Molecular mapping of a non-host resistance gene *YrpstY1* in barley (*Hordeum vulgare* L.) for resistance to wheat stripe rust

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Cultivated barley (*Hordeum vulgare* L.) is considered as a non-host or inappropriate host species for wheat stripe rust caused by *Puccinia striiformis* f. sp. *tritici*. Most barley cultivars show a broad-spectrum resistance to wheat stripe rust. To determine the genes for resistance to wheat stripe rust in barley, a cross was made between a resistant barley line Y12 and a susceptible line Y16. The two parents, F_1 and 147 BC_1 plants were tested at seedling stage with Chinese prevalent race CYR32 of *Puccinia striiformis* f. sp. *tritici* by artificial inoculation in greenhouse. The results indicated that Y12 possessed one dominant resistance gene to wheat stripe rust, designated *YrpstY1* provisionally. A total of 388 simple sequence repeat (SSR) markers were used to map the resistance gene in Y12 using bulked segregant analysis. A linkage map, including nine SSR loci on chromosome 7H and *YrpstY1*, was constructed using the BC_1 population, indicating that the resistance gene *YrpstY1* is located on chromosome 7H. It is potential to transfer the resistance gene into common wheat for stripe rust resistance.

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Wheat stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (PST), is one of the most devastating diseases of wheat (*Triticum aestivum* L.) in many cooler and wetter regions of the world (Line 2002; Wellings et al. 2003; Chen 2005; Wan et al. 2007). In China, stripe rust has caused widespread damages in wheat since the first major epidemics in 1950, particularly in the northwestern and southwestern regions (Li and Zeng 2000; Wan et al. 2007). It can cause 10% of yield loss, and up to 20 to 30% in severe epidemics. Therefore, much attention has been paid to the control of wheat stripe rust by breeders, pathologists and farmers.

Use of resistant wheat cultivars is the most effective, economical and environmentally friendly way to control stripe rust. To date, more than 40 genes for stripe rust resistance have been catalogued and mapped to different chromosomes in wheat (McIntosh et al. 2009). Most of the genes are race-specific and easy to be overcome by new PST races in the pathogen population. In China, with the dramatical increase of the PST race CYR32 in a wide virulence spectrum, most of commercial wheat cultivars have become susceptible (Wan et al. 2007). Only a few genes such as *Yr5*, *Yr10*, *Yr15*, *Yr24* or *Yr 26*, and *YrZH84* are still effective and can be used to combat stripe rust in breeding programs (Ma et al. 2001; Li et al. 2006; Wan et al. 2007). On the other hand, some adult-plant resistance (APR) genes with race non-specific and durable resistance were identified, mapped and isolated (Fu et al. 2009; Lin and Chen 2009; Lu et al. 2009). Pyramiding APR genes is an effective way to control stripe rust. However, the cultivars with APR genes are susceptible at seedling stage, and not preferred by breeders and farmers in the Longnan of Gansu province, a hotspot area for stripe rust in China. The stripe rust oversummers in Longnan and then a large amount of PST spores spread to the main wheat growing areas in Yellow and Huai valleys, resulting in the epidemics of stripe rust in the whole country. In order to reduce the PST spores in the winter, major genes that confer resistance at both seedlings and adult plant stage are employed in Gansu province. Hence, it is crucial to explore and identify new resistance genes, particularly, major genes with durable resistance.

Non-host resistance is the most common form of disease resistance exhibited by plant against the majority of pathogens of other species. The durable and broad-spectrum defense of non-host resistance suggests that non-host resistance in plant has great potential of agricultural applications (Niks 1988; Mysore and Ryu 2004). Studies on the genetics and molecular basis of non-host resistance

