

RESEARCH ARTICLE

Genetic analysis and location of gene for resistance to stripe rust in wheat international differential host Strubes Dickkopf

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Abstract

Strubes Dickkopf is the sixth differential in the world set for wheat stripe (yellow) rust. It is very important to clarify its genetic character of resistance to stripe rust and to develop the molecular markers linked to resistance genes. The NIL Taichung 29*6/Strubes Dickkopf, which was obtained by Strubes Dickkopf as the gene donor and Taichung 29 as the genetic background through backcross breeding, was crossed with the recurrent parent Taichung 29, inbred, and backcrossed to obtain the F₁, F₂ and BC₁ population. The genetic analysis of the cross Taichung 29/(Taichung 29*6/Strubes Dickkopf) was assessed by inoculating the rust race CYR26 at seedling stage. Bulked segregant analysis (BSA) and F₂ segregation analysis were used for detecting polymorphic primers to locate the gene. The resistance of the NIL Taichung 29*6/Strubes Dickkopf to CYR26 was controlled by a single dominant gene, named *YrSD*. The primer pair Xbarc59 on 5B was linked to *YrSD* and the genetic distance between Xbarc59 and *YrSD* was 2.4 cM. The molecular marker Xbarc59 closely linked to the gene *YrSD* could be used in marker-assisted selection for resistance to stripe rust in wheat breeding programmes.

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Introduction

Wheat stripe (yellow) rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is an important disease of wheat and is widely distributed with large-scale epidemics (Chen 2005; Hadi *et al.* 2012). Wheat stripe rust has repeatedly broken out in major wheat production areas in China and caused a wide range of serious yield losses (Wan *et al.* 2004). *Pst* is a highly specific parasitic species and can adapt very effectively to host pressures with rapid evolution of virulence. Moreover, the sexual phase of stripe rust has not yet been discovered, the genetic analysis of pathogenic genes cannot be conducted through sexual hybridization (Kang *et al.* 2010). The only way to identify pathogenic genes is to use the resistance genes of differential hosts. The method of using differential hosts to identify the stripe rust physiological race is useful for studies of pathogen population and resistance breeding. Therefore, the genetic analysis of stripe rust resistance gene in the differential host and locating the rust resistance gene with microsatellite technology are useful for

monitoring changes of wheat stripe rust race, improving the levels of identification race from varieties to genes and extending international exchanges and cooperation.

The identified and named races throughout the world differ in many respects. Moreover, in China wheat stripe rust is a relatively independent prevalent system. Thus, China has its own independent set differential hosts. There are presently four sets of differential hosts in the world, which is used in Europe (including Australia), North America, China and India. Each of them has its own characters, in which *Yr1*, *Yr3*, *Yr4*, *Yr5*, *Yr9*, *Yr10* and *YrSu* are common in the differential host of China and other international regions. This is the reason that the international differential host is not suitable for China, and the host in China is not suitable for Europe (Yang and Stubbs 1990). It must point out the need for studying the genetic resistance of the differential sets. Thus further research about the world sets can clearly determine pathogenic genotype of physiological race, monitor variation of pathogen populations and predict effectiveness of new types of resistance.

To date, many genes have been identified and located by simple sequence repeat (SSR) such as *Yr5* (Sun *et al.* 2002),

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Yr17 (Robert et al. 2000), *YrH52* (Peng et al. 2000), *Yr26* (Ma et al. 2001), *Yr15* (Sun et al. 1997), *Yr28* (Singh et al. 2000), *Yr32* (Eriksen et al. 2004). Currently, the differential set has undergone changes in number and needs deeper research. More genes have been identified in them, *Yr1* in Chinese 166 (Lupton and Macer 1962), *Yr7* and *Yr22* in Lee (Chen et al. 1995a), *Yr2* and *Yr6* in Heines Kolben (Macer 1966; Johnson et al. 1986), *Yr3* and *YrV23* in Vilmorin 23 (Chen et al. 1996), *Yr10* and *YrMor* in Moro (Macer 1975), *Yr25* in Strubes Dickkopf (Calonnec and Johnson 1998), *YrSu* in Suwon92/Omar, and *Yr2*, *Yr9* and *YrCle* in Clement (Chen et al. 1995b). The evidence from race surveys and genetic analyses showed that additional resistance genes were also present in some of the differentials.

