

Review Article



Novel Gene Pyramiding to Combat Rusts in Global Wheat Varieties against Prevalent Virulence: A Review

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Abstract | Epidemics caused by leaf, stripe and stem rust have significant threat to agro-ecosystems and worldwide food security. Semi-dwarf wheat varieties with major gene resistance could not continue for longer period due to emergence of new rust races. However, genotypes such as Inqilab-91, Bluebird, Kenya Plume and Hope developed in early part of green revolution retained their resistance for longer period due to presence of non-specific rust resistance genes. Until now, 187 rust resistance genes (80 leaf rust, 49 stripe rust, 58 stem rust) have been described from different wheat and durum cultivars and related local species using different molecular approaches. This review provides a detailed discussion of the different aspects for controlling three rust diseases caused by *P. recondita* Rob. exdesm f. sp. *tritici*, *P. striiformis* West. f. sp. *tritici*, *P. graminis* Pers. f. sp. *tritici* and the importance of race specific and non-specific rust resistance genes in global wheat varieties. This knowledge will help as basis for plant pathologist, plant breeders and genetics to develop non-specific rust resistant wheat varieties through gene pyramiding or marker assisted breeding.

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Introduction

Leaf, stripe and stem rusts are major diseases of wheat (*Triticum aestivum* L. and *Triticum turgidum*) causing severe epidemics worldwide. These pathogens are highly specific and significant pathotypes occurs in their populations for virulence to a virulence against specific resistance genes. Appearance of novel rust races and their variant through recombination of their genetic material, migration, mutation followed by selection is also common (Brown, 2015). The phenomenon of the breakdown of major gene host resistance has led researchers to look for alternative management strategies. Mainly two approaches have been widely used for controlling rust diseases, genetic and chemical resistance. Genetic resistance further categorized as race specific and race non-specific re-

sistance. Race-specific (vertical resistance) resistance is attained due to existence of major genes and can be easily detected at a seedling or adult plant stage while race non-specific resistance also known as horizontal resistance is accomplished through minor genes and remains effective to all prevalent pathotypes of pathogen and is expressed at adult plant stage (Singh, 1992).

Race specific resistance has been broadly used by numerous wheat improvement programs and easily overcome by the pathogen. However, such type of resistance is often defeated by the evolution of new highly virulent variant of the pathogen by single-step mutation or sexual recombination (Kolmer and Acevedo, 2016). Horizontal or race non-specific resistance provides long lasting durable resistance (Singh et al., 2005). Such type of resistance is most effec-

tive, economically safe and eliminates the need to use fungicides and reduce the cost of production (Oliver, 2014). Though, progress on breeding and other genetic approaches for non-specific resistance is slow, demanding pyramiding durable resistance genes into desirable genotypes. Until now, few non-specific resistance genes have been described and catalogued in wheat (Bansal et al., 2014).

Recent advances in molecular marker technology have created effective tools for solving such complex problems. For example, the utilization of polymerase chain response (PCR) based DNA robust markers has numerous advantages than conventional phenotypic trait selection for resistance (Todorovska et al., 2009). Breeding through marker assisted selection (MAS) has also been generally used to achieve partial resistance. For example, to facilitate breeding for race non-specific rust resistance against all three types of rust robust molecular markers are useful for producing resistant varieties, particularly in addition to the pyramiding several rust resistance genes. MAS can be used at seedling stage with multiple DNA robust markers to evaluate numerous genes simultaneously (Anderson et al., 2013).

The main goal of current review is to describe most recently developed approaches for rust resistance into wheat varieties. To achieve this, we collected current information on rust resistance genes (leaf, stripe and stem) including their types of resistance, primer sequence with base-pair and discuss their potential applications for producing non-specific resistance wheat varieties through MAS.

Breeding for rust resistance

Major genes were the 1st category of resistance genes that to be genetically defined and rapidly used in breeding strategies by plant breeders. Though, not long after these race specific resistance genes started to be utilized as a part of breeding schemes in the early to mid-twentieth century it became very clear that new harmful pathotypes would emerge that defeated these genes in new releasing wheat varieties within few years. The highly virulent pathotypes were either exists at a very low frequency in pre-existing pathogens populaces or were evolved later by changing their genetic make-up through mutation or sexual recombination. In other words, race specific (major genes) being used individually are not race non-specific in breeding strategies (Ellis et al., 2014).

However, with high level of resistance, race specific genes have been utilized with great achievement to manage wheat stem rust in Australia, North America and other areas worldwide (Leonard and Szabo, 2005). Interestingly, compared with stem rust control, a race specific resistance gene has been failed to control yellow rust disease in various regions worldwide. In North America, Europe and Australia yellow rust lines of basic wheat cultivars indicate less genetic variation compare to stem rust genes (Ellis et al., 2014).