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could give new insights on the durable resistance. In the well-studied *Arabidopsis-Bgh* non-host interaction, a complex genetic basis with three genes *PEN1*, *PEN2* and *PEN3*, involved in biosynthetic and secretion processes, have been shown to control prehaustorial resistance (Ellis 2006). Meanwhile, major gene based on gene-for-gene interaction was also proven to condition non-host resistance. In the genetic study of resistance in bean against tomato leaf spot, a single dominant gene, induced by avirulence gene *avrRxv* of leaf spot pathogen, was identified (Whalen et al. 1988). For plant breeding, the major gene is more interesting because it is easily transferred into targeting parents. Actually, non-host resistance was already proven very effective for crop improvement in resistance breeding. For example, a non-host wheat stripe rust resistance gene *Yr9* from rye played a very important role in controlling wheat stripe rust worldwide for a long time (Niks 1988; Wan et al. 2004), although the gene is now not effective any more for stripe rust resistance in China due to the increase of CYR32. Therefore, it is important to explore new stripe rust resistance genes for wheat breeding programs in other species, especially in related species such as barley and rye.

Barley (*Hordeum vulgare* L.) is a related species of wheat. The pathogens (*Puccinia striiformis*) of stripe rust in barley and wheat were subdivided into different formae speciales based on their host ranges (Eriksson 1894). Evaluation of barley germplasm by *P. striiformis* f. sp. *tritici* showed that most barley cultivars are resistant to wheat stripe rust, indicating barley contains resistance genes to combat PST (Chen et al. 1995). Two non-host genes in barley conferring resistance to wheat stripe rust were identified by Pahalawatta and Chen (2005a), indicating that it is a feasible strategy to identify resistance genes in barley for wheat stripe rust.

Previously, we investigated 104 Chinese barley cultivars and lines with 30 PST races at seedling stage, and found 101 lines were highly resistant to all races tested, whereas three were susceptible to them. The objective of this study was to map a resistance gene to wheat stripe rust in a barley line Y12 that is highly resistant to all the PST races surveyed.

MATERIAL AND METHODS

Plant material

When inoculated with 30 PST races at seedling stage, the Chinese barley line Y12 showed immune reaction to 18 races with infection type IT 0 and highly resistant to 12 races with IT 0, whereas Y16 was susceptible to all the races tested, with IT 3 to 3^+. A cross was made using Y12 as female and Y16 as male, and the BC_1 population was generated from $F_1 \times$ Y16. The F_1 and 147 BC_1 plants were used for mapping the resistance gene to wheat stripe rust. A highly susceptible wheat cultivar Mingxian169 was used as a control for evaluating the inoculation of wheat stripe rust.

Seedling test with PST race CYR32

The seedling test for stripe rust resistance was conducted with artificial inoculation in greenhouse. The PST race CYR32 was used to test F_1 and BC_1 plants from the Y12/Y16 cross and their parents. Fifteen seeds of each parent, eight F_1 and 147 BC_1 plants were grown in small pots with about 15 plants each, and three plants of susceptible cultivar Mingxian 169 were used as control in each pot. Seedlings were inoculated with the PST race CYR32 when the first leaf was fully expanded. After inoculation, the seedlings were placed in a dew chamber at 9–11°C and 100% of relative humidity for 24 h and then transferred to a greenhouse maintained with 16 h light/8 h dark photoperiod at 13–17°C. Infection types were scored 14–15 days after inoculation when rust was fully developed on the susceptible check Mingxian 169.

Infection types were scored based on a 0–4 scale in wheat stripe rust (Li et al. 2006). Rating of the seedling reactions was simplified into two classes (resistant and susceptible) as there was a clear distinction between these two categories. Based on the reactions of BC_1 plants to the race CYR32, plants with IT 0 to 2 were considered to be resistant and those with IT of 3^- to 4 be susceptible.

DNA extraction and bulk construction

Genomic DNA was extracted from green leaves as described by Sharp et al. (1988). Resistant and susceptible bulks for bulked segregant analysis were made by pooling equal amounts of DNA from 10 resistant and 10 susceptible plants, respectively, of the segregating BC_1 population (Michelmore et al. 1991).