The wheat cultivar Strubes Dickkopf is the international differential host for wheat stripe rust. There is one major gene and a minor resistance gene postulated in it (Calonnec et al. 1997). The gene was designated as *Yr25*, which is located on chromosome 1D (Calonnec and Johnson 1998). However, there are still other genes, not yet described in it. The gene *Yr25* is not found in near-isogenic line (NIL) Taichung 29*6/Strubes Dickkopf, indicating an unknown resistance gene to wheat stripe rust in it. In this study, the classical genetic methods combined with SSR markers were used to test the resistance gene in the NIL Taichung 29*6/Strubes Dickkopf, which was obtained by Strubes Dickkopf as the resistance donor and Taichung 29 as recurrent parent for six back-crosses. An assessment of the stripe rust reaction of seedling plants in the F₁, F₂ and BC₁ population for the cross between Taichung 29 and Taichung 29*6/Strubes Dickkopf was conducted to locate the *YrSD* in Strubes Dickkopf gene by molecular markers.

Material and methods

Material

The resistance gene donor Strubes Dickkopf, whose resistance gene may be derived from cv. Blé Rouge d'Ecosse, was introduced from the United Kingdom; and the recurrent parent Taichung 29 lacking stripe rust resistance gene was from China. The NIL Taichung 29*6/Strubes Dickkopf was obtained by Strubes Dickkopf as the resistance donor and Taichung 29 as recurrent parent for six back-crosses. The NIL as male parent was crossed with Taichung 29 to obtain F₁, and F₁ hybrids were self pollinated to produce F₂ and were crossed with Taichung 29 to obtain BC₁ generation. It consisted of 10–15 plants of each parent, 25 plants of backcross, and 296 plants of F₂. The race CYR26 (Chinese yellow rust) of *Puccinia striiformis* f. sp. *tritici* (*Pst*) was used to assess the resistance of populations. The seeds and the tested race CYR26 were offered by the Institute of Plant Protection, Chinese Academy of Agricultural Sciences (Beijing, China).

Identification of the resistance

Identification resistance was tested in the greenhouse at the seedling stage. The varieties Strubes Dickkopf, Taichung 29, the NIL Taichung 29*6/Strubes Dickkopf, F₁, F₂ and BC₁ population were soaked in 1% H₂O₂ for seed germination, with seven seeds in one pot of 10 cm diameter. After the first leaf fully developed, the plants were inoculated with the smearing method (Stubbs 1988) with pre-prepared fresh rust race at 9 ± 1°C in 100% relative humidity for 24 h and then turned to room temperature (day 15~19°C / night 10~14°C, photoperiod 14 h/d, light intensity 6000 Lx) for latent disease. When the susceptible Taichung 29 was fully developed, the infection type was scored. Infection type, divided into 11, i.e., 0, 0₁, 0₂, 1, 1⁺, 2, 2⁺, 3⁻, 3, 3⁺, 4 (Liu 1988). Plus (+) and minus (-) were added for reactions above or below the class. F₂ progeny was resistant to 0–3, 3⁺–4 is susceptible. Chi-square test for goodness of fit was used to separate the proportion of fitness tests to determine whether the data fit a theoretical ratio for resistance genes contained.

Genomic DNA extraction and the resistant and susceptible pool construction

Wheat genomic DNA was extracted from fresh leaves following Rogers and Bendich (1985), Röder et al. (1998), and slightly modified CTAB protocol, with 0.8% agarose gel electrophoresis for detection of its quality and concentration. DNA from the F₂ generation of resistant–susceptible group in randomly selected 10 resistant plants DNA (R-pool) and 10 susceptible plants DNA (S-pool) were mixed, respectively. Its DNA equivalent mixed pools were established resistant and susceptible pools for screening the polymorphic markers with the parents DNA.

PCR amplification

The microsatellite markers were chosen according to published microsatellite primers (Röder et al. 1998; Somers et al. 2004) and synthesized by ShangHai Boya Company (Beijing, China). The total volume of amplification reaction 10 μL, the reaction solution composed of: 10 mmol·L⁻¹ Tris-HCl (pH 9.0), 1.8 mmol·L⁻¹ MgCl₂, 50 mmol·L⁻¹ KCl, 200 μmol·L⁻¹ dNTP, 300 μmol·L⁻¹ primer, 1 U Taq enzyme (TaKaRa Cot.), 50–80 ng genomic DNA. Reaction conditions: 94°C denaturing first 4 min, 94°C denaturation 1 min, 55°C or 60°C annealing ranging from denaturation 1 min, 72°C extension 1 min, 35 cycles, 72°C balance on the last 10 min. PTC-200-DMJ Research (USA) and Eppendorf Master cycler (Germany) gradient were used for PCR amplification.

