

Review paper

Wheat rusts in India: Resistance breeding and gene deployment - A review

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Abstract

This review paper presents the history of rust resistance breeding and deployment of resistant cultivars in different geographical areas of India. Much has been accomplished in controlling the wheat rusts through deploying resistant cultivars carrying diverse resistance genes in India. The genetic diversification in wheat has not only proved critical in developing resistant cultivars but also in the understanding of disease epidemiology and its dynamics and has gradually reduced the magnitude and frequency of epidemics. The gene *Lr26* in combination with *Lr13*, *Lr23* and *Lr34* and the *Agropyron* segment carrying *Lr24/Sr24* have played a crucial role in providing durable resistance and protecting wheat from any epidemic threat to stable wheat production. In recent years, wheat has achieved relatively higher production stability as compared to other cereal crops by adopting strategic gene deployment. Only marginal increase in wheat area is recorded but the strategic deployment of rust resistance genes is most protective of crop production and crucial in sustaining the production levels.

Key words: Wheat, rust, gene deployment, resistance genes, rust races/pathotypes

Introduction

Wheat is the most important winter cereal crop in India and serves as the staple food for more than 1 billion population. It contributes approximately 14% to the world wheat basket and holds the global share of 11% area under cultivation of wheat. As a result of consistent efforts made during the last 50 years, India recorded an all time high wheat production of 94.88 million tons from 29.8 m ha area during 2011-12 [1] and is maintaining the second position among wheat producing nations next only to China. During 2012-13,

both production and area declined marginally to 92.46 mt and 29.65 mha respectively with an average productivity of 3.12 t/ha which is higher than the global average productivity [2]. For sustaining and realizing future goals, wheat crop will have to be protected against biotic stresses. Among biotic stresses, the rust pathogens challenge wheat production globally with highly virulent and diverse races. In India too, wheat crop is subjected to severe attack of all the three rust endemics to India viz., black or stem rust (*Puccinia graminis* f. sp. *tritici* Erik. & Henn), the brown or leaf rust (*Puccinia triticina* Erik.) and the yellow or stripe rust (*Puccinia striiformis* West).

Indian wheat programme started around 1900 and progressed towards one of the most successful programs in the world achieving self sufficiency in wheat. On the way to this achievement, many important steps like breeding for higher yields and protection against rusts were taken. Other steps which accompanied these activities like race identification, screening pre-released material against virulent races, using major genes and then incorporating minor gene based resistance also contributed to this successful story. Therefore, the association of breeders and pathologists helped to protect wheat against rusts and steady increase in wheat yields made India achieve its position of being the second largest wheat producer in the world. Present review deals with these attempts from a historical perspective to the modern status.

History of rust epidemics in India

Historically, India has witnessed several rust epidemics

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in past resulting into heavy yield losses where the harvest even fell short of the quantity of seed sown [3]. Mehta [4] estimated the loss of about 200 million rupees due to rusts' damage of the wheat grain every year. The first stem rust epidemic record goes back to 1786 A.D. in central India [5]. Losses due to the epidemics of black rust were significant during pre-independence period [6]. Widespread occurrence of leaf rust was observed during 1971-73 in popular cultivar Kalyansona in northern plains [7] and during 1993-94 in HD2285 and HD2329 covering approximately 4 million hectares in NEPZ [8]. Nayar *et al.* [9] reported that both leaf rust and stripe rust occurred each year from 1967 to 1974 but the losses were estimated only twice. Sporadic high incidences of stripe rust are recorded in some parts of Punjab and recently in 2011 in north-western areas [10].

Stem rust of wheat is a significant disease in south, central, and peninsular India. When stem rust epidemics occur, losses can be significantly higher. Leaf rust has a wide spread occurrence in the country and is the most dynamic of all the rusts. Stripe rust is destructive and important in the northern areas of India, where frequent epidemics have occurred recently. However, these occurrences were confined to local regions. Although, it is a disease of cooler climate, new races tolerant to high temperature have recently been identified [11, 12], which enhances the damage potential considerably. Losses of significant magnitude can occur in fields of susceptible cultivars, generally in northwestern regions, northern foothills, and adjacent plains, and in the Nilgiri and Pulney hills in the south [13]. Under optimum climatic conditions prevailing in the particular locality one or more of these rusts may damage the wheat crop during years of epidemic(s). Losses in yield are generally attributed to several factors, namely, early appearance of rust, congenial environment and load of inoculum and the type of variety grown in the area [14].

