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Review

Genes for resistance to stripe rust on chromosome 2B and their application in wheat breeding

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Abstract

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is one of the most damaging diseases of wheat worldwide. Growing resistant cultivars is the most economic and environmental friendly way to control the disease. There are many resistance genes to stripe rust located on wheat chromosome 2B. Here, we propose a strategy to construct the recombinant wheat chromosome 2B with multiple resistances to stripe rust by making crosses between wheat lines or cultivars carrying *Yr* genes and using marker-assisted selection, based on the reported information about resistance spectrum, chromosomal location, and linked markers of the genes. Pyramiding the resistance genes on 2B would afford a valuable strategy to control the disease by cultivating varieties with durable resistance. The possibility, efficiency, and prospect of the suggested strategy are reviewed in the paper.

Keywords: *Puccinia striiformis*; *Yr* gene; 2B chromosome; Stripe rust; Marker-assisted selection

1. Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most widely devastating wheat (*Triticum aestivum* L.) diseases in the world, especially in areas with cool and moist environments. The fungus is hemicyclic, a sexual cycle has not been identified, and host species other than wheat (and perhaps a few very closely related species in areas of their occurrence) are not significant in epidemiology and survival [1]. Wind dispersal of its spores for hundreds or thousands of kilometers has caused its widely spread on a continental or global scale and allows the regular reestablishment of this disease in regions where the climate is seasonally unfavorable [2]. Stripe rust of wheat and barley led to yield losses as high as 50% due to shriveled grain and weakened plant development [3]. In southwestern China, stripe rust is the most devastating disease of wheat [4,5], and caused yield losses of 20–30%. Although chemical control and wheat cultivation measures can reduce the loss caused by stripe rust at some degree, the most economic and environmental friendly way to control the disease is through deployment of genetic resistance [6,7].

There are more than 40 stripe rust resistance (*Yr*) genes designated so far [8], most of which are associated with the hypersensitive reaction and interact with the pathogen in a gene-for-gene fashion [9]. Virulence in the pathogen population has been detected following the deployment of many such resistance genes. Therefore, the effective exploitation and utilization *Yr*s, such as pyramiding different resistant genes, would be advantageous to develop durable and broad-spectrum resistant wheat cultivars.

Southwest China is the largest epidemic region in the world because of the temperate environmental condition in wheat growing season [4,5,10]. In recent years, stripe rust

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has become the most devastating disease in the region due to the epidemics of new physiological races of the pathogen CYR31 and CYR32 [11]. Most of the resistance genes used in wheat production of southwestern China have become ineffective to the two races [3,4,12]. Therefore, it is essential to develop cultivars with durable and broad-spectrum resistant varieties. The purpose of the present paper is to summarize the recent progress made on the research of *Yr* genes on wheat chromosome 2B and to propose a strategy to use them in wheat resistance breeding to stripe rust.

2. *Yr* genes on chromosome 2B

Many resistance genes to stripe rust have been mapped on chromosome 2B, including *Yr5*, *Yr7*, *Yr27*, *Yr31*, *YrV23*, *YrSp*, *YrQz*, *YrTp1*, *YrCN19*, and the resistance gene in genotype YW243 has been identified [4,13,17]. They are still effective in conferring resistance to all or to some races of *P. striiformis* f. sp. *tritici* in China.

2.1. Yr5

Yr5, originally derived from *T. spelta album*, was first localized on chromosome 2B by Macer [18] with monosomic analysis, and then it was further mapped on the 2B long arm, 21 cM away from the centromere [19]. At present, almost all isolates of *P. s. tritici* in the world except a few from India and Australia are avirulent to *Yr5* [12,20]. So it has been used widely in wheat breeding programs (X.M. Chen, personal communication). Several microsatellite markers on wheat chromosomal arm 2BL linked to *Yr5* had been identified by Sun et al. [21]. To combine *Yr5* with other seedling resistance genes and with high temperature adult plant (HTAP) resistance for providing durable and superior resistance, three resistance gene analog polymorphism (RGAP) markers, co-segregated with the *Yr5* locus, and four markers tightly linked to the locus have been developed [22]. Further, some more valuable makers including sequence tagged site (STS) and cleaved amplified polymorphic sequence (CAPS) markers have also been developed [23]. Undoubtedly, these studies would accelerate transferring of *Yr5* into commercial cultivars and combining *Yr5* with other *Yr* genes by marker-assisted selection.