Electrophoresis analysis and genetic distance calculation

The 10 μL PCR products were mixed with 4 μL loading buffer consisting of 98% w/v formamide, 10 mM

Table 1. Infection type for the cross Taichung29/(Taichung29*6/Strubes Dickkopf) to CYR26 in seedling.

Parents or cross	Generation	Infection type												Expected Ratio (R:S)	χ^2	P
		0	0;	0; ⁺	1	1 ⁺	2 ⁻	2	2 ⁺	3 ⁻	3	3 ⁺	4			
Taichung29	P ₁												18			
Taichung29*6/ Strubes Dickkopf	P ₂	20												1:0		
Taichung29/ (Taichung29*6/ Strubes Dickkopf)	F ₂	39	6	12	28	4	41	28	12	16	42	29	39	3:1	0.6486	0.25~0.50
	BC ₁	9					2	2	1			1	10	1:1	0.36	0.50~0.75

EDTA, 0.005% w/v each of xylene cyanol and bromophenol blue, and were denatured for 5 min at 95°C. After denaturing, the mixture was placed on ice cooling until use. Denaturing polyacrylamide gel electrophoresis and silver staining analysis were adapted from the methods of Bassam *et al.* (1991). The amplified products were separated on 6% denaturing polyacrylamide gel electrophoresis in 1 × TBE buffer (90 mmol/L of Tris-borate, 90 mmol/L of boric acid, 2 mmol/L of EDTA pH 8.0), with 80 W about 30 min for the pre-electrophoresis and 1–2 h for the electrophoresis, and visualized with silver staining. The linkage distance was computed using software Mapmaker 3.0. The Kosambi mapping function was used (Lander *et al.* 1987). The linkage map was drawn using software Mapdraw (Wuhan, China).

Results and analysis

The genetic analysis

The gene donor *Strubes Dickkopf*, the recurrent parent Taichung 29 and its progenies were tested by CYR26 at seedling stage for resistance identification. The statistical analysis is shown in table 1. The results showed that: the NIL Taichung 29*6/*Strubes Dickkopf* was resistance to CYR26, with infection type 0; recurrent parent Taichung 29 was susceptible, with infection type 4; and F₂ progenies showed resistance segregation. According to infection type

and the number IT 0-3 plants was resistant type, and IT 3⁺-4 classified as susceptible type. There were 225 resistant and 68 susceptible in the 296 F₂ plants. The χ^2 test showed goodness of fit for one dominant gene controlling the resistance of 3R: 1S ratio theories (χ^2 (3:1) = 0.5488; P = 0.50–0.75). There were 14 plants resistant and 11 susceptible in the 25 test cross, consistent with the one dominant genes control with 1R: 1S ratio theory (χ^2 (1:1) = 1.041; P = 0.25–0.50). The result of F₂ generation and backcross are consistent.

Genomic DNA polymorphism analysis and genetic linkage

For SSR analysis, a total of 765 primers on all chromosomes were used to analyse polymorphism in the genomic DNA and R-pool and S-pool. The SSR primers on chromosome 5B produced polymorphic DNA bands between the parents and resistant DNA pool and susceptible DNA pool. Eighty eight microsatellite primers on chromosome 5B were selected for further analysis. The four pairs of SSR primers (Wmc640, Barc59, Wmc783 and Wms497) on chromosome 5B showed polymorphism, which were used for F₂ segregation population.

