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GENETIC ANALYSIS OF WHEAT-RUST INTERACTIONS AND STRATEGIES TO BREED FOR DURABLE RESISTANCE

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ABSTRACT

Assessment of designated series of genes for resistance against Indian pathogen populations of all the three rusts and genetic basis for rust resistance in released cultivars have revealed that several of the effective genes, mostly derived from species related to *T. aestivum*, remained unexploited. A number of these genes have been successfully introgressed into formerly popular wheat cultivars that provided easily usable diverse resistances for tailoring new generations of high yielding rust resistant cultivars. Some of these stocks when employed as parents in several cross combinations in a breeding programme have generated a number of promising cultivars with diverse resistances. Deployment of diverse resistances in a crop population has helped in suppressing the intensity, effectiveness and frequency of rust epiphytotics and thus served as a buffer in checking disease spread.

It is well recognized that most resistances are eroded by the new pathogenic races soon after the cultivar is extensively grown. Evolution of new virulences in each of the pathogen populations as influenced by resistance genes deployed in the local cultivars has been described.

Adult plant resistance (APR) is conferred by genes that are ineffective in seedlings but becomes operative in adult plants. They are implicated in durability but usually confer partial resistance. A number of cultivars both from national and international programmes and certain near-isogenic lines carrying specific leaf-rust resistance genes as possessing diverse sources of APR to leaf rust have been identified. A new source Federation* 4/Kavkaz carrying novel complementry genes, seperately derived from Federation and Kavkaz, determined adult plant resistance to leaf rust. Some of these sources, besides *Lr34/Yr18, Sr2, Sr26* and Sr31 that are recognized to confer durable resistance, have potential to be durable. In certain cultivars *Lr34* and *Sr2* in combination with other specific genes have been successfully utilized for durable resistance. A novel adult plant resistance gene associated with durability to leaf rust in cv. Arjun has been identified.

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Combination of more than one resistance genes each conferring resistance to existing race spectrum in a cultivar is one strategic approach to achieve durable resistance. Identification of markers linked to different resistance genes for selection of plants with such genic combinations in a segregating population of resistance breeding is important. Molecular marker selection techniques that have become recently available are still emerging with tremendous potential to pyramid desired gene combinations. However, until the molecular marker selection techniques become routinely available, conventional means of pyramiding some highly effective genes in the background of adult plant durable incomplete resistance is a more practical approach of breeding durable and adequate levels of resistance. Durable resistances controlled by *Lr34/Yr18* and *Sr2* that are linked with morphological markers can be more easily manipulated in the presence of more effective genes. In absence of any associated marker with partial or incomplete resistance, combination of these two distinct types of resistance can be achieved by following a two step breeding strategy.

For stripe rust resistance, resistances that were transferred from durable resistant cultivars across widely different genotypes into the formerly popular wheats WL 711 and Kalyansona, ,offer well adapted materials for imparting durable resistance, in addition to use of the gene *Yr18*.

Key words : *T. aestivum, Puccinia recondita, P. graminis, P. striiformis*, Rust Genetics, Breeding durable resistance.

Wheat is the major winter cereal all over the world. Of the total world wheat production of 590.3 million tonnes, India harvested 68.9 million tonnes in 1996-97. With the spread of high yielding variety (HYV) technology, the control of disease assumes greater concern because intensive agriculture provides most congenial environment for disease build up. Among the diseases that attack wheat, rusts are the most damaging and development of high yielding, rust resistant cultivars provides the most practical and economical approach in achieving yield stability at higher levels of productivity. Breeding for durable resistance has special significance for developing economy where the frequent replacement of cultivars entails an enormous expenditure on limited resources. All the three rusts, namely stem rust (*Puccinia graminis Pers.*), leaf rust (*P. recondita* Rob. ex *Desm*), and stripe rust (*P. striiformis Westend*) are prevalent in the country. Each rust species has a unique optimum temperature requirement for disease development. Stem rust is a warm temperature rust, leaf rust a moderate temperature rust and stripe rust a cool temperature rust. The losses due to rusts can be large and can vary from year to year and region to region.

A very intimate interaction exists between wheat and the obligate parasites that cause three rust diseases. A complete study of wheat rust genetics demands the genetics of both host and pathogen. Although genetics of the rust pathogens is difficult to study, the genetics of the host (wheat) can be studied from the interaction between host and pathogen which produce incompatible (resistance) and compatible (susceptible) reactions. The work of Flor [1] demonstrated that the pathogenic range of each physiologic race of the pathogen is conditioned by pairs of factors that are specific for each different resistance factor possessed by the host variety which led to the concept of *gene-for-gene* interactions. These interactions indicate that incompatibility or resistance reaction depends upon the presence of an allele (usually dominant) determining resistance in the host and the corresponding allele, also usually dominant, for avirulence in the pathogen. All other interactions of host and pathogen genotype result in compatibility and generally cannot be distinguished. Furthermore, when more than one resistance genes are combined together, the pathogen rust evade the effect of each gene by change at a specific corresponding locus. This operation of a gene-for-gene system [2] has the implication that resistance will not remain effective if the pathogen acquires the corresponding virulence by losing the avirulence allele that elicits resistance, either by deletion or by genetic change following evolution in pathogen strain. These interactions also permit gene postulation of pathogen strains for avirulence/virulence, corresponding to the resistance genes in the host and provide a basis for molecular genetic analysis of a host-parasite interaction.

Sawhney [3] recently described the concepts related to major categories of resistances in wheat rust systems including the various techniques, procedures that are followed in management of genetic control to rust diseases. The terms race-specific and race-non-specific resistance, that are descriptive of the way the resistance functions, is briefly described here. Race-specific resistance is conferred either by genes that are effective in seedlings and throughout the life of a plant or by genes that become effective only in adult plants. It imparts resistance to some pathogen isolates and not to others and has relatively simple inheritance. When resistance is effective to all isolates of a disease organism it can be termed as race-non- specific. It has potential to be durable and resistance is usually effective partially at adult stages of plant growth. Nevertheless, resistance can only be classified as non-specific as long as no pathogen genotype is discovered that can overcome it [4]. Johnson [5] argued that it is almost impossible to prove that resistance is non-specific because it requires the demonstration that the pathogen is incapable of evolution towards increased pathogenicity specific for that resistance. Additional problems may occur if the differential interactions are small and are obscured by large uncontrolled variation [6].

