INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
12–1231/2013/15–6–1209–1220
http://www.fspublishers.org

Review Article

Prospects of Wheat Breeding for Durable Resistance against Brown, Yellow and Black Rust Fungi

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Abstract

Wheat leaf, stripe and stem rusts have devastating role in reducing crop yield resulting in socio-economic instability many times across the world. The semi-dwarf wheat varieties with race specific resistance could not survive longer due to the evolution of new rust races. However, varieties like Lerma Rojo-64, Yaqui-50 and Lyalpur-73 developed in early part of green revolution retained resistance for longer time due to presence of adult plant resistance (APR) genes. Evolution of new rust races like virulence's *Yr9* and *Yr27* followed by the emergence of Ug99 and its mutants lead the breeders to revise their breeding strategy. Breeders are now depending on accumulation of minor genes or their use in combination with major genes for durability of rust resistance in wheat varieties. The minor genes/APR genes, *Sr2/Yr30*, *Lr34/Yr18*, *Lr46/Yr19* are being exploited in wheat breeding at CIMMYT and other places. The germplam with this type of resistance have shown survival consistency over space and time. At Ayub Agriculture Institute, Faisalabad the home of green revolution in Pakistan, this strategy has been adopted since 1995. The partial resistance varieties were crossed in a top cross/back cross scheme and the segregating populations were advanced by selected bulk method, which resulted in the development of material having better yield and rust resistance than the pre-exiting varieties (e.g., Inqlab-91, MH-97). Three varieties, Shafaq-06 and Lasani-08 and AARI-11 from these crosses have been approved for general cultivation. Similarly, the material developed and distributed by CIMMYT, Mexico having this type of resistance is being globally adopted. The SSR markers for above mentioned minor genes are available and can be used as an aid in the early selection of superior genotypes.

Keywords: Durable resistance; Rust; Wheat; Breeding

Introduction

Wheat along with rice and maize is fulfilling half of the calories demands of the human population around the world. The projected global wheat production for the year 2009-2010 is 656 million tones, which is slightly higher than the demand of 642 million tones. Global Wheat production has increased tremendously since green revolution in 1960's and helped in minimizing hunger and malnutrition. Developing countries, which consume 60% of the global wheat production, have shown higher yield increase than the developed countries in the past (Heisey *et al.*, 2002). It was driven by the hunger prevalence in these countries and is attributable to the introduction of high yielding and rust resistant semi dwarf varieties developed under the collaborative efforts of International and National research systems during last 50 years. Whereas, climate change and emergence of new pests and diseases are threatening the food sustainability. The evolution of new races of pathogens like Ug 99 of stem rust are of serious concern. In order to feed the ever growing population increase in wheat production at the rate 1.6% can be achieved by developing high yielding varieties having good tolerance level for biotic and abiotic stresses.

Wheat rusts have major historical and economic importance worldwide. Yield losses due to rusts had been reported in many wheat producing countries in most years and periodic epidemics during last century resulted in famine situation in many parts of the world (Brennan and Murray, 1988). The control of rust diseases of wheat in Australia has been estimated to save farmers income over $ 200 million annually (Brennan and Murray, 1988). The yield losses due to black rust (*Puccinia graminis f. sp. tritici*) were independently reported by Italian scientists Fontana and Tozzeti in the 18th century. The rusts affect the photosynthetic ability of the plant and transportation of photosynthates from green part of the plant, which results shriveled grains (Fig. 1). This adversely affects the yield, moreover, the grain quality is also badly affected resulting lower price in market. Therefore, to sustain wheat productivity and farmers income some strategies must be adopted to control these menaces. In developed countries

To cite this paper: Rehman, A.U., M. Sajjad, S.H. Khan and N. Ahmad, 2013. Prospects of wheat breeding for durable resistance against brown, yellow and black rust fungi. *Int. J. Agric. Biol.*, 15: 1209–1220

the use of chemicals is common for controlling rusts but it is unaffordable by the poor farmers of Africa, Asia and other developing countries. The only way left unblocked is the development of rust resistant stock, which had been the major breeding strategy since the early 1900's. Genetic manipulation of resistance genes has resulted in more stable pattern of resistance (Macindoe and Brown, 1968; Lupton, 1987; Singh and Dubin, 1997) and helped in feeding ever increasing world population. It has been estimated that wheat genetic improvement has generated at least 27 times its value in benefits from leaf rust (brown rust) resistance breeding in spring wheat alone (Marasas *et al.,* 2004).

After the birth of Mendelian Genetics in the beginning of 20th Century, Biffen (1905) demonstrated that inheritance of wheat yellow rust (stripe rust), caused by *Puccinia striiformis* f. sp*. tritici* (*Pst*) followed Mendelian principles. After devastating rust epidemics in North America in the early part of 20th century, Stalkman and Piemeisel (1917) demonstrated that stem rust pathogen has various forms and races. These races varied in their ability to be virulent on different wheat varieties which were later found to carry distinct resistant gene or gene combinations. Flor (1942, 1956) demonstrated that incompatibility between host and pathogen involved corresponding genes in each organism. This consideration of gene for gene relationship led to the development of following two fundamental rules parallel to basic Mendelian Principles by Loegring in 1966 justified by McIntosh *et al.* (1995), and stated as:

a). Incompatibility between host and pathogen is the consequence of interaction between the products of at least one host resistant and at least one corresponding pathogen avirulence gene: LIT=LP:LR.

LIT is low infection type, LP is low pathogenicity, and LR is low reaction.

b). When more than one interacting gene pairs are involved the level of incompatibility as low as, or lower than, the level produced by the most incompatible interacting gene pair acting alone, that is: LIT1,2< L1T1 where:LIT1<L1T2.