The knowledge regarding the annual recurrence of cereal rusts was inadequate [15] and was mainly based on the work done by Dr. K.C. Mehta and his associates during early 1920s [16, 17]. Systematic work on race analysis and testing of varieties against wheat rusts in India started in 1931 [18, 19] and the knowledge about the physiological races of three rusts of wheat in India first became available in 1930s. Two stem rust races, 15 and 27 were identified by M.N. Levine from wheat samples collected from Pusa in 1923 [18]. Higher hills of north India, though harbor stem rust infection, but due to very low temperature,

have been suggested not to play any significant role in epidemics of north India. In south India, the spread of air borne stem rust inoculum occurs continuously to neighbouring plains from Nilgiri hills to as far as the plains in central India. However, stem rust is able to survive on susceptible local durums occupying a very small area in the hills of Karnataka and the infection is almost endemic in this area.

Subsequently, races 10, 63, 106, 107 and 108 of leaf rust were identified from 1931 to 1935. The presence of a relatively smaller number of races of the three rusts in India [20], the likelihood of their number continuing to remain relatively small [18] and the resistance to a group of physiologic races being controlled by a few genes that are simply inherited were some of the hopeful features for resistance breeding. Attempts to understand the genetic basis of rust resistance began in 1960s, although the work on identification of rust races began in 1931 [21]. With a view to test the varieties against multiple diseases, plant pathological screening nurseries were started in 1969 in hot spot locations [22]. Since 1967, disease surveillance has been conducted by the All India Co-ordinated Wheat Improvement Programme at Indian Agricultural Research Institute, New Delhi [23], using mobile and trap plot nurseries and has continued since then [24].

Distribution and prevalence of rust races

Leaf rust

The resistance of Democrat and Mediterranean (both carrying *Lr3*) was overcome by a new virulent pathotype 77 [25], when these sources were exploited in resistance breeding programme. After the introduction of dwarf wheats from Mexico, the new virulences were picked up for the genes *Lr1*, *Lr10* and *Lr23*. Matching virulence(s) in the races 12, 77 and 104 for *Lr23* were evolved after 1974 [26, 27] when the resistance of Gabo was utilized. Later, when *Lr26* was utilized, pathotypes with matching virulence appeared [28] and these pathotypes later combined virulence for *Lr23* overcoming the resistance of these genes [29]. Changes in the population of *Puccinia recondita* (now *P. triticina*) have also been recorded and documented for 49 races of leaf rust. The elegant example being the evolution of new races 12-1 and 77-1, which overcame the resistance of *Secale cereale* derived gene *Lr26*. Prior to this, race 77 was identified on Sonalika, 77A-1 on WL711 and HD2009 (Arjun), 77-2 and 77-4 on HD2285, 77-5 and 104-2 on UP2338 (*Lr26*). Durability of resistance was lost because of the

extensive deployment of gene combination *Lr23+Lr26*. More than 40% of the leaf rust isolates identified possessed the combined virulence for these two genes [30]. Emergence of virulence 77-7 for the genes *Lr9* and 77-10 for *Lr28* (both from Nilgiris 1998) could not be related to introgression of these resistance genes since they were used for breeding later than the identification of virulent races on these. So, it is not always necessary that the evolution of new race will take place after a new resistance gene either of native or alien origin is deployed in the field. Mutation, being spontaneous and random event, continues to occur even without the deployment of a particular resistance gene. Once mutated, it is likely to get selected on a differential host present and will build up over a period of time. A typical example of *Yr8* in United Kingdom can be cited as a new race virulent on *Yr8* which was discovered even before it was introgressed into common wheat from *Aegilops comosa*. [31].