The typical amplification pattern generated by Xbarc59 is shown in figure 1. There was obviously cosegregation between the primer Xbarc59 and the resistant phenotypes of F₂ plants. The results showed that 9 of 10 resistant were

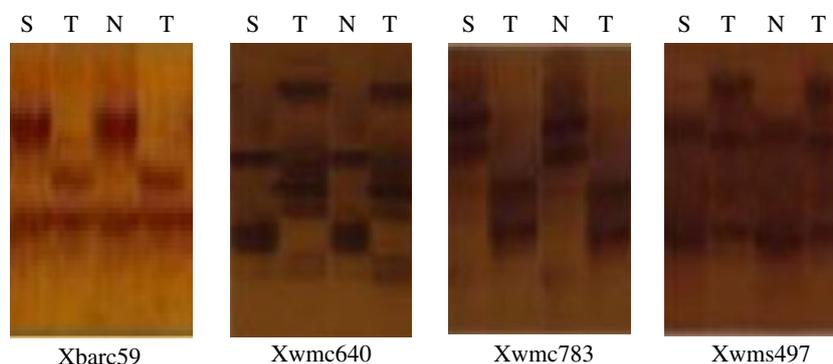


Figure 1. The SSR result of DNA polymorphism from parents and NIL amplified by four pairs of primers. S, *Strubes Dickkopf*; T, Taichung29; N, Taichung29*6/*Strubes Dickkopf*.

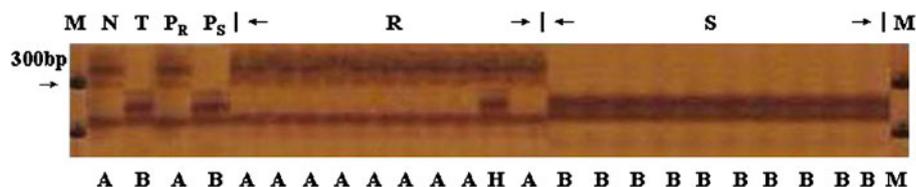


Figure 2. Amplification of part F_2 plants using SSR primer Xbarc59. M, marker; T, Taichung29; N, Taichung29*6/Strubes Dickkopf; R, resistant plant; S, susceptible plant; P_R , resistance pool; P_S , susceptible pool.

amplified with the same resistant parent type, one with resistant and susceptible types, indicating these plants were presumably heterozygous type. In the homozygous 10 susceptible plants in all were amplified with the same type (figure 2). It is suggested that the linkage relationship existed between the amplified differences DNA fragments by primer Xbarc59 and the stripe rust resistance gene *YrSD* gene.

The linkage map of *YrSD*

The NIL Taichung 29*6/Strubes Dickkopf and resistant donor Strubes Dickkopf were amplified with type A, the recurrent parent Taichung29 amplified with B-type. Total wheat genomics DNA of 296 F_2 plants was extracted and amplified by PCR using selected primers Xbarc59. Among the 225 resistant plants of F_2 population, there were 217 amplified with A or H band and eight amplified with the same B as Taichung 29; besides two plants amplified with type A, the remaining 66 in 68 susceptible plants were amplified with the recurrent parent with the same B. To determine the linkage pattern among Wmc640, Barc59, Wmc783, Wms497 and *YrSD*, all F_2 population were analysed by these primers to obtain genotype data, which were used for molecular map construction.

The software Mapmaker 3.0 was applied to establish the linkage map. The genetic distance between the SSR primers Xwmc640, Xbarc59, Xwmc783, Xwms497 and stripe rust resistance genes *YrSD* were 3.6, 2.4, 5.4 and 12.4 cM, respectively. The primer Xwmc640 located at one side of stripe rust resistance gene, Xbarc59, Xwmc783 and Xwms497 at the other side. It can be identified that *YrSD* was located on chromosome 5B in the order: Wmc640-*YrSD*-Barc59-Wmc783-Wms497-. The map is shown in figure 3.

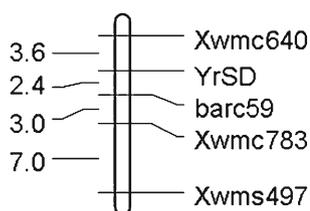


Figure 3. Linkage map of stripe rust resistance gene *YrSD* and four SSR markers on chromosome 5B. Locus names and corresponding locations on the genetic map are indicated on the right side. Map distances (Kosambi) in centi morgans are shown on the left side.

Discussions

Currently using RAPD, RFLP, SSR, RGAP and other molecular markers, many stripe rust resistance genes were located on wheat chromosome (Wang *et al.* 2002; Suenaga *et al.* 2003). Among them, SSR markers were polymorphic, stable, high technology, simple and easy to operate, and strong anchor qualitative characteristics, so the gene can be directly located on the wheat genetic map. Also, the sequences of SSR primers are open for easy genome research application and have become second-generation molecular markers (Gupta *et al.* 2002), and play an important role in the wheat stripe rust resistance genes and molecular assisted breeding.