Wheat Breeding in Pre-green Revolution Era

There was no serious attempt in wheat improvement until the early years of 19th century. Twenty five types (T1-T25) belonging to *T. durum*, *T. Sphaerococum* and *T. vulgare* (*T. aestivum*) were isolated from the mixture of genotypes and species (Aziz, 1966; Rehman *et al.,* 2009). The mixture of genotypes was commonly known as landraces, which evolved as a result of natural selection and some times assisted by farmers own selection of better heads for the seed of next year crop. These landraces remained under cultivation until the first decade of 20th century (Rehman *et al.,* 2009). Main breeding method used by the breeders of nineteenth century was isolation of pure lines from local land races following Johnson's pure line theory. Hybridization in most part of the world was started by the end of nineteenth century. Some crosses had also been reported to be made to combine contrasting characters of parents in hybrid varieties. Farrer (1898), in Australia, gave due consideration for breeding rust resistant wheat varieties. He carefully selected the parents for hybridization work and mainly concentrated on the development of early maturing varieties to avoid rusts. He also imported some early maturing germplasm from India and crossed with Australian material. He used back cross approach for introgression of rust resistance into Australian material. He listed as components of rust resistance: size of stomata, presence of leaf wax, thickness of cuticle, leaf angle (erect leaves offering a less suitable site for spore deposition) and leaf width. These characteristics are remarkably similar to those now considered likely to determine durable disease resistance. He also developed interspecific crosses of wheat with *T. monococcum* (Einkorn) for transferring rust resistance in wheat. In India these crosses were imported during 1896-1901 but could not acclimatize in Indian conditions and wheat land races or their derivatives mostly predominated. Some varieties of sub-continent like Mundia, Pissi, Bansi, Nagpur hybrid, Bakhshi, Majhi were found moderately resistant but not immune (Howard and Howard, 1909), which indicated that they may posses few minor genes for rust resistance. As the main breeding method used for the development of wheat varieties in those days was isolation of pure lines, therefore, it can be assumed that these minor genes were co-evolved with the bread wheat.

In Russia, scientific breeding dates back to 1902 but early work was confined to the selection from local or introduced populations. Hybridization with collected wild and cultivated forms from areas of primitive agriculture for introgression of alien alleles was also conducted in this part of the world. Their interest in wide crosses is clearly shown by the parentage of famous variety Besostaja and its derivatives Aurora and Kavkaz. The variety Kavkaz had shown wide adaptability in different climatic conditions (Lupton, 1987) and was used extensively as a donor of rust resistance genes all over the world.

In spring wheat areas of North America, varieties released since early days of breeding have adult plant resistance or combination of adult plant resistance and seedling resistance. The varieties Webster, Ceres and several Hope and H-44 derivatives are typical examples of adult plant resistance. Other varieties released were combination of adult plant resistance of one parent and seedling resistance of the other parent: an example is New-Thatcher. Another method called analytical in those days was also used, which targets combining partial resistance of two or more varieties to develop rust resistant varieties (da Silva, 1958; Knott, 1958). Lupton (1987) revealed that in North America the history of spring wheat breeding after the 1916 black rust epidemic showed the rise and fall of many varieties carrying major gene, each displaced following the spread of rust race virulent to their respective genes. A major advancement followed the introduction of variety

Selkirk in 1954, which maintained its resistance for more than 25 years and appeared to carry factors for durable resistance in addition to major gene resistance for which it was originally selected.

In Germany, some early winter wheat hybrids varieties such as Strube-56 and Carstens-5 with good level of field resistance were developed in 1934. In Indian sub-continent, then it was considered that no further development was possible through pure line selection and therefore, hybridization was started for breeding still better varieties in 1926 (Aziz, 1966), by combining all maximum desirable characters in a variety present in more than one types. The varieties including C-591, C-518, C-217, C-250, C-271 and C-273 were developed by crosses using local and exotic germplasm. These varieties were superior to pre-existing stock in all respects. The variety C271 contains Lr34 (Kolmer, 2009), a durable rust resistance gene. This showed that this gene has been used in wheat breeding consciously or unconsciously since long.

So it can be concluded that in the early days of wheat breeding, although the knowledge regarding genetics of rust resistance was not much advanced but due consideration was given for the selection of varieties having better resistance. Many selections from land races also possessed good resistance (30-40M). After the establishment of hybridization programs, varieties with adult plant resistance (race non-specific resistance) and race-specific resistance were developed. The varieties, developed with race specific resistance, were not long-living therefore, development of varieties with adult plant resistance (APR) remained the effective breeding strategy. Sometimes breeder accumulated APR genes, while targeting a major gene, which gave their varieties long life. Some inter-specific crosses were also developed for introgression of alien genes in wheat genome.

Green Revolution and Breeding for Rust Resistance

The semi-dwarf and dwarf varieties developed at CIMMYT, Mexico in the early days of green revolution (Penjamo 62, Pitic 62, Lerma Rojo 64, Sanora 64 and Siete Cerros etc.) had been responsible for yield breakthrough in Pakistan, India, Turkey, Afghanistan and many other parts of the world. The life time of most of these Mexican varieties was short as appearance of new stem rust race has terminated their useful life time however, there were some exceptions also. The variety Lerma Rojo 64 had life time of eleven year, while others like Yaqui 50, Champingo 52 and Champingo 53 retained their resistance until they were displaced from commercial cultivation by new high yielding varieties (Borlauge, 1968). The long life of these varieties is attributable to their genetic background. They had combination of Hope and Thacher type and Kenya type resistance (Borlauge, 1958). During the period 1965-1985, the CIMMYT wheat breeding program has incorporated diversity of genes. Most of the material distributed during this period contains *Sr2* and two to four additional genes for stem rust resistance (Table 1). These additional genes include *Sr5*, *Sr6*, *Sr7a*, *Sr7b*, *Sr8a*, *Sr9b*, *Sr9d*, *Sr9e*, *Sr9g*, *Sr10*, *Sr11*, *Sr12*, *Sr17*, *Sr24*, *Sr26*, *Sr30*, *Sr31*, *Sr36* (Green and Dyck, 1979; Rajaram *et al.*, 1988; Knott, 1988). The parallel strategy was also adopted by many national programs.

