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Genetics and Breeding for Durable Resistance to Leaf and Stripe Rusts in Wheat

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Abstract: Yellow (or stripe) and leaf (or brown) rusts, caused by *Puccinia striiformis* and *P. triticina*, respectively, are important diseases of wheat worldwide. Growing resistant cultivars is the most economical and environmentally safe control measure and has no cost to growers. Wheat (*Triticum aestivum*) cultivars that have remained resistant for a long time, or in other words carry durable or race-nonspecific resistance, are known to occur. Inheritance of resistance indicates that these cultivars often carry a few slow rusting genes that have small-to-intermediate, but additive, effects. Our genetic studies show that a high level of resistance (approaching immunity) to both rusts could be achieved by accumulating from 4 to 5 such genes. We recommend that a group of winter and spring wheat cultivars known to carry adequate levels of durable resistance to yellow and/or leaf rusts are assembled and further evaluated in the region to identify those cultivars that show resistance stability. Resistance from these cultivars should then be transferred in a planned manner to the susceptible but locally adapted cultivars through a 'Single Backcross Breeding Approach', that allows the simultaneous accumulation of desired number of slow rusting genes with increased grain yield potential and other traits.

Key Words: *Puccinia triticina*, *Puccinia striiformis*, *Triticum aestivum*, resistance, rust

Introduction

Yellow (or stripe) and leaf (or brown) rusts, caused by *Puccinia striiformis* and *P. triticina*, respectively, are important diseases of wheat worldwide. This is mainly due to the pathogens' ability to mutate and multiply rapidly, and to use their air-borne dispersal mechanism from one field to another and even over long distances. With the discovery of the genetic resistance by Biffen (1905), physiological specialization in rusts by Stakman and Levine (1922), and gene-for-gene interaction by Flor (1956), the utilization of the hypersensitive (race-specific) type of resistance has predominated in wheat improvement. The phenomenon of the loss of effectiveness of such genes, or their combinations, led scientists to look for alternative approaches to resistance management. The concept of horizontal, or race-nonspecific, resistance was widely used in breeding stem rust resistance in wheat by Borlaug (1972) and leaf rust resistance by Caldwell (1968).

Application of such a concept in breeding for leaf rust resistance, commonly known as slow rusting (Caldwell, 1968), or partial resistance (Parlevliet, 1975), has dominated in CIMMYT's bread wheat (*Triticum aestivum* L.) improvement for more than 25 years. Our results indicate that durable resistance (Johnson, 1988) to leaf and stripe rusts of several cultivars is based on the slow rusting genes having additive effects. In this paper we briefly explain how slow rusting resistance can be used in wheat improvement and our thoughts on what needs to be done in the Central Asian region to achieve a long-term control of yellow and leaf rusts.

Identification and characterization of slow rusting resistance

Slow rusting to leaf rust is characterized by slow disease progress in the field despite a compatible, or high or susceptible, infection type. Cultivars carrying slow

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rusting resistance show high infection type in the seedling growth stage. For stripe rust, which progresses in plants also in a systemic manner, it is often not possible to identify fully compatible stripes in adult growth stages. Johnson (1988) presented examples of adult resistance genes that are race-specific in nature. It is difficult to distinguish such resistance from the resistance conferred by genes of race-nonspecific nature based on the adult plant infection type. At least some reduction in infection type is most often associated with low disease severity to stripe rust. However, we have observed that in the case of potentially durable slow rusting resistance, the first uredinia to appear are moderately susceptible to susceptible. Subsequent growth of the fungal mycelium causes some chlorosis or necrosis; therefore, the final infection type of the stripe, not uredinia, is usually rated as moderately resistant to moderately susceptible (MR-MS).

Slow rusting can be readily identified within the improved germplasm (Singh and Rajaram, 1991). The existence of slow rusting resistance in most cultivars is often a chance inheritance from their ancestors. This was clearly demonstrated in Australia where stripe rust did not exist before 1979 but where several cultivars developed before 1979 carry moderate, and a few high, levels of adult plant resistance. Searching for slow rusting resistance in land races and alien sources should be considered only if it is not available in improved germplasm.

