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Molecular mapping of two quantitative trait loci for adult-plant resistance to powdery mildew in common wheat (*Triticum aestivum* L.)

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ABSTRACT

Powdery mildew is one of the major wheat diseases in regions with maritime or semi-continental climate and can strongly affect grain yield. Breeding wheat varieties with quantitative resistance to powdery mildew would be relatively more durable and promising than varieties with only major resistance genes (*Pm* genes). The chief aim of the present study is to map the quantitative trait loci (QTLs) for adult plant resistance (APR) to powdery mildew. A population of 176 recombinant inbred lines was developed from a cross of "Shannong 0431 × Lumai 21" (SN0431 × LM21) and evaluated for disease severity of powdery mildew under two cropping seasons. Two major QTLs (*QPm.sdau*-2A and *QPm.sdau*-2B) for APR to powdery mildew were mapped on chromosomes 2A and 2B, which were contributed by LM21 and SN0431. The molecular markers associated with the QTLs will be useful for selecting partial and potentially durable resistance genes against powdery mildew.

1. Introduction

Powdery mildew caused by *Blumeria graminis* f.sp. *tritici* (*Bgt*) is a destructive wheat foliar disease worldwide, which is prevalent in regions with temperate and maritime climates, such as Europe, North and South America, Africa, and China (Everts et al., 2001; Li et al., 2014). Powdery mildew is now a major disease in the winter wheat areas of China (Cao et al., 2012). The common occurrence of this disease causes significant reductions in both grain yield and quality in susceptible wheat cultivars by reducing photosynthesis and altering the carbon flux within the infected leaf (Conner et al., 2003; Swarbrick et al., 2006). The grain yield loss can be 5%–34% each year in China (Li et al., 2014). Considering the damage of wheat powdery mildew to yield, thousand-kernel weight was most seriously affected by powdery mildew of three yield components assessed (Cao et al., 2014).

The use of powdery mildew resistance genes in elite cultivars is the most cost-effective and sustainable strategy to control this disease (Wang et al., 2012). In recent decades, most studies have focused on major genes (*Pm* genes) that are also often qualitative or race-specific resistance genes. These genes are simply inherited and easy to manipulate in breeding programmes, as they express complete resistance and are usually associated with hypersensitive responses that limit pathogen growth (Gustafson and Shaner, 1982). Until recently, 54 powdery mildew resistance loci have been located, including 78 resistance genes (Hao et al., 2015; Li et al., 2017; McIntosh et al., 2014). Race-specific resistance is often transient owing to the occurrence of new pathogen races arising from mutations or increases in the frequency of previously rare variants (Menardo et al., 2016).

One of the principal challenges in wheat breeding is to develop cultivars with durable disease resistance. Adult-plant resistance (AP) offers race non-specific and therefore durable resistance based on the additive effects of several genes that delay infection and reduce the growth and reproduction of the pathogen at the adult-plant stage (Lillemo et al., 2012; Marone et al., 2013). Molecular markers make it easier to locate APR genes on chromosomes and to estimate the effect of each locus (Lan et al., 2010). More than 119 quantitative trait loci (QTLs) for powdery mildew resistance have been identified and mapped on almost all wheat chromosomes (Li et al., 2014). Although many race-specific major resistance genes (*Pm* genes) have been widely used in breeding programmes (Bennett, 1984), but this kind of resistance is generally of short durability, since it can be overcome by pathogen races with matching virulence alleles (Roberts and Caldwell, 1970; Shaner, 1973; McDonald and Linde, 2002; Skinnes, 2002). Adult plant resistance is potentially more durable than race-specific major resistance (Bennett, 1984), and exhibits quantitative variation, but it is limited to be widely used in breeding programmes since the assessment

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phenotypically is difficult (Gustafson and Shaner, 1982; Yu et al., 2001), and its QTL is not consistent across environments (Keller et al., 1999; Mingeot et al., 2002) to date. Therefore, there is an urgent need for the continuous exploration of new powdery mildew resistance genes or QTLs, especially those with a broader resistance spectrum.

We have developed a new wheat germplasm, 'Shannong 0431' (SN0431), with resistance to multiple diseases including powdery mildew, and better agronomic traits, which could be a useful parent in wheat breeding programmes. Using SN0431 and the famous cultivated variety 'Lumai 21' (LM21), a set of recombinant inbred lines (RILs) was constructed. The objective of this study is to identify QTLs for APR to powdery mildew using these RILs.

2. Materials and methods

2.1. Plant and fungal materials

The mapping population was a composed of 176 RILs originated from the cross "SN0431 × LM21" (F_{10} in 2013) through the method of single-seed descent (SSD). SN0431 was developed from the cross "Grtpi85504//MI76-77-S29/ALD", which came from "International Winter × Spring Wheat Screening Nursery" (IWSWSN) in 1994, Cornell University, USA. SN0431 has resistance to multiple diseases (powdery mildew, stripe rust, leaf rust, and sharp eyespot) and better agronomic traits in general. LM21 is a cultivar released by the Yantai Academy of Agricultural Science of China in 1996 with high grain yield and drought resistance, but it is moderately susceptible to powdery mildew. This cultivar has been planted on more than 30 million hectares in the Huang-huai winter wheat region of China.