The importance of *Lr13* gene for leaf rust (*Puccinia triticina*) resistance was recognized in the early 1970's when it was transferred along with other genes into many wheat varieties. Some varieties containing *Lr13* in combination with other genes developed in Mexico, India and Pakistan are given in Table 2. The gene, *Lr13* itself does not provide desired level of resistance but when present in combination with other genes it provides a degree of resistance of high probability of being durable. The mode of action of *Lr13* complex in CIMMYT program is non race-specific resistance. Its presence in combination with *Lr34* in some members of Bluebird series gave them long life. Another example of this combination is a Pakistani variety Lyalpur 73 (Fig. 2), which although replaced in the farmers field by the introduction of new high yielding varieties but even after 36 years of release, it still has very good resistance for leaf rust (20M) in screening nurseries. The varieties like Genero 81 and Torim 73, which remained resistant to leaf rust in Mexico for long time also have *Lr 34* gene in combination with other genes.

The adult plant resistance to leaf rust of the Brazilian wheat cultivar "Frontana" was first described as due to the gene *Lr13* (effective in the adult plant stage) and one or two modifiers (Dyck *et al.*, 1966). Subsequent studies (Dyck and Samborski, 1982; Dyck, 1987) revealed the presence of *Lr 34* and *Lr13* in "Frontana". Pretorius *et al.* (1984) showed that *Lr13* could confer low seedling reaction at elevated temperature. The gene *Lr13* appears to be common in cultivars from Australia (Hawthorn, 1984); India (Gupta and Saini, 1987); and Brazil, Argentina and Unites States (Roelfs, 1988); and in cultivars derived from CIMMYT germplasm (Singh and Rajaram, 1991). The interaction of *Lr13* with other genes such as *Lr16* and *Lr34* have also been reported (Dyck and Samborski, 1982; Ezzahiri and Roelfs, 1989). The interaction of *Lr13* with other *Lr* genes has been considered as the cause of durable resistance to leaf rust in many cultivars (Rajaram *et al.*, 1988; Roelfs, 1988). Singh and Rajaram (1992) investigated the inheritance of adult plant resistance in "Frontana" and 3 globally leaf rust resistant CIMMYT spring bread wheat varieties, the genetic test for the presence of *Lr34*, the postulation of the other known *Lr* genes, and the role of *Lr13* and other known *Lr* genes in conferring adult plant resistance. They concluded that resistance was independent of major genes.

The material developed during mid 1960's had acquired resistance for yellow rust from Andean region varieties which possessed high level of resistance. The Anza was derived from cross LR/N10B//3*ANE and released in North Africa, Sudan, South Africa and New Zeland.

Table 1: Stem rust resistance genes in old wheat varieties (after McIntosh *et al.*, 1995)

Varieties	Year of release	Country/Region	Genes
Selkirk	1954	Canada	*Sr2,Sr6,Sr7b,Sr9d,Sr17*
Hope	1927	USA	*Sr2,Sr7b,Sr9d,Sr17*
Newthach	-	USA	*Sr2,Sr5,Sr7b,Sr12*
Lerma Rojo 64	1964	Mexico	*Sr2,Sr6,Sr7b,Sr9e*
Penjamo T 62	1962	Mexico	*Sr5,Sr6,Sr8a, Sr9b*
Kenya Plume	-	Kenya	*Sr2, Sr5, Sr6, Sr7a, Sr8a , Sr12, Sr17*
Maxipak	1965	Pakistan	*Sr17*
Kalyansona		India	
Sonalika	1967	India	*Sr2*
Bluesilver	1971	Pakistan	
Bluebird	1976	Mexico	*Sr2, Sr5, Sr6, Sr8a*
Yecora 70	1975	Pakistan	
PARI 73	1973	Pakistan	
Nuri 70	1975	Pakistan	
Pavon F 76	1976	Mexico	*Sr2, Sr8a, Sr12, Sr30*
Hartog	1983	Australia	*Sr2, Sr8a, Sr9g, Sr30*
Songlen	1975	Australia	*Sr2, Sr5, Sr6, Sr8a, Sr36*
Qing Chung 5	-	China	*Sr5, Sr6, Sr11*
Hochzucht	-	Eurpian Union	*Sr5, Sr9g, Sr12*
Karl	1988	USA	*Sr2, Sr9d , Sr24*
Frontana	1943	South America	*Sr8a, Sr9b*
Sunco	2006	Australia	*Sr5, Sr6, Sr8a, Sr24, Sr36*
Sunelg	1984	Australia	*Sr24, Sr26*

Table 2: Leaf rust resistance genes in old wheat varieties as described by McIntosh *et al.* (1995)