Slow rusting can be characterized in greenhouse experiments by evaluating latent period, infection frequency (number of uredinia per unit area or receptivity), size of uredinia or infection, inoculum production, etc. under quantitative inoculation. Characterization of 27 bread wheats of CIMMYT origin by Singh et al. (1991) indicated that this was phenotypically diverse for all components measured (Table 1). The area under disease progress curve of these wheat lines in field ranged from 1 to 50% of the very susceptible check cultivar Morocco (Table 1). Singh et al. (1991) also reported the likelihood of pleiotropic genetic control of the components of slow rusting because of highly significant positive or negative phenotypic correlation among latent period, number of uredinia and size of uredinia. If it is assumed that same gene controls various components of slow rusting, then it can be hypothesized that perhaps only a few genes with additive

Table 1. Range of variability for components of slow rusting (partial resistance to leaf rust observed in 28 bread wheats (given as % of susceptible check variety Morocco)

Component	Variability range
Latent period	+14 to +49
Uredinium number	-42 to -98
Uredinium size	-34 to -78
Area under the disease progress curve	-50 to -99

effects could retard disease progress to a rate that final disease level remains to an acceptable low level.

Linked genes *Lr34/Yr18* and *Lr46/Yr29* for slow rusting to leaf and stripe rusts

Dyck (1987) designated gene *Lr34* located in chromosome 7DS, which is now known to be present in several cultivars with durable resistance to leaf rust. Singh (1993) identified its presence in several CIMMYT-derived Mexican wheat cultivars. The heterogeneous Mexican wheat cultivar Jupateco 73 was reselected for the presence and absence of *Lr34* by Singh (1992a). These isogenic Jupateco 73R (*Lr34* present) and Jupateco 73S (*Lr34* absent) genotypes and those of Thatcher developed by Dyck (1987) have yielded useful information on the nature of slow rusting resistance. Our studies, using the Jupateco pair have shown that *Lr34* affects all three components of slow rusting, i.e. it increases latent period and decreases number and size of uredinia (Table 2). The effect was more pronounced in post seedling growth stages, although measurable differences also occurred in the seedling stage. Temperature can influence the expression of resistance conferred by the gene *Lr34* (Singh and Gupta, 1992). Comparison of grain yields of Jupateco isolines in leaf rust protected (by fungicide) and non-protected plots indicated that though leaf rust could significantly reduce grain yield by approximately 15% in the presence of *Lr34*, the reductions in the absence of *Lr34* were substantially higher and ranged between 42.5 to 84% depending on planting date and year (Singh and Huerta-Espino, 1997).

Studies of Singh (1992b) and McIntosh (1992) have shown that gene *Lr34* is closely linked with gene *Yr18*, which confers slow rusting to stripe rust. Using the Jupateco 73 near-isogenic reselections, studies at CIMMYT have shown that the gene *Yr18* also increases

Table 2. Comparison of the three components of slow rusting resistance to leaf rust in seedling and flag leaves of the near-isogenic *Lr34* Jupateco 73 reselections tested at 15 °C

Genotype	Latent period (Days)		Uredinia/cm ²		Size of uredinia (mm ²)	
	Seedling	Flag	Seedling	Flag	Seedling	Flag
Jupateco + <i>Lr34</i>	13.8b ^A	18.0b	21a	6a	0.21a	0.07a
Jupateco - <i>Lr34</i>	12.8a	12.7a	47b	30b	0.38b	0.27b

^A Different letters following the values indicate significant difference between the means at P=0.05

latent period, and decreases infection frequency and length of infection lesions (stripes) to stripe rust in greenhouse experiments (Table 3). The conclusion again was that these components were under pleiotropic genetic control. Comparison between stripe rust protected and non-protected treatments showed that stripe rust infection caused grain yield losses of 31 to 52% in *Yr18* carrying Jupateco 73R and 74 to 94% *Yr18* lacking Jupateco 73S (Ma and Singh, 1996). This shows that slow rusting resistance based on *Yr18* protected grain yield in the range of 36 to 58% depending on the year and sowing date. This level of protection was not considered sufficient in the environment of Toluca, Mexico where the experiments were conducted.