It is a common experience that specific resistance is often neutralised by the evolution of new pathogenic race soon after a new resistant cultivar is extensively grown, which makes resistance breeding an ever continuous process. Nevertheless, both evidence and knowledge is accumulating about durable resistance and how it can be exploited. So far, for the rust diseases of wheat most durable resistance is characterised being effective in adult plants, partial, slow rusting and apparently race-non-specific. Identification and use of durable resistance or on the continuing use of resistances in different gene combinations offer possible alternative approaches to breeding for durable resistance to rust diseases. The discussion that follows will mostly relate to studies likely to help breeding for durable resistance. This communication also describes the genetic basis of rust resistance for commonly grown cultivars in India and the evolution of new pathotypes in each of the Indian population of rust pathogen with virulence for the specific resistance genes currently deployed in wheat cultivars. For purpose of discussions the three rusts of wheat, due to three different fungi, are considered separately with some cross references where relevant. They are presented in the sequence, leaf, brown rust; stem, black rust; stripe, yellow rust.

II. *Puccinia recondita* (Leaf rust)

Leaf rust is the most widely distributed of the three rusts and is found in almost all areas where wheat is grown [7]. Genetic studies have led to the naming of 43 resistance gene loci by 1993 [8]. Samborski [7] described changes in the pathotypes of the pathogen that occurred when cultivars with newly introduced resistance were extensively grown. He further emphasised that the pathogen population evolve more rapidly to new virulences when cultivars with single genes are released. Nevertheless, some adult plant, incomplete resistances have been recognised as genes/sources of durable/ potentially durable resistances.

1. *Genetic basis of adult plant partial leaf-rust durable resistance*

Roelfs [9] described cultivars from South America that displayed durable resistance to leaf rust. Among these cultivars was Frontana which had a high level of resistance and was used in North American, CIMMYT, and Indian breeding programmes. One of the genes possessed by Frontana is *Lr13* described as a gene for adult plant resistance located on chromosome 2BS. Use of Frontana in North American wheats led to the evolution of virulences for *Lr13*. In contrast to the failure of *Lr13* in North America, it was highly effective in Australia since 1973. Egret was released as the first cultivar carrying *Lr13* in Australia, the resistance of which was overcome by an exotic pathotype of *P. recondita* in 1981 [10]. *Lr13*, the most commonly identified gene in the Indian wheat varieties [11, 12] was reported to be completely ineffective in India at least when present alone [3]. *Lr13* is also reported to be interactive in nature and produce enhanced resistance in combination with certain other genes [13]. The resistance conferred by *Lr13* was referred as due to the *Lr13* complex [14]. The term *Lr13* complex has created some confusion by suggesting that *Lr13* is a complex gene. There is no evidence for this [6] but interaction for enhancement of the effect of *Lr13* with other genes is recognised [13]. Further, studies of Frontana and other wheats led to the recognition of another gene *Lr34* located on chromosome 7D. Evidence accumulated to suggest that this gene contributes durability for resistance to leaf rust. Like *Lr13* expression of *Lr34* is strongly affected by the presence of some other genes [15]. A non-differential interaction response in near-isogenic lines carrying *Lr34* with a number of genetically diverse pathotypes of *P. recondita* produced uniformly moderate resistance responses (Unpublished data as reported in [16]). However, considerable differences in levels of resistance have been observed in lines carrying *Lr34* alone or in combination with certain other genes due to the interaction effect between the genes [6]. The Chinese Spring substitution lines with the single genes *Lr10* and *Lr23* were shown to be more resistant than the isogenic Thatcher lines with *Lr10* and *Lr23* respectively [17]. This enhanced resistance was postulated to be due to the combination of Chinese Spring adult plant resistance of *Lr34* and *Lr12* and additional resistance gene [18]. Sawhney [19] showed that neither *Lr12* nor *Lr31*, two of the other genes in the cultivar Chinese Spring has a role in conferring resistance either alone or in combination with *Lr34*. However, in the presence of complementary genes (*Lr27* + *Lr31*), *Lr34* produced enhanced resistance. Cultivar Shortim with *Lr27* and *Lr31* was highly susceptible (score 50S to 60S in different years), a line with *Lr34* was moderately resistant (20MS to 40MS) and lines with all three of these genes together were very resistant (trace R to 10MS). *Lr34* on its own conferred a slow rusting effect [20] and under the most conducive conditions can develop high levels of infection [6]. As with gene *Lr13* referred to above, the term *Lr34* complex [21], used in CIMMYT programmes has no supporting evidence except that like *Lr13*, it interacts with other genes for enhanced effect and is also very influenced in its expression by environmental conditions. For example, high disease intensities in South Africa and low intensities in the U.K. were reported (R. Johnson, personal communication 1997). A number of cultivars possessing *Lr34* in combination with other genes maintained acceptable levels of resistance to leaf rust in India [22]. A Thatcher line carrying *Lr34* (Tc + *Lr34*) showed adult plant stem rust resistance in Canada [23] and in India [24]. *Lr34* is also associated with the stripe rust resistance gene *Yr18* [25, 26]. These associations of resistance to all the three rusts are likely to be due to closely linked genes, which not only offer aid in breeding for combined resistance to all three rusts but can also assist in the identification of genetic diversity in instances where resistance to these diseases are not associated. A visible effect of slight necrosis on the tips of the flag leaves of cultivars with *Lr34* provided a useful marker in the selection of this gene under field conditions [27]. A number of cultivars Kundan, HD 2160, HD 2189, HP 1209, Kanchan, DL 802-3, VL 616 carrying *Lr34* in combination with other genes were reported [28]. Singh and Huerta-Espino [21] showed that the presence of *Lr34* which is linked with leaf tip necrosis of adult plants, may cause a slight yield reduction in some disease free environments.