SSR analysis

The 388 pairs of SSR primers of barley used in this study were obtained from the GrainGenes database (<www.graingenes.org/GG2/index.shtml>), MPBCRC of Australia (Hearnden et al. 2007) and IPK of Germany (Thiel et al. 2003). At first, 332 SSRs covering all the genome were used to screen two parents, as well as the resistant and susceptible bulks. After two SSR markers on chromosome 7H were found to be linked to the resistance gene, we then just chose the markers on 7H to screen the parental lines and the resistant and susceptible bulks. Subsequently, the nine polymorphic markers on 7H were used to genotype the BC_1 population and construct the linkage map.

The PCR reactions were performed in an MJ Research PTC-200 Peltier Thermal Cycler in a volume of 15 µl containing 1.0 U *Taq* DNA polymerase (Tiangen, Beijing, China), 1.5 µl of 10 × PCR buffer (200 mM KCl, 200 mM Tris–HCl, pH 8.4, 100 mM $(NH_4)_2SO_4$, 15 mM $MgCl_2$), 400 µM of each of dNTPs, 6 pmol of each primer, and 30 ng of template DNA. The PCR conditions were an initial denaturation at 95°C for 5 min, followed by 35 cycles of 94°C for 1 min, 50–60°C (depending on annealing temperature of the primer pair) for 1 min, 72°C for 1 min, and a final extension at 72°C for 10 min. The PCR products were kept at 4°C in the DNA cycler until removal and stored at 4°C for use.

The 4.5 µl of PCR product of each sample was mixed with 4 µl of formamide loading buffer (98% formamide, 10 mM EDTA, 0.25% bromophenol blue, 0.25% xylene cynol, pH 8.0) and heated at 94°C for 5 min, and loaded on 6% denaturing polyacrylamide gels and run at 80 W for approximately 1 h, and then resolved by the silver staining method as described by Bassam et al. (1991).

Statistical analysis and linkage map construction

χ^2 analysis was used to test the goodness of fit for the observed segregation to expected ratios. The 'χ-test' procedure in the data analysis of Microsoft Office 2003 Excel was used to calculate χ^2 and P-values. A linkage map was constructed using Mapmaker ver. 3.0 (Lander et al. 1987). Two-point analysis with a logarithm of odds (LOD) threshold of 3.0 was used to determine the linkage among markers whereas multipoint analysis was used to determine the best locus order in linkage groups. Recombination values were converted to map distance using the Kosambi mapping function (Kosambi 1944). The linkage map was drawn with the software Mapdraw V2.1 (Liu and Meng 2003). Map positions found in the present study were compared with those reported by Hearnden et al. (2007) and Varshney et al. (2007).

RESULTS

Inheritance of wheat stripe rust resistance in Y12

In seedling tests with CYR32, Y12 was highly resistant (IT 0;) with hypersensitive response and Y16 was susceptible (IT 3^+). Eight F_1 plants of the cross Y12/Y16 were highly resistant (IT 0;), indicating that the stripe rust resistance in Y12 was conferred by dominant genes. In the BC_1 population, 147 plants segregated into 77 resistant (IT 0 to 2) and 70 susceptible (IT 3 to 3^+), fitting to a 1:1 ratio ($\chi^2_{1:1} = 0.43$, df = 1, P = 0.51). These suggested that the stripe rust resistance in Y12 was conditioned by a single dominant gene, designated *YrpstY1* tentatively.

Linkage analysis and genetic map of YrpstY1

Of the 388 SSR markers, 102 were polymorphic between Y12 and Y16. Nine SSR markers (viz. *HvACL0003*, *Bmag0507*, *EBmac0764*, *AWBMS0022*, *EBmac0755*, *HvGLB0002*, *GBM1065*, *EBmac0655* and *Bmag0733B*)