Rubiales and Niks (1995) studied the infection process and indicated that partial resistance due to *Lr34* was based on reduced rate of haustorium formation in the early stages of infection, in association with no or relatively little plant cell necrosis. Electron microscopic studies of Alvarez-Zamorano (1995) on Jupateco 73 isolines have shown an accumulation of unknown electro-dense substances in the cells of *Lr34* line near the site where haustorial mother cells try to dissolve the cell wall of mesophyll cells for the formation of haustoria. It would

appear that the accumulation (cell wall apposition) causes a thickening of cell wall, which reduces the establishment of haustorial tube. If haustoria are formed, the slow mycelial growth may be due to a restricted movement of fungus from one cell to other by a similar phenomenon. Alvarez-Zamorano (1995) also observed structural change in the *Lr34* line leading to invagination, or contraction of cell wall, which may delay the completion of infection process. These observations indicate a different mechanism for *Lr34* based slow rusting than hypersensitivity, which is associated with race-specific genes. Because pathogen isolates can vary for aggressiveness (Lehman and Shaner, 1996), it may be difficult to differentiate pathogenic variation for increased capability to overcome slow rusting resistance of this type from aggressiveness.

One of the slow rusting genes present in Mexican wheat cultivar Pavon 76, which has moderate levels of durable adult-plant resistance to leaf and yellow rusts, was recently designated as *Lr46* (Singh et al., 1998). Gene *Lr46* is located in chromosome 1BL and is linked (or pleiotropic) to gene *Yr29* that confers moderate levels of adult-plant resistance to stripe rust (William et al., 2003). Gene *Lr46* also affects all components of slow rusting resistance to leaf rust (Martinez et al., 2001).

Table 3. Comparison of the three components of slow rusting resistance to stripe rust in flag leaves of the near-isogenic *Yr18* Jupateco 73 reselections tested at 15 °C

Genotype	Latent period (Days)	Infection frequency (stripes/cm ²)	Length of stripes (mm)
Jupateco + <i>Yr18</i>	20.1b ^A	0.7a	12.5a
Jupateco - <i>Yr18</i>	15.9a	7.1b	47.7b

^A Different letters following the values indicate significant difference between the means at P = 0.05

Combinations of *Lr34*, *Lr46* and other genes for durable leaf rust resistance

The South American cultivar 'Frontana' is considered to be one of the best sources of durable resistance to leaf rust (Roelfs, 1988). Genetic analysis of Frontana and various CIMMYT wheats possessing excellent partial resistance to leaf rust worldwide has indicated that adult plant resistance is based on the additive effects of *Lr34* and two or three additional slow rusting genes, commonly known as the *Lr34* complex (Singh and Rajaram, 1992). In Mexico, leaf rust severity on most cultivars can be related to the number of slow rusting genes they carry (Table 4). Cultivars with *Lr34* and three or four additional genes show a stable response in environments tested so far, with final leaf rust ratings lower than 5% even under heavy rust pressure. The presence of *Lr34* can be indicated by the presence of leaf tip necrosis in adult plants, which is closely linked with it (Singh, 1992a). Results of Sayre et al. (1998) show that 7.7 to 10.4% losses in grain yield of cultivars that carry such combinations of 2 or 3 genes with *Lr34* were similar to 6.6 to 10.2% losses in cultivars that carry hypersensitive types of resistance under high leaf rust pressure.

Our genetic studies have shown that at least 10-12 different slow rusting genes are involved in the adult plant resistance of a group of CIMMYT wheats. We have also identified lines where *Lr34* is absent, but whose level of resistance is high. We therefore believe that durable resistance is feasible even in the absence of *Lr34*, as in the case of Pavon 76 (Table 4).

Combinations of *Yr18*, *Yr29*, *Yr30* and other genes for durable stripe rust resistance

