

Review Article

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Advanced Breeding Strategies to Mitigate the Threat of Yellow Stripe Rust of Wheat

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ABSTRACT

Stripe or yellow rust of wheat, caused by *Puccinia striiformis* f. sp. *Tritici* (Pst), is an important disease in many wheat-growing regions of the world. Although, the pathogen has overcome resistance offered by more than 90 genes and QTLs still, aggregation of resistant genes in future wheat genotypes is the most practical and efficient means of tackling the rapidly evolving virulent races of Pst. The germplasm of non-progenitor qwr4567890 *Aegilops* species with substantial amount of variability has been exploited to a limited extent. Various *Aegilops* species have been reported to possess resistance to several wheat diseases. A number of genes imparting resistance to various rusts have been transferred to cultivated wheats from their wild relatives. The Lr34/Yr18/Sr57/Pm38 gene is a globally important genetic resource for wheat resistance breeding against leaf rust and stripe rust. A total of 67 leaf rust resistance genes (Lr) and 48 stripe rust resistance genes (Yr) have been catalogued so far. Several genes for resistance to leaf rust and stripe rust have been introgressed from *Aegilops* and *Thinopyrum* species to cultivated wheat. Lines with adult plant resistance, gene pyramiding and shuttle breeding have been practised to have resistance against various races of the rust pathogen. Marker-assisted selection (MAS) methods for APR would be useful, however, the multigenic nature of APR impedes the use of MAS efforts that aim to pyramid only a few target genes.

Keywords

Stripe rust,
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Introduction

Stripe or yellow rust (YR), caused by *Puccinia striiformis* f. sp. *tritici*, has reportedly caused significant yield losses in more than 60 countries (Stubbs 1985; Chen 2005). Recently, YR has become a serious threat to wheat, causing 50–100 % yield losses due to the breakdown of existing resistance genes and gradual adaptation of new strains in warmer regions, particularly the Central and West Asia and North Africa (CWANA) region (ICARDA, 2011). The

breakdown of the widely used race-specific genes (R-genes) *Yr17* (Bayles *et al.*, 2000; Wan *et al.*, 2004; Chen 2007), *Yr27* (Singh *et al.*, 2004; Wan *et al.*, 2004), *Yr31* (Singh *et al.*, 2011; Rosewarne *et al.*, 2012), and *Lr24* (Park *et al.*, 2002) has created a serious challenge for wheat scientists and growers worldwide. Introducing genetic resistance into cultivars is the most economic and environmentally safe measure of rust disease management in wheat. To date, more than 71

LR and 53 YR resistance genes have been identified and catalogued in different *Triticum* and related species or genera (McIntosh *et al.*, 2012; Singh *et al.*, 2013; Xu *et al.*, 2013). Most of the formally designated genes confer race-specific resistance, which often loses effectiveness within a few years of deployment because cultivars with single R-genes facilitate selection for virulent races (Bolton *et al.*, 2008). Though most R-genes display high levels of resistance against the pathogen, and selection is therefore a relatively easy task, the longevity of those genes is only 3–5 years in a new cultivar (Singh, 2012). In the current scenario, the genes *Yr5* and *Yr10* may play a crucial role in the yellow rust breeding programme as they have shown field resistance and are effective against the prevalent races of yellow rust pathogen. Hence, detection of these genes can be very useful in wheat improvement programmes (Talha *et al.*, 2016)

Currently, the most effective methods for disease management are cultural control, fungicide applications and resistance, the latter being the most environmentally friendly and cost-effective approach (Roelfs *et al.*, 1992). Cytogenetic and mapping studies to identify resistance in wheat have led to the naming of more than 70 Yr genes, but there are many more with temporary designations (McIntosh *et al.*, 1995). The identification and incorporation of Yr genes has significantly benefited wheat growing regions affected by stripe rust. Efforts to develop markers for Yr genes have helped facilitate marker-assisted selection (MAS) and introgression of APR and ASR into elite breeding lines (Distelfeld *et al.*, 2006; Murphy *et al.*, 2009).