Many resistance genes had been transferred into novel wheat germplasm from its cultivated and wild species by interspecific hybridization to combat leaf, stripe and stem rust virulent races. For example, in Russia, in 1902 wide crosses were performed between collected wild and introduced population as a result Kavkaz, Aurora and Besostaja varieties were developed which remained under cultivation worldwide over a longer period of time (Lupton, 1987). In North America, Hope, Ceres, and Webster wheat varieties were released subsequently the early days of plant breeding which confer the both seedling and adult plant resistance. During 1965-1985, International Maize and wheat Improvement Centre have incorporated many rust resistance genes so called "alien genes" into wheat from its local and cultivated landraces through interspecific hybridization. Most of germplasm distributed during this era (1965-1985) contain *Sr36*, *sr31*, *Sr6*, *Sr5*, *Sr30*, *Sr7a*, *Sr24*, *Sr7b*, *Sr17*, *Sr8a*, *Sr12*, *Sr10*, *Sr9g*, *Sr9d*, *Sr11*, *Sr9e*, and *Sr2* genes against stem rust resistance (Rajaram et al., 1988; Knot, 1988).

The importance of adult plant or race non-specific resistance gene *Lr13* against leaf rust was perceive in the mid-1970, when it was transferred along with other genes into a large number of wheat cultivars. Some genotypes having *Lr13* gene along with some other minor genes developed in Pakistan, Mexico and India when present individually does not give race non-species type resistance against leaf rust but in association with different genes showed high level of non-specific or durable resistance. Its occurrence with gene *Lr34* in certain member from Bluebird succession provides longer resistance. Another case of non-specific resistance is variety Lyalpur-73 which though swapped in agriculture fields with the arrival of high rust resistant cultivars but even after 37 years of release until now have very high level of resistance in testing plots.

Adult plant or non-specific resistance genes give incomplete resistance with less pathogen growth and without hypersensitive response merely in adult plants and this is known as durable or slow rusting. Thus, such type of resistance is attained by wheat breeders in field instead of glasshouse. The masking of non-specific resistance by race specific gene with effective resistance phenotypes can prevent high level of non-specific resistance selection unless specific virulent variant of pathogen are utilized to produce high rust outbreaks. All such influences make breeding with non-specific resistance more complex rather by specific resistance genes. Though, the resistance showed by single non-specific resistance genes conferred varying level of durable resistance, it has been described that by combining some undefined partial resistance genes resistance near to immunity can be attained (Singh et al., 2014).

The best known non-specific resistance genes utilized as a part of wheat breeding are *Lr34*, a leaf, stripe and powdery mildew resistance gene and *Sr2* provide resistance to stem rust. These *Sr2* and *Lr34* genes have been utilized for commercial wheat breeding programs for almost more than hundred years. Essentially either non-specific resistance genes on their own give suitable resistance levels under high rust outbreak and often non-specific resistance expression is prolonged in field to effectively maintain yield (Yildirim et al., 2012).

International Maize and Wheat Improvement Center (CIMMYT) researchers have supported and effectively adopted breeding for partial rust resistance for several years and use single back cross method (Singh et al., 2014). The germplasm developed during mid-1960s achieved resistance against stripe rust from Andean local genotypes which had high level of rust resistance. The variety Anza was developed after crossing LR/N10B//3*ANE and cultivated in South Africa, New Zealand, North Africa and Sudan. It was considered as non-specific resistance against stripe rust by Johnson (1988). Such type of resistance was recognized due to existence of *Yr18* and widely developed in winter and spring wheat varieties (Singh et al., 1992). The genotypes released during early years of green revolution carried *Yr18* gene. The *Yr7* in association with *Sr9g* also presents in a number of winter and spring wheat varieties providing non-specific resistance. It is reported in many genotypes such as Pak-81 (*Yr9*, *Yr7*), Seri-82 (*Yr9*, *Yr7*, and *Yr2*), Pavon-76 (*Yr29*, *Yr7*, and *Yr6*), PBW-12, Barani-83, WL-

2265 (Badebo et al., 1990). Varieties Pavon-76 and Veery having *Yr7* had been released in many countries including Mexico, Morocco, Pakistan, Iran, Nepal, Turkey, Yemen, Zambia, Brazil, Bangladesh, Egypt, India and China which show a wide use of *Yr7* gene.

Evolution of new rust races

The widespread use of semi-dwarf wheat genotypes having major gene resistance results in the emergence of new high virulent races. A stripe rust race (*Yr9*) was first detected in East Africa during 1986 and consequently moved to South Asia and North Africa. Once it observed in Yemen during 1991 it took only 4 years to move field of south Asia (Singh et al., 2000a). On its way, it brought on significant grain losses in Turkey, Syria, Egypt, Iraq, Iran, Pakistan, and Afghanistan beyond one billion \$. Similarly, another race of *Puccinia striiformis* (*Yr27*) evolution and its spread, adopted the similar pathway posed significant yield losses to wheat cultivation in Pakistan and India where main genotypes PBW-343 and Inqlab-91 were cultivated. During 2005, the wheat cultivation in North-Pakistan was mostly attacked *Yr27* where the greater part of the range was under Inq-91 (Rehman et al., 2013).