Singh (1992b) and McIntosh (1992) have indicated that the moderate level of durable adult plant resistance of the CIMMYT-derived US wheat cultivar Anza is controlled by gene *Yr18*, which is also present in winter wheats such as Bezostaja. As mentioned earlier, this gene is completely linked with the *Lr34* gene. The level of resistance it confers is usually not adequate when present alone. However, combinations of *Yr18* and 3-4 additional slow rusting genes (the *Yr18* complex) result in adequate resistance levels in most environments (Singh and Rajaram, 1994). Cultivars carrying such *Yr18* complexes are listed in Table 5. Our genetic study on a few selected cultivars indicated the presence of genes different from *Yr18*. We believe that these slow rusting genes can be pyramided to achieve adequate resistance levels. The durability of such slow rusting genes is not known; however, when combinations are deployed, the longevity of the resistance can be expected to be high as evident in Australia for wheat cultivars Cook and Hartog (=Pavon). Recent studies at CIMMYT (William et al., 2003) have shown that gene *Lr46* is either closely linked (or pleiotropic) to gene *Yr29*, which confers slow rusting to yellow rust. Another minor gene, *Yr30*, involved in the adult plant resistance of several CIMMYT wheats was found to be in the chromosomal region carrying durable stem rust resistance gene *Sr2* (Singh et al., 2000). Genes *Yr29* and *Yr30* are widely distributed in CIMMYT wheat germplasm.

Table 4. Some seedling susceptible bread wheats that carry good adult plant resistance to leaf rust in Mexico and other countries

Genotype(s)	Usual leaf rust response ^A	Additive genes ^B for resistance
Jupateco 73S	100S(N)	Highly susceptible
Jupateco 73R	50MSS	<i>Lr34</i>
Nacozeni 76	30MSS	<i>Lr34</i> + 1 gene
Sonoita 81, Bacanora 88, Rayon 89	20MSS	<i>Lr34</i> + 1 or 2 genes
Frontana, Parula, Trap, Tonichi 81	10MSS	<i>Lr34</i> + 2 or 3 genes
Chapio, Tukuru, Kukuna, Vivitsi	1MSS	<i>Lr34</i> + 3 or 4 genes
Pavon 76	40MSS	<i>Lr46</i> + 1 gene
Genaro 81, Attila	40MSS	2 genes
Amadina	5MSS	4 genes

^A Leaf rust response evaluated in Mexico has two components: % severity based on the modified Cobb scale (Peterson et al., 1948) and reaction based on Roelfs et al. (1992). The reactions are: MSS = moderately susceptible to susceptible, i.e., medium to large sized uredinia without chlorosis or necrosis; S = susceptible, i.e. large uredinia without chlorosis or necrosis; N = necrotic leaves following high leaf rust severity.

^B Minimum number estimated from genetic analysis.

Table 5. Some seedling susceptible bread wheats that carry good adult plant resistance to stripe rust in field trials in Mexico and other countries

Genotype(s)	Usual yellow rust response ^A	Additive genes ^B for resistance
Jupateco 73S	100MS	Moderately susceptible
Jupatco 73R	50M	<i>Yr18</i>
Parula, Cook, Trap	15M	<i>Yr18</i> + 2 genes
Tonichi 81, Sonoita 81, Yaco	10M	<i>Yr18</i> + 2 or 3 genes
Chapio, Tukuru, Kukuna, Vivitsi	1M	<i>Yr18</i> + 3 or 4 genes
Pavon 76	20M	<i>Yr29</i> , <i>Yr30</i> + 1 gene
Attila, Amadina	30M	3 genes

^A Yellow rust response data from Mexico has two components, % severity based on modified Cobb scale (Peterson et al., 1948) and reaction based on Roelfs et al. (1992). The reactions are M = moderately resistant to moderately susceptible, sporulating stripes with necrosis and chlorosis; and S = sporulating stripes without chlorosis or necrosis.

^B Minimum number estimated from genetic analysis.

Molecular markers for genes conferring slow rusting resistance

Although advances in finding closely linked markers are notable with race-specific genes, especially those transferred into wheat from alien sources, progress with slow rusting genes has been slow and limited. QTL analyses have shown several chromosomal regions that enhance resistance to leaf or yellow rust (William et al., 1997; Nelson et al., 1997; Messmer et al., 2000; Singh et al., 2000; William et al., 2003; Suenaga et al., 2003). Chromosomal regions involved in slow rusting resistance to leaf and yellow rusts in Pavon 76 and Parula were identified at CIMMYT by testing RILs (recombinant inbred lines) from the crosses of these wheats with susceptible

cultivar Avocet S (Table 6). The linkage between *Lr46* and *Yr29* was in fact first identified in the Avocet S/Pavon 76 cross. Other interesting features included the presence of additional QTLs that conferred resistance to both leaf and yellow rusts, and QTLs which were disease specific (Table 6). It is also worth mentioning that presence of *Agropyron elongatum* segment carrying stem rust resistance gene *Sr26* had minor but significant effects in reducing leaf and yellow rust severities in at least Pavon population. This relationship was also found in the Avocet/Tonichi 81 cross (data not presented). A total of at least 6 distinct additive genes for leaf and yellow rusts were identified between Pavon 76, Parula and Tonichi 81. Such mapping efforts have been useful to understand