Molecular markers allow breeders to identify and select the presence or absence of genes in early generation populations, and only carry forward material indicative of resistance. These lines are then followed up with disease

phenotyping to confirm resistance. They are especially valuable in identifying quantitative traits or screening seedlings for APR resistance (Chen *et al.*, 2013). Molecular markers are also valuable when combining APR into a line with ASR, which because of its high level of resistance and continuous expression masks the effect of APR. In addition, MAS can facilitate more lines screened in earlier generations, pyramiding of resistance genes, and potentially reduces the time to release a new variety (Collard *et al.*, 2008). By improving the efficiency of disease resistance breeding, MAS may be a key part of increasing wheat production in the future as new *Puccinia striiformis* f. sp. *tritici* (Pst) races evolve.

Many prominent APR genes, such as *Lr34/Yr18/ Sr57/Pm38* (Dyck 1987; McIntosh 1992; Singh 1992; Spielmeier *et al.*, 2005; Lillemo *et al.*, 2008; Krattinger *et al.*, 2009), *Lr46/Yr29/Sr58/Pm39* (Singh *et al.*, 1998; William *et al.*, 2003; Lillemo *et al.*, 2008), *Lr67/Yr46/ Sr55/Pm46* (Herrer Foessel *et al.*, 2011; Hiebert *et al.*, 2011), *Yr36* (Fu *et al.*, 2009), *Sr2/Yr30* (Singh *et al.*, 2000; Suenaga *et al.*, 2003), and *Lr68* (Herrera-Foessel *et al.*, 2012), have been well characterized. Similarly, during the last 15 years, several molecular mapping studies have reported dozens of quantitative trait loci (QTL) distributed throughout all 21 chromosomes for YR resistance, and at least in 20 chromosomes for LR resistance in hexaploid wheat germplasm (Naz *et al.*, 2008; Basnet 2012; Singh 2012). Nonetheless, the identification of new sources of durable resistance and their molecular characterization is a continual process in ensuring genetic diversity in breeding programs that aim to develop advanced lines or cultivars with high and stable yield potential, besides having durable rust resistance and other desirable characteristics.

Quaiu 3, a high-yielding spring wheat line developed by the International Maize and Wheat Improvement Center (CIMMYT), displays a high level of resistance against LR and YR under field conditions. Recently, two sister lines of Quaiu 3 were released as the cultivars Koshan 09 (Afghanistan) and Gambo (Ethiopia) (CIMMYT Wheat Atlas: <http://wheatatlas.cimmyt.org/country/varieties/AFG/0>). Quaiu 3 does not seem to carry any effective seedling resistance genes for YR resistance, as it displays high infection type (IT) ratings in seedling screenings (IT 6–8 on the 0–9 scale, depending on Mexican *P. striiformis* races and the greenhouse environment). However, it carries a moderately effective race-specific LR resistance gene (*Lr42*), initially transferred from *Aegilops tauschii* to the winter wheat line KS91WGRC11 (Basnet *et al.*, 2013). In a previous study, Basnet *et al.*, (2013) also estimated a minimum of three genes conferring resistance to both LR and YR in Quaiu 3. In addition to *Lr42*, they also suggested that Quaiu 3 carries two APR genes, *Yr29* and *Yr30*, based on closely linked molecular markers. However, these known genes alone were not able to display near immune resistance to both LR and YR as in resistant parent Quaiu 3 (Basnet *et al.*, 2014).

Sr2/Yr30 Gene

The gene, *Sr2* was transferred to hexaploid wheat from tetraploid emmer wheat cultivar Yaroslav in 1920. It is present on chromosome 3BS and is also reported to be associated with *Lr27* (Singh and McIntosh 1984). It is completely linked with pseudo black chaff (*Pbc*), which is used as morphological marker for identification of lines carrying this gene. The genotypes with *Pbc* show varying level of stem rust infection. The maximum severity level of 60–70% has been noted as compared to 100% severity of susceptible check in disease screening

nurseries in Kenya. When present alone it does not provide sufficient level of resistance but in combination with other genes desirable level of resistance can be achieved. Much information is not available about the interaction of *Sr2* and other genes in *Sr2* complex. The adequate resistance level can be achieved by accumulating 4–5 minor genes. *Sr2* was detected in several highly resistant old, tall Kenyan cultivars like Kenya plume and semi dwarf CIMMYT, cultivars Pavon F 76, Parula, Kingbird, Dollar bird etc. These cultivars show maximum disease severity of 10–15% with moderately resistant reactions. The gene *Sr2* is tightly linked with *Yr30* or has pleiotropic effects (Singh and Huerta-Espino, 2000). A microsatellite (SSR) marker *gwm533* is tightly linked and associated with the presence of this gene, which can be used to facilitate selection of this difficult to score gene (Spielmayer *et al.*, 2003).