2.2. Yr7

Yr7 was first identified in wheat (*T. aestivum* L.) cultivar 'Lee', and genetic analysis suggested that it is a single dominant gene [24]. It was mapped on the chromosome 2B by monosomic analysis [18,25]. It is one of the *Yr* genes used widely by CIMMYT during the 1970s and 1980s, and has been deployed in many commercial cultivars in North America [26–28] and in Eucador [29]. Many of the varieties in France and China also carry *Yr7* [30]. It played an important role in protecting wheat yield when the epidemic occurred both in 1984 and 1985 [31]. To accelerate its application in wheat breeding programs in China, Xu et al. have developed the near isogenic line of *Yr7* using Taichung29 as the recurrent parent [32] and to enhance the efficiency of selection, Yao et al. [33] identified a microsatellite marker *Xgwm* 526 on the chromosome arm 2BL, linked closely with *Yr7* locus.

2.3. Yr27

Yr27 was traced to a Canadian farmer's selection named McMurachy from where the gene was transferred to Selkirk, and subsequently to a range of CIMMYT cultivars [34]. The gene responsible for the resistance to stripe rust in Selkirk was first described and named *YrSk* by Wellings [35]. Thereafter, McIntosh et al. [36] further illustrated its existence and found a difference in symptoms between homozygosity and heterozygosity for the gene by isolating avirulent races. *Yr27* was located on wheat chromosome arm 2BS, closely linked to leaf rust resistance genes *Lr13* and *Lr23* in the proximal region [34]. It is apparently quite effective in conferring resistance to avirulent races under field conditions, and it is present in a number of CIMMYT generated wheat selections including Ciano 79, Nacozari 76, Crow, Tesia 79, Opata 85, Bacanora 88, Bakhtawar, WH542, Atrak, Memof, PBW343, MH97, Chamaran, Kubsa, and Shirudi [35]. Although some cultivars in Iran, Syria, Pakistan and India, whose resistance is based largely on *Yr27*, have become highly vulnerable because some new races are virulent to *Yr27* in the regions [34], many stripe rust races except for CYR30, CYR31, and CYR32, are avirulent to *Yr27* in China [4,5,11,12]. Therefore, *Yr27* would be a valuable component of gene combination for conferring durable resistance of wheat to stripe rust in China.

2.4. Yr31

Yr31, first found in a CIMMT cultivar 'Pastor', was mapped on the chromosomal arm 2BS [37]. Genetic analysis showed that *Yr31* also is located in or near a cluster of resistance genes in the proximal region on the short arm of wheat chromosome 2BS, and the genes located in the region include leaf rust resistance genes *Lr13* and *Lr23*, stripe rust resistance genes *YrSp* and *Yr31*, and stem rust resistance gene *Sr10* [34]. The recombinant values of *Yr31* and *Yr27*, of *Yr31* and *Lr23*, and of *Yr27* and *Lr23*, are 0.148, 0.295, and 0.131, respectively (http://www.wheat.pw.usda.gov). In addition, *Yr31* would also have large potential to wheat resistance breeding because it has adult plant resistance to stripe rust [38]. In China, *Yr31* is effective against many stripe rust races except for some newly emerged races such as CYR31 and CYR32 [4,5,11,12]. In China wheat resistance breeding programs, *Yr31* may have a role in crop protection when in gene combinations.

2.5. YrSp

YrSp is one of the three resistance genes to stripe rust in wheat cultivar 'Spaldings Prolific', which is a UK cultivar with unknown pedigree [39] and one of the 15 wheat cultivars in the set of differential cultivars proposed by Johnson et al. [40] and is currently used widely for identifying *P. striiformis* f. sp. *tritici* races in the word. The resistance of 'Spaldings Prolific' to European race 4 and North American race 61–1 is conferred by a single dominant gene [41]. Further genetic analysis of resistance to two races of the pathogen showed that there are three pairs of resistance genes to stripe rust in the 'Spaldings Prolific' [39]. One of them was designated *YrSp* by McIntosh [36], which is located on wheat chromosomal arm 2BS [34,42]. Then some authors reported new virulent races on *YrSp* [20,29,43]. In China, *YrSp* is still effective to many races of *P. striiformis* f. sp. *tritici* including CYR31 and CYR32 [11,12,44]. Hence, *YrSp* may be an important resistance resource against stripe rust worldwide [45]. This gene has been mapped to the region SSR marker *Xwmc441* by Guan et al. [46].