2. Novel durable adult plant partial leaf-rust resistance gene

A wheat cultivar Arjun (HD2009), under cultivation since 1970 over large areas, has continued to show field resistance and thus qualifies for being described as durably leaf rust resistant wheat [29]. Inheritance of resistance in Arjun revealed that its durable leaf rust resistance is attributable to a novel dominant adult plant resistance gene [30]. *Lr13*, another gene reported in the cultivar [31] has played no role in conferring durable resistance to this cultivar. The new gene is also established to be different from *Lr34*, the only effective adult plant resistance gene from *T. aestivum* which is known for durability.

3. Postulation of new resistance genes/sources of potential durability

Durable resistance is often associated with genes giving incomplete resistance. This applies to *Sr2* and *Lr34/Yr18*, but not to *Sr26* and *Sr31*. Nevertheless, it could be considered that new genes of unknown durability could be assessed as being more likely to provide durable resistance if they provide incomplete resistance rather than extreme hypersensitive resistance. In the following section this argument has been applied and genes providing incomplete resistance, slow rusting or apparently non-specific are designated as more likely to give durable resistance than those producing extreme hypersensitive reactions. However, there can be no certainty about these diagnosis - the durability of resistance will only be tested by widespread and prolonged use in a cultivar according to the definition of Johnson [32].

3(i). Diverse sources for adult plant leaf-rust resistance

Field resistance in adult plants which cannot be recognised in the seedling is very important because most sources of durable resistance to leaf rust have been described as carrying resistance of adult plant type. In an attempt to identify adult plant resistance sources, studies carried out on sixtyone Indian wheats released for cultivation, six diverse sources of adult plant leaf-rust resistance were recognised. *Lr34* individually or interacting with other APR genes for enhanced and prolonged resistance was postulated in a number of these sources [16]. A similar study on Australian wheat cultivars had recognised 7 cultivars in four groups, each group carrying diverse group of genes for resistance. Analogously to the postulations for Indian wheats, it was suggested that Australian wheat cultivars possibly also carried *Lr34* individually or in combination with other APR genes constituting four diverse groups [33]. More information on these wheats, and whether they could themselves provide prolonged resistance or only through association with *Lr34* may determine new components contributing to durability.

3(ii). Adult plant leaf-rust resistance genes

Sawhney *et al.* [34, 35] showed that resistance due to *Lr35* from *T. speltoides/T. monococum* and of *Lr37* having its origin from *T. ventricosum* were identified to be effective in adult plants. Seedling tests of lines with *Lr35* [34] and *Lr37* (unpublished data) produced IT3, a compatible reaction with all the pathotypes when used individually. *Lr35* was identified as a race-non-specific adult plant gene when tested with six genetically diverse pathotypes and thus likely to impart durability [34]. The expression of resistance in lines carrying *Lr37* through decreased rate of uredinial appearance, fewer uredina and smaller uridinium size [36] indicated this gene as conferring slow rusting. *Lr37* which is reported to be linked with stem rust resistance gene Sr38 and stripe rust resistance gene *Yr17* has been extensively used in the Australian breeding programme where rust resistance due to these genes is still remaining effective. Cultivar Sunbri [37] Sunstate and Trident carrying these resistances has been developed/released.

3(iii). Federation/Kavkaz (1BL-1RS) novel adult plant complementary leaf-rust resistance genes

The wheat-rye translocation chromosome (1BL/1RS), which carries *Lr26/Yr9/Sr31*, has been the most widely exploited source of rust resistance in the world in the development of wheat cultivars. Even with the loss of resistance to leaf rust conferred by *Lr26* in many parts of the world, including India [38] most breeders still used this 1BL-1RS translocation stock because apparently this segment gave higher yields than genotypes lacking the translocation [39, 40]. In addition, 1B-1R genotypes imparted environmental stability for yield [41]. An adult plant resistance response on a line derived from Federation (*Lr10*)/Kavkaz (*Lr26*), to a pathotype with virulence for adult plants of both Federation and Kavkaz was determined to be due to the undescribed novel complementary genes of resistance, seperately derived from Federation and Kavkaz [42]. Resistance due to gene interactions, as in this case, is likely to be more stable than resistance determined by a single gene pair [43].

3(iv). Novel adult plant partial leaf-rust resistances in near-isogenic lines with known seedling genes

Thatcher near-isogenic lines with *LR14b*, *Lr14ab*, and *Lr30* were identified in India (16) as also in Australia (37) as novel adult plant resistance sources. Adult plant resistance responses on all the three lines to pathotype 77-5, a highly virulent and newly evolved pathotype, have indicated that these sources are likely to impart durability [35]. The resolution of the question that either each allele was capable of conferring adult plant resistance or that an additional gene(s) was transferred in each instance during back-crossing would be interesting. Seedling resistance in each of these lines could not be identified.

4. Basis of leaf rust resistance in Indian Wheats

Several studies to investigate the leaf-rust resistance genes commonly found in the currently grown wheats suggested that these contain *Lr1, Lr3, Lr10, Lr13, Lr14a. Lr23, Lr26, Lr34,* either singly or in combination of two or three genes and also some adult plant resistance components, besides *Lr13* and *Lr34* [16, 12, 28]. All these known genes except *Lr34* have become less effective. Table 1 gives leaf-rust resistance genes/sources identified in some major wheats under cultivation since 1967. Average coefficient of infection on these wheats that were observed recently in All-India Coordinated Programme revealed that the varieties possessing *Lr34*, in combination with other genes, had low-coefficients of infection. A few of the other wheats also postulated to possess *Lr34*, with high level of infection were subsequently reported to be lacking *Lr34* [28]. Low level of infection on Arjun, however, was atttributed to novel adult plant resistance gene with durability as described earlier in the preceding section. Three of the wheats Sonali (*Lr9*), Vaishali (DL 784-3) and Vidisha (DL 788-2) both possessing Lr24, which were derived from *Agropyron* also showed very low co-efficients of infection demonstrating that these genes have continued to be highly effective [44].