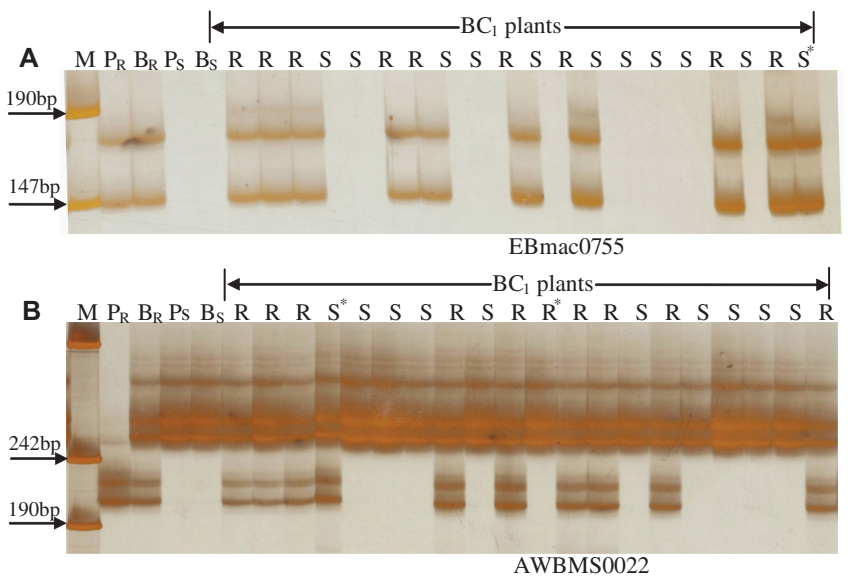

Fig. 1 A–B. Electrophoresis of PCR products amplified with SSR markers EBmac0755 (**A**) and AWBMS0022 **(B)** linked with the resistance gene *YrpstY1*. M = PUC18 DNA/*Msp*I ladder, P_R = resistant parent Y12, B_R = resistant bulk, Ps = susceptible parent Y16, B_S = susceptible bulk. For BC_1 plants, R = resistant, S = susceptible. Arrows on the left side indicate the fragment sizes of ladders. *indicates the plants with recombination event between the resistance gene *YrpstY1* and SSR loci.