The virulence's in wheat cultivars with *Sr6*, *Sr9b*, *Sr11* and *Sr17* in Australia was observed by Watson (1958) for independent mutational changes occur in *Puccinia graminis tritici*. Though, the exact genetic mechanism of this process in *Puccinia graminis* is unknown, it is now believed that race advancement against resistant genotypes includes involvement of effectors that stop the recognition of signaling pathways from pattern associated recognition receptors (Dodds and Rathjen, 2010). It has also been shown that changes in host EDS1 gene increase the susceptibility to virulent pathogens (Falk et al., 1999). This demonstrates that pathogens' effector based destruction of host pathogen associated molecular pattern (PAMP) induced resistance is not comprehensive due to apparent perfect host pathogen interactions which become more compatible because of host gene mutation (Ellis et al., 2014).

A new race of Ug99 of fungus *Puccinia graminis* was first identified in Uganda in 1998 that showed a significant danger to grain production. Based on North American Nomenclature System this race was named as TTKSK (Wanyera et al., 2006) that showed virulence to *Sr31*, *Sr21*, *Sr24*, *Sr36* in Iran (2007), Yemen (2006), Sudan (2006), Ethiopia (2003) and in Kenya (2001). Other variants of this race TTKST (*Sr24*),

TTTSK (*Sr36*), PTKST, TTKSP (*Sr31*, *Sr21*, *Sr24*), detected in Kenya and Ethiopia in 2007 and TTKSF (*Sr31*, *Sr21*) is identified in Zimbabwe and South Africa in 2009 (Jin et al., 2008; Singh et al., 2011). Significantly, studies in Turkey and Egypt in recent years have failed to identify any of such destructive variants. In 2009, three *Puccinia graminis* strains were identified from Pakistan that clearly shown difference from TTKSK (Fetch et al., 2009 unpublished). In India a new race (*Sr25*) PKTSC have been identified (Jain et al., 2009). The identification of these harmful races frightened the wheat breeders that they should breed for partial or race non-specific resistance or combine two to three minor genes to increase the field life of wheat genotypes.

Monitoring of virulence pattern for rust resistance

Wheat rust pathogens surveillance, including virulence characterization through either pathotype (race) surveys or trap nurseries and assessment of rust incidence, has provided information and strategies in rust pathogen research and plant breeding. Based on recent survey in China, genes *Yr41*, *Yr39*, *Yr36*, *Yr24*/*Yr26*, *Yr18*, *Yr15*, *Yr10* and *Yr5* as well as the advance lines having *Yr16*, *Yr14*, *Yr13* and *Yr12* are still effective and could be used in breeding techniques. Resistance genes *Yr25*, *Yr22*, *Yr21*, *Yr20*, *Yr17*, *Yr9*, *Yr8*, *Yr7*, *Yr6*, *Yr4*, *Yr3*, *Yr2*, and *Y1* are ineffective against currently prevalent pathotypes (Wang et al., 2007). In several regions of the world including Australia, India, China and Pakistan virulence to these genes is recognized as race specific, but some genes including *Yr15* and *Yr5* were found resistant to all rust races in the USA which have been observed until now (Chen, 2007).

Flath and Bartles (2002) in 1998-1992 observed the various virulence's of yellow rust to *YR17*, *YR9*, *YR4*, *YR2*, *YR3*, *Su*, *YR1* and *Sd* genes which exhibited race non-specific resistance up to 1989. Afterward, in 1999-2000, rust outbreaks occurred and collapse resistance of *YR8*, *YR17* including *Yr9*, and *Yr17*, correspondingly. The dominant resistant genes absent in Australia and Germany were *YRA*, *YrSp*, *YR15*, *YR5* and *YR10*. The most common rust virulence's were detected in Australia (8%) and Germany (34%) in which they enclosed a combined virulence to *YR17*, *YR9*, *YR4*, *YR3*, *YR2*, *YR1*, *Su* and *Sd*.