5. Effective genetic leaf-rust resistance variation of potential use in resistance breeding

Of the known genes up to *Lr34* for resistance to leaf rust, *Lr9, Lr19, Lr21, Lr22a, Lr24, Lr28, Lr29, Lr32, Lr34* were reported to be effective [45, 46, 47, 24]. All these genes except *Lr34*, are alien in origin and were effective throughout plant life except *Lr22a* and *Lr34*, that operate at adult plant stage. *Lr34* is known to be associated with durability.

In certain experiments, resistance genes from alien species have been associated with reduced grain yields. Sawhney and Sharma [48] have attempted a backcross breeding programme where it was demonstrated that with limited backcrosses and selection of desirable rust resistant plants in each selfed and backcross generation it became possible to produce lines with certain alien resistance genes which yielded higher or comparable to the recurrent parent Kalyansona in disease free conditions. A similar set of Sonalika backcross derived lines with diverse alien resistance genes

Table 1. Leaf rust resistance genes in some important Indian wheats and average coefficient of infection (ACI) in field conditions

Year of release	Cultivar	Gene(s)*	ACI**
Resistances from *T. aestivum*			
1967	Kalyansona	*Lr14a*	56.0
1967	Sonalika	*Lr13*	56.0
1973	NI 5439	*Lr34#*	42.0
1974	Arjun	*Lr13,APR1+*	16.4
1977	WH 147	*Lr13,34#*	65.0
1977	UP 262	*Lr23,34#*	35.0
1979	WL 410	*Lr13*	57.0
1979	WL 711	*Lr13*	72.0
1979	HD 2189	*Lr13,34*	16.2
1979	HP 1209	*Lr1,3,34*	19.2
1981	LOK-1	*Lr13*	30.0
1984	HUW 234	*Lr14a*	22.4
1985	HD 2285	*Lr23*	22.5
1985	HD 2329	*Lr10,13,34#*	29.0
1985	Kundan	*Lr23,34*	08.3
Resistances from alien sources			
Wheat-rye translocated chromosome (IBL/IRS) wheats			
1982	HUW 206	*Lr23*	26
1989	HS 240	*Lr1,26,34*	17.6
1991	MACS 2496	*Lr1,23,26*	27.2
1992	WH 542	*Lr23,26,34*	20.8
1993	GW 190	*Lr1,23,26*	31.5
1993	Kanchan	*Lr23,26,34*	05.5
1993	UP 2338	*Lr26,34*	13.6
1994	PBW 343	*Lr26,34*	09.8
Triticum umbellulatum resistance wheat			
1992	Sonali	*Lr9*	0.2
Thinopyrum ponticum resistance wheats			
1993	Vaishali	*Lr24*	0.0
1996	Vidisha	*Lr24*	5.2

*Source: Nayar *et al.* (1994). Research Bulletin 32, Regional Station, Directorate of Wheat Research, Flowerdale, Shimla-171 002.

**Source: Plant Pathological Screensing Nurseries (AICWIP); # Other tests indicated absence of *Lr34*

+ Novel APR gene (Sawhney and Sharma (1997) Plant Breeding. 116 : 598-599.

were also developed (Sawhney *et al.* unpublished). These derivatives have served and will continue to serve as useful pre-breeding stocks in tailoring a new generations of high yielding rust resistant wheats embodying diverse gene combinations. Cox *et al.* [49] have shown that the backcross derived common wheat lines with alien gene *Lr41* (*T. tauschii*) produced increased grain yield and milling quality under heavy leaf rust infection with no negative effect on these traits in disease free plots. Resistances *Lr35* and *Lr37* from alien sources were effective in adult plants [34, 35]. *Lr35* has potential for durability [34].

In the expanded series of newly described genes, *Lr41* (source: *T. tauschii*), *Lr42* (source: *T. tauschii*), *Lr44* (source: *T. spelta*) and *Lr45* (Source: Japanese wheat-rye translocation), all of alien origin and available in agronomically undesirable background, were effective both in seedlings and adult plants, thus conferring over-all resistance to leaf rust [50]. Transfer of these genes into the background of popular but currently susceptible wheats through backcross should provide easily usable additional alien diversity for resistance to leaf rust.

6. Evolution of pathotypes in *P. recondita* in India

Mehta [51] described leaf rust pathotypes that were predominently avirulent for *Lr3*. Use of Democrat (*Lr3*) resulted in the evolution of pathotype 77 that infected *Lr3* in 1954. At present, there are 22 different pathotypes that match *Lr3* in different gene combinations [12]. Similarly, pathotypes matching *Lr1* increased from 5 in 1972 to 19 in 1994 [12]. The use of Gabo and Timstein in early seventies, both carrying *Lr10* + *Lr23*, led to the appearance of 77A and 77A-1 that were pathogenic for *Lr10*. Likewise, matching virulence for *Lr23* was first detected in 1974. By 1994, 9 pathotypes with virulence for *Lr23* were known [12]. Another important gene *Lr13* in Frontana used in breeding for the first time in the mid seventies was at that time susceptible to only pathotype 77. The number of pathotypes attackng this resistance has now increased up to 10 [12]. In the early 80s, use of 1B/1R translocation carrying *Lr26* led to the evolution of virulences matching *Lr26*, 12-1 in 1983 and 77-1 in 1985. Subsequently Nayar *et al.* [38] described five pathotypes with virulence for *Lr26* which has now arisen to 8. The frequency of pathotypes with virulence for *Lr26* increased from 7.8% in 1991 to 23.9% in 1996. Likewise, frequency of pathotypes with virulence for *Lr23* increased from 46.3% in 1991 to 81.6 per cent in 1996 (S. K. Nayar *et al.* unpublished data). More recently, pathotypes with combined virulence for both *Lr23* and *Lr26* (104-2, 77-5, 77-6) have appeared resulting in the susceptibility of most current Indian wheats to leaf rust.