Table 6. QTLs for slow rusting, additive genes involved in resistance to leaf and yellow rust diseases of wheat mapped by evaluating RILs from crosses of susceptible wheat 'Avocet S' and resistant 'Pavon 76' and 'Parula' for three years at field sites in Mexico

Cultivar	Location	Marker	Disease severity reduction (%) ^C		Named genes
			Leaf rust	Yellow rust	
Pavon 76	1BL	Wms259	35	27	<i>Lr46</i> , <i>Yr29</i>
	4B	Wms495	18	15	
	6A ^A	Wms356	14	18	
	6B	PaggMcaa	-	18	
	3BS	PacgMcgt	-	11	<i>Yr30</i> , <i>Sr2</i>
Parula	7DS	Wms295, <i>Ltr</i> ^B	56	46	<i>Lr34</i> , <i>Yr18</i>
	7B or 7D	Pcr156	29	-	
	1BL	Wms259	15	16	<i>Lr46</i> , <i>Yr29</i>
	Unknown	PaagMcta	22	14	
	3BS	Gik2	-	12	<i>Yr30</i> , <i>Sr2</i>

^A Source of resistance is Avocet S.

^B Leaf tip necrosis, a morphological marker linked to gene *Lr34*.

^C Reduction is the mean difference in severity of lines with and lines without the marker allele.

the genetic basis of interactions among genes and their mapping. All attempts to find a diagnostic marker for slow rusting genes *Lr34* and *Yr18* have failed so far. The closest markers for *Lr34/Yr18* and *Lr46/Yr29* genes are about 10 cM away. We recommend that more efforts should be made in the future to find markers for slow rusting resistance genes rather than investing in race-specific resistance genes.

Incorporation of resistance based on additive slow rusting genes: the single backcross approach

It is often believed that selecting for resistance based on additive minor genes is difficult. However, at CIMMYT we have launched a program to incorporate additive genes based durable resistance into important wheat cultivars/genotypes that have unacceptable levels of resistance to Mexican leaf and/or yellow rust races. We use one backcross approach where such cultivar/genotype is crossed with a group of about ten resistance donors (some listed in Tables 4 and 5) and then 20 spikes of the F_1 plants from each cross are backcrossed to obtain 400-500 BC_1 seeds. Selection is practiced from BC_1 generation onwards for resistance and other agronomic features under high rust pressure. Because the additive genes are partially dominant – partially recessive, BC_1 plants carrying most of the genes show intermediate resistance and can be selected. About 1600 plants per cross are space grown in the F_2 whereas population sizes of about 1000 plants are maintained in the F_3 - F_5 populations. Plants with low to moderate terminal disease severity in early generations (BC_1 , F_2 and F_3), and plants with low terminal severity in later generations (F_4 and F_5) are retained. We use a selected-bulk scheme where one spike from each selected plant is harvested as bulk until the F_4 generation and plants are harvested individually in the F_5 . Because high resistance levels require the presence of 4 to 5 additive genes, the level of homozygosity from the

F_4 generation onwards is usually sufficient to identify plants that combine adequate resistance with good agronomic features. Moreover, selecting plants with low terminal disease severity under high disease pressure means that more additive genes may be present in those plants. Selection for seed characteristics is carried out on seeds obtained from individually harvested F_5 plants. Small plots of the F_6 lines are then evaluated for agronomic features, homozygosity of resistance, etc. before conducting yield trials. By using the above methodology resistant derivatives of Baviacora 92, Seri 82, Attila, PBW343, Inqalab, and Pastor were developed recently. Some of the derived lines not only carry high levels of resistance to leaf rust or yellow rust or both diseases, but also carry about 5-15% higher yield potential than the original cultivar. We believe that this approach of wheat improvement allows us to maintain the characteristics of the original cultivar while improving its yield potential and rust resistance.