Varieties	Year	Country/Region	Genes
Lerma Rojo	1964	Mexico	*Lr13*, Lr17
Champingo 53	1953	Mexico	Lr34
Penjamo 62	1962	Mexico	Lr14a, Lr34
Pitic62	1962	Mexico	Lr14a
Sonora64	1964	Mexico	Lr1
Mexipak 65	1965	India	Lr 14a
Kalyansona		Pakistan	
Sonalika	1967	India	*Lr13*,Lr14a
Bluesilver	1971	Pakistan	
Lyalpur 73	1973	Pakistan	Lr1,*Lr13*,Lr34
Bluebird	1976,	Mexico	Lr1,*Lr13*, Lr34
Yecora 70	1975	Pakistan	
PARI 73	1973	Pakistan	
Nuri 70	1975	Pakistan	
Ciano 79	1979	Mexico	Lr16
Arz	1973	Lebnon	Lr17
Pavon F 76	1976	Mexico	Lr1, Lr10, *Lr13*, Lr 46 *
Hortog	1983	Australia	
Dollarbird	1987	Australia	
Parula	1981	CIMMYT	Lr34, Lr46*
Punjab 81	1981	Pakistan	Lr10, *Lr13*, Lr34
Era	1970	North America	Lr10, *Lr13*, Lr34
Frontana	1943	South America	*Lr13*,Lr34
Chines Spring	-	China	Lr12, Lr34
Bezostaya	-	Europe	Lr3a, Lr34
Hobbit	-	UK	*Lr13*, Lr17

* Singh *et al.* (1998)

It was regarded as durable resistant for yellow rust by Johnson (1988) and may have derived durable resistance from Anderson (Rajaram *et al.*, 1988). Durable resistance of Anza is widely deployed in spring wheat and in some winter wheat varieties. This durable resistance was attributed to the presence of gene *Yr18* by Singh (1992a). The varieties, developed in early days of green revolution, carrying *Yr18* are given in Table 3. The gene, *Yr7* is also present in a range of spring wheat and winter wheat varieties and it is frequently associated with *Sr9g*. It is reported in number of varieties such as Barani 83, PBW12, WL2265, Seri 82 (*Yr2*, *Yr7*, *Yr9*), Pavon76 (*Yr6*, *Yr7*, *Yr29*), Pak. 81(*Yr7*,*Yr9*) (Dubbin *et al.*, 1989; Perwaiz and Johnson, 1986; Wellings 1986; Badebo *et al.*, 1990; Singh *et al.*, 1990). It is usually present in many cultivars as a combination as mentioned in Table 3. Veery and Pavon containing *Yr7* had been released in 31 and 16 countries, respectively with different names (Table 4, 5), which show the wide use of *Yr7* gene.

Table 3: Yellow rust resistance genes in old wheat varieties (McIntosh *et al.*, 1995)

Varieties	Year	Country/ Region	Genes
Lerma Rojo	1964	Mexico	*Yra*
Champingo 53	1953	Mexico	*Yr 18*
Sonalika	1967	India	*Yr2,YrA,*
Lyalpur 73	1973	Pakistan	*Yr 18*
Bluebird	1970	Mexico	*Yr6, YrA, Yr18,*
Pavon F 76	1976	Mexico	*Yr6,Yr7,Yr29**
Hortog	1983	Australia	
Dollarbird	1987	Australia	
Ciano79	1979	Mexico	*Yr Sulkirk (Yr 27)*
Veery	1980,S	Worldwide	*Yr7,Yr9*
Barani 83	1983	Pakistan	*Yr7*
PBW343 (Attilla)	1995	India	*Yr Sulkirk (Yr 27)*
Inqilab 91	1991	Pakistan	*Yr Sulkirk (Yr 27)*
Era	1970	North America	*Yr 18*
Frontana	1943	South America	*Yr 18*
Chines Spring	-	China	*Yr 18*
Bezostaya	-	Europe	*Yr 18*

* Singh *et al.* (1998)

Table 4: Derivatives of Veery (CM 33027- KVZ/BUH//KAL/BB) released in different parts of the world (Skovmand *et al.*, 1997)

Country	Varieties
Bangladesh	SERI 82- BGD
Bolivia	CHANE CIAT
Brazil	BR26-SAO GOTARDO, BR31-MIRITI, IAC 289-MARRUA, IAPAR28-IGAPO, OCEPAR 18
Chile	MILLALEAU INIA, NOBO INIA, SNA 204, SNA 205, SNA 206, SNA 210
China	GOU JI 13, JING XUAN 9, YUN ZHI 437
Egypt	GIZA 164
Ethiopia	DASHEN, HAR 407
Guatemala	ICTA OLINTEPEQUE 86
India	HS 207, HUW206, MACS2496,MALAVIYA206
Iran	FALAT
Lebanon	SERI 82-LBN
Libya	BOHOOTH 202
Mexico	GENARO T 81, GLENNSON M 81, SERI M 82, URES T 81
Morrocco	TILILA
Myanmar	YEZIN WHEAT 6
Nepal	ANNAPURNA 1, NL 459
Pakistan	PAK 81, PIRSABAK 85, MEHRAN 89
Paraguay	CORDILLERA 3
Peru	LA MOLINA 82
Portugal	LIMA 1, TAMEGA
Rawanda	GICINYA
South Africa	GAMTOOS
Spain	ARGANDA, CARTHAYA
Sudan	SASARAIB
Tanzania	TAUSI, VIRI
Turkey	ANADOLU, KAKLIC 88, SERI 82-TUR
Uaaan	NARRO F.86
Uruguay	ESTANZUELA CARDENAL
Yemen	AZIZ, MUKHTAR
Zambia	LOERIE, LOERIE II, SERIC
Zimbabwe	NATA, RUSAPE, SCW 101

1B-1R Translocation

Driscoll and Sear (1965) and Sears (1967) produced several lines having a translocation between a segment of hairy neck chromosome of rye 5R and different wheat chromosome segments. Due to genetic relationship between rye chromosome 5R and wheat chromosome of homology group 1, the designation 1R was proposed for this chromosome (Shephered, 1968, 1973; Shephered and Jennings, 1971). The rye chromosome 1R was reported to be containing powdery mildew and stripe rust resistance genes in its short arm (Riley and Macer, 1966). It was found that these genes were linked with stem rust and leaf rust resistant genes and cultivars Salzmunder, Baertweizen and Weique have identical genes (Bartos and Bares, 1971). A sister line of these 'Neuzutch' was used for breeding in Soviet Union and gave rise to Russian cultivars Kavkaz, Aurora, Besostaya 2, Skorospelka and many others.