III. *Puccinia graminis* (Stem rust)

1. Genetic basis of adult plant partial stem-rust durable resistance

A total of 40 genes for resistance to stem rust were described by 1993 [8]. Hare and McIntosh [52] concluded that the gene *Sr2*, first reported by McFadden derived from Yaraslav emmer via Hope and H-44 with other genes, displayed durable resistance to stem rust. D. R. Knott, however, doubted a role for *Sr2* of this nature in Canada [53]. Johnson [6] reported a personal communication from R.A. McIntosh attributing this difference of opinion to a possible effect of late scoring in which high infection levels were recorded, and earlier scores would make the detection of effects of *Sr2* clearer which was considered very important for recognising resistance conferred by Sr2. Johnson [6] argued that *Sr2* on its own, probably does not provide sufficient resistance when conditions very conducive to stem rust are prevalent. Sawhney [3] further argued that resistance by *Sr2* is not recognised in Canada possibly because Canadian wheats have a much longer growing period and/or the Canadian stem rust population is quite different from those where *Sr2* has demonstrated potential for durability through interaction with other genes. A number of cultivars grown in India [11, 12] and other parts of the world indicated that when *Sr2* is present in the background with other more effective but less durable genes has provided durability for resistance to stem rust. *Sr2*, alone, however, is not sufficiently effective in India under highly conducive conditions [11] and produces high terminal disease scores. Hare and McIntosh [52] reported the close linkage of melanin pigmentation on spikes and lower leaves with *Sr2*. It has also been shown that seedlings with *Sr2* also develop a distinctive mild chlorosis when grown at temperature above 22°C [10]. These markers are helpful for determining the presence of *Sr2* in both field and laboratory. Rajaram *et al.* [14] stated that *Sr2* interacts with other genes in the achievement of increased and durable resistance to stem rust and exploitation of *Sr2* in combination with other genes therefore continues to be an important objective of CIMMYT wheat breeding programmes. Using the associated blackening of the ear, a gene that provides only incomplete resistance, in combination with other genes that confer higher levels of resistance could possibly contribute to the ability for prolonged resistance. Development of linked markers such as RFLPs could contribute to the ability to combine genes that could not be detected in the presence of a resistance gene of universal effectiveness. Stem rust resistance due to *Sr2* is, however, referred to as the *Sr2* complex in CIMMYT programme, which is likely to be misconstrued to mean that *Sr2* is a complex gene. The term *Sr2* complex only denotes that *Sr2* interacts with other genes/modifying genes for enhanced resistance [3]. Analysis of the effects on yield of genes that provide only moderate resistance like *Sr2* showed that their presence can enhance yield even when terminal infections become high, due to the delay in the build- up of disease (R. Johnson, personal communication, 1997).

2. Durable over-all stem-rust resistance gene derived from *Agropyron elongatum*

The over-all resistance gene *Sr26* was derived from *Agropyron elongatum (Host) Beav.* The gene was used in the Australian breeding programme for resistance to stem rust and has remained effective since 1967 [54] when it was initially deployed. A number of cultivars including Eagle, Avocet, Flinders, Harrier, Jabiru, King, Kite and Takari [8] carrying *Sr26* were released and widely grown. All efforts to find a susceptible infection in the field on lines with *Sr26*, or to produce one by mutation failed but a laboratory culture from the United States, that has virulence for plants with *Sr26*, was found [55]. No exceptional durability was expected for this resistance gene when it was first introduced into the Australian wheat breeding programme ([6], a personal communication of R.A. McIntosh). A Kalyansona backcross derivative with *Sr26* from Eagle was developed. Transfer of *Sr26* in a popular wheat without depression in yield will encourage the use of this gene in future breeding programmes [48].

3. Durable over-all stem-rust resistance gene derived from rye

The gene *Sr31* derived from Kavkaz and Aurora linked with *Lr26* and *Yr9* also confers over-all resistance to stem rust. Although, many cultivars with these genes have been widely grown, no race has yet been detected with virulence for *Sr31* [37]. In the Indian Plant Pathological Screening Nurseries, however, many cultivars with these genes are screened every year and variable stem rust infection, higher than expected, has been observed. There has been some other reports of virulence on lines supposed to possess *Sr31*. These have not so far been found to be due to virulence for *Sr31* but appears to have happened from other causes. One important feature of the 1B-1R translocated chromosome is that it is reduced in transmission through the male gamete in heterozygotes of some crosses [56]. In outcrosses this chromosome can therefore become reduced in frequency soon. The stem rust infection could therefore have been on plants lacked *Sr31*, rather than indicating virulence for the gene. Lines supposed to carry *Sr31* should be more intensively studied to establish whether there are pathogen isolates with increased virulence or environmental effects such as high temperature, giving rise to these infections and whether these lines are genetically homogeneous for presence of *Sr31*. However, no race with virulence for *Sr31* has yet been detected in India.

Despite the many failures recorded for single genes for resistance to stem rust, the three most durable stem rust resistances described above were largely due to what are apparently single genes. Two of these *Sr31* and *Sr26* confer high levels of over-all resistance. They are both located on alien segments of chromosome that possibly do not pair with wheat chromosomes under the normal conditions of pairing control existing in hexaploid wheats. Although they behave as single, they may be more complex but lack of recombination of the alien chromosome segment on which they are carried could cause them to have the appearance of single genes [57].

4. Polygenically controlled durable stem-rust resistance

Knott [4] suggested the possibility of achieving durable resistance to stem rust through polygenic resistance. These are currently less genetically defined than those described above. Also, polygenically controlled resistance is more difficult for breeders to manipulate than simpler genetic systems.

5. Basis of stem rust resistance in Indian wheats

Table 2 lists important Indian cultivars with stem rust resistance genes and average co-efficients of infection to stem rust determined in the multilocation field tests. Most of the earlier developed wheats that carry *Sr2, Sr7a, Sr8, Sr9b, Sr11,* except HUW 234 and HD 2285, possessing *Sr9b* and *Sr11*, singly or in combination, showed high levels of infection. Low infection in HUW 234 and HD 2285 with same known genes for resistance as those showing high infection indicated the possibility of additional resistance in them which needs further investigation. Wheats with 1B/1R translocation showed stem rust resistance due to *Sr31*, a gene known to confer high degree of resistance with durability. Increased resistance in MACS 2496 and GW 190 in comparison to HUW 206, HS 240, WH 542 and UP 2338, can be attributed to *Sr2*, in addition to *Sr31* present commonly in all these wheats. Higher levels of resistance in Kanchan and PBW 343, also carrying *Sr31* is attributed to possible additional unidentified resistance. Nevertheless, the use of *Sr31* in many cultivars constitutes a case of genetic vulnerability as change in the virulence spectrum of the pathogen can be directly influenced by resistance genes incorporated in the local cultivars. It is, therefore, necessary that this gene be used in combination with other genes. A combination of *Sr31* and *Sr2*, as in certain wheats, is likely to contribute longevity of resistance. Both Vaishali and Vidisha with resistances *Sr24, Sr2,* and *Sr5* were resistant to newly evolved stem rust pathotype with virulence for *Sr24* [58], which may be due to additional stem rust genes in these cultivars.