In Pakistan, Hussain et al. (2004) observed the leaf rust virulence in Kaghan and Faisalabad for five years which showed that at both places, resistance genes

Lr33, *Lr32*, *Lr26*, *Lr23*, *Lr22b*, *Lr20*, *Lr18*, *Lr16*, *Lr15*, *Lr14a*, *Lr13*, *Lr11*, *Lr10*, *Lr3*, *Lr3k*, *Lr3bg*, and *LrB* were ineffective while, genes *Lr37*, *Lr27*, *Lr36*, *Lr25*, *Lr19* and *Lr24* were effective. Fayyaz et al. (2008) monitor leaf rust population during 2004-2006 at 5 different places and exhibited that lines with *Lr* genes *Lr28*, *Lr19* and *Lr9* were avirulent while *Lr32*, *Lr30*, *Lr29*, *Lr26*, *Lr25*, *Lr24*, *Lr23*, *Lr21*, *Lr20*, *Lr18*, *Lr17*, *Lr16*, *Lr15*, *Lr14bg*, *Lr12*, *Lr11*, *Lr10*, *Lr3bg*, *Lr3ka*, *Lr3*, *Lr2a*, *Lr2b*, *Lr2c* and *Lr1* were virulent at most of the location. In Nawabshah and Karachi *Lr35*, *Lr34*, *Lr22a* and *Lr13* demonstrated virulent pattern and partial virulence was detected in *Lr37* and *Lr36* at all places.

Rattu et al. (2009) reported the leaf rust virulence pattern from different places of Pakistan. The resistance genes *Lr37*, *Lr33*, *Lr32*, *Lr30*, *Lr26*, *Lr25*, *Lr23*, *Lr18*, *Lr17*, *Lr15*, *Lr14a*, *Lr14b*, *Lr10*, *Lr11*, *Lr3*, *Lr3bg*, *Lr2a*, *Lr2c*, *LrB* revealed great virulence incidences (75-100%) while, resistance genes *Lr34*, *Lr28*, *Lr19* and *Lr9* provide effective resistance to leaf rust. *Lr29*, *Lr24*, *Lr16*, and *Lr13* showed virulence frequency between 51 to 75 percent and the resistance genes *Lr36* and *Lr23* demonstrated virulence frequency ranging from 26 to 51 percent respectively. Bux et al. (2011) monitor the virulence analysis of *Yr* genes in CIMMYT tester lines under field conditions at various regions including Faisalabad, Sakrand, Quaid-i-Azam University and Pirsabak (KPK) and indicated that *Yrsp*, *Yrcv*, *Yr26*, *Yr15*, *Yr10*, *Yr5* and *Yr3* were found most effective while *Yr27*, *Yr17*, *Yr9*, *Yr8*, *Yr7*, *Yr6*, *Yr2*, *YrA* and association of Super Kauz (*Yr27*, *Yr18*, *Yr9*) and Opata (*Yr18*/*Yr27*) were susceptible. The gene *Yr18* demonstrated slow to moderate level of rust resistance at all places.

Despite the progress that has been made through different surveys and in establishing the global wheat rust monitoring system (GCRMS) to date, many challenges remain. A global decline in the incidence of stripe, leaf and particularly stem rust over the last forty years attributes the widespread development of resistance genes through different breeding techniques and led to many countries abandoning these rusts surveillance and an alarming reduction in the global skill base in rust race analysis and general rust pathology.

Genetic basis of rust resistance

To date, more than 81 *Lr* genes (Roelf et al., 2002),

58 *Sr* (Haile et al., 2013) and more than 70 *Yr* resistance genes (McIntosh et al., 2008) have been reported; most confer major genes with race specific resistance and some confer minor genes and indicated race non-specific resistance (Lin and Chin, 2009). A brief description of the detail of some of these leaf, stripe and stem rust resistance genes and their presence in existing global wheat varieties are described in Table1, Table2 and Table3 respectively.

Table 1: List of identified leaf rust resistance genes and presence in existing global wheat varieties.

Resistance genes	Varieties	Types of resistance	Country	References
Lr1, Lr2,	Pavon-F76, Dollabard	Specific resistance	Mexico	Khan et al. 2013
Lr9	Aegilops umbellulata	Specific resistance	USA	McIntosh et al. 2003
Lr11, Lr13, Lr34	Lyalpur-73, Bluebird	Non-specific resistance	Pakistan, Mexico	McIntosh et al. 1995
Lr11, Lr12,	Lerma rajo, pujab-81, Giza -164	Specific resistance	Mexico, Paistan., Egypt	Prins et al. 2001
Lr14a, Lr14b	Arz	Specific resistance	Lenanon	McIntosh et al. 2003
Lr34+ Lr18+pm8	FKlein Castor	Non-specific resistance	Argentina	Lagudah et al. 2006
Lr67+Yr46	Brazilian wheat cultivar	Specific resistance	Brazil	Herrera-Foessel et al. 2012
Lr56+Yr38	Chinese spring wheat	-	China	Marais et al. 2010
Lr62+Yr42	Aegilops neglecta	-	California	Marais et al. 2009

Understanding the molecular basis for partial (durable) resistance to rust diseases is necessary for improving the efficiency of wheat breeding (Long et al., 2014). The incomplete (durable) resistance mainly depends upon slow rusting minor genes which express at adult plant stage. Work done at CIMMYT (Mexico) has showed that at least ten to twelve various types of genes are tangled in a group of CIMMYT wheat germplasm and by gathering four to five partial resistance genes an effective level resistance can be attained. However, 2-3 minor genes with partial resistance in a line/genotype demonstrate moderate level of rust resistance (Singh et al., 2005). A substantial number of partial resistance genes have been characterized; only *Lr34/Yr18*, *Sr2/Yr30* and *Lr46/Yr29*

which are pleiotropic are given names and selected to exact chromosomal location (Martinez et al., 2001).