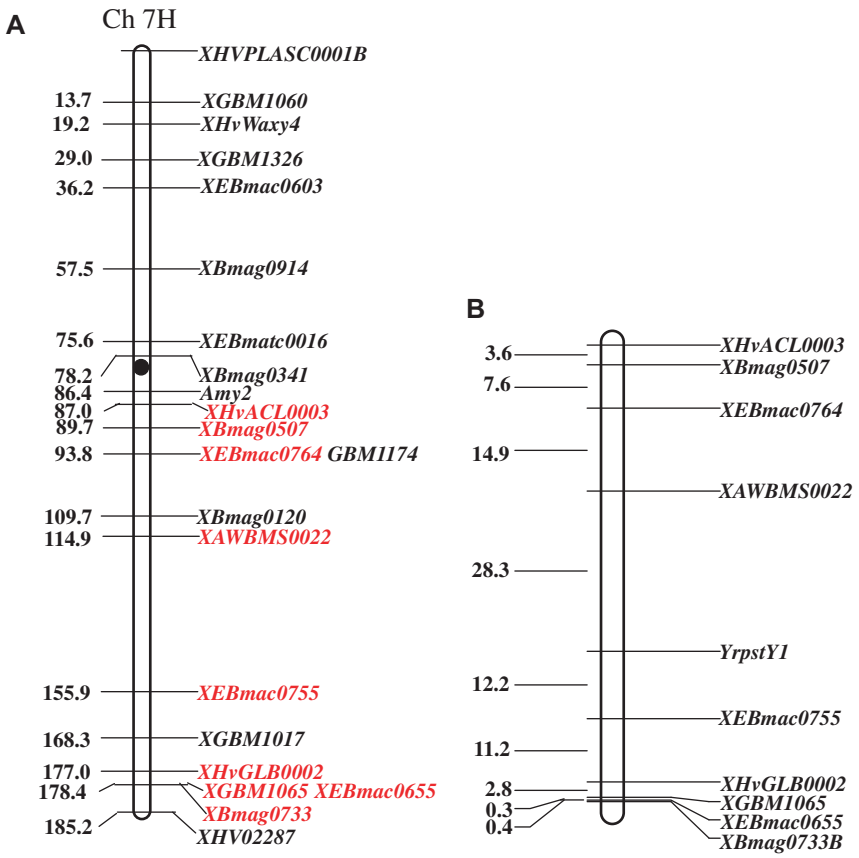

Fig. 2 A–B. (**A**) Linkage map of barley chromosome 7H based on Hearnden et al. (2007) and Varshney et al. (2007). The red color indicated the SSR loci linked with *YrpstY1*. (**B**) Linkage map involved in the resistance gene *YrpstY1* and nine SSR loci on chromosome 7H in the present study. SSR loci names are indicated on right side of the map. Kosambi map distances (cM) are shown on the left side. Centromere position was based on barley BinMap 2005 (<http://barleygenomics.wsu.edu/>).

on chromosome 7H showed clear polymorphisms between the resistant and susceptible DNA bulks as well as their parents. The entire BC_1 population was then genotyped with the nine polymorphic markers (Fig. 1). Of the nine SSR loci, only *XEBmac0755* exhibited dominant allele in Y12, and the other loci were co-dominant in the BC_1 population. All the nine SSR markers showed 1:1 segregation ratio in the BC_1 population.

Using the multipoint analysis of Mapmaker 3.0, a highly reliable linkage group, comprising nine SSR loci and *YrpstY1*, was established in a threshold of LOD score 3.0 and a maximum recombination frequency of 0.5. The linkage group spanned a total of 81.3 cM (Fig. 2). The genetic distances between the resistance gene *YrpstY1* and the flanking SSR loci *XEBmac0755* and *XAWBMS0022* were 12.2 cM and 28.3 cM, respectively. Compared with the map published by Hearnden et al. (2007) and Varshney et al. (2007), all the nine SSR loci linked to *YrpstY1* are located on chromosome 7H. Therefore, the resistance gene *YrpstY1* might be located on chromosome 7H.

DISCUSSION

Wheat stripe rust pathogen *Puccinia striiformis* f. sp. *tritici* and barley stripe rust pathogen *Puccinia striiformis* f. sp. *hordei* belong to different formae speciales based on their distinct host range (Rodrigues et al. 2004; Pahalawatta and Chen 2005a, 2005b). Chen et al. (1995), using random amplified polymorphic DNA, demonstrated that the two formae speciales fell into evidently different groups. Based on this result, barley is a non-host of *Puccinia striiformis* f. sp. *tritici*. Barley and wheat are related species of *Poaceae*. Most of barley cultivars are resistant to wheat stripe rust (Chen et al. 1995; Li and Zeng 2000). Occasionally, some barley cultivars, such as US cultivar Russell and Chinese cultivar Xiyin 2, are susceptible to PST races (Li and Zeng 2000; Pahalawatta and Chen 2005a). Some landrace and naked barley accessions have been reported to have higher chance of susceptibility to heterologous rust fungi than modern cultivars (Atienza et al. 2004). In our study, 104 Chinese barley cultivars and lines were inoculated with 30 PST races at seedling stage in greenhouse. Only three lines were

Table 1. *R-genes on chromosome 7HL around YrpstY1 in barley.*

Gene/ QTL	Combating disease	Closest marker	Reference
Rrs15	Scald	HVM49	Genger et al. 2005
Rph3	Leaf rust	Albino lemma (eburatum)	Jin et al. 1993
Rph19	Leaf rust	HVM11	Park and Karakousis 2002
QBLR-P	Leaf rust	Ris44	Rossi et al. 2006
Mlf	Powdery mildew	MWG539	Schönfeld et al. 1996
QPM-P	Powdery mildew	Bmac156	Rossi et al. 2006

susceptible, and two of them are hull-less naked barley (data not shown), which is consistent with Atienza et al. (2004). Barley was considered to be a near-nonhost of *Puccinia striiformis* f. sp. *tritici* (Jafary et al. 2008). Barley-PST represents an intermediate case in between host and full non-host status. It is very convenient to study the inheritance of resistance genes to heterologous pathogen using the cross of resistant and susceptible parents, which does not need interspecific crosses or mutant creation.

