

# Genetic analysis and molecular mapping of a stripe rust resistance gene derived from *Psathyrostachys huashanica* Keng in wheat line H9014-121-5-5-9

Dongfang Ma · Xinli Zhou · Lu Hou ·  
Yaobo Bai · Qiang Li · Haige Wang ·  
Mingshuang Tang · JinXue Jing

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**Abstract** Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most devastating diseases worldwide and is also an important disease in China. The wheat translocation line H9014-121-5-5-9 was originally developed from interspecific hybridization between wheat (*Triticum aestivum* L.) line 7182 and *Psathyrostachys huashanica* Keng. This translocation line showed resistance to predominant stripe rust races in China when it was tested with nine races of *Pst*. To determine the inheritance and map the resistance gene, segregating populations were developed from the cross between H9014-121-5-5-9 and the susceptible cultivar Mingxian 169. The seedlings of the F<sub>1</sub>, F<sub>2</sub>, and F<sub>2</sub>:3 generations were tested with race CYR31. The results showed that the resistance in H9014-121-5-5-9 was conferred by a single dominant gene. Bulked segregant analysis and simple sequence repeat (SSR) markers were used to identify

polymorphic markers associated with the resistance gene locus. Seven polymorphic SSR markers were linked to the resistance gene. A linkage map was constructed according to the genotypes of the seven SSR markers and the resistance gene. Based on the SSR marker positions on the wheat chromosome, the resistance gene was assigned on chromosome 1AL, temporarily designated *YrHA*. Based on chromosomal location, reaction patterns and pedigree analysis, *YrHA* should be a novel resistance gene to stripe rust. The molecular markers of the new resistance gene in H9014-121-5-5-9 could be useful for marker-assisted selection in breeding programs against stripe rust.

**Keywords** Genetic analysis · SSR molecular mapping · Resistance genes · *Puccinia striiformis* f. sp. *tritici* · *Psathyrostachys huashanica*

## Introduction

Stripe rust (yellow rust), caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most devastating diseases of wheat (*Triticum aestivum* L.) worldwide. China is the largest region of epidemic wheat stripe rust in the world, especially the northwest, southwest and Yellow-Huai wheat regions of China. Stripe rust has become a major threat to wheat production due to the appearance of new virulent races (Wan et al. 2004; Wellings 2011). Growing resistant cultivars is the most effective, economic and environment-friendly

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Dongfang Ma and Xinli Zhou made equal contributions to this study.

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D. Ma · X. Zhou · L. Hou · Y. Bai · Q. Li ·  
H. Wang · M. Tang · J. Jing (✉)  
State Key Laboratory of Crop Stress Biology for Arid Areas, College of Plant Protection, Northwest A & F University, Yangling 712100, Shaanxi, China  
e-mail: jingjinxue@163.com

strategy for controlling the disease. However, the race-specific resistance gene(s) are usually overcome by new virulent *Pst* races shortly after the genes are widely deployed in commercial cultivars (Li and Zeng 2002; Lin and Chen 2008). It is therefore an important task to identify new stripe rust resistance genes and develop molecular markers for efficient incorporation and pyramiding of the genes into new wheat varieties.

To date, 53 stripe rust resistance genes have been officially named, of which 14 genes were introgressed into wheat from alien species, viz. *Yr5*, *Yr7*, *Yr8*, *Yr9*, *Yr15*, *Yr17*, *Yr24*, *Yr26*, *Yr28*, *Yr35*, *Yr36*, *Yr37*, *Yr38* and *Yr40*. These genes enrich the stripe rust resistance gene pool, and some genes (e.g. *Yr9*, *Yr15*) have made great contributions to wheat improvement (Li and Zeng 2002). Chinese geneticists and breeders have successfully introgressed the chromosomes or chromosomal fragments from alien species into wheat and developed several valuable cultivars. For example, Xiaoyan 6 and Guinong 22, which carry stripe rust resistance genes from *Elytrigia elongata* and *Haynaldia villosa*, respectively, remained resistant for many years (Shang 1998; Jing et al. 2007; Zhang et al. 1998). Our group has been working on genetics of alien species resistance to wheat stripe rust since the 1990s. In genetic stock resistance screening, over 40 resistant lines from progenies of wheat hybridizations with *Psathyrostachys huashanica*, *Haynaldia villosa*, *Leymus mollis* (Trin.) Hara, *Elytrigia elongata* and *Thinopyrum intermedium* were identified (Jing et al. 1999). Sixteen genes from these genetic stock lines have been mapped, viz. *YrZL93444* (Wang et al. 2011a), *Yr93447* (Yang et al. 2010b), *Yr88375* (Yang et al. 2008c) and *YrZhong22* (Yang et al. 2008b) derived from *Thinopyrum intermedium*; *YrElm1-4* (Yang et al. 2010a), *YrEml4* (Yang et al. 2009a), *YrElm2* (Yang et al. 2008a), *YrLm2* (He et al. 2010) and *YrLm1* (Song et al. 2009) derived from *L. mollis* (Trin.) Hara; *YrWV* (Wang et al. 2011b) and *YrV1* (Zhou et al. 2008) derived from *H. villosa*; *Yrcy54-1* (Hou et al. 2010) and *Yrxyh* (Yang et al. 2009b) derived from *E. elongata*; and *YrHy* (Yao et al. 2010), *Yrhua* (Cao et al. 2008) and *YrH9020* (Li et al. 2012) derived from *P. huashanica*, and these genes are effective against the current *Pst* population in China.