The genotypes having non-specific rust resistance retain their resistance level for longer period of time and space. Genotype Lyalpur-73 were included in mega varieties of Pakistan in 1970s to date, have effective level of rust resistance in tested plots. Though, the genotypes having race-specific resistance are short lived resistance and distorted frequently after four to five years of release. Varieties having durable resistance exhibit similar response to all prevailing rust races and their effective level of resistance endured in various environmental conditions. The yellow and leaf rust response of some genotypes having partial resistance is alike at Faisalabad-Pakistan and CIMMYT-Mexico. The race non-specific Frontana wheat variety which was released about fifty year ago, up till now has high level of resistance worldwide. There are rare cases in which resistance based on major genes have been continued for longer period of times. William et al. (2006) described six distinct chromosomal loci with race non-specific resistance against yellow and leaf rust in a genotype resulting from crosses of Pavon and Avocet S. The reputed characteristics recognized on chromosomal location 4BL, 6AL and 1BL affect resistance level of both leaf and yellow rust. The chromosomal location 6BL and 3BS have a sustainable effect against yellow rust. In another genotype, the chromosomal loci identified on distal area of 1BL provide effective level of resistance to yellow rust (Suenaga et al., 2003). In some other research studies, the alteration pleotropic to chromosomal location 4B association map have also been identified (Suenaga et al., 2003). Even Avocet S and Morocco have some kind of phylogenetic association that ensure race non-specific resistance that resulted in major delay in becoming entirely vulnerable (William et al., 2006).

The stem and yellow rust resistance genes *Sr2/Yr30* are pleiotropic to each other (Singh et al., 2000b). Spiel-mayer et al. (2003) reported that a molecular marker Xgwm-533 (a microsatellite) is strongly linked to particular gene *Sr2* that is being utilized in selection of genotypes in breeding technologies. In wheat breeding, still various resistance genes showing conflict to rust races have been recognized and are being used. In spring wheat grown in USA *Lr34* has been widely used, Pathotypes of leaf rust with virulence to *Lr34* had not been observed (Kolmer, 2009a). In US, *Lr34* identified in soft red winter wheat is associated

Table 2: List of identified stripe rust resistance genes and presence in existing global wheat varieties.

Resistance genes	Varieties	Types of resistance	Country	References
Yr18, YrSulkirk(Yr27)	Champigo-53, Inqilab 91	Non-specific resistance	Mexico, Pakistan	McIntosh <i>et al.</i> 1995
Yr1	European cultivars	Specific resistance	Europe	Johnson <i>et al.</i> 1975
YrA	Funo	Specific resistance	China	Stibbs, 1985
Yr2	HeineseVII	Non-specific resistance	North America	Line and Qayoun, 1991
Yr3	Danish 1	Specific resistance	China	Stibbs, 1985
Yr4	Hybrid46	Specific resistance	India	Nagarajan <i>et al.</i> 1986
Lr18, Yr3c, Yr5, Yr9, Yr10, Yr15 and Yr17	Bezostaya	Both specific and non-specific resistance	Russia	Babyants <i>et al.</i> 2009
Yr6, Yr7, Yr18	Pavon F76	Non-specific resistance	Mexico	McIntosh, 1992
Yr26	Chuannong 19	Non-specific resistance	China	Luo <i>et al.</i> 2008

Table 3: List of identified stem rust resistance genes and presence in existing global wheat varieties.

Resistance genes	Varieties	Types of resistance	Country	References
Sr2, Sr6, Sr7b, Sr9d, Sr17	Hope	Non-specific resistance	USA	McIntosh <i>et al.</i> 1995
Sr5, Sr9g, Sr21, Sr9e, Sr27	Marquis, Acme, Einkorn, Vernal, Triticale	Specific-resistance	Australasia	Park and Wellings, 1992
Sr11, Sr8a, Sr16, Sr30	North America cultivars	Specific-resistance	North America	Singh, 1991
Sr2, Sr6, Sr7a, Sr8a, Sr12, Sr17	Kenya Plume	Non-specific resistance	Kenya	McIntosh <i>et al.</i> 1995
Sr13, Sr28, Sr30, Sr37	Indian Cultivars	Specific-resistance	India	Nargana <i>et al.</i> 1986
Sr13, Sr22, Sr26	Khapli, Sebatel, Eagle	Specific-resistance	Ethopia, Australia	Haile <i>et al.</i> 2013 Liu <i>et al.</i> 2010
Sr2	Bluesilver	Non-specific resistance	Pakistan	McIntosh <i>et al.</i> 1995
Sr39+ Sr35	Canadian Cultivars	Specific-resistance	Canada	Gold <i>et al.</i> 1992; Niu <i>et al.</i> 2011
Sr58+ Sr46+ Yr29+Pm39	Pavon-76	Non-specific resistance	Mexico	Long <i>et al.</i> 2014