Table 5: Details of parents selected and utilized in gene pyramiding crosses at AARI, Faisalabad-Pakistan

Varieties/Lines	Characteristics		
	Leaf rust	Yellow rust	Av. Yield (Kg/ha)
Inqilab-91	20 M	70S	4000-4500
V-87094(Wattan)	40M	40M	4000-4500
Kohistan-97	30M	50 M	4000-4500
Luan	30M	40M	3000
MH-97	50MSS	60MSS	4000-4500
Shalimar-88	60M	40M	3500-4000
Punjab-96	40S	40M	4000-5000
Weaver	20M	10MR	3000

S=susceptible, MS moderately susceptible, MR Moderately resistance
M moderately resistant moderately susceptible

Table 6: Yield performance of selected durable rust resistant elite lines of AARI, Faisalabad- Pakistan

Line	Parentage	trials	Testing years	Av. Yield (Kg/ha)	Check (Inqilab)	% inc./ dec over check
V-00183R (Shafaq-06)	V87094/2* Inq-91	120	5	4110	4031	+2.70
V-02192	SH88/V87094//MH97	124	5	4049	3970	+2.44
V-02156	SH-88/Weaver	50	4	4236	4046	+4.5
V-03007	Pb96/V87094//MH97	37	4	4505	4288	+5.06
V-04179	Pb96/V87094//MH97	37	4	4658	4488	+4.7
V -03138	Luan/Koh.97	125	3	4141	3983	+3.96

Table 7: Potential rust reactions of finally selected elite lines of AARI, Faisalabad at hot spots in Pakistan

Line	Parentage	Leaf rust		Yellow rust	
		Bahwalpur	Faisalabad	Islamabad	Pirsabak
V-00183R (Shafaq-06)	V87094/2* Inq-91	0	0	10MR	20MR
V-02192	SH88/V87094//MH97	0	20M	10R	5RMR
V-02156	SH-88/Weaver	5MR	40MS	10RMR	20RMR
V-7096	Pb96/V87094//MH97	5MRMS	30MRMS	10R	40RMR
V-04179	Pb96/V87094//MH97	0	40M	10R	40RMR
V -03138	Luan/Koh.97	10MR	30M	5R	15MR
Mumtaz#1	LU26/PRL// LU26/TRAP	10MR	5R	5M	10MR
Mumtaz#2	LU26/PRL// LU26/TRAP	15M	20M	10M	20M
Morrocco		100S	100S	100S	100SN

Neuzutch possesses a complete 1R chromosome, whereas Kavkaz and Aroura have an interchange chromosome having 1B segment and a rye chromosome 1R segment. (Mettin *et al.*, 1973; Zeller, 1973; Zeller and Hossam, 1983). Kavkaz was introduced into CIMMYT germplasm where a high yielding spring wheat cultivar "Veery" was released. This segment was also transferred to several Europian cultivars. These cultivars were found possessing resistance to wheat streak mosaic virus and its vector wheat curl mites. There was good compensation of Rye chromosome 1R for the elimination of wheat chromosome 1B. The 1B.1R translocation appears to be more stable and superior in agronomic properties. It was easy for the breeders to work with this translocation as there was no cytological problem associated with it (Zeller and Hossam, 1983). Therefore, this translocation became widespread in wheat cultivars released in China and USA, India, Pakistan and several other countries during the mid-1980s and later. The Veery derivatives due to their superior agronomic feature and disease resistance were widely cultivated in different parts of the world (Table 4).

This germplasm showed significant grain yield advantage and wide adaptation with superior disease resistance attributes due to the presence of the 1B-1R translocation. The higher yielding ability of 1B-1R germplasm was attributed to post-anthesis stress tolerance of this material resulting in higher Kernal weight (Morenosevilla, 1995). The frequency of 1B.1R translocation went up to approximately 70% at one stage in CIMMYT's spring wheat germplasm but has declined to about 30% in more recent advanced lines (Singh *et al.*, 2006; Rehman *et al.,* 2013). Introgression of 1B-1R translocation and wide spread adoption of the material carrying it on global basis, probably enhanced the emergence of new devastating races like *Yr9*, *Yr27* virulence's of yellow rust and stem race Ug 99. Although the genes *Sr31*, *Lr26* and *Yr9* present in this translocation remained effective for long period of time but their breakdown forced the scientist to devise some alternative strategy of gene deployment in wheat varieties for rust resistance.

This translocation, derived from imperial Rye carries genes *Sr31*, *Lr26*, *Yr9* and *Pm8*. (Zeller and Hossam, 1983; McIntosh *et al.,* 1995), when used initially it provided resistance to stem rust, leaf rust and yellow rust but with the development of new virulent races, these genes are ineffective now (Singh *et al.,* 2006). Despite, its successful use it was not widely deployed in Australia due to sticky dough, poor mixing characteristics resulting poor bread making qualities (Roelfs, 1988; McIntosh *et al.,* 1995; Rehman *et al*., 2013).

Emergence of New Rust Races

The wide spread global popularity of the germplasm with 1B-1R translocation created monoculture situation. This lead to the evolution of some new devastating rust races resulting a serious threat to global wheat production. A race of *P. striiformis*, *Yr9* was 1^{st} observed in East Africa in 1986 and subsequently migrated to North Africa and South Asia. Once it appeared in Yemen in 1991 it took just four years to reach wheat fields of south Asia (Singh and Huerta-Espino, 2000). On its way it caused major yield losses in Egypt, Syria, Turkey, Iran, Iraq, Afghanistan and Pakistan exceeding USD 1 billion. Similarly, *Yr27* emergence and its movement following the same pathway posed major threat to wheat production in India and Pakistan, where mega cultivars PBW343 and Inqilab-91 were having *Yr27* gene based resistance. In 2005, the wheat crop in Nothern Pakistan was severely hit by this race of Yellow rust where most of the area was under Inqilab-91.