What should be done in Central Asia to achieve a long-term solution to rust diseases?

We recommend that wheat breeders, rust geneticists and pathologists working in Central Asia assemble a group of winter and spring wheat cultivars known to carry adequate levels of durable resistance to yellow and/or leaf rusts and evaluate them in the seedling stage in the greenhouse with relevant rust races and in field trials at hot-spot locations to identify those cultivars that show resistance stability in the Central Asian environment. Resistance from these cultivars could then be transferred in a planned manner to the susceptible but locally adapted cultivars through a 'Single Backcross Breeding Approach', described above. In our view, any breeding program in the region can adopt this simple breeding methodology to achieve a long-term rust control.

References

- Alvarez-Zamorano, R. 1995. Patogenesis de *Puccinia recondita* Rob. Ex Desm. f. sp. *tritici* y la resistencia en trigo. Ph.D. thesis. Colegio Postgraduados., Montecillos, Mexico. p. 76.
- Biffen, R.H. 1905. Mendel's laws of inheritance and wheat breeding. J. Agric. Sci. 1: 4-48.
- Borlaug, N.E. 1972. A cereal breeder and ex-forester's evaluation of the progress and problems involved in breeding rust resistant forest trees: "Moderator's Summary". Biology of Rust Resistance in Forest Trees: Proc. of a NATO-IUFRO Advanced Study Institute. Aug. 17-24, 1969. USDA Forest Service Misc. Publication 1221, pp. 615-642.