to seedling resistance genes *Lr2a*, *Lr9* and *Lr26* which demonstrate an effective resistance level and adult plant resistance genes including *Lr10*, *Lr11* *Lr18* which exhibit moderate level of rust resistance (Kolmer *et al.*, 2009b). *Lr34* is closely linked to, powdery mildew resistance, barley yellow dwarf virus and leaf tip necrosis (Liang *et al.*, 2006). The genetic linkage of *Lr34* is linked to genotype Ardito and Mentana released in Italy during early nineteenth century (Kolmer *et al.*, 2008). The *Lr34* was replicated and showed that *Ltn1/Yr18/Lr34* has similar genetic characteristics and are linked to each other (Krattinger *et al.*, 2009). *Lr46/Yr29* the leaf and yellow rust resistance genes are also firmly pleiotropic (William *et al.*, 2003). Suenaga *et al.* (2003) identified that molecular marker Xwmc44 is closely linked to *Lr46/Yr29* which is located on chromosomal arm1BL. Its importance is alike *Yr18/Lr34* gene which provides partial/non-specific resistance to plants rather than complete immunity. In the absence of *Lr34* genotypes

having *Lr46* demonstrate long lasting resistance over control (Martinez *et al.*, 2001). Without any necrotic or chlorotic effects, the plants with *Lr34/Yr18* also reduce the spore production of the pathogen.

Gene pyramiding

Until now, discussion has dealt with major and minor gene resistance mostly individually but now we need to consider them together in terms of gene pyramids of both types of resistance genes either singly or in combination. A few however, not all major genes resistance act additively (Roelfs, 1988). For example, *Sr26* and *Sr24* both important for stem rust resistance, when present separately provide race specific resistance but in combination reaction is different as every gene alone. However, the use of pathogen races susceptible to *Sr26* and resistant to *Sr24* in pyramid association and vice versa demonstrated that each gene response individually (Roelf, 1988). Though whether the race specific and partial resistance genes show

Table 4: List of some triple rust resistance genes and their presence in existing wheat cultivars/varieties worldwide.

Varieties/Cultivars	Leaf rust resistance	Stripe rust resistance	Stem rust resistance
Frontana	2-3 minor genes including <i>Lr34</i>	<i>Yr18</i> and <i>Yr9</i>	<i>Sr8a</i> , <i>Sr9b</i> , <i>Sr2</i> in various combination
Bluebird	-	<i>Yr6</i> , <i>YrA</i> , and <i>Yr18</i> minor gene	<i>Sr5</i> , <i>Sr6</i> , <i>Sr8a</i> including <i>Sr2</i>
Arina/Forno derivatives	3 minor genes including <i>Lr34</i>	3-4 minor genes including <i>Yr18</i>	<i>SrFn</i> , <i>Sr</i> minor genes
LERMA RAJO-64	<i>Lr17a</i> <i>Lr17b</i> minor genes in various combinations <i>Lr13</i> , <i>Lr17</i>	<i>Yra</i> in combination <i>Yr18</i>	<i>Sr2</i> , <i>Sr6</i> , <i>Sr7b</i> , <i>Sr9e</i>
SUNCO	4-6 minor genes including <i>Yr18</i>	<i>Lr13</i> , <i>Lr24</i> , 2-3 minor genes including <i>Lr34</i> , <i>Lr46</i> in various combinations	<i>Sr2</i> , <i>Sr24</i> , <i>Sr36</i> , <i>Sr30</i> in various combination
Pavon F76	<i>Lr46</i> , <i>Lr10</i> minor genes	-	<i>Sr2</i> , <i>Sr8a</i> , <i>Sr12</i> , <i>Sr30</i> including <i>Sr58</i>
CRANKBROOK	2 or more minor genes including <i>Lr46</i>	3-4 minor genes including <i>Yr29</i>	<i>Sr2</i> , <i>Sr30</i>

*Source: McIntosh et al., 1995; Bariana et al., 2007

interaction or not, their individually response is the source of getting moderate level of resistance when resistant race specific genes are utilized in pyramid.