2.6. YrV23

YrV23 was first identified in the wheat cultivar 'Vilmorin 23' [47], an important species that has a strong ability to differentiate races and carries *Yr3* besides *YrV23* [36]. Monosomic analysis showed that *Yr4a* and *YrV23* were located on 1B and 2B respectively [13]. The near isogenic line of *YrV23* has been established using Taichung29 as the recurrent parent [32], and SSR analysis identified a microsatellite marker *Xwmc356*, located on the chromosomal arm 2BS (http://www.wheat.pw.usda.gov), was linked with the resistance gene *YrV23*, with 9.4 cM genetic distance [48]. This would be very useful for pyramiding resistance genes with marker-assisted selection.

2.7. YrQz

YrQz was first identified in a common wheat line Qz180 by Deng et al. [15]. The resistance segregation of *YrQz* followed the single dominant gene mode, which was located within the region flanked by microsatellite Xgwm388 and *Xgwm526* on the long arm of wheat chromosome 2B. Amplified fragment length polymorphism (AFLP) analysis showed that two markers P35M48 and P36M61were closely linked to *YrQz* with 3.4 and 4.1 cM genetic distance, respectively [15]. *YrQz* is effective to CYR30 and would have an important role in counterbalancing the fasting evolution of stripe rust pathogens if it is combined with other *Yr* genes.

2.8. YrTp1

YrTp1, derived from *Thinopyrum ponticum*, was mapped on 2BS, 0.4 cm from SSR *WMC477* [17]. It is effective against many races of *P. striiformis* f. sp. *tritici* in China, including CYR31 and CYR32 [17]. Hence, it is a valuable resistance resource for improvement of controling stripe rust in wheat.

2.9. The resistance gene in YW243

A resistance gene to stripe rust was identified in a Chinese resistance source YW243, and was identified to be linked to *Xgwm388* and *Xgwm501* on chromosome 2B with 27.9 and 23.5 cM genetic distance, respectively [16]. YW243 is effective to CYR31, and would have large potential for developing durable resistance cultivars by combining the resistance gene in YW243 with other *Yr*s.

2.10. YrCN19

YrCN19 on 2BS displayed a high resistance throughout the wheat growth stages to almost all the Chinese races of *P. striiformis* f. sp. *tritici* [4,5], which was first identified in several wheat lines and cultivars originating from the southwestern region of China. Linkage analysis showed that SSR marker *Xgwm410*, on the short arm of chromosome 2B, co-segregates with the resistance gene *YrCN19* and could be used as a diagnostic marker for it, which has potential for application in the marker-assisted breeding [4]. Further genetic analysis proved that the resistance expression and separation of *YrCN19* is dependent on the background or cross combination [5]. Cultivar Chuan-nong 19 (CN19), carrying the resistance gene *YrCN19*, has been released in Sichuan Province of China in 2003. *YrCN19* is one of the resistance genes used currently in wheat resistance breeding programs of Southern China [49,50].

3. Prospect of *Yr* genes on chromosome 2B for stripe rust resistance breeding

Growing resistance varieties is the most-efficient and environmentally sustainable means of reducing losses due to the disease. The most common form of resistance employed is race-specific all-stage (also called seedling) resistance, which can be detected at the seedling stage and remains effective at all stages of plant growth. It is conferred by single genes following the gene-for-gene interaction model [9]. A significant problem with this type of resistance is virulence changes in the pathogen population, which can overcome the resistance. Therefore, such race-specific resistance genes have a limited effective life. The combination of different sources and types of resistance within a single genotype should assist in the development of durable resistant varieties and prolong the life of race-specific resistance genes [51]. However, certain gene pyramids have been shown to fail after widespread exposure to the pathogen population [20,37,52,53] because of the lack of basic information such as the virulence to

Yr genes, and the origins and genetic diversity of combined *Yr* genes [54].

