

Genetic analysis revealed a quantitative trait loci $(QTL_{2A,K})$ on short arm of chromosome 2A associated with yellow rust resistance in wheat (*Triticum aestivum* L.)

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Abstract

Yellow rust, caused by Puccinia striiformis, is one of the most devastating diseases in wheat. A synthetic by elite recombinant inbred line (RIL) population derived from a cross, Botnol/Aegilops squarrosa (666)//Kachu was evaluated for yellow rust resistance in two different environments in Mexico. The population was subjected to DArT-seq analysis for an in-depth genetic characterization. A major effect rust resistance QTL (QTL_{2A,K}) explaining up to 45% phenotypic variance was found to be contributed by Kachee, an elite line of International Maize and Wheat Improvement Center (CIMMYT) Mexico. The QTL_{2A.K} was found to be contributed by a segment of 2NS Chromosome of Triticum ventricosum translocated into the short arm of bread wheat chromosome 2A ($QTL_{2A,K}$). The position of QTL_{2A,K} was confirmed using *T. ventricosum* specific primer VENTRIUP-LN2. Identified genomic regions are being introgressed in to the popular but susceptible wheat varieties through marker-assisted breeding for enhancing yellow rust resistance.

Key words: Wheat, rust, genotyping, Quantitative Trait Locus, *Puccinia striiformis*

Introduction

Wheat (*Triticum* spp.) is one of the most important cereal crop in the world. Globally, wheat is cultivated in an area of about 220 mh with the total grain production of about 763 mt (Ramadas et al. 2019). Genetic yield potential increment of wheat at global level is below 1% per annum which is insufficient to meet the demands of growing population across the world (Ray et al. 2013). The yellow rust of wheat caused by the fungus *Puccinia striiformis* sp. *tritici* can be disseminated thousands of kilometers by wind and

are capable of causing considerable economic loss throughout the world (Kolmer, 2005; Goyal and Prasad 2010). The most effective and environmentally sustainable method of controlling wheat rust is through the transfer of resistance genes into modern cultivars (Fetch 2011). A goal in breeding programs should be to screen germplasm for durable resistance genes, and then attempt to combine them in a cultivar for long-term durable resistance (McCallum 2007).

Currently there are 80 designated stripe rust resistance genes (*Yr1-Yr80*) and approximately 40 temporarily designated genes (Cheng 2014; Coriton et al. 2020). Some of the permanently designated genes that confer adult plant resistance are *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr16*, *Yr18*, *Yr29*, *Yr30*, *Yr34*, *Yr36*, *Yr39*, *Yr46*, *Yr48* and *Yr52* (Xu, 2013). These genes are not race specific so that, they can provide partial protection against several races of stripe rust and are more durable.

An important rust resistance gene cluster (*Lr37-Sr38-Yr17*) which confers resistance of wheat against leaf rust (caused by *Puccinia triticina*), stem rust (caused by *Puccinia graminis*) and stripe rust (caused by *Puccinia striiformis*), respectively (Dyck and Lukow 1988; McIntosh et al. 1995; Robert et al. 1999) is located within a segment of short arm of chromosome 2N of *Triticum ventricosum* (Tausch). This 2NS chromosome segment was translocated to the short arm of bread wheat chromosome 2A (Helguera et al. 2003). This cluster has been widely used in breeding programs in the US and has provided durable resistance

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to stripe rust for years (Hao 2011; Coriton et al. 2020) however, now the resistance has been overcome by newly evolved races of stripe rust. The gene *Yr17* has also been introduced onto chromosome 2D and recombinant with double dose of gene has displayed better resistance than single dose.

Progress in molecular marker technology and the development of quantitative trait analysis software have permitted researchers to construct genetic maps in wheat to identify and estimate the effects of quantitative trait loci (QTL) associated with important agronomic traits including yellow rust. QTLs for stripe rust resistance on chromosome 2A have also been detected earlier on the *Sr38, Lr37* and *Yr17* segment (Zang et al. 2019). Genomics assisted approaches offer promise of fast track precision breeding in wheat.

The aim of this research was to detect quantitative traits (QTLs) associated with yellow rust resistance in a bi-parental population derived from a cross involving a synthetic wheat line with common wheat. This population was subjected to DArT-seq for an in-depth genetic characterization in order to identify genomic regions associated with yellow rust resistance.

