located toward the telomeric ends, and all 14 agronomically important genes in group 1 chromosome are distributed in gene-rich regions at the distal end of these chromosomes. Huang and Gill (2001) mapped two leaf rust resistance genes, *Lr21* and *Lr40* derived from *Ae.Tauschii* accessions, to the distal, high recombination "hot spot" region of wheat chromosome 1DS using RFLP marker KSUD14 (locus *Xksud14*). The data of genetic linkage and physical mapping of *H22*-linked markers in the present study indicate that *H22* is located in the same or nearby gene-rich region where the *Lr21* and *Lr40* leaf rust-resistance genes are located. More recently, Huang et al. (2003) reported that *Lr21* encodes a protein (with 1,080 amino acids) containing a conserved nucleotide-binding site (NBS) domain, 13 imperfect leucine-rich repeats (LRRs), and a unique N-terminal domain with an 151-amino-acid sequence that is not present in other known NBS–LRR proteins. Considering the fact that Hessian fly–wheat interaction operates in a typical gene-for-gene model like the interactions between pathogens and host plants, the colocalization of *H22* and the leaf rust-resistance gene *Lr21* may suggest that the *H22* might be a gene with a structure similar to these disease resistance genes. This postulation is currently being tested by molecular and genetic analysis in our laboratory.

Current breeding is advancing rapidly from phenotypic selection towards MAS (Melchinger 1990; Yencho et al. 2000). MAS is particularly important in breeding for durable resistance to the Hessian fly because of the dynamic changing of Hessian fly population in the fields. The resistance conferred by single genes to the Hessian fly is short-lived, with effective period of only 6–8 years. As a result, more durable resistance can only be achieved via pyramiding of multiple genes into single cultivars. It is difficult to pyramid multiple genes through traditional phenotypic selection because of the lack of biotype populations specific to individual resistance genes in a laboratory. The source for Hessian fly resistance is relatively abundant, with 32 different resistance genes identified and many potential new genes in the pipeline. The limiting factor for pyramiding is the lack of markers specific for individual resistance genes. Together with the molecular markers linked to other Hessian fly resistance genes (Ma et al. 1993; Dweikat et al. 2002; Williams et al. 2003; Liu et al. 2005a, b, c; Sardesai et al. 2005), the *H22* linked markers identified in this study should be useful for gene pyramiding through MAS. The two flanking markers, *Xhor2kv* and *Xgdm33*, are linked to *H22* at 0.3 and 1.0 cM, respectively (Fig. 2). The recombination frequency (RF) between *Xhor2kv* and *H22* is 0.5% (with a Kosambi map distance of 0.5 cM, Kosambi 1944). The RF between *Xgdm33* and *H22* is 1.0%. The two RFs for *Xhor2kv* and *Xgdm33* translate into selection accuracies of 99.5 and 99.0%, respectively, if they are used separately. According to the product rule of the probability, the selection accuracy will increase to nearly 100% (i.e., 1–0.5 × 1%) when these two flanking markers are used together.

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