6. Effective genetic stem-rust resistance variation of potential use in resistance breeding

A number of genes, among those described, effective to the Indian population of stem rust pathogen were mostly of alien origin [59, 60, 61]. Bhardwaj *et al.* [62] reported that lines carrying *Sr25, Sr26, Sr27 Sr31, Sr32* continue to maintain resistance

Table 2. Stem rust resistance genes in some important Indian wheats and average coefficient of infection (ACI) in field conditions

Year of release	Cultivar	Gene(s)*	ACI**
Resistances from *T. aestivum*			
1967	Kalyansona	*Sr11*	68.5
1967	Sonalika	*Sr2,11*	53.8
1973	NI 5439	*Sr11*	53.0
1974	Arjun	-	23.0
1977	WH 147	*Sr7a,11*	61.0
1977	UP 262	*Sr11*	43.0
1979	WL 416	*Sr11*	48.0
1979	WL 711	*Sr7b*	69.0
1979	HD 2189	-	11.2
1979	HP 1209	*Sr9b*	30.0
1981	LOK-1	*Sr2,9b,11*	40.0
1984	HUW 234	*Sr9b,11*	16.6
1985	HD 2285	*Sr9b,11*	08.0
1985	HD 2329	*Sr8,9b,11*	52.0
1985	Kundan	*Sr8,9b,11*	42.5
Resistances from alien sources			
Wheat-rye translocated chromosome (IBL/IRS) wheats			
1982	HUW 206	*Sr31*	12.7
1989	HS 240	*Sr31*	17.7
1991	MACS 2496	*Sr2,31*	07.0
1992	WH 542	*Sr31*	03.9
1993	GW 190	*Sr2,31*	05.5
1993	Kanchan	*Sr31*	05.5
1993	UP 2338	*Sr31*	15.7
1994	PBW 343	*Sr31*	08.2
Thinopyrum ponticum resistance wheats			
1993	Vaishali	*Sr2,5,8a,24*	0.1
1996	Vidisha	*Sr2,5,24*	0.6

*Source: Nayar *et al.* (1994). Research Bulletin 32, Regional Station, Directorate of Wheat Research, Flowerdale, Shimla-171002. **Plant Pathological Screening Nurseries (AICWIP) to all stem rust pathotypes and, in addition, *Sr39* was identified for the first time as conferring resistance to all the field isolates of stem rust. Patel and Deokar [63] reported ineffectiveness of *Sr32* to pathotype 40A which was perhaps due to the incorrect seed stock as this gene showed complete resistance in other tests (S. C. Bhardwaj, pers. comm.). In India, till recently, most of the alien genes that were effective, except *Sr31*, have not yet been exploited. Resistance conferred by *Sr26* and *Sr31* were recognised to be durable because cultivars carrying these genes individually remained effective for a long time even when grown over large areas in different parts of the world. *Sr31* carried by 1RS-1BL wheat-rye translocation has been extensively exploited. Transfer of *Sr26* in a popular wheat without depression in yield [48] provided useful stock carrying this gene in future breeding programmes.

7. Evolution of pathotypes in *P. graminis* in India

Evolution of stem rust pathotypes during the last 25 years of cultivation of dwarf wheats produced mostly races 21, 40, 42, and 117.

Cultivation of ChhotiLerma in the Nilgiri Hills in the early days of dwarf wheat cultivation, led to evolution of pathotype 40A in 1975 with virulence for this wheat. Pathotype 40A was the most virulent pathotype and possessed virulence for a number of potentially useful *Sr* genes. This pathotype, in addition to having avirulence for the universally resistant genes (*Sr25, Sr26, Sr27, Sr31, Sr32, Sr39*) was also reported to have avirulence for lines carrying *Sr21, Sr22 Sr24* and *Sr33* [63]. A newly evolved pathotype (40-1) with virulence for *Sr24* was detected on advanced generation breeding material from the Nilgiri Hills in 1990 [58]. Recently, this was the predominant stem rust pathotype in the Nilgiri Hills [62].

The race 21 group constituted pathotypes 21A and 21A-1, 21-1 and 21A-2. This group was predominent in Karnatka and Maharashtra. Genes *Sr5, Sr9e, Sr21, Sr24, Sr33,* and *Sr37* (*SrTt2*) and six other genes for resistance to all the Indian pathotypes were effective against race group 21.

Pathotype 117A-1 of the race 117 group with virulence for *Sr9b* and Charter (*Sr11*) was identified in 1977 [64]. In 1987, a pathotype with combined virulence for *Sr9b* + *Sr37* (*SrTt2*) was also identified as 117A-1. Since 1990, five more variants viz. 117-1, 117-3, 117-4, 117-5, 117-6 with additional virulence for different stem rust genes/gene combinations were identified [65]. Pathogenecity of four of these variants of 117, except 117-6, for *Sr37*, a gene rarely used in the Indian wheat programme is interesting. Evolution of a number of variants in 117 group was largely helped by the cultivation of Bijaga Yellow and rendered most of the *durum* wheats susceptible (S. C. Bhardwaj, per. comm.).

Pathotype 42B of the race 42 group is predominant in Karnataka and Maharashtra. Interestingly, 42B was absent in Tamil Nadu which serves as a main focus of stem rust infection [66]. Pathotype 42B was observed to be avirulent to a number of known genes *Sr5, Sr23, Sr24, Sr28, Sr29, Sr30, Sr35, Sr37,* besides six other genes that were identified for resistance to all the Indian stem rust pathotypes.