- Caldwell, R.M. 1968. Breeding for general and/or specific plant disease resistance. In: 'Proc. 3rd Int. Wheat Genetics Symp.' (Eds: K.W.Finley and K.W. Shepherd). Aust. Acad. Sci., Canberra: Australia, pp. 263-272.
- Dyck, P.L. 1987. The association of a gene for leaf rust resistance with the chromosome 7D suppressor of stem rust resistance in common wheat. *Genome*. 29: 467-469.
- Flor, H.H. 1956. The complementary genetic systems in flax and flax rust. *Adv. Genet.* 8: 29-54.
- Johnson, R. 1988. Durable resistance to yellow (stripe) rust in wheat and its implications in plant breeding. In: 'Breeding strategies for resistance to the rusts of wheat'. (Eds: N.W. Simmonds and S. Rajaram). CIMMYT: Mexico, D.F. Mexico, pp. 63-75.
- Lehman, J.S. and G. Shaner. 1996. Genetic variation in latent period among isolates of *Puccinia recondita* f. sp. *tritici* on partially resistant wheat cultivars. *Phytopathology*. 86: 633-641.
- Ma, H. and R.P. Singh. 1996. Contribution of adult plant resistance gene *Yr18* in protecting wheat from yellow rust. *Plant Dis.* 80: 66-69.
- Martinez, F., R.E. Nicks, R.P. Singh and D. Rubiales. 2001. Characterization of *Lr46*, a gene conferring partial resistance to wheat leaf rust. *Hereditas*. 135: 111-114.
- McIntosh, R.A. 1992. Close genetic linkage of genes conferring adult-plant resistance to leaf rust and stripe rust in wheat. *Plant Pathol.* 41: 523-527.
- Messmer, M.M., R. Seyfarth, M. Keller, G. Schachermay, M. Winzler, S. Zanetti, C. Feuillet and B. Keller. 2000. Genetic analysis of durable leaf rust resistance in winter wheat. *Theor. Appl. Genet.* 100: 419-431.
- Nelson, J.C., R.P. Singh, J.E. Autrique and M.E. Sorrells. 1997. Mapping genes conferring and suppressing leaf rust resistance in wheat. *Crop Sci.* 37: 183-285.
- Parlevliet, J.E. 1975. Partial resistance of barley to leaf rust, *Puccinia hordei*. I. Effect of cultivar and development stage on latent period. *Euphytica*. 24: 21-27.
- Peterson, R.F., A.B. Campbell and A. E. Hannah. 1948. A diagrammatic scale for estimating rust intensity of leaves and stem of cereals. *Can. J. Res. Sect. C*. 26: 496-500.
- Roelfs, A.P. 1988. Resistance to leaf rust and stem rust in wheat. In 'Breeding strategies for Resistance to the Rusts of Wheat'. (Eds: N.W. Simmonds and S. Rajaram). CIMMYT: Mexico, D.F. Mexico, pp.10-22.
- Roelfs, A.P., R.P. Singh and E.E. Saari. 1992. Rust diseases of wheat: concepts and methods of disease management. CIMMYT: Mexico, D.F. Mexico, pp. 81
- Rubiales, D. and R.E. Nicks. 1995. Characterization of *Lr34*, a major gene conferring nonhypersensitive resistance to wheat leaf rust. *Plant Dis.* 79: 1208-1212.
- Sayre, K.D., R.P. Singh, J. Huerta-Espino and S. Rajaram. 1998. Genetic progress in reducing losses to leaf rust in CIMMYT-derived Mexican spring wheat cultivars. *Crop Sci.* 38: 654-659.
- Singh, R.P. 1992a. Association between gene *Lr34* for leaf rust resistance and leaf tip necrosis in wheat. *Crop Sci.* 32: 874-878.
- Singh, R.P. 1992b. Genetic association of leaf rust resistance gene *Lr34* with adult plant resistance to stripe rust in bread wheat. *Phytopathology*. 82: 835-838.
- Singh, R.P. 1993. Resistance to leaf rust in 26 Mexican wheat cultivars. *Crop Sci.* 33: 633-637.
- Singh, R.P. and A.K. Gupta. 1992. Expression of wheat leaf rust resistance gene *Lr34* in seedlings and adult plants. *Plant Dis.* 76: 489-491.
- Singh, R.P. and J. Huerta-Espino. 1997. Effect of leaf rust resistance gene *Lr34* on grain yield and agronomic traits of spring wheat. *Crop Sci.* 37: 390-395.
- Singh, R.P., A. Mujeeb-Kazi and J. Huerta-Espino. 1998. *Lr46*: A gene conferring slow-rusting resistance to leaf rust in wheat. *Phytopathology*. 88: 890-894.
- Singh, R.P., J.C. Nelson and M.E. Sorrells. 2000. Mapping *Yr28* and other genes for resistance to stripe rust in wheat. *Crop Sci.* 40: 1148-1155.
- Singh, R.P., T.S. Payne and S. Rajaram. 1991. Characterization of variability and relationship among components of partial resistance to leaf rust in CIMMYT bread wheats. *Theor. Appl. Genet.* 82: 674-680.
- Singh, R.P. and S. Rajaram. 1991. Resistance to *Puccinia recondita* f. sp. *tritici* in 50 Mexican bread wheat cultivars. *Crop Sci.* 31: 1472-1479.
- Singh, R.P. and S. Rajaram. 1992. Genetics of adult-plant resistance to leaf rust in 'Frontana' and three CIMMYT wheats. *Genome*. 35: 24-31.
- Singh, R.P. and S. Rajaram. 1994. Genetics of adult plant resistance to stripe rust in ten spring bread wheats. *Euphytica*. 72: 1-7.
- Stakman, E.C. and M.N. Levine. 1922. Analytical key for the identification of physiologic races of *Puccinia graminis tritici*. (Processed) Div. of Cereal Crops and Dis., U.S. Dept. Agr. and Minn. Agr. Exp. Sta. 7 pp.
- Suenaga, K., R.P. Singh, J. Huerta-Espino and M. William. 2003. Microsatellite markers for genes *Lr34/Yr18* and other quantitative trait loci for leaf rust and stripe rust resistance in bread wheat. *Phytopathology*. 93: 881-890.
- William, H.M., D. Hoisington, R.P. Singh, D. Gonzalez-de-Leon. 1997. Detection of quantitative trait loci associated with leaf rust resistance in bread wheat. *Genome*. 40: 253-260.
- William, H.M., R.P. Singh, J. Huerta-Espino, S. Ortiz-Islas and D. Hoisington. 2003. Molecular marker mapping of leaf rust resistance gene *Lr46* and its association with stripe rust resistance gene *Yr29* in wheat. *Phytopathology*. 93: 153-159.