Stem rust resistance in wheat cultivars with *Sr31* remained effective for more than 30 years**.** In 1990's, most of the wheat varieties were having 1B-1R translocation which created a monoculture situation in Africa, Asia and other parts of the world. Isolates of *pgt*, which were virulent on *Sr31* were collected for the 1^{st} time in Uganda during 1999 and then spread throughout East Africa (Pretorius *et al*., 2000). It subsequently spread to Kenya and Ethiopia in 2005 (Waynera *et al.,* 2006). The race, named as TTKS (Ug99), is virulent on majority of mega wheat varieties and can cause 100% yield losses whereas, up to 80% yield losses have been reported in Kenya. A new variant of this stem rust race has been found in Kenya since 2006, which is virulent on *Sr24* (Jin *et al.,* 2007, 2008). Now-a-days fungicides are being used to control stem rust in Kenya (Singh *et al.,* 2008). It ultimately jumped the red sea and its presence has been reported in Yemen since 2006 and was also found in Sudan in the same year. In March 2007, isolates of *pgt* were collected from different locations in Iran and the collections from Borujerd and Hamadan were identified as TTKSK (Nazari *et al.,* 2009). The race identified, produced high IT's of 3 to 4 on wheat genotypes carrying 1BL-1Rs translocation (Falat and PBW343). Subsequently, FAO announced its existence in Iran and alarmed a threat for, the bread-basket zone of the world, South Asia and other neighboring regions.

A new race of stem rust virulent on *Sr25* gene, have been detected in India (Jain *et al*., 2009). This isolate collected from Karnataka, has shown IT's 3+ to 4 on primary leaves of differential types with *Sr25* gene. This race is named as PKTSC according to North American system. The detection of *Sr25* virulent race alarmed the breeders that they should breed for adult plant resistance or pyramid 2 or 3 major genes to enhance the field life of wheat cultivars.

Durable Rust Resistance

The problem of ever changing races of pathogens led the breeders to evolve alternative forms of resistance that would be more durable such as slow rusting or partial resistance (Broers, 1989; Singh *et al.,* 2000a, b). It has been demonstrated that durable rust resistance is more likely to be of adult plant type rather than of seedling type and is not linked with the genes producing hypersensitive reaction (McIntosh, 1992; Bariana *et al.*, 2001). Durable rust resistance is a mechanism conferring resistance to a cultivar for long period of time during its widespread cultivation in a favorable environment for a disease (Johnson, 1978, 1988). This type of resistance is mainly associated with the minor genes, which are also known as slow rusting genes. The concept of slow rusting in wheat was recommended by Caldwell (1968), analogous to partial resistance to late blight of potato proposed by Niederhauser *et al.* (1954).

Many researchers have emphasized the need to identify and exploit durable resistance. Johnson and Law (1975) defined durable resistance as a resistance source that remained effective after widespread deployment over a considerable period. A general concept of a durable resistance source for cereal rusts is that it is polygenic, likely to express at adult plant stage, non-race-specific and produce non-hypersensitive response to infection. A typical example of durable resistance is the resistance to stem rust transferred from tetraploid emmer to North American bread wheat cultivars Hope and H-44 (Hare and McIntosh, 1979), and resistance to leaf rust in the South American wheat cultivar Frontana (Rajaram *et al.,* 1988).

Genetic Basis of Durable Resistance

The durable resistance is based on additive effect of partial resistant minor genes, usually polygenic in nature and active in adult plant stage. Genetic studies conducted at CIMMYT, Mexico has shown that at least 10-12 different genes are involved in group of CIMMYT germplasm, and by accumulating 4-5 minor genes resistance level near to immunity can be achieved. However 2-3 genes in a line provide moderate level of resistance (Singh *et al.,* 2005). Most of these genes are undesignated only the genes *Lr34*/*Yr18*, *Lr46*/*Yr29* and *Sr2*/*Yr30* have been given names and designated to specific chromosomes. Each of these genes pairs are tightly linked or pleotropic.

The varieties possessing minor gene based resistance show almost same level of resistance over space and time. For example Lyalpur-73, which was among major varieties of Pakistan in 1970's still show very good level of resistance in screening nurseries (Fig. 2). Whereas, the varieties having

Table 8: Comparison of leaf rust reaction of varieties having minor gene based resistance in Maxico and Pakistan

Variety/Line	Minor Genes possessed	Usual rust reactions	
		Mexico	Pakistan
Nacozari 76	*Lr34*+1	30MSS	30M
Sonoita	*Lr34*+1	20MSS	10M
Baconora 88	*Lr34*+1 or 2	10MSS	20M
Frontana	*Lr34*+ 2 or 3	10MSS	15M
Trap#1	*Lr34*+ 2 or 3	10MSS	20M
Kukuna	*Lr34*+ 3 or 4	1M	5MR
Parula	*Lr34*+*Lr46*+1or 2	10MS	10M
Pavon 76	*Lr46*+1	30MS	40M
Amadina	4	5M	10M

Table 9: Comparison of leaf rust reaction reactions of some varieties having minor gene based resistance in Mexican and Pakistani conditions