Materials and methods

Experimental location

Experiments were conducted at two different experimental stations of International Maize and Wheat Improvement Center (CIMMYT)-EI Batán and Toluca, Mexico in 2015. Each station has unique environmental conditions. El Batán is located at an elevation of 2250m above sea level with an average daily temperature of 16.6°C, dew point 11.8°C and humidity of 75%. Toluca is located at an elevation of 2660 m amsl, monthly average temperature of 14.8°C, dew point around 9.0°C and humidity of 74%, (Weather Underground web site: https://www.wunderground. com/). The experiments were sown under well managed irrigated conditions. The experimental design was "Control of local variability - by blocking" following an alpha lattice design. Two replications of each trials were followed.

Plant material and its evaluation for yellow rust severity

A set of two hundred sixty $F_{4:6}$ recombinant inbred lines (RILs) derived from a cross of synthetic line Botno/*Ae. squarrosa* 666 with an elite line 'Kachu' from

CIMMYT, was developed using single seed descent (SSD) method. Leaf tissue from each RIL (F_4) were sampled for DNA extraction. DNA samples were subjected to DArT-seq genotyping. F_5 generation was planted and harvested as bulk in order to obtain $F_{4:6}$ seeds for phenotyping purpose.

The set 260 RILs and parental lines were evaluated for yellow rust resistance under field conditions at El Batán and Toluca, Mexico in the year 2015. Experiments were performed in two replications with repeated checks after every 50 plots using an alpha lattice breeding design. At the very first step, plots (blocks) that showed resistance and susceptibility to yellow rust were observed to confirm the presence/absence of fungus. Observations were recorded at seedling and adult plant stages. The average percentage of leaf area of adult plants covered by stripe rust was visually estimated according to the scale described by Peterson (1948). The proportion of vegetative damage was also estimated in relation to the total area of each plot using a scale of 0% to 100%.

Simple Sequence Repeat (SSR) genotyping and segment analysis

DNA was extracted using a protocol standardized by CIMMYT (2005). SNP genotyping was carried out using DArT-Seq technology at CIMMYT's SAGA platform SAGA ("Servicio de AnálisisGenético para la Agricultura") following methodology delineated by Vikram et al. (2016).

PCR reactions were made using SSR markers, GoTag® DNA polymerase (Promega Corporation). Buffer 5X (1.55µL), MgCl₂ 25mM (0.75µL), dNTP's 100mM (0.6µL), Primer 1µM (2µL) and Taq enzyme (0.4µL). The annealing temperature of each SSR was obtained from Grain Genes 2.0 (https://wheat.pw. usda.gov/cgi-bin/GG3/browse.cgi?class= marker). The PCR program used for SSR markers was 30 cycles (94°C-5 min//94°C-1 min/60°C-2 min/ 72°C-1 min//72°C-7 min/10°C-"); only annealing temperature (highlighted in bold) change for each marker. The PCR product was resolved using agarose gels (3%) electrophoresis performed for 2 h at 150 volts. The banding pattern in the population was scored according to each parent, genotype parent 1 and genotype parent 2, a mix of two genotypes is heterozygous genotype. To identify the fragment containing Yr17, two PCR primers URIC, VENTRIUP, LN2 were used.

Statistical analysis

Statistical analysis was performed using SAS 9.4 software (SAS Institute, Cary, NC). Best Linear Unbiased Predictors (BLUPs) were calculated, using Restricted Maximum Likelihood (REML) in a Mixed Model Framework. The corresponding linear models were implemented in PROC Mixed of SAS using REML to estimate the variance components.

For analyses of individual locations using a lattice design the model was:

$$Y_{ijk} = \mu + Rep_i + Block_j(Rep_i) + Gen_k + \varepsilon_{ijk}$$
 [Eq 1]

where Y is the trait of interest, μ is the mean effect, Rep_i is the effect of the ith replicate, $Block_j$ (Rep_i) is the effect of the jth incomplete block within the ith replicate, Gen_k is the effect of the kth genotype, and ε_{ijk} is the error associated with the ith replication, jth incomplete block, and kth genotype, which is assumed to be normally and independently distributed with mean zero and homoscedastic variance σ^2 .