Lr34/Yr18

Numerous genes conferring resistance to wheat rusts have been identified and used in wheat (*T. aestivum* L.) breeding. However, several of these genes have been rendered ineffective due to emergence of new virulent races. Cultivars with the rust resistance gene *Lr34* such as Frontana had effective durable rust resistance to leaf rust (*P. triticina*). Although *Lr34* has been used extensively in spring wheat grown in US, isolates of *P. triticina* with complete virulence to this gene had not been detected (Kolmer *et al.*, 2003). It has been found that soft red winter wheats having *Lr34* in combination with seedling resistant *Lr2a*, *Lr9*, *Lr26* were highly resistant while in combination with *Lr10*, *Lr11*, *Lr18* were moderately to low resistant in USA (Kolmer, 2009).

Lr34, which has recently been cloned and found to encode an ATP-binding cassette (ABC) transporter of the ABC transporter

subfamily G (ABCG), formerly known as pleiotropic drug resistance (PDR) subfamily (Krattinger *et al.*, 2009), is known to confer broad-spectrum resistance to at least four biotrophic diseases: leaf rust (Dyck *et al.*, 1966), stripe rust (Singh, 1992b), stem rust (Dyck, 1987) and powdery mildew (Lillemo *et al.*, 2008; Spielmeier *et al.*, 2005). *Lr34* is also associated with a premature senescence of the leaf tips, commonly referred to as leaf tip necrosis (LTN) (Singh, 1992a).

Lr46/Yr29

A slow rusting gene identified in the cultivar Pavon and was found located on chromosome 1B by crossing with a monosomic series of adult plant leaf rust susceptible cultivar Lal Bahadur (Singh *et al.*, 1998). This is the 2nd named minor gene involved in slow rusting. The leaf rust resistance gene *Lr46* and yellow rust resistance gene *Yr29* are tightly linked or Pleiotropic (William *et al.*, 2003). Its effect is similar to *Lr34/Yr18* as it does not provide complete immunity to plants. Infected adult plants carrying *Lr46* have longer latency period as compared to control without this gene (Martinez *et al.*, 2001). The plants with this gene also show higher rate of fungal colonies abortion with out any chlorotic or necrotic effects and also decrease the colony size. The resistance conferred by this gene is not of hypersensitive type (Suenaga *et al.*, 2003) determined that the microsatellite locus Xwmc44 is located 5.6-cM proximal to the putative QTL for *Lr46*. Leaf tip necrosis (Ltn) has been reported to be highly correlated with the presence of *Lr46/Yr29* gene (Rosenwarne *et al.*, 2010). Efforts are underway to clone this gene.

Lr34/Yr18/Sr57/Pm38

The *Lr34/Yr18/Sr57/Pm38* gene is a globally important genetic resource for wheat resistance breeding against leaf rust and stripe