*Psathyrostachys huashanica* Keng (2n = 2x = 14, NN) is a perennial wild grass native to Huashan Mountain in Shaanxi Province, China. *P. huashanica* is a useful breeding material for wheat improvement

due to its valuable characters such as early maturity, tolerance to drought stress and disease resistances. Various types of wheat—*P. huashanica* hybrid genetic stocks have been successfully created through interspecific hybridization and chromosomal engineering, including nullisomic heptaploid lines, alien chromosomal substitution lines, addition lines and translocation lines (Chen et al. 1991, 1996; Hou et al. 1997). In our disease resistance assessments, we found most of the translocation lines had a high level of resistance to Chinese *Pst* races (Jing et al. 1999). To make the resistance sources more useful for breeding programs, our group studied the inheritance of these resistance genes, and identified and molecular-mapped four stripe rust resistance genes from *P. huashanica* (Tian et al. 2011; Yao et al. 2010; Cao et al. 2008; Liu et al. 2008).

Wheat line H9014-121-5-5-9 was developed from interspecific hybridization between common wheat line 7182 and *P. huashanica* accession 0503383 and subsequent backcrossing with 7182 (Cao et al. 2008). The objective of this study was to identify the stripe rust resistance gene(s) in H9014-121-5-5-9, map the resistance gene using simple sequence repeat (SSR) markers and develop molecular markers in wheat breeding.

## Materials and methods

### Plant and pathogen materials

The translocation line H9014-121-5-5-9, which originated from interspecific hybridization between *Triticum aestivum* line 7182 and *P. huashanica* accession 0503383, was created and kindly provided by Professor Jie Fu (Northwest A & F University, Yangling, China). The segregating populations were made from the cross between H9014-121-5-5-9 and Mingxian 169. H9014-121-5-5-9 is a resistant donor. Mingxian 169 is a Chinese winter wheat cultivar and susceptible to all Chinese *Pst* races identified so far. The F1, F2 and F2:3 progenies were developed in a greenhouse. Chinese Spring (CS) and its complete set of 21 nulli-tetrasomic lines were used to determine the chromosomal position of the molecular markers related to stripe rust resistance gene in H9014-121-5-5-9. Four wheat—*P. huashanica* translocation lines, H9020-17-15, H9020-1-6-8-3, H9020-20-12-1-8 and H122, were used to determine the gene's origin and relationships.

Nine predominant Chinese *Pst* races (CYR25, CYR27, CYR29, CYR30, CYR31, CYR32, CYR33, Su11-4 and Su11-11) representing various virulence combination patterns reported in China in recent years were used to test H9014-121-5-5-9 and Mingxian 169 at the seedling stage in a greenhouse.

### Seedling tests

The seedling tests were conducted under a controlled greenhouse condition. About 10 seeds for each parent and the F1, 228 seeds for the F2 and 20 seeds for each of the F3 lines were used for tests. Seeds were planted in several 10-cm-diameter pots. About 10 days after planting, seedlings were inoculated by dusting with a mixture of urediniospore and talc at a 1:50 ratio and kept in a dark dew chamber at 10 °C for 24 h. The inoculated plants were transferred to an environmentally controlled greenhouse with 16 h light/8 h dark photoperiod at 12–17 °C. Infection types (IT) were recorded 17–18 days after inoculation when rust had fully developed on the susceptible check Mingxian 169. Infection type was based on a 0–4 scale where the plants with IT 0–2<sup>+</sup> were considered to be resistant and those with IT 3<sup>–</sup>–4 susceptible (Li et al. 2006).