For the analyses combined across locations, new terms are added to the above model. For a lattice design, the model is [Eq. 2]

| [Eq | 2] |
|-----|----|
| | |

where the new terms Loc_i and $(Loc_i \times Gen_i)$ are the effects of the ith location and the location × genotype interaction, respectively.

Analysis of variance (ANOVA) test were performed, using the general linear model, for disease rating obtained from each location and for estimating genetic and environmental effect of lines. The variance components were carried out in the field trials in which two replications in Batan were evaluated and one replication for Toluca.

Genetic analysis

Genotyping of the population was made through 2694 SNPs markers, and 11 SSR markers were used to identify and validate the linkage maps. Software lciMapping 4.0 was employed for construction of a genetic linkage map. Map distances between markers were calculated using the Kosambi (1944) mapping function. The positions of detected QTLs were determined by inclusive composite interval mapping (ICIM). A logarithm of odds (LOD) of 3.0 was set to declare significance of QTLs. QTL effects were estimated as the proportion of phenotypic variance explained (PVE) by the QTL.

Results

Phenotypic evaluation of RIL population for yellow rust

The RILs of Botno/*Ae. squearosa* // Kachu population, were screened for yellow rust in two different dates. 'Kachu', the resitant parent showed 10% of disease severity at the adult plant stage whereas, for synthetic

 Table 1.
 Summary of phenotypic evaluation of the disease severity (%) for yellow rust recombinant inbred line (RIL) population in two environments

| Parent, parameter | Yellow rust severity, % | Yellow rust severity, % |
|--|---|--------------------------|
| | | (Toluca, México 2015) |
| | , | , |
| Kachu | 10 | 10 |
| Botno/Ae.squarrosa (66 | 6) 37.5 | 35 |
| Population F ₆ grand me | an 37.78 | 33.86 |
| Population range: low $Y_{ijkl} = \mu + Loc_i + Rep_i(Loc_i)$ - | + Block _k (Loc _i Re | p_i) 5 |
| Population (range: chigh- | +ε _{ijkl} 80 | 85 |

parent it ranged between 35-37.5%. Mean values of yellow rust ranged from 33.86% to 37.78% in the RILs population. Results for both environments are presented in Table 1. Heritability of yellow rust in





Table 2.Summary of heritability, variance components,
least significant difference and coefficient of
variation for combined analysis in Batán and
combined across both locations Batán and
Toluca, Mexico

| Parent, parameter (E | Combined analysis Batán, México 2015) | Combined analysis across both locations (Toluca, México 2015) |
|--|--|--|
| Population F ₆ grand mean | n 37.77 | 36.52 |
| Genotype variance (σ^2_{g}) | 248.78 | 333.33 |
| Location × genotype variance (σ^2_{ge}) | 76.13 | 106.01 |
| Residual variance (σ_e^2) | 73.71 | 86.92 |
| Heritability (h ²) | 0.81 | 0.77 |
| LSD | 18.78 | 18.30 |
| CV | 22.73 | 25.53 |

combined analysis in Batán between two replications was 0.81 and across both locations 0.77. Coefficient of variation within and across the replications were 22.73 and 25.53, respectively (Table 2).

The frequency distribution for disease severity was determined and plotted for both environments. The frequency distribution of RILs for yellow rust severity was continuous in the two field experiments, Batán and Toluca (Fig. 1).

Genotypic analysis of mapping population for yellow rust

Genotyping of the population was made through 2694 SNPs markers and 11 polymorphic SSR markers to validate the linkage maps construction. The chromosome position was defined based on the BLAST of clone ID sequences with wheat reference genome. Number of markers on chromosomes and length of chromosomes in centimorgans (cM) alongwith the total length of 21 chromosomes, 3816.57cM is given in Table 3.