In this experiment, the wheat NIL Taichung 29*6/Strubes Dickkopf, in which the resistance donor is Strubes Dickkopf and the recurrent parent is Taichung 29 in which resistant gene has not been found, was constructed and obtained after six successive generation of backcrossing, identification and screening. In theory, the directional selection of the target stripe rust resistance gene in Strubes Dickkopf was transferred to NIL Taichung 29*6/Strubes Dickkopf up to 99% probability, indicating that one dominant resistant gene to CYR26 in Taichung 29*6/Strubes Dickkopf came from Strubes Dickkopf.

Using classical genetic analysis, one dominant gene was found in the wheat NIL Taichung 29*6/Strubes Dickkopf to rust race CYR26. The gene *YrSD* in Strube Dickkopf resistant to stripe rust CYR26 using SSR method was located on chromosome 5B. There are four pairs (Wmc640, Barc59, Wmc783 and Wms497) polymorphic SSR primers on chromosome 5B which produced polymorphic DNA bands between the parents, resistant DNA pool and susceptible DNA pool. They were linked with wheat stripe rust resistance gene *YrSD* by PCR amplification and polyacrylamide gel electrophoresis. The genetic distance between primers Xbarc59 and *YrSD* was 2.4 cM.

Strubes Dickkopf is the differential host in the world set and may have derived its resistance from cv. Blé Rouge d'Ecosse which was used as a tester in the early work of Gassner and Straib (McIntosh *et al.* 1995). Studies have shown that the resistance donor Strubes Dickkopf contains *Yr25* gene, which is located on chromosome 1D and also is probably present in several of the cultivars currently widely used. Boshoff and Pretorius (1999) concluded that Strubes Dickkopf, Heines VII and Heines Peko share a gene (maybe allelic) which is present in Line TP981 and was common in European wheats (Johnson and Minchin 1992). Whether

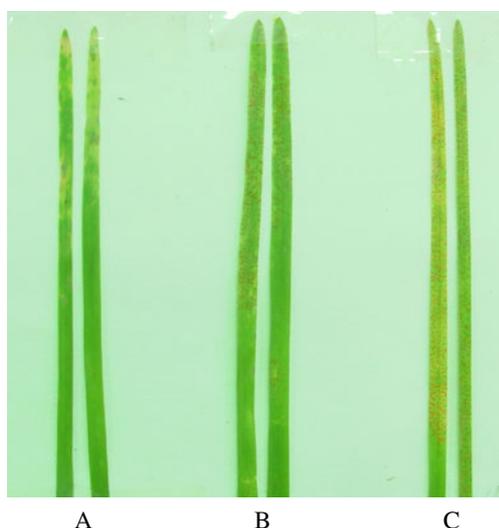


Figure 4. Comparison of the infection type in wheat Strubes Dickkopf, NIL Taichung 29*6/Strubes Dickkopf and Compair, inoculated with Chinese yellow rust 33.

they were indeed the same needs more research to be determined. It can be excluded that the gene in NIL Taichung 29*6/Strubes Dickkopf to CYR26 is the same dominant resistant gene with *Yr25*.

Now, there are two resistance genes to stripe rust that has been officially named on chromosome 5B, *YrDru* and *Yr19* (Chen *et al.* 1995a, 1996; Chen 2005). Chen *et al.* (1995a) positioned a stripe rust resistance gene *YrDru* in spring varieties Druchamp on 5B by the monosomic analysis of Chinese spring. For the origin of cultivars Strubes Dickkopf and Druchamp was different, *YrDru* and *YrSD* is different. Also Chen *et al.* (1995a) located the other gene *Yr19* in Compair on 5B, whose carrier was also different from the origin of *YrSD*. Moreover, the resistance spectrum was different, for Compair (IT 4) was susceptible but NIL Taichung 29*6/Strubes Dickkopf with IT 2⁺ and Strubes Dickkopf with IT 0₁ to CYR33, indicating the the gene was different (figure 4).

Therefore, the resistance gene in Strubes Dickkopf to stripe rust CYR26 is different from *YrDru* and *Yr19*, named *YrSD*.

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