2.2. Powdery mildew evaluations

The 176 RILs and their parents were evaluated for disease severity in Beijing at the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS) during the 2013–2014 and 2014–2015 cropping seasons, defined as E1 and E2 in chronological order. The field trial was conducted in randomized complete blocks with two replicates each year. The susceptible control was 'Jingshuang 16', one row of which was planted after every 20 test rows. Around the tested lines, 'Zhongzuo 9504' was planted as a disease spreader. The composite *Bgt* isolates (Li et al., 2011), which was collected from different wheat-producing areas in China and derived from single pustule, was used as inoculums. This composite *Bgt* isolates is virulent to *Pm3a*, *Pm3b*, *Pm3e*, *Pm5a* and *Pm1+2 + 9*, but avirulent to *Pm1c*, *Pm13*, *Pm20*, *Pm21*, *Pm24*, *Pm2+6* and *Pm5+6*. In the pre-erecting stage, 'Zhongzuo 9504' was inoculated with an isolates mixture (the virulence spectrum was *V1*, *V3a*, *V3b*, *V3c*, *V3d*, *V3e*, *V3f*, *V4a*, *V4b*, *V5*, *V6*, *V7*, *V8*, *V17*, *V19*, *V23*, *V24*, *V25*, *V30*, *V34* and *V35*). In the milk-ripening stage, the percentage of the penultimate leaf area affected was recorded as the powdery mildew severity, which was used as the maximum disease severity (MDS); then, the powdery mildew infection type (IT) was scored on a 0–6 scale (0: 0% of leaf coverage; 1: < 5%; 2: < 10%; 3: < 25%; 4: < 50%; 5: < 80% and 6: more than 80% of leaf coverage) according to Yu et al. (2001). According to the MDS and IT of each line, we calculated the disease index (DI) using the following formula (Zhang et al., 2014):

$$DI = \frac{\sum n_i \times i}{N \times X} \times 100$$

where n is the number of investigated leaves at i scale, i is the score at i scale, N is the number of all assessed leaves, and X is the highest scale. The average value of the two replicates represented the performance of each RI line in E1 or E2. AV represented the average value of MDS/DI across E1 and E2.

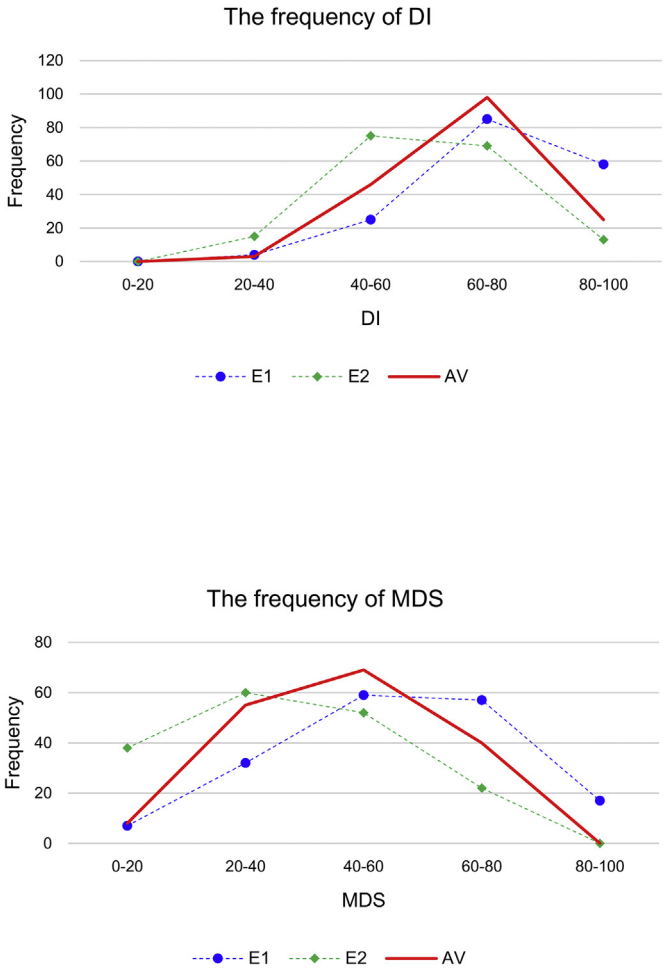

Fig. 1. The frequency distributions of MDS and DI among the RILs derived from "SN0431 × LM21". E1, MDS or DI of each line in environment E1; E2, MDS or DI of each line in environment E2; AV, the average value for MDS or DI across environment E1 and E2.

Table 1
Pearson correlation coefficients among phenotypic traits and broad sense heritability estimates.

	Correlation coefficients			Heritability (H_B^2)
	MDS-E2	DI-E1	DI-E2	
MDS-E1	0.446[a]	0.981[a]	0.461[a]	0.44
MDS-E2		0.437[a]	0.981[a]	
DI-E1			0.456[a]	0.48
DI-E2			1.000	

[a] Highly significant at 1% level.

2.3. Statistical and QTL analysis

The experimental data were analyzed using the SPSS (version19.0, SPSSInc, Chicago, IL, USA) software. Analysis of variance (ANOVA) was performed using GLM procedure in SPSS and simple correlation coefficients between DI and MDS were calculated. Heritability in the broad sense (H_B^2) was computed through analysis of variance using the formula: $H_B^2 = \sigma_G^2/(\sigma_G^2 + \sigma_e^2/n)$, where σ_G^2 is genetic variance, σ_e^2 is environment variance, n is the number of replicates per RIL.

A high-resolution genetic map we constructed before (Gao, 2014) was used for the QTL analysis. The map consisted of 7955 loci (4530 unique loci) distributed on 21 chromosomes, giving a total map length of 2929.96 cM with a density of 0.63 cM/marker. The majority of