### SSR analysis

Genomic DNA was extracted from green leaves using the CTAB method as modified by Yan et al. (2003). Two hundred and twenty-eight F2 plants and the corresponding F3 lines from the cross Mingxian 169/H9014-121-5-5-9 were used as a mapping population. Based on the F3 disease phenotypic data, DNA from 10 resistant lines and 10 susceptible lines was used for constructing resistant and susceptible bulks, respectively. Each bulk was composed of equal amounts of F2 plant DNA (Michelmore et al. 1991).

The SSR procedure was used to identify markers linked to the resistance loci. SSR primer sequences were obtained from the GrainGenes website (<http://wheat.pw.usda.gov>). A total of 660 wheat SSR markers were screened on the two parents and the resistant and susceptible bulks for detecting polymorphisms. A 15 µL reaction mixture consisted of 1.5 µL PCR 10× buffer (containing 5 mmol Mg<sup>2+</sup>), 2.0 µL DNA template (25 ng/µL), 1.2 µL dNTPs (2.5 mM each), 1.5 µL each of forward and reverse primers (5 µM), 0.3 µL Taq DNA polymerase (5 U/µL) and 7.0 µL ddH<sub>2</sub>O.

PCR amplification of SSRs was performed in a MJ Research PTC-200 thermal cycler. The PCR conditions were the following: initial denaturation at 94 °C for 5 min, followed by 35 cycles of 30 s denaturation at 94 °C, 1 min annealing at 50–68 °C depending on primers and 45 s extension at 72 °C, and a final extension at 72 °C for 10 min. After amplification, 6 µL of formamide loading buffer [98 % formamide, 10 mM EDTA (pH 8.0), 0.5 % (w/v) xylene cyanol and 0.5 % (w/v) bromophenol blue] was added to the PCR product. About 5–7 µL mixture of the PCR product and loading buffer for each sample was loaded for electrophoresis on 8 % polyacrylamide gels. The gel was stained and visualized as previously described (Bassam et al. 1991).

### Data analysis and linkage map construction

Segregation of markers and resistance gene locus was tested for goodness-of-fit to the expected ratio using the Chi squared test with the Excel data analysis software of Microsoft Office 2007. Linkage analysis was performed with MAPMAKER 3.0b (Lincoln et al. 1992). The recombination frequency was converted to map distance (in centiMorgans) according to the Kosambi mapping function (Kosambi 1943). The linkage map was drawn using the software Mapdraw v2.1 (Liu and Meng 2003).

### Validation of the close marker in wheat—*P. huashanica* translocation lines

The closest SSR markers to the stripe rust resistance gene in H9014-121-5-5-9 were used to test four wheat translocation lines (H9020-17-5, H9020-1-6-8-3, H9020-20-12-1-8 and H122), which also contained the stripe rust resistance genes from *P. huashanica* (Tian et al. 2011; Yao et al. 2010; Cao et al. 2008; Liu et al. 2008). The DNA isolation of the four translocation lines and *P. huashanica* accession 0503383 were as previously described.

## Results

### Genetic character of stripe rust resistance in line H9014-121-5-5-9 in the seedling tests

H9014-121-5-5-9 was resistant (IT 0–1) to nine *Pst* races. The reaction to seven races was light necrosis with IT 0. The reaction to race Su11-4 was immune.

**Table 1** Observed numbers of resistant, segregating and susceptible plants or lines for F1, F2 and F2:3 progeny from cross M169/H9014-121-5-5-9 tested with race CYR31 of*Puccinia striiformis* f. sp. *tritici* under greenhouse conditions: Chi squared tests of goodness of fit

Parent <sup>a</sup> or progeny	Observed number of plants or lines <sup>b</sup>			Expected ratio Res:Seg:Sus	$\chi^2$	P
	Res.	Seg.	Sus.			
Mingxian 169	0	0	10			
H9014-121-5-5-9	9	0	0			
F1	10	0	0			
F2	173		55	3:1	0.05	0.76
F2:3	50	96	46	1:2:1	0.17	0.92

<sup>a</sup> H9014-121-5-5-9 is the male parent, Mingxian 169 is the female parent<sup>b</sup> Res resistant, Seg segregating, Sus susceptible. For parents, F1 and F2, the values are numbers of plants. For F3, the values are numbers of lines. The segregating lines included plants with IT 0–2<sup>+</sup> and 3<sup>–</sup>–4. The F2 ratio is for resistant and susceptible plants, and the F3 ratio is for homozygous resistant, segregating and homozygous susceptible lines