Variety/Line	Minor genes possessed	Usual rust reactions	
		Mexico	Pakistan
Pavon 76	*Yr29*+*Yr30*+1	40M	30M
Parula	*Yr18*+*Yr29*+*Yr30*+1	10M	20M
Kukuna	*Yr18*+ 3-4	10MR	TR
Trap#1	*Yr18*+2	10MR	20M
Amadina	*Yr29*+*Yr30*+1	30M	20M
Kakatsi	3-4	10MR	5M

major gene based race specific resistance did not have long life and collapsed usually after 4-5 years. Varieties having durable type of resistance show almost same level of reaction against different races and their resistance remained effective in different climatic conditions. The leaf rust and yellow rust reaction of some varieties having durable rust resistance are same at CIMMYT, El Batan, Mexico and Faisalabad, Pakistan (Table 8, 9). The variety Frontana being released about half century ago still have effective rust resistance almost every where. There are very rare examples that resistance based on major genes had been effective for a longer period of time. William *et al.* (2006) identified 6 independent loci, contributing to adult plant resistance (APR) or slow rusting contributing to two rusts in a population derived from cross of Avocet 'S' and Pavon. The putative loci influencing resistance to stripe and yellow rust were identified on chromosomes 1BL, 4BL and 6AL. The loci on chromosome 3BS and 6BL had significant effect on stripe rust. In another population a locus on the distal region of chromosome 1BL was identified with highly significant effects on stripe rust resistance (Bariana *et al.*, 2001; Suenaga *et al.*, 2003). Even Morocco and Avocet S have some genetic factors that contain some slow rusting resistance which results in significant delay in becoming completely susceptible (William *et al.*, 2006). The material having minor gene based resistance near to immunity (<10M) for leaf and yellow rust was developed and distributed worldwide in 1990's by CIMMYT (Singh *et al.*, 2000a).

Sr2/*Yr30* Gene

The gene, *Sr2* was transferred to hexaploid wheat from

From left to right: (1). Disease intensity 0%, 1000 grain weight 45 g.
(2) Disease intensity 20-30%, 1000 grain weight 40 g
(3) Disease intensity 40-50%, 1000 grain weight 30 g
(4) Disease intensity 50-60%, 1000 grain weight 25 g
(5) Disease intensity 70-80% 1000 grain weight 20 g

Fig. 1: Grano-gram showing grain shriveling at various intensity levels of stem rust

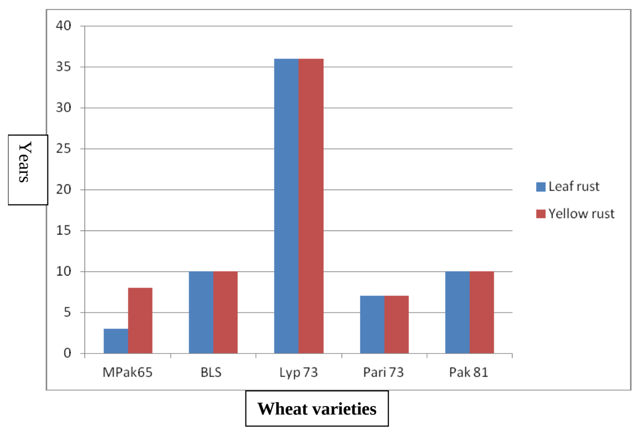

Fig. 2: Field life of wheat varieties in Pakistan

tetraploid emmer wheat cultivar Yaroslav in 1920. It is present on chromosome 3BS (Hare and McIntosh, 1979) 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 (Knott, 1988). *Sr2* was detected in several highly resistant old, tall Kenyan cultivars like Kenya plume (Singh and McIntosh, 1986) and semidwarf CIMMYT, cultivars Pavon F 76, Parula, Kingbird, Dollarbird etc. These cultivars show maximum disease severity of 10-15% with moderately resistant reactions. The gene *Sr2* is tightly linked with *Yr30* or has pleotropic effects (Singh *et al.*, 2000b). 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 (Spielmeyer *et al.*, 2003).

***Lr34/Yr18*:** A number of genes conferring resistance to rusts have been identified and used in wheat (*T. aestivum* L.) breeding programs. However, many of these genes have become ineffective because of the emergence of new virulent races of rusts. Cultivars such as Frontana with the rust resistance gene *Lr34* had operative durable rust resistance to leaf rust (*P. triticina*) (Dyck *et al.*, 1966; Singh and Rajaram, 1992). Although *Lr34* has been used extensively in spring wheat grown in US, isolates of *P. tiriticina* with complete virulence to this gene had not been identified, therefore, the resistance in Frontana might be due to escape from a complete virulent leaf rust race (Kolmer *et al.*, 2003). It has been reported that soft red winter wheats having *Lr34* in combination with seedling resistant *Lr2a*, *Lr9*, *Lr26* were highly resistant, whereas, in combination with *Lr10*, *Lr11*, *Lr18* were moderately to low resistant in USA (Kolmer, 2009).