Many researchers use this technique to develop rust resistance to all three types of wheat rusts worldwide. Several genes pyramids became successful and provide good source of resistance against all rust diseases (Table 4), though few genes have rapidly been reduced their resistance. Rarely, such as *Lr16*, *Lr13* and undesignated genes for leaf rust (Grama et al., 1984; Samborski and Dyck, 1962) *Lr2a*, *Lr13*, *Lr16*, *Lr27*, *Lr31* and *Lr34* seem to have an additive impact in combination (Ezzahiri and Roelfs, 1989; German and Kolmer, 1990; Singh and McIntoch, 1984).

Combination of some rust resistance genes i.e. the 'Frontana complex' for leaf rust, the 'Sr2 complex' for stem rust resistance, an association of Little Joss and Anza assortments for stripe rust, have demonstrated prolonged stability (Johnson, 1988; Rajaram et al., 1988; Roelfs, 1989). A special set of germplasm lines were developed in CIMMYT to carry two to four non-specific resistance genes against yellow/ stripe rust (Bariana et al., 2001). A few of these cultivars have race specific resistance to leaf rust, which do not exhibit resistant response in Mexico, but provide effective response against leaf rust of Australian wheat germplasm. Stem or black rust resistance generally depends on *Sr2* or/and *Sr30* genes. Occurrence of *Lr34/Yr18* and *Sr2* in these germplasms was identified through using genetic markers associated with these genes. These complexes provide high level of rust resistance in the developing new wheat elite lines

at CIMMYT and worldwide. Such race non-specific resistance genes can be combined with some major genes to deliver genetic diversity (Roelfs et al., 1992).

Marker assisted selection (MAS)

MAS has been broadly used for selecting durable resistance in wheat germplasm to rust diseases; however, the mostly breeding schemes depend on phenotypic selection due to lack of DNA robust markers, high cost of reliable molecular DNA marker and high accuracy of phenotypic selection. Through using a robust molecular marker firmly linked with resistance genes *Lr30*, *Lr26*, *Lr20*, *Lr14b*, *Lr10*, *Lr9*, *Lr3*, *Lr3ka* and *Lr1* (Anderson et al., 2013) were capable to identify and screen a greater number of fifty one varieties/cultivars to capably enhance the level of partial resistance. Closely linked markers give phenotype unbiased selection of associated gene in breeding population. Such molecular markers certify selection of a mark gene relying on the close genetic occurrence of the connected genotype.

The achievement of selection is reliant on the nearby chromosomal association and a particular marker over diverse genetic linkage. Firmly associated molecular DNA markers are accessible for numerous major and minor rust resistance genes. The list of some mostly used robust and approved DNA markers in Mexico, Pakistan and worldwide for leaf, stripe and stem rust resistance genes are illustrated in Table 5 together with their primer sequence, base pair, and the references.

In winter bread wheat, molecular DNA markers for *Lr3* and some other assessable trait loci to stem, yellow

Table 5: List of robust DNA markers tightly linked with triple rust resistance genes, with their primer sequence, base pair, and the references.