Only a few tiny unopened stripe rust pustules of race Su11-11 were formed on H9014-121-5-5-9. The resistant donor *P. huashanica* accession 0503383 had a similar reaction to stripe rust as H9014-121-5-5-9. Wheat line 7182, as recurrent parent for developing H9014-121-5-5-9, was highly susceptible, with IT 4. Mingxian 169, as the susceptible control, was also highly susceptible (IT 4). When inoculated with CYR31, F1 plants had IT 0, and in the 228 F2 plants 173 plants were resistant and 55 susceptible, fitting a resistant:susceptible ratio of 3:1 ( $\chi^2 = 0.09$ ,  $P = 0.76$ ). Of 192 F3 families, 50 were homozygous resistant, 96 segregating and 46 homozygous susceptible lines, showing a 1:2:1 ratio ( $\chi^2 = 0.17$ ,  $P = 0.92$ ). Both F2 and F3 segregation data indicated that a single dominant gene conferred the stripe rust resistance to CYR31 in H9014-121-5-5-9 (Table 1). We tentatively designated this gene as *YrHA*.

#### Molecular linkage map for *YrHA*

A total of 660 SSR markers covering all 21 wheat chromosomes were screened for polymorphisms between H9014-121-5-5-9 and Mingxian 169. Seven markers, *Xbarc240*, *Xwmc312*, *Xwmc93*, *Xwmc9*, *Xwmc469*, *Xgwm497* and *Xwmc59*, showed clear polymorphisms between the resistant and susceptible DNA bulks as well as the parents. The entire F2 population was then genotyped with the seven polymorphic markers. All of them are co-dominant markers except *Xwmc469* and *Xwmc312* (Table 2). The genotypes of the seven SSR markers fitted 3:1 (dominant) or

1:2:1 (co-dominant) ratio, indicating that each of the seven SSR markers inherited as the single locus. A linkage group was constructed using these markers and the resistance gene *YrHA*. The linkage map spanned 25.1 cM, and the resistance gene *YrHA* was closely linked to *Xwmc469* and *Xgwm497* with map distances of 3.4 and 4.6 cM, respectively (Table 2, Fig. 2). The markers *Xwmc469* and *Xgwm497* are shown in Fig. 1 as an example. Based on the wheat SSR consensus map (<http://wheat.pw.usda.gov>), the seven linked markers were located on the long arm of chromosome 1A. The marker *Xwmc312* was used to test 21 CS nulli-tetrasomic lines. The target fragment was present in all lines except N1AT1B, confirming that the resistance gene in H9014-121-5-5-9 was located on chromosome 1A (fig. S1).

#### Origin of the stripe rust resistance gene *YrHA*

The wheat line H9014-121-5-5-9 was derived from consecutive backcross between *P. huashanica* accession 0503383 and common wheat line 7182. Seedling tests showed that the recurrent parent 7182 was susceptible to nine stripe rust races and pathotypes, whereas H9014-121-5-5-9 and *P. huashanica* accession 0503383 were resistant to all the stripe rust races and pathotypes. Therefore, from the pedigree and the resistance to stripe rust, we conclude that the resistance gene in H9014-121-5-5-9 was derived from *P. huashanica* accession 0503383. To determine the origin of the resistance gene in H9014-121-5-5-9, the two closest flanking SSR markers (*Xwmc469*,

**Table 2** SSR markers linked to resistance gene to *Puccinia striiformis* f. sp. *tritici* and their genotype, presence (+) and absence (–) in H9014-121-5-5-9 ( $R_P$ ), Mingxian 169 ( $S_P$ ) and Chinese Spring (CS), number of F2 lines of the cross with orwithout the bands, and  $\chi^2$  and probability values for goodness of fit to 3:1 ratios for dominant markers and 1:2:1 ratios for co-dominant markers