IV. *Puccinia striiformis* (stripe rust)

1. Genetic variation of stripe rust resistance

The number of named stripe rust resistance genes is much less than for the other two rusts with only 18 listed by 1993 [8]. In addition, Chen and Line [67] allocated a number of temporary designations to uncatalogued genes when a number of differentials and other wheats were analysed with North American *P. striiformis* accessions. Inheritance studies on the differentials such as T. spelta var. alba [68], Moro [69] and Heines VII [70] with Indian pathotypes suggested that more than one described genes for resistance in each of these differential wheats is present. Earlier Singh and Johnson [71] reported the presence of additional undescribed genes in Heines VII that is known to possess *Yr2* which did not allow the detection of pathogenicity of some races for *Yr2* of P. striiformis. These studies emphasised the need for developing ideal tester stocks each carrying a single different gene for differential of pathogen population and in identifying new sources for resistance. McIntosh *et al.* [8] listed *Yr11* to *Yr16* as adult plant resistance genes. Nayar [72], however, observed the effectiveness of these genes at the seedling stage with Indian stripe rust pathogen population.

Effectiveness of described resistance genes was recently discussed: it was argued that the major genes effective so far in India may not provide lasting resistance when exploited in breeding programmes because pathogenicity for all those resistances described so far is available in different parts of the world pathogen population [3, 28]. *Yr18,* the only genetic component controlling durable resistance to stripe rust was reported recently [73]. R. Johnson communicated that under the environment of New Zealand, *Yr18* alone does not provide adequate resistance to stripe rust under all circumstances. Its resistance however, was variable in different plots in Norwich (England) (R. Johnson, per. comm.). Singh and Rajaram [74] also found that cultivars with *Yr18* alone confer inadequate level of resistance but when combined with two to three additional slow rusting genes can confer an acceptable level of adult plant resistance even under high disease pressure [75].

2. Exploitation of durable resistant sources to stripe rust

Many of the cultivars described so far as possessing durable resistance to stripe rust are of winter habit and the resistance of these wheats is therefore difficult to exploit in breeding spring habit wheats. Through a collaborative programme between the Plant Breeding Institute (PBI), Cambridge (currently called Cereals Research Department, JI Centre for Plant Research, Norwich, involving Dr. R. Johnson) and the Indian Agricultural Research Institute (IARI), New Delhi, an attempt was made to transfer durable resistance to stripe rust, controlled by genes other than those known to be race-specific, from 10 red grained, winter habit types (Atou, Avalon, Bounty, Cappelle Desprez, Elite Lapeuple, Flanders, Flinor, Hybride de Bersea, Hybrid 46, Maris Widgeon) and two spring habit types (Atle and Highbury) into two of the formerly popular Indian spring wheats, Kalyansona and WL711. The backcross F2 and subsequent populations were exposed at the PBI Cambridge to race/races with pathogenicity matching the known specific genes in the cross. The material was exchanged between PBI and IARI and in each generation selection for promising amber (white) grained and rust resistant plants was made using the same plant families in each location. Thus, it was made possible to transfer durable resistance to stripe rust across widely different genotypes while retaining the high yield potential, appropriate maturity of spring wheats and amber grain colour of Indian wheats. These wheats provide excellent sources for breeding durable resistance to stripe rust in India and other spring wheat breeding programmes. Johnson and Law [76] reported that 5BS-7BS translocated pair of chromosomes in European cultivars such as Hybride de Bersee and Cappelle Desprez provided sufficient amount of resistance to stripe rust. Cytological examination of the lines from the PBI-IARI programme would be of interest to know whether this chromosome structure has entered these selections.

Cultivars reported to have durable resistance to stripe rust in the Pacific northwest of the USA were described as temperature sensitive with resistance expressed at higher temperature and described as high temperature adult plant resistance (HTAP). It was suggested that resistance in these cultivars that include Gaines, Nugaines and Luke was controlled by a minimum of 2 to 3 genes [77, 78]. The exact identity and location of these genes are yet to be established.

3. Basis of stripe-rust resistance in Indian wheats

Table 3 lists important cultivars with stripe rust resistance genes and average coefficients of field infection to stripe rust. It is revealed that most of the wheats with low coefficient of infection belong to a class of wheats with 1B/1R translocation which carries *Yr9*. *Yr2* another gene which occurs predominently in Indian wheats, is at present not playing any significant role for the control of stripe rust. Cultivars carrying the 1BL/1RS translocation with *Yr9*, *Sr31* and *Lr26* have been extensively grown world over, including India, and have conferred a high degree of stripe rust resistance. In 1992-93, severe epidemics of yellow rust in several middle eastern countries including Iran and Pakistan were observed [79] due to *Yr9* virulence. Nayar *et al.* [80] detected the virulence for *Yr9* in 1996 in India bordering West Pakistan and subsequently named 46S119. A number of lines possessing this chromosome translocation (1B/1R), and also lines which do not possess 1B/1R, are resistant to the *Yr9* attacking virulence [80]. Resistance to this newly evolved race could therefore be utilised selectively in the future breeding programmes.

4. Evolution of pathotypes in *P. striiformis* in India

In the early seventies three variants namely 14A, 20A and 38A of existing races 14, 20, 38 were picked up on Kalyansona [81]. Similarly, virulence I on Sonalika was identified [82]. In 1982 virulence K, that has virulence for *Yr1*, *Yr2+*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, and *Yr8* in the series up to *Yr9*, was identified from Punjab [83]. Pathotype N was found in 1989 and differed from pathotype K by the loss of virulence for *Yr1*. In the nineties, two of the pathotypes designated as L [84] and P [85] possessed virulence for Hybrid 46 that contains *Yr4b* and a new gene [86] and not at *Yr3* locus, as reported earlier. Pathotype P, compared to pathotype L, possesses additional virulence for *Yr3* and Sonalika. Pathotype T with additional virulence for *Yr1* may have evolved from pathotype P. *Yr9* virulence was detected in 1996 [80] and named as 46S119.