Mapping and characterization of QTL

Composite interval mapping (CIM) revealed quantitative trait loci ($QTL_{2A.K}$) on chromosome 2AS significantly associated with the yellow rust resistance in Botno/*Ae. squarrosa* × Kachu RIL population. $QTL_{2A.K}$ explained phenotypic variance up to 48.8 %. Additive effect up to 18.2 % was observed. LOD score

| Chromosome | No. of markers | Chromosome length |
|------------|----------------|-------------------|
| 1A | 125 | 187.09 |
| 1B | 186 | 241.68 |
| 1D | 122 | 170.04 |
| 2A | 308 | 318.63 |
| 2B | 340 | 423.02 |
| 2D | - | - |
| 3A | 126 | 191.84 |
| 3B | 51 | 71.39 |
| 3D | 117 | 169.06 |
| 4A | 79 | 171.48 |
| 4B | 118 | 127.11 |
| 4D | 91 | 154.36 |
| 5A | 194 | 260.74 |
| 5B | 112 | 252.35 |
| 5D | 90 | 176.86 |
| 6A | 109 | 126.76 |
| 6B | 120 | 124.21 |
| 6D | 83 | 182.79 |
| 7A | 192 | 239.75 |
| 7B | - | - |
| 7D | 98 | 227.41 |

Table 3. Linkage map construction details for

recombinant inbred line (RIL) population

-= Not recorded

in mapping ranged between 18.6-34.7 in different trials. The positive QTL allele was contributed from elite parent of the population, 'Kachu'. $QTL_{2A,K}$ was located on proximal end of chromosome 2A short arm as shown in Fig. 2. Markers linked with this QTL were BARC122, 1028859|F|0-50:G>C and VENTRIUP-LN2. Genetic linkage map showed that marker interval bracketed by BARC122-1028859|F|0-50:G>C-VENTRIUP-LN2(3.3 cM) in different experiments. Results were consistent across two environments. Summary of QTL mapping results in different experiments have been presented in Table 4.

The banding pattern of PCR amplification corresponding to 2NS-specific dominant marker VENTRIUP/LN2 for *Yr17* were used to evaluat the complete population (Fig. 3). Results clearly indicated involvement of *Aegilops venticrossa* allele in controlling the effect of the candidate QTL.



Fig. 2. Likelihood plot of quantitative trait loci (QTL) for stripe rust on chromosome 2As, identified by lciMapping 4.0 program in F6 RIL population Botno/Ae.squarrosa (666) x KACHU; detected in two locations Batán and Toluca, Mexico. The significant logarithm of odds (LOD) threshold was detected based on 1,000 permutations, is shown on the vertical axis. Positions (in centimorgans) of the molecular markers along the chromosome is shown on the horizontal axe. MYR/ BV 2015: Mean Yellow rust, Batán 2015; MYR /MV 2015: Mean Yellow rust, Toluca 2015



Fig. 3. PCR amplification with 2NS-specific marker VENTRIUP/LN2 for Yr17. The arrow indicates the 2NS specific 262-bp PCR amplification product. This marker was evaluated for the entire F6 RIL population, but in the figure only fifteen lines are shown randomly to show how the score was performed; 2: presence of 2NS translocations and 0: Absence of 2NS translocations. The white color numbers show the phenotypic values of yellow rust disease severity from day 2 Batán, México 2015

should be due to presence of major genes in the population (Fig. 1). Study of phenotypic and genotypic coefficient of variation, heritability and genetic variance for yellow rust have been presented in Tables 1 and 2. Heritabilities of the yellow rust observed in this study

Table 4. Summary of quantitative trait loci (*QTL*_{2A,K}) for stripe rust in the F₆ RIL population, Batán and Toluca, México; position and effect of quantitative trait loci using composite interval mapping

| Trait | Chr | Pos | Left marker | Right marker | LOD | PVE (%) | Add |
|--------------|-----|-----|-------------|--------------|-----|---------|-------|
| M-YRBatan-1 | 2A | 11 | BARC122 | 1028859 F | 35 | 48.8 | -11.7 |
| M-YRBatan-2 | 2A | 12 | 1028859 F | VENTRIUP-LN2 | 19 | 22.2 | -10.2 |
| M-YRToluca-1 | 2A | 11 | BARC122 | 1028859 F | 32 | 46.1 | -18.3 |

Chr. = Chromosome, Pos = Position

Discussion

Kachu is one of the most important elite genotype of CIMMYT extensively used in crosses due to its combining ability and yellow rust resistance. The study aimed to understand the genetic basis of yellow rust resistance of 'Kachu' using [*Botno/Ae. squarrosa* (666])/kachu F_{4:6-}RIL population.