Non-host resistance as a prevalent resistance phenomenon is durable and broad-spectrum. Upon genetics of the non-host resistance, many studies suggest that non-host resistance is multi-component, genetically complicated, and race nonspecific. Using three barley populations for the identification of resistance genes to heterologous rust fungi, Jafary et al. (2008) confirmed the resistance is controlled by sets of QTLs, most of which were different and a few were overlapping among the populations. The complication of these resistance genes suggested a high diversity of genes conferring non-host resistance to heterologous pathogens and the loci were significantly associated with QTL for partial resistance to the pathogen *Puccinia hordei*. Both non-host resistance gene *PEN3* cloned from *Arabidopsis* and host resistance genes *Yr18/Lr34/Pm38* for adult-plant resistance to stripe rust, leaf rust and powdery mildew of wheat, shared the same structure of ABC transporter (Stein et al. 2006; Krattinger et al. 2009). Therefore, race non-specific resistance QTLs are involved in host and non-host resistance. On the other hand, major resistance genes were also involved in non-host resistance. Rodrigues et al. (2004) identified two major resistance genes in wheat conferring non-host resistance to barley stripe rust, which accounted for 76.7% of phenotypic variance for resistance. In addition, a non-host resistance gene *Rac4* cloned from *Arabidopsis* resistant to *Brassica oleracea* pathogen *albugo candida* showed a similar structure to the R-genes with NBS-LRR nature (Holub 2002). These studies provided evidence that non-host resistance may be similar to that of host resistance, which was also confirmed by the present study that a major gene in barley conferred the resistance to wheat stripe rust with hypersensitive response.

In barley, a similar study was carried out by Pahalawatta and Chen (2005a). Two non-host resistance genes *RpstS1* and *rpstS2*, conferring resistance to wheat stripe rust, were identified from barley cultivar Steptoe. The dominant gene *RpstS1* was mapped by molecular markers on chromosome 4H. In the present study, we identified a single dominant gene in the barley line Y12 conferring resistance to wheat stripe rust and it was mapped on chromosome 7H. Therefore, we can conclude that the resistance gene *YrpstY1,* interacted with PST pathogen with hypersensitive response, is a new resistance gene different from *RpstS1*. Based on the barley linkage map of Hearnden et al. (2007), the resistance gene *YrpstY1* is on the position of about 142 cM on chromosome 7HL. To date, four R-genes have been mapped on chromosome 7HL around *YrpstY1*, including two leaf rust resistance genes *Rph3* and *Rph19*, a powdery mildew resistance gene *Mlf* and a scald resistance gene *Rrs15*, (Table 1). In addition, two QTLs including one leaf rust resistance locus and a powdery mildew resistance locus were detected (Table 1). No stripe rust resistance gene has been identified at this position yet. Further studies are needed to determine whether these R-genes have any relationship with *YrpstY1* and the genetic distance between them.

According to the linkage map for *YrpstY1*, two flanking markers were relatively far from the resistance gene, with genetic distances of 12.2 cM and 28.3 cM, respectively. This is due to a lack of SSR markers around the location of *YrpstY1*. No SSR markers were available in a large gap of 40 cM on this chromosome region (Hearnden et al. 2007). To get more closely linked markers for cloning or fine mapping of the resistance gene, other molecular markers such as RGAP, AFLP and EST may be alternative choices.

One of the objectives to study resistance in a non-host is to transfer durable and broad-spectrum resistance gene into host plants. The major gene *YrpstY1* might be introgressed into wheat by crossing barley and wheat lines, although the hybrid seeds can be got from only 0.05% of pollinated embryos (Yuan and Chen 2004). Of course, fine mapping and cloning the resistance gene will be a direct approach to transform the gene from barley to wheat. It may provide effective resistance to current *Puccinia striiformis* f. sp. *tritici*, when introduced into wheat from barley.

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