rust. It has also been shown to confer partial resistance to powdery mildew, and in some genetic backgrounds to stem rust. The locus has further been associated with tolerance to barley yellow dwarf virus. *Lr34* has been widely used in wheat cultivars worldwide and its resistance has remained effective over many years (possibly more than 100), making it one of the few known resistance genes with a generally large effect and durability despite large-scale, agricultural use. The gene was first described as *LrT2* (Dyck, 1977, 1987) and later identified in several distinct groups of genetic material, *e.g.* CIMMYT lines, Chinese landraces and Eastern European winter wheat material (Kolmer *et al.*, 2008; Krattinger *et al.*, 2009). The *Lr34/Yr18* gene acts quantitatively, *i.e.* it confers only partial resistance and generally has to be used in combination with other quantitatively acting resistance genes to provide sufficient resistance under heavy disease pressure. *Lr34* is active specifically in the adult plant stage and the flag leaf is usually evaluated in assays of plants containing the gene against leaf and stripe rust as well as powdery mildew (McIntosh 1992; Singh 1992; Spielmeier *et al.*, 2005). *Lr34/Yr18* activity is correlated with leaf tip necrosis (LTN) on the flag leaf which can be used as a phenotypic marker for *Lr34/Yr18* and which is also expressed in the absence of the pathogen (Dyck 1991; Lagudah *et al.*, 2006). However, the expression of LTN is environmentally dependent and can vary greatly in different environmental conditions and genetic backgrounds. *Lr34/Yr18* was cloned by bi-parental mapping and positional cloning using integrated molecular marker information from several crosses as well as physical maps from the D genome of *Aegilops tauschii* and hexaploid wheat (Krattinger *et al.*, 2009).

Based on the knowledge of the *Lr34/Yr18* gene sequence, gene-specific markers were developed and have proven to be highly

diagnostic for the *Lr34* gene (Lagudah *et al.*, 2009; Dakouri *et al.*, 2010). The analysis of eight independent mutants revealed that the same gene is in fact responsible for leaf and stripe rust resistances as well as LTN (Krattinger *et al.*, 2009). Henceforth, we will refer only to *Lr34*, keeping in mind that it is a multi-pathogen resistance gene with a pleiotropic effect of leaf tip necrosis.

***Lr34/Yr18* compared to other cloned leaf rust or stripe rust resistance (R) genes**

No major gene against stripe rust (Yr genes) has yet been isolated. The cloned *Yr36* is a temperature-dependent resistance gene with no race specificity detected to date (Fu *et al.*, 2009). *Yr36* encodes a protein with an N-terminal kinase domain a C-terminal lipid transfer (START) domain. Thus, the protein structure and possibly molecular mode of action is very different from *Lr34*.

Characterization and molecular mapping of *Yr52* for high-temperature adult-plant resistance to stripe rust in spring wheat germplasm PI 183527

High-temperature adult-plant (HTAP) stripe rust resistance has proven to be race non-specific and durable. However, genes conferring high-levels of HTAP resistance are limited in number and new genes are urgently needed for breeding programs to develop cultivars with durable high-level resistance to stripe rust. Spring wheat germplasm PI 183527 showed a high-level of HTAP resistance against stripe rust in germplasm evaluations over several years. To elucidate the genetic basis of resistance, we crossed PI 183527 and susceptible wheat line Avocet S. Adult plants of parents, F1, F2 and F2:3 progeny were tested with selected races under the controlled greenhouse conditions and in fields under natural infection. PI 183527 has a single dominant gene conferring HTAP

resistance. Resistance gene analog polymorphism (RGAP) and simple sequence repeat (SSR) markers in combination with bulked segregant analysis (BSA) were used to identify markers linked to the resistance gene. A linkage map consisting of 4 RGAP and 7 SSR markers was constructed for the resistance gene using data from 175 F2 plants and their derived F2:3 lines. Amplification of nulli-tetrasomic, ditelosomic and deletion lines of Chinese Spring with three RGAP markers mapped the gene to the distal region (0.86–1.0) of chromosome 7BL. The molecular map spanned a genetic distance of 27.3cm, and the resistance gene was narrowed to a 2.3cm interval flanked by markers Xbarc182 and Xwgp5258. The polymorphism rates of the flanking markers in 74 wheat lines were 74 and 30 %, respectively; and the two markers in combination could distinguish the alleles at the resistance locus in 82 % of tested genotypes (Ren *et al.*, 2012).

To determine the genetic relationship between this resistance gene and *Yr39*, a gene also on 7BL conferring HTAP resistance in Alpowa, a cross was made between PI 183527 and Alpowa. F2 segregation indicated that the genes were 36.5 ± 6.75 cm apart. The gene in PI 183527 was therefore designed as *Yr52*. This new gene and flanking markers should be useful in developing wheat cultivars with high level and possible durable resistance to stripe rust (Ren *et al.*, 2012).