The yellow rust traits evaluated in present study showed a normal distribution in the population. This kind of distribution of genotypes in the population clearly suggests towards presence of sufficient recombinants. Deviation from normal for yellow rust were at higher score providing another line of evidence of presence of major gene(s) for yellow rust resistance.

The phenotypic variance explained by RIL population subjected to the QTL analysis study also indicated towards presence of large number of recombination events which is the most important and pre requisite for a breeding/breeding program. This is most likely due to the combining ability of elite parent 'Kachu'. This population can be analyzed for a number of adaptive traits to identify suitable trait donors as well as useful alleles governing adaptive traits.

Further, to harness potential of the large number

of recombination events, genetic characterization was carried out using high density genotyping platform DArT-seq. Linkage map construction was done using polymorphic marker scores in the population. Marker polymorphism in wheat is reportedly lower than in other major crops such as corn and soybean. Studies have shown that SSR marker polymorphism in corn and soybean is over 50%, whereas it is around or even below 40% in wheat (Sa 2012; Singh 2010). Common hexaploid wheat also has extremely low levels of polymorphism at DNA marker loci compared to its parent species, especially Ae. squarrosa (Nishikawa 1980). Polymorphism also depends on the parents. In the present study two contrasting parents, synthetic wheat and an elite variety were crossed so as to obtain large number of polymorphic markers. Polymorphic markers used in this study covered a genetic distance of 3816.57 cM among total of 21 chromosomes which is in complaince with previous reports (Li et al. 2015).

A major QTL $(QTL_{2A,K})$ for yellow rust resistance was identified on short arm of chomosome 2A using DArT-seq marker data (Table 4). Based on the pedigree of elite parent 'Kachu' we hypothesized that positive allele might be contributed from the wild ancestor (Ae. ventricosa). To test this hypothesis, SSR markers, Barc-122 and VENTRIUP-LN2 were amplified in the population lines to determine their possible association with yellow rust resistance. Specifically, VENTRIUP-LN2 was used to detect the presence of chromosome 2N of T. ventricosum (Tausch). 'VENTRIUP-LN2' is a SSR marker designed from the sequence of *Aegilops* ventricosa. Characterization by SSR marker confirmed that the effect of yellow rust resistance QTL in RIL population is contributed from 2NS of T. ventricosum (Tausch).

An important translocation 2NS/2AS from *Aegilops ventricosa* carrying the linked genes *Sr38*, *Lr37* and *Yr17* has been very useful in wheat improvement. Fang et al. (2011) had developed recombinant inbred lines (RILs) population involving Jagger carrying 2NS segment from *Ae. ventricosa* and an accession 2174 (1L 71-5662/PL145) and tested for stripe rust resistance under varied field conditions; the population segregated for *Yr17*, and effective resistance to common stripe rust pathogen(s). Later, Cavangh et al. (2013) had genotyped the above mentioned RIL population using a wheat bead chip which facilitated the discovery of additional resistance gene in the population. Avni et al. (2017) had also developed a marker for translocated segment of 2NS

region which may show close association with linked genes, *Sr38, Lr37* and *Yr17*. Xue et al. (2018) also characterized the 2NS region for rust resistance genes in wheat. All these works contributed enormously towards the wheat improvement using marker-based technology.

The results of present study are quite important for current and future genomic studies related to rust resistance. Ample number of elite wheat genotypes used in breeding or varietal pipelines are harboring segments from one or the other wild accessions. Genetic understanding of such germplasms should provide better understanding of genetic basis of resistance genes in wheat. The approach we followed in this study for yellow rust can be successfully applied for other traits such as grain quality, heat, drought or other traits.

Author contribution

Conceptualization of research (SuS, PV); Designing of the experiments (SuS, PV); Contribution of experimental materials (PV, CO, SuS); Execution of field/lab experiments and data collection (PV, SuS, CO); Analysis of data and interpretation (PV, SuS, SAS); Preparation of the manuscript (CO, PV, SuS, SAS)

Declaration

The authors declare no conflict of interest.

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