3.1. The resistance spectrum of Yr genes on chromosome 2B

The formae speciales *P. striiformis* f. sp. *tritici*, the pathogen causing stripe rust on wheat, is further separated into races based on avirulence or virulence to cultivars or genotypes of wheat. Allison et al. [55] first reported the physiological specialization of this pathogen. Races are differentiated by infection types produced on a set of selected plant genotypes or single gene lines that are referred as differentials. The combined effects of mutations and migration or influxes of new genotypes with subsequent sexual reproduction or somatic hybridization between or within the immigrant and local populations is believed to be responsible for genetic variation in rust fungi, which gives rise to new races [56]. In 1980, Wright and Lennard reported that somatic recombination of whole nuclei during germ tube fusion could result in new pathotypes and produced a novel pathotype of yellow rust by mixing urediniospores of two pathotypes and inoculating them on the same plant [57]. Airborne spread of urediniospores between countries growing a wide array of different wheat cultivars contributes to pathotype diversity [1,2]. The stepwise mutation model, suggested by Steele et al. [1], indicates that spontaneous mutation from avirulence to virulence may be the other important mechanism for generating variation in virulence characteristics. At present, there are a total of 67 Chinese races (32 CYR races and 35 "pathotypes") have been identified based on their virulence and avirulence patterns on the 17 differential genotypes (Trigo Eureka, Fulhard, Letescens 128, Mentana, Virgilio, Abbondanza, Early Premium, Funo, Danish 1, Jubilejina 2, Fengchan 3, Lovrin 13, Kangyin 655, Shuiyuan 11, Zhong 4, Lovrin 10, and Hybrid 46) [12]. The fast evolution of virulence in rust populations makes pyramiding different resistant genes with various spectrum resistances to stripe rust races, as well searching new resources of rust resistance, be necessary in wheat breeding programs for resistance to stripe rust.

In terms of the resistance spectrum, *Yr5* has broad-spectrum resistance to stripe rust [12,20,58]. Though some new races reported in Eucador have virulence on *Yr7*, it still has large potential for wheat resistance breeding to stripe rust worldwide [29]. *Yr7* is also effective against some races such as CYR23 and CYR27 [24,30,32,33] in China. Many stripe rust races in China except for CYR30, CYR31, and CYR32, are avirulent to *Yr27* [4,5,11,12]. This implicates that *Yr27* would be a valuable gene for conferring durable resistance by pyramiding wheat resistance breeding programs in China. *Yr31* is still effective to stripe rust races except for some newly emerged races such as CYR31 and CYR32 [4,5,11,12], and the potential of *Yr31* to wheat resistance breeding to stripe rust is also embodied by its adult plant resistance against wheat stripe rust [38] as well as race-specific resistance [4,5,11,12]. *YrSp* is still effective to many Chinese races of *P. striiformis* f. sp. *tritici* including the current predominant race CYR31 and CYR32. Hence, *YrSp* is being used as an important resistance resource [45]. The resistance gene *YrV23* can be effective against race 2E16 [48]. *YrQz* is effective against CYR30 [15]. The gene temporarily designated as *YrTp1* is effective to many Chinese races of *P. striiformis* f. sp. *tritici*, including CYR31 and CYR32 [17]. The resistance gene against stripe rust in YW243 is effective against CYR31 [16]. *YrCN19* displayed a high resistance at seedling and adult stages to almost all the currently prevalent races in China [4,5,49,50].

3.2. Genetics of Yr genes

Since Biffen [59] first demonstrated that resistance to stripe rust in wheat follows Mendel's laws, the genetics of resistance to stripe rust has been studied for a century. Genetic analysis showed that segregation of *Yr* genes on wheat chromosome 2B complied with the single dominant gene mode with 3:1 resistant: susceptible ratio [4,13–17]. In pyramiding for resistant genes, the genetic model would be advantageous to enhance the efficiency by marker-assisted selection.

3.3. Genetic diversity of Yr genes

P. striiformis f. sp. *tritici*, as an airborne fungal pathogen, can disperse in long-distance in the air [2,60], which enables races of the pathogen to spread to new geographic areas. We strongly suggest using resistance genes with large genetic diversity to pyramid with multiple resistance genes. As far as pedigrees of the *Yr* genes on chromosome 2B are concerned, these genes are derived from wheat [4,5,15–18,26–28,37,47], except for *Yr5* from *T. spelta album* [18], and *YrTp1* from *Th. ponticum* [17]. Based on their different geographic origins, pedigrees, and reactions to stripe rust races, these genes on chromosome 2B are largely diverse.

We would assume that pyramiding these genes on 2B may lead to development of varieties with durable resistance, which may play an important role in protecting wheat crops from yield losses caused by stripe rust in the world, especially in China.