Genes	Marker	Primer code	Primer sequence (5' to 3')	Base pair	References
Lr9	J13-F	21F 21R	CCACACTACCCCAAAGAGACG TCCTTTTATTTCCGCACGCCGG	110	Schachermayr <i>et al.</i> (1994)
Lr19-Sr25	GB	16F 18R	CAT CCT TGG GGA CCT C CCA GCT CGC ATA CAT CCA	130	Cherukuri <i>et al.</i> (2003)
Lr21	D14	20F 20R	CGC TTT TAC CGA GAT TGG TC CCA AAG AGC ATC CAT GGT GT	885	Huang and Gill, (2001)
Lr34/Yr18	Xbarc352	20F 21R	AGCTCTGCTTCACGAGGAAG CTCCTCTTTATATCGCGTCCC	250	Roder <i>et al.</i> (1998)
Lr34/Yr18	Cs5fr5	21F 21R	GTTGGTTAAGACTGGTGATGG TGCTTGCTATTGCTGAATAGT	150	Lagudah <i>et al.</i> (2006)
Lr35-Sr39	Sr39	20F 18R	AGA GAG AGT AGA AGA GCT GC AGA GAG AGA GCA TCC ACC	900	Gold <i>et al.</i> (1999)
Lr46/Yr29	Xwmc44	22F 22R	GGTCTTCTGGGCTTTGATCCTG TGTTGCTAGGGACCCGTAGTGG	242	Somers and Isaac, (2004)
Lr47	PS10R PS10L2	19F 19R	GCTGATGACCCTGACCGGT GGGCAGGCGTTTATTTCCAG	224	Helguera <i>et al.</i> (2000)
Yr1	stm673acag	24F 22R	TAACTCACAACACGTTCTGGTTCGT ACACACACACACAGAGAGAG	120	Bansal <i>et al.</i> (2009)
Yr5	STS-7/8	18F 18R	GTACAATTCACCTAGAGT GCAAGTTTTCTCCCTATT	439	Zhang <i>et al.</i> (2009)
Yr9	H20	21F 22R	GTTGGAAGGGAGCTCGAGCTG GTTGGGCAGAAAGGTCGACATC	-	Liu <i>et al.</i> (2008)
Yr10	Yr10	20F 21R	TCAAAGACATCAAGAGCCGC TGGCCTACATGAACTCTGGAT	543	Liu <i>et al.</i> , (2010)
Yr15	gwm413	21F 19R	TGCTTGTCTAGATTGCTTGGG GATCGTCTCGTCCTTGCCA	390	Murphy <i>et al.</i> (2009)
Yr29	bac17R	21F 21R	CCCATGCTGACATGGCCACAT CTCTGCTCTTTAGTAGTTGCC	500	Rosewarne <i>et al.</i> (2006)
Yr46	gwm165	21F 20R	GGTGGGGTTGGGAAGACAACG TGCAGTGGTCAGATGTTTCC	236	Herrera-Foessel <i>et al.</i> (2014)
Yr51	sun104	20F 20R	TGCTATGTGCGTGATGATGA TTACATGCTCCAGCGACTTG	250	Randhawa <i>et al.</i> (2014)
Yr57	gwm389	21F 20R	ATCATGTGATCTCCTTGACG TGCCATGCACATTAGCAGAT	117	Randhawa <i>et al.</i> (2015)
YrSP	dp269	18F 20R	CTGCTGTCACCGCTCTCC AGTCACACGCCCTACTCTCC	343	Yin <i>et al.</i> (2009)
Sr2/yr30	gwm53	20F 20R	AAG GCG AAT CAA ACG GAA TA GTT GCT TTA GGG GAA AAG CC	120	Spielmeier <i>et al.</i> (2006)
Sr2/yr30	stm598tcac	20F 21R	GTTGCTTTAGGGGAAAAGCC TCTCTCTCTCTCACACACAC	56	Hayden <i>et al.</i> (2004)
Sr2	csSr2	24F 28R	CAAGGGTTGCTAGGATTGGAAAAC AGATAACTCTTATGATCTTACATTTTCTG	172	Mago <i>et al.</i> (2002)
Sr22	Cfa2019	20F 20R	GACGAGCTAACTGCAGACCC CTCAATCCTGATGCGGAGAT	234	Khan <i>et al.</i> (2005)
Sr24-Lr24	Sr24#12	19F 23R	CACCCGTGACATGCTCGTA AACAGGAAATGAGCAACGATGT	500	Mago <i>et al.</i> (2005)
Sr26	Sr26#43	20F 21R	AATCGTCCACATTGGCTTCT CGCAACAAAATCATGCACTA	270	Mago <i>et al.</i> (2005)
Sr31-Lr26-Yr9	Iag95	24F 24R	CTCTGTGGATAGTTACTTGATCGA CCTAGAACATGCATGGCTGTTACA	1100	Mago <i>et al.</i> (2002)
Sr35	CFA2170	20F 20R	TGGCAAGTAACATGAACGGA ATGTCATTCATGTTGCCCT	190	Babiker <i>et al.</i> (2009)

and leaf rust were identified. Israeli x Fukuhokomugi wheat oligoculm cross and Japanese CV with double haploid population were used for commercial cultivation. The results exhibited the certain genetic variation of genes which confer slightly effects to stripe rust resistance, and useful documentation of these microsatellite DNA marker are helpful for both combining such partial resistance genes and selecting wheat germplasm effectively (Suenaga et al., 2003). Molecular mapping of *Lr46/Yr29* were identified on chromosome 1B provides the durable resistance against both leaf and yellow rust (William et al., 2003). A set of molecular markers were used for genetic efficacy in breeding programs, two markers pleiotropic to *Sr2* a stem rust resistance gene, several linked with chromosomal loci having *Sr38/Lr37/Yr17* resistance gene, one for *Lr28*, two specified DNA markers for the associated genes *Lr35/Sr39*. Gene *Sr2*, provides durable resistance to black rust and generally under field conditions (Sharp et al., 2001).

Conclusions and Recommendations

Information in regards to characteristics and distribution of rust resistance genes is useful for developing new wheat varieties with durable rust resistance. Gene pyramiding through MAS and the utilization of various molecular methodologies is necessary to combat partial rust resistance in wheat varieties. Combining information on race non-specific resistance varieties and their mechanism for controlling rust disease, which is the focus of this paper, is also important for the development of new disease-resistant varieties with high yielding capabilities. Overall, this work aims to support pathologists, plant breeders, and wheat researchers by increasing consideration of the recent state of the field of wheat research.

Authors Contributions

Yasir Ali: Conceptualize the main idea and wrote the article.

Muhammad Aslam Khan: Helped in conceptualize the main idea and supervised the entire work:

Muhammad Atiq and Muhammad Hussain: Helped in collection and management of data.

All authors read and approved the final manuscript.

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