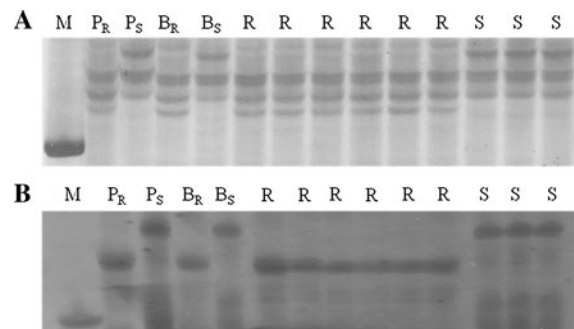
Marker	Size <sup>a</sup> (bp)	$R_P$	$S_P$	CS	Number of markers in			$\chi^2$	P value	
					A <sup>b</sup>	H	B			
<i>Xbarc240</i>	310/290	A (310 bp)	B (290 bp)	+	(290 bp)	60	109	59	0.45	0.80
<i>Xwmc312</i>	330	A (330 bp)	B	+	(330 bp)	175		53	0.28	0.54
<i>Xwmc93</i>	235/260	A (235 bp)	B (260 bp)	+	(260 bp)	54	119	56	0.39	0.82
<i>Xwmc9</i>	210/220	A (210 bp)	B (220 bp)	+	(220 bp)	56	114	58	0.04	0.98
<i>Xwmc469</i>	220	A (220 bp)	B	+	(220 bp)	172		56	0.01	0.88
<i>Xgwm497</i>	130/140	A (130 bp)	B (140 bp)	+	(140 bp)	55	112	61	0.38	0.82
<i>Xwmc59</i>	320/310	A (320 bp)	B (310 bp)	+	(310 bp)	51	121	55	1.13	0.57

<sup>a</sup> Fragment size was visually estimated based on the 100-bp DNA ladder<sup>b</sup> A, resistant parent allele; H, both resistant and susceptible parent allele; B, susceptible parent allele

*Xgwm497*) were tested with the four translocation lines, 7182 and *P. huashanica* accession 0503383. SSR analyses showed that *P. huashanica* accession 0503383 possessed the same bands as that of H9014-121-5-5-9, whereas the target bands were absent in 7182 and the four translocation lines H9020-17-5, H9020-1-6-8-3, H9020-20-12-1-8 and H122 (Fig. 3). These results indicated that the resistance gene in H9014-121-5-5-9 was originated from *P. huashanica* accession 0503383 and different from the other translocation lines that also derived from *P. huashanica*. The resistance gene in H9014-121-5-5-9 was a novel effective gene to current stripe rust pathogen population, temporarily designated *YrHA*.

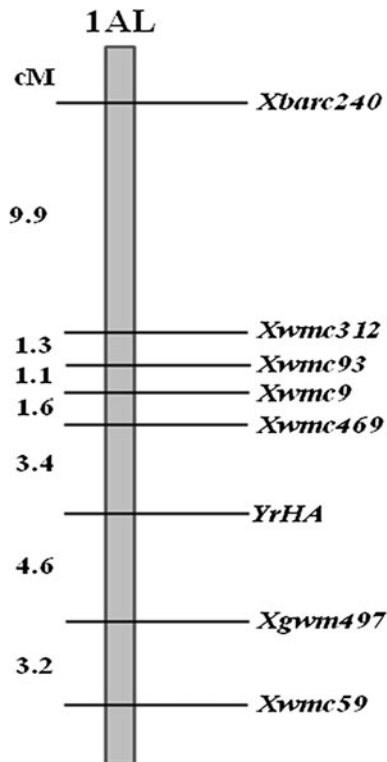
## Discussion

To date, none of the officially named *Yr* genes is located on chromosome 1A. Only one temporarily named gene, *YrDal* from cultivar Daws, has been located on chromosome 1A by monosomic analysis (Chen et al. 1995). The wheat cultivar Daws is developed from a three-way cross, CI14484/CI13645/PI178383 (Zeven and Zeven-Hissink 1976). The gene in Daws could have been from CI14484, CI13645, and/or Washington Selection 101, which was used to develop CI14484. All of the wheat genotypes in the Daws pedigree are common wheat. *YrHA* is derived from *P. huashanica* and should be different from *YrDal*.



**Fig. 1** PCR profile of *Xwmc469* (a) and *Xgwm497* (b) in F2 plants from the cross Mingxian 169 × H9014-121-5-5-9. M DNA ladder,  $P_R$  H9014-121-5-5-9,  $P_S$  Mingxian 169,  $B_R$  resistant pool,  $B_S$  susceptible pool, R resistant plant, S susceptible plant