Stem rust

For stem rust in India, two races namely 40 and 42 were identified in 1932. Virulence (7G35) against stem rust resistance in *Khapli* was identified in 1947 [32]. Subsequently, races evolved against stem rust resistance genes *Sr5* (11 syn. 79G31), *Sr8b* (14 syn. 16G2), *Sr30* (17 syn. 73G7), *Sr11* (117 syn. 37G3) and *Sr9e* (117 syn. 37G3) rendering them ineffective [25, 32]. So far, 32 races of *Puccinia graminis tritici* have been identified. The gene *Sr2* provides partial but broad-spectrum APR and has remained effective worldwide. When the cultivars Safed Lerma (S307), Chhoti Lerma (S331) both carrying *Sr11*, HD2135(*Sr2+*), HW517(*Sr2+Sr11*) and HW741 (*Sr2+Sr8b+Sr11*) were grown in cyclic shifts in the Nilgiri hills, within 3-4 years of cultivation, Safed Lerma became susceptible to races 42B and 122 of stem rust. By 1974, these cultivars lost their resistance to race 40A of stem rust. Subsequently, varieties HD2135 (1974) carrying *Sr2*, *Sr8a* and *Sr30*, HW517 (1978) and HW741 (1982) having *Sr2*, *Sr8b*, and *Sr11* became susceptible to race 40A [33]. A virulent pathotype, 40-1 syn. 62G29-1 was isolated from the Nilgiris in 1990 (Bhardwaj et al, 1990), which overcame the gene *Sr24* before the cultivars Vaishali (DL784-3) in 1993 (NEPZ) and Vidisha (DL788-2) in 1996 (CZ) were commercially deployed. A new race in group 117 syn. 37G3 was detected showing virulence for *Sr37* [34]. Virulence 40-2 syn. 58G13-3 collected from Karnataka state in 2006 overcame the resistance of *Sr25* [35].

Stripe rust

Stripe rust races 31 syn. 67S64, 13 syn. 67S8 and 20 syn. 70S0 were identified from northern and southern hills in 1936 and 1937. Race A syn. 70S4 was identified from Gurdaspur [36, 37]. Since then, 28 races of stripe rust have been documented. Kalyansona released in 1967 showed resistance to all the prevailing pathotypes of stripe rust (except 31), but soon in 1970 it became susceptible to three pathotypes viz., 14A syn. 66S84, 20A syn. 70S64 and 38A syn. 66S64-1 [38]. Presumably, all these pathotypes had migrated from across the border [39]. The wide spread cultivation of Sonalika (*Yr2Sk*) and Kalyansona (*Yr2Ks*) in India exposed the resistance against stripe rust pathogen I syn. 38S102 [40]. Subsequently, race K syn. 47S102 and N syn. 46S102 evolved [41] and thus the new races were either evolved indigenously or migrated from across the border. Later, the gene present in Hybrid 46 was also overcome by a new virulence L syn. 70S69 [42] and a virulence P-1 syn. 46S119 for *Yr9* was picked up from Gurdaspur, Punjab [43]. Pathotype CIII-1 syn. 78S84 attacking *Yr9* was later identified [32]. This pathotype was also hinted to have been introduced into India from adjoining country. The gene *Yr27* present in popular cultivars PB343 and PBW 373 was overcome by the virulence 78S84 [44]. Testing of materials against physiological races of all the rusts in seedling stage, gene identification and incorporation of rust resistance genes led to the development of resistant cultivars.

Nature of the pathogen

Maximum variation has been reported in brown rust of wheat in India. Some of the races like 12 group, 77 group and 104 group have changed very frequently giving rise to number of variants. These variants have rendered most of the resistance genes in Indian wheats ineffective. The rate at which these variations are emerging is really a worry for the wheat researchers as new sources of resistance are very scarce. The reasons for such frequent changes in these race groups is not understood, yet efforts are on to combat this phenomenon.

Possible forces involved in evolution

New pathogenic races may emerge through sexual hybridization, mutation, heterokaryosis and somatic hybridization or race flora shifts may happen when races are introduced from neighbouring countries as a large number of urediospores are produced by the rust

fungi. The role of sexual hybridization was ruled out, as epidemiological studies on wheat rusts done by Dr. K. C. Mehta showed that alternate hosts of wheat rusts do not exist in India. Mutations being random and continuous in nature have been implicated as possible mechanism giving rise to new patterns of virulence(s). Many workers since then, have expressed that mutations play an important role in *Puccinia* spp. Johnson and Newton [45] and Sharma and Prasada [46] indicated that changes in pathogenicity may occur either through mutation or parasexuality in wheat rusts. Studies with asexual stages done by Flor [47] also provided information that virulence changes occurred due to mutations in the natural rust population. Flor, in fact, was the first to report induced mutations for virulence in rust fungi in *Melampsora lini*. Later, an important observation made by Watson [48] indicated that the chance of emergence of new pathotypes related to the earlier biotypes of a race is greater than for the change of an entire race. Similar observations have also been made in India. Later, Gabriel *et al.* [49] suggested that if genes function for specific avirulence then mutations to increase virulence against specific genes should be more frequent than mutations to decreased virulence. However, Statler [50] reported mutations to avirulence when he used N-methyl-N'-nitro-N-nitrosoguanidine (MNNG) on uredospores. In addition, most avirulent mutants have very little or no sporulation and can easily be lost in a screening programme in the presence of normal parental sporulation. However, there is no evidence that new races have arisen through mutation in nature in India. Somatic hybridization may also play a significant role in producing genetic variation, particularly in association with hyphal fusion and nuclear exchange. Several such new races of leaf rust have been identified by various workers [51, 52].