A major leaf rust resistance gene *Lr34* first described by (Dyck, 1977, 1987) has been established to improve leaf rust resistance in combination with other genes (German and Kolmer, 1992). Another salient characteristic of *Lr34* resistance is that it is genetically tightly linked with *Yr18* gene, which confers adult plant resistance (Singh, 1992a, b; McIntosh, 1992). This gene co-segregates with leaf tip necrosis *(Ltn1)*, powdery mildew resistance (*Pm38*), Barley yellow dwarf virus (*Bydv1*) genes (McIntosh, 1992; Singh *et al.*, 1992a, b, Spielmeyer *et al.*, 2005; Liang *et al.*, 2006). These multi-pathogen resistance traits have made the *Lr34/Yr18* locus one of the highly valuable regions for disease resistance in wheat (Kolmer *et al.*, 2008). If *Lr34/Yr18* complex is present alone the disease level may go high but in combination with other genes it could give effective control (Ma and Singh, 1996). At low temperature the resistance level conferred by plants with *Lr34* is higher under growth chamber and green house condition. The gene seems to be effective under field conditions at average daily temp 0-20Ċ and helps in reducing disease progress (McIntosh *et al.*, 1995). Singh and Rajaram (1991) had indicated that environment has a significant influence on terminal disease reaction for leaf rust. Singh (1992b) showed that *Yr18* may display inadequate resistance under some environmental conditions. It is present in many sub-continental varieties including some released in pre-green revolution era. A marker associated with *csLV34* locus on chromosome 7D was found associated with *Lr34/Yr18* gene. Two predominant allelic size variants *csLV34a* and *csLV34b* were identified. A strong association was observed with the presence *Lr34/Yr18* gene and csLV34b allele. However, lines having *Lr34/Yr18* gene and positive for *csLv34a* allele were rare. The lineage of this gene is tracked back to varieties Mentana and Ardito developed in Italy during early 1990's (Kolmer *et al.*, 2008). This gene has been cloned and was shown that *Lr34/Yr18/Pm38/Ltn1* is the same gene (Krattinger *et al.*, 2009).

***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.*, 1998a). 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 pleotropic (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 (Rosenwarne *et al.*, 2010) and efforts are underway to clone this gene (www.ars.usda.gov).

Combining Minor Genes

Accumulating minor genes for attaining desired level of resistance in a variety is a challenging task (Singh and Trethewan, 2007) as it requires identification of parents with minor genes, crossing them in specific schemes following back cross or top cross approach, maintaining desirable population size and selection of desirable genotypes from segregating populations. The crossing schemes and selections strategies used for breeding major genes based resistance are not suitable for breeding minor gene resistance. The modified pedigree method used for breeding major gene based resistance can not give any progress for minor gene based resistance. Singh *et al.* (1998b) compared different crossing and selection schemes for working out their efficiency in terms of genetic gains and cost efficiency. The influence of type of cross and selection scheme was minimal on main grain yield. They found that selection of parents was the most important feature in breeding for achieving desirable results. They also reported that mean rust severity of top cross progenies was less as compared to simple cross because two parents contributed resistance factors to the top cross progenies. Non selected bulk method was found to be least effective and selected bulk method as the most attractive schemes in terms of genetic gain and cost efficiency. An example of breeding for minor gene based resistance is the development of wheat stock resistant to leaf and yellow rust at CIMMYT.

Since early days of breeding for minor genes, plants and lines with infection intensity of 20-30% and compatible infection type were targeted. This led to the development of wheat varieties Nacozari F 76, Pavon F 76 and several others (Singh and Trethewan, 2007), which were released not only in Mexico but also in Ethiopia, Bangladesh, Pakistan and other countries. Pavon was released in 16 countries with different names (Table 5). This material provided the foundation for breeding for minor gene resistance. In Pakistan the varieties Uqab-2000 (CROW'S'/NAC/BOW'S'), Bhakkar-02 (P-102/PIMA//F3.71/TRM/3/PVN) and Seher-06 (CHIL/2* STAR/BOW/CROW//BUC/PVN/3/VEE#10) have this type of resistance. Bhakkar-2002 has dominated the mega wheat cultivar Inqlab-91 since 2005 after Inqlab-91 was hit by yellow rust epidemic and Seher-06 is gaining popularity now, due to its higher yield and better resistance to leaf and yellow rusts. The variety, Uqab-2000 proved the best option for the rain- fed northern Pakistan after severe epidemic of yellow rust in 2005.

An example of breeding for durable rust resistance out side CIMMYT is the wheat breeding program of Ayub Agricultural Research Institute, Faisalabad-Pakistan. The collection of 1200 accessions was screened under artificial inoculation with mixture of all prevailing rust races in Pakistan like *Yr9*, *Yr27*, *Lr10*, *Lr13*, *Lr26* virulences etc. The accessions (Table 6) with partial resistance for leaf/yellow rust were selected (Hussain *et. al.*, 2006). The selected parents were crossed to combine genes for high yield and rust resistance. The major objective was the accumulation of minor genes for longer-lasting rust resistance. The selected parents were used to create back crosses, double crosses and top crosses. Bulk selection as described by Singh *et al.* (2005), was used to advance the filial generations conserving maximum genetic diversity. The spikes were harvested from the plants having rust intensity ranging 0-30% preferably with R/MR/MS type of reaction. Many lines were selected from this material and tested for yield and disease reaction (Table 6, 7). From this material two varieties Shafaq-06 and Lasani-08 with durable resistance based on unknown minor genes were accepted for general cultivation in the Punjab-Pakistan (Hussain *et al.*, 2007; 2009). These varieties are high yielding and have shown durable resistance to leaf and yellow rust races like *Yr9*, *Yr27*, *Lr10*, *Lr13*, *Lr26* virulences etc. Lasani-08 was also found resistance to stem rust (Ug 99) in the year 2007 at Kenya.

Conclusion

The ever changing nature of wheat leaf, stripe and stem rusts poses a serious threat to future wheat production. Learning from wheat breeding history and epidemic losses by wheat rusts, breeders devised the strategy of pyramiding APR/minor genes. The strategy of pyramiding APR genes was developed by understanding rust resistance mechanism prevalent in historical wheat varieties like Lerma Rojo-64, Yaqui-50 and Lyalpur-73 which retained resistance due to then unknown APR genes. CIMMYT and AARI devised a strategy of pyramiding APR genes alone or in combination with major genes to combat the recently emerged races of stem and yellow rust. Recent wheat cultivars bred at AARI, Faisalabad such as Shafaq-06, Lasani-08 and AARI-11 are strong evidences of potential of APR gene pyramiding strategy to cope with threats of leaf, stripe and stem rusts.

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(Received 15 November 2012; Accepted 06 April 2013)