V. Approaches for breeding durable resistance to all the three rusts

It is well established that use of a single set of resistance genes is more vulnerable to widespread disease attack of epidemic proportion. There is no evidence to suggest that even alien resistances and/or stable resistances when used individually will always prove durable. Breeding for durable resistance, therefore, requires accumulation within the same cultivar more than one resistance genes offering protection against a given race spectrum, first emphasised by Watson and Singh [87] which would require more than a single mutational event for the pathogen to overcome the combined resistances which is expected to take a longer period [88]. Breeding to incorporate a combination of fully resistance genes is, however, difficult because identification of various genes in the segregating population is often not possible. Recent developments in molecular markers have provided new opportunities to breeders for managing highly variable diseases such as rusts. For instance, Schachermayr *et al.* [89] recently identified molecular markers linked to leaf rust resistance gene *Lr24*. The molecular marker-aided selection technique involves tagging of resistance gene with a DNA marker which is expected to facilitate indirect selection of desired segregants. Until molecular marker-aided selection techniques become routinely available, morphological traits associated with resistance genes, such as leaf tip necrosis in cultivars with *Lr34/Yr18* [27] and appearance of pseudo black chaff on spikes and lower leaves of lines with *Sr2* [52] can be utilised effectively in

Table 3. Stripe rust resistance genes in some important Indian wheats and average coefficient of infection (ACI) in field conditions

Year of release	Cultivar	Gene(s)*	ACI**
Resistances from *T. aestivum*			
1967	Kalyansona	*Yr2(KS)*	63.3
1967	Sonalika	*Yr2*	40.0
1973	NI5 439	*Yr2*	63.3
1974	Arjun	*Yr2*	60.0
1977	WH 147	-	63.3
1977	UP 262	*Yr2*	46.6
1979	WL 410	-	11.6
1979	WL 711	*Yr2(KS)*	26.6
1979	HD 2189	*Yr2,18*	11.3
1979	HP 1209	*Yr2,18*	-
1981	LOK-1	*Yr2(KS)*	60.0
1984	HUW 234	*Yr2(KS)*	23.1
1985	HD 2285	*Yr2*	10.0
1985	HD 2329	*Yr2,18#*	23.3
1985	Kundan	*Yr18*	13.3
Resistances from alien sources			
Wheat- translocated chromosome (1BL/1RS) wheats			
1982	HUW 206	*Yr9*	7.2
1989	HS 240	*Yr9,18*	1.5
1991	MACS 2496	*Yr9*	0.8
1992	WH 542	*Yr9,18*	0
1993	GW 190	*Yr9*	1.7
1993	Kanchan	*Yr9,18*	0
1993	UP 2338	*Yr9,18*	3.4
1994	PBW 343	*Yr9,18*	0

*Source: Nayar *et al.* (1994) Research Bulletin 32, Regional Station, Directorate of Wheat Research, Flowerdale, Shimla 171 002.

**Plant Pathological Screening Nurseries (AICWIP); #Other tests indicated absence of *Yr18* pyramiding at least these two genes for durable resistance with other fully resistance genes in breeding programmes for control of leaf and stem rusts. When durable/potentially durable partial resistance is not associated with any phenotypic marker, combining two distinct types of resistance involves two steps breeding strategy. Since higher resistance is epistatic to incomplete resistance, the presence of both types of resistance cannot be guaranteed in a single step breeding programme. Hence, in the first step, durable/potentially durable incomplete resistance should be transferred into high yielding and agronomically desirable wheat. Once this is achieved, complete resistance genes, that are earlier transferred in the formerly popular wheats can be combined with partially resistant high yielding type using the latter line as a recurrent parent in a backcross breeding programme. This procedure would ensure that durable/potentially durable resistance is not lost in the breeding process.

Surveys of the stripe rust pathogen in different parts of the world show that multiple pathogenicity is common in isolates of the pathogen. As only one genetic component (*Yr18*) controlling durable resistance to stripe rust has so far been established, and this also does not provide adequate resistance in all circumstances, it is necessary to use techniques for selecting additional unidentified genes from durably resistant sources. The procedure of selection of resistance in segregating population of crosses involving durable resistant wheats, in the presence of race/races with combination of pathogenicity genes making all the known specific genes in all the parents of a cross ineffective, can achieve resistance likely to be durable.

CONCLUSIONS

Production of wheat cultivars with single genes for resistance even stable ones, is not likely to lead to durable resistance and new pathogenic race may emerge after the cultivar is widely grown. Durable resistance of adequate level can, however, be achieved by use of durable resistance which is mostly adult plant and incomplete, in combination with more effective genes or on the use of complete resistances in different gene combinations. Accumulation of more than one resistance gene within the same cultivar, each conferring resistance to existing race spectrum is often difficult because identification of different genes in the segregating population is not easy. Molecular markers selection techniques that have been recently emerging should help indirect selection of segregants with combination of genes each conferring resistance to a common race spectrum. Until molecular marker technology become routinely available, the adult plant durable/potentially durable resistance as the background resistance, with other set of resistance genes may be continuously combined to provide higher levels of resistance with diversity. More particularly, adult plant durable incomplete resistances controlled by *Lr34/Yr18* and *Sr2* that are linked with morphological markers, can be easily mainpulated even in the presence of more effective genes. Combination of an adult plant incomplete durable/potentially durable resistance not associated with any morphological marker with other set of resistance genes can also be achieved by following a two step breeding strategy. This approach should not only guarantee longevity of resistance but could also enhance the effectiveness of the background resistance, thus contributing to durability for resistance. Backcross derivatives of formerly popular wheats with alien resistance genes could serve as improved stocks for developing high yielding lines with diverse resistances, which act as a safeguard against genetic vulnerability. These backcross derivatives could also serve as readily usable material when high degree of resistance needs to be transferred into agronemically desirable genotypes of adult plant incomplete durable/potentially durable resistance.

For stripe rust resistance, resistances that were transferred from durably resistant cultivars across widely different genotypes into two popular Indian wheats, could provide adapted materials for imparting durable resistance in India, in addition to incorporation of the gene *Yr18*.

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