Characterization of a major QTL for adult plant resistance to stripe rust in US soft red winter wheat

Pioneer 26R61 has provided effective resistance to stripe rust for 10 years. To elucidate the genetic basis of the resistance, a mapping population of 178 recombinant inbred lines (RILs) was developed using single-seed descent from a cross between Pioneer 26R61 and the susceptible cultivar

AGS 2000. A genetic map with 895 markers covering all 21 chromosomes was used for QTL analysis. One major QTL was detected, explaining up to 56.0% of the mean phenotypic variation, flanked by markers Xbarc124 and Xgwm359, and assigned to the distal 22% of the short arm of wheat chromosome 2A. Evidence showed that it was different from *Yr17* derived from *Ae. ventricosa*, the only formally named Yr gene in 2AS, and the QTL was temporarily designated as *YrR61*. In addition, a minor QTL, QYr.uga-6AS, probably conditioned high temperature adult plant resistance. The QTL explained 6–7% of the trait variation. Preliminary test of the flanking markers for *YrR61*, in two cultivars and two promising breeding lines with Pioneer 26R61 in their pedigree, indicated that *YrR61* was present in these cultivars and lines, and these markers could therefore be used in marker assisted selection (Hao *et al.*, 2011).

Characterization of *Yr54* and other genes associated with adult plant resistance to yellow rust and leaf rust in common wheat Quaiu 3

Quaiu 3, a common wheat line developed at the International Maize and Wheat Improvement Center (CIMMYT), is immune to YR in Mexico despite seedling susceptibility to predominant races. Quaiu 3 also shows immunity to LR in field trials and is known to possess the race-specific gene *Lr42*. A mapping population of 182 recombinant inbred lines (RILs) was developed by crossing Quaiu 3 with susceptible Avocet- YrA and phenotyped with LR and YR in field trials for 2 years in Mexico. Quantitative trait loci (QTL) associated with YR and LR resistance in the RILs were identified using Diversity Arrays Technology and simple sequence repeat markers. A large-effect QTL on the long arm of chromosome 2D explained 49–54 % of the

phenotypic variation in Quaiu 3 and was designated as *Yr54*. Two additional loci on 1BL and 3BS explained 8–17 % of the phenotypic variation for YR and coincided with previously characterized adult plant resistance (APR) genes *Lr46/Yr29* and *Sr2/Yr30*, respectively. QTL on 1DS and 1BL corresponding to *Lr42* and *Lr46/Yr29*, respectively, contributed 60–71 % of the variation for LR resistance. A locus on 3D associated with APR to both diseases explained up to 7 % of the phenotypic variance. Additional Avocet- Yr A-derived minor QTL were also detected for YR on chromosomes 1A, 3D, 4A, and 6A. *Yr54* is a newly characterized APR gene which can be combined with other genes by using closely linked molecular markers (Basnet *et al.*, 2013).

Genetic mapping of a putative *Thinopyrum intermedium* derived stripe rust resistance gene on wheat chromosome 1B

Rust resistance was transferred from *Thinopyrum intermedium* to common wheat, and the resulting introgression line (L693) exhibited all-stage resistance to the widely virulent and predominant Chinese pathotypes CYR32 and CYR33 and to the new virulent pathotype V26. There was no cytological evidence that L693 had alien chromosomal segments from *Th. intermedium*. Genetic analysis of stripe rust resistance was performed by crossing L693 with the susceptible line L661. F1, F2, and F2:3 populations from reciprocal crosses showed that resistance was controlled by a single dominant gene. A total 479 F2:3 lines and 781 pairs of genomic simple sequence repeat (SSR) primers were employed to determine the chromosomal location of the resistance gene. The gene was linked to six publicly available and three recently developed wheat genomic SSR markers. The linked markers were localized to wheat chromosome 1B

using Chinese Spring nulli-tetrasomic lines, and the resistance gene was localized to chromosome 1B based on SSR and wheat genomic information. A high-density genetic map was also produced. The pedigree, molecular marker data, and resistance response indicated that the stripe rust resistance gene in L693 is a novel gene, which was temporarily designated *YrL693*. The SSR markers that co-segregate with this gene (Xbarc187-1B, Xbarc187-1B-1, Xgwm18-1B, and Xgwm11-1B) have potential application in marker-assisted breeding of wheat, and *YrL693* will be useful for broadening the genetic basis of stripe rust resistance in wheat (Huang *et al.*, 2014).