4. Control of stripe rust by constructing recombinant 2B chromosome with multiple resistance genes

More durable resistance against stripe rust can be achieved by pyramiding resistance genes, those alone may be ineffective but together provide resistance to the current pathogen population, so that the usefulness of the seedling resistance genes can be prolonged. Some of the *Yr* genes on 2B have a broad resistance spectrum against stripe rust. If they can be pyramided into a single genotype by genetic recombination, the *Yr* genes would have great potential to enhance the durability of resistance and prolong the lives of them.

4.1. Possibility of the construction of recombinant 2B chromosome

The possibility to genetically recombine genes depends upon their genetic distance. Though the data show that *Yr27*, *Yr31*, and *YrSp* are in a same cluster of resistance genes, which does not mean no crossing-over occurrences, the recombinants with various frequencies between them have been reported [34,42]. Information on chromosomal locations of genes on 2B shows that they have different position on chromosome [4,5,15–18,26–28,37,47]. Moreover, some data from allelic analysis of stripe rust resistance genes on 2BS showed recombinant values with the frequency ranging from 0.062% to 0.192% (unpublished data from P.G. Luo). This suggests that crossing-over event would occur during meiosis. Breeders could choose the recombinant plants by increasing the number of the segregating population to overcome the problem caused by the low frequency of recombination in breeding selection.

4.2. Efficiency of recombinant chromosome 2B construction

Pyramiding of resistance genes becomes possible by conventional breeding methods only under the condition that suitable races of the pathogen are available to test for the presence of each resistance gene [51]. In the absence of isolates carrying the corresponding combination of virulence and avirulence factors, molecular markers closely linked to each resistance gene, can be used to select for given combinations of genes. So, the development of molecular markers for mapping resistance genes to stripe rust and of marker-assisted selection has been among the most active areas of research on stripe rust. Molecular markers have been identified for *Yr5* [21,22], *Yr7* [33], *YrSp* [46], *YrV23* [48], *YrQz* [15], *YrTp1* [17], *YrCN19* [40], and the resistance gene in YW243 [16]. Several SSR markers were closely linked to *Yr5* [21], three RGAP markers co-segregated with the *Yr5* locus and four markers tightly linked to the locus [22], and some STS and CAPS markers have also been developed [23]. In addition, many authors have identified many markers for marker-assisted selection, such as SSR marker *Xgwm* 526 closely linked to *Yr7*, with 5.3 cM genetic distance [33]; SSR marker *Xwmc441* linked with *YrSp* with 12.1 cM genetic distance [46]; SSR *Xwmc356* linked with the resistance gene *YrV23*, with 9.4 cM genetic distance [48]; two SSR markers *Xgwm388* and *Xgwm526* linked to *YrQz* and two AFLP markers P35M48 and P36M61 closely linked to this locus with 3.4 and 4.1 cM genetic distance, respectively [15]; SSR *WMC477* closely linked to *YrTp1* with 0.4 cM genetic distance [17]; two SSR markers *Xgwm388* and *Xgwm501* linked to the resistance gene in YW243 with 27.9 and 23.5 cM genetic distance, respectively [16]; and SSR marker *Xgwm410* co-segregated with the resistance gene *YrCN19* [4]. Most of these markers are SSR markers which would be helpful for marker-assisted selection because their good duplication and high polymorphisms within species [4]. Though there is no molecular marker reported for *Yr27*, its unique characteristic and the low infection type with avirulent property in host screening are readily recognized [37], so it can be used as a phenotypic marker. The availability of molecular markers for *Yr* genes on 2B would shorten time and decrease cost to construct the recombinant chromosome with multiple resistance genes. In the future to develop resistant cultivars by marker-assisted selection needs to identify new markers linked to *Yr27* and *Yr31*, and some more markers closely linked to *Yr7*, *YrV23*, *YrSp* in YW243.

5. Conclusions

This review highlights the importance to construct the artificial chromosome 2B with multiple resistance genes to stripe rust by pyramiding the *Yr* genes on the chromosome. This strategy has a higher efficiency than that the other *Yr* genes on different chromosomes in wheat breeding. The broad resistance spectrum of the *Yr* genes to stripe rust races, and their diversity would contribute to develop highly durable wheat varieties if they are pyramided. Furthermore, the knowledge we obtained about genetic background of the resistance and the availability of molecular markers linked to *Yr*s on chromosome 2B would accelerate the construction of recombinant wheat chromosome 2B with multiple resistance genes. To further determine their positional effects on chromosome 2B and identification of more molecular markers closely linked to the *Yr* genes and their application in marker-assisted selection are needed to accomplish the task.

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