Our group has identified four stripe rust resistance genes from wheat—*P. huashanica* translocation lines (Tian et al. 2011; Yao et al. 2010; Cao et al. 2008; Liu et al. 2008). All of these four genes have a high level of resistance to the tested races. *Yrhua* is identified in the translocation line H9020-17-5 against CRY30, and mapped on chromosome 6AL. *YrH9020*, identified from translocation line H9020-1-6-8-3, is resistant to CYR32 and located on chromosome 2D. *YrHy* is identified in translocation line H9020-20-12-1-8 and confers resistance to CYR32, which is located on chromosome 2BS. *YrH122* in translocation line H122 is resistant to *Pst* pathotype Sun11-4 and mapped on chromosome 1DL. In this study, we identified a new resistance gene *YrHA* in translocation line H9014-121-5-5-9. Comparing the SSR genotypes with the other



**Fig. 2** Linkage map of stripe rust resistance gene *YrHA* and SSR markers on chromosome 1AL in wheat

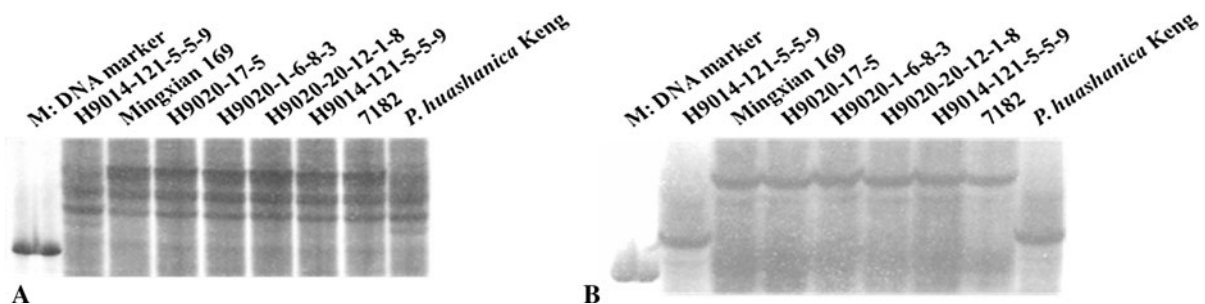
identified *Yr* genes from *P. huashanica*, *YrHA* is different from other *Yr* genes and is deduced to be a novel resistance gene to stripe rust.

Zhao infers that chromosomes of *P. huashanica* can substitute for the wheat chromosomes 5A, 3B or 3D to generate a common wheat genotype (Zhao et al. 2003), which means that it is easy to create a relatively stable substitution lines between *P. huashanica* and common wheat. In other words, the chromosomes of *P. huashanica* can be transferred to common wheat and

could be recognized as relatively fixed common wheat chromosome groups. Resistance assessments over several years also confirm that resistance of H9014-121-5-5-9 to stripe rust is stable, and *YrHA* is stably inherited.

Wheat wild relatives have various disease resistances and play important roles in wheat improvement. The wheat cultivars derived from wheat-rye (*Secale cereal* L.) 1BL/1RS translocation lines carry several disease resistance genes such as *Lr26*, *Sr31*, *Yr9* and *Pm8* which provide many benefits to modern wheat breeding (Singh et al. 1990; Villareal et al. 1991). Almost 90 % of predominant Chinese wheat cultivars in 1990s are developed from this translocation line (Li and Zeng 2002). In China, another wild wheat relative, *Elytrigia elongata*, is used in wheat improvement and batches of cultivars benefit from the wheat—*E. elongata* translocation. The wheat—*E. elongata* translocation lines carry both race-specific and non-race-specific resistance. Wheat cv. Xiaoyan 6 derived from this translocation has high-temperature durable rust resistance and has remained resistant over 20 years since its release in the 1980s (Ma and Shang 2000).

*Psathyrostachys huashanica* has similar resistance characteristics to *E. elongata* against multiple races at seedling stage and also remains resistant in multiple-year rust evaluation in the field. However, it is not known whether *P. huashanica* has high-temperature resistance. *P. huashanica* possesses several stripe-rust resistance genes, but they have not been deployed in current wheat cultivars. In our studies we found that several wheat—*P. huashanica* translocation lines not only have disease resistance but also have other favorable agronomic traits such as drought tolerance and good seed quality. They are a valuable genetic source for wheat improvement. With



**Fig. 3** PCR amplification profiles of H9014-121-5-5-9, Mingxian 169, H9020-17-5, H9020-1-6-8-3, H9020-20-12-1-8, H9014-121-5-5-9, 7182 and *P. huashanica* Keng using SSR markers *Xgwm469* (a) and *Xgwm497* (b)

the SSR markers in this study, the resistance gene *YrHA* will be easily introgressed into elite wheat lines in breeding programs.

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