Novel QTL for stripe rust resistance on chromosomes 4A and 6B in soft white winter wheat cultivars

Stripe rust of wheat is a devastating disease in temperate regions when susceptible varieties are grown and environmental conditions sustain high disease pressures. With frequent and severe outbreaks, disease resistance is a key tool for controlling stripe rust on wheat. The identification of quantitative trait loci (QTL) involved in stripe rust resistance from the important US Pacific Northwest soft white winter wheat varieties "Eltan" and "Finch" was carried out. An F2:5 recombinant inbred line (RIL) mapping population of 151 individuals derived from the Finch-Eltan cross was developed through single seed descent. A linkage map comprising 683 unique single nucleotide polymorphism (SNP) loci and 70 SSR markers were used to develop 22 linkage groups consisting of 16 of the 21 chromosomes. Stripe rust data were collected on the RILs during the summers of 2012 to 2014. QTL analysis identified two genomic regions on chromosomes 4A (QYrel.wak-4A) and 6B (QYrfi.wak-6B) associated with resistance from Eltan and Finch, respectively. The results of the QTL

analysis showed that QYrel.wak-4A and QYrfi.wak-6B reduced infection type and disease severity. Based upon both molecular and phenotypic differences, QYrel.wak-4A is a novel QTL for adult plant resistance (APR) to stripe rust (Klarquist *et al.*, 2016).

Genetic architecture of resistance to stripe rust in a global winter wheat germplasm collection

Virulence shifts in populations of *Puccinia striiformis* f. sp. *tritici* (Pst), the causal pathogen of wheat stripe rust, are a major challenge to resistance breeding. The majority of known resistance genes are already ineffective against current races of Pst, necessitating the identification and introgression of new sources of resistance. Germplasm core collections that reflect the range of genetic and phenotypic diversity of crop species are ideal platforms for examining the genetic architecture of complex traits such as resistance to stripe rust. We report the results of genetic characterization and genome-wide association analysis (GWAS) for resistance to stripe rust in a core subset of 1,175 accessions in the National Small Grains Collection (NSGC) winter wheat germplasm collection based on genotyping with the wheat 9K single nucleotide polymorphism (SNP) iSelect assay and phenotyping of seedling and adult plants under natural disease epidemics in four environments. High correlations among the field data translated into high heritability values within and across locations. Population structure was evident when accessions were grouped by stripe rust reaction. GWAS identified 127 resistance loci that were effective across at least two environments, including 20 with significant genome-wide adjusted P-values. Based on relative map positions of previously reported genes and QTL, five of the QTL with significant genome-wide adjusted P-values in this study represent potentially new loci. This

study provides an overview of the diversity of Pst resistance in the NSGC winter wheat germplasm core collection, which can be exploited for diversification of stripe rust resistance in breeding programs (Peter *et al.*, 2016).

Markers assisted selection for multiple stripe rust resistance genes in spring bread wheat lines

In order to stack combination of effective stripe rust resistance genes in future wheat genotypes, 99 spring wheat lines derived from the cross of Khyber-87 × Suleman-96 were screened with five closely linked PCR-based markers with stripe rust resistance genes *Yr5*, *Yr10*, *Yr17* and *Yr9*. Out of 99 experimental lines, S19M93 and S23M41 markers revealed the presence of *Yr5* gene in 86 and 70 genotypes, respectively. While, Xpsp3000 suggested presence of *Yr10* gene in 66 genotypes, excluding two heterozygous lines PBS-07-60 and PBS-07-64. VENTRIUP-LN2 marker revealed that all genotypes were negative for *Yr17* gene, while iag95 marker revealed presence of rye origin *Yr9* gene in all genotypes. The presence of 1RS fragments were related to the poor bread making quality in certain wheat backgrounds. Furthermore, coexistence of both Xpsp3000 and iag95 markers are indicative of the potential interstitial recombination between wheat 1BS and rye 1RS chromatin or the presence of 1RS fragments on more desirable wheat chromosomes 1A or 1D (Ullah *et al.*, 2016).

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