The rusts, being obligate parasite requires the live host. Hills of southern and northern India and, neighbouring country Nepal act as foci, from where dissemination takes place to peninsular and central India as well as Indo-Gangetic plains [53, 54]. The nature of the pathogen and diversity of virulence in the population, availability of genetic resistance and its diversity, screening methodology, breeding and selection procedure for tracking resistance in a given environment are some of the important factors to be considered for breeding resistant varieties and their deployment. Presently about 126 races comprising 32 of stem rust, 49 of leaf rust and 28 of stripe rust are being maintained at DWR, RS Flowerdale [10].

The frequent arisal of new pathotypes render the cultivars susceptible and each wheat zone in India has different pathotypes showing a definite distribution. The distribution of pathotypes and their frequency has been worked out periodically [55, 56]. The races of leaf rust commonly distributed across the country during the last 15 years are: 12-4, 12-5, 12-7, 77-1, 77-2, 77-5, 77-9, 104A, 104-2 and 104-3, 162A, 162-1 and 162-2 of *Puccinia triticina*, whereas stripe rust races, namely, I, L,T, U, 47S102, 47S103, 46S102, 78S84, 46S119 and 67S64 are commonly occurring across the zones prone to *Puccinia striiformis*. The stem rust is a problem of warmer areas and for last 30 years the races 21-1, 40A, 40-1, 40-2, 117-A, 117-1, 117-2, 117-3 117-4 117-5 and 117-6 have been identified. At different times, distribution pattern of races has been different in the zones with some races occurring with >60 of frequency [57]). Varying degree of prevalence of different races has been reported in different years [24, 56, 58-61].

Generally, when a new pathotype evolves, it takes few years for its population to become predominant. Nayar *et al.* [62] reported that pathotypes 77A and 77A-1 identified in 1974 and 1976, respectively, became predominant during late 1980s and about 38% of samples in 1990 contained the above races. Pathotypes 77-5 and 104-2 of leaf rust identified in 1991 [63] continues to have very high frequency.

In a given time there are not more than 2-3 races of any wheat rust prevailing across the zones. Sinha *et al.* [57] reported 96% of samples carried 40A and 40-1 pathotypes of stem rust in southern hills zone. The moderate to high incidence of particular rust was sporadic and localized. Also most of the time, the stem rust appears at the terminal stage of crop growth and hence, not of much consequence. However, stripe rust is a real threat in north western India, while leaf rust is a potential threat all over the country. The low incidence or no incidence of rust is mainly ascribed to existing diversity of resistance genes present in the cultivars grown in a mosaic pattern in each wheat zone.

Gene postulation

The work on postulation of genes present in the varieties prior to their release was initiated in the beginning of 1980s [64]. The pedigree analysis indicated further evidence for the presence of the postulated genes. Genes for leaf rust resistance, namely, *Lr1*, *Lr3*, *Lr10*, *Lr14a* or *Lr22*, *Lr15* and *Lr26* were detected either independently or in combination.

The presence of resistance genes, *Yr2*, *Yr7*, and *Yr9* for stripe rust; *Sr5*, *Sr7a*, *Sr8*, *Sr11* and *Sr31* for stem rust in various combinations were also postulated. Leaf rust races in India were identified based on the response of 13 hosts with different *Lr* genes [65]. However, during the early phase of resistance breeding i.e., before the introduction of Mexican dwarfs, stem rust pathotypes virulent on Vernal, Khapli and Kota were detected. These isolates were virulent on *Sr9d* and *Sr9g*, however, another allele *Sr9e* showed differential behavior. Stem rust resistant Australian varieties Gabo and Ridley were identified to carry *Sr11* and the same resistance was introgressed into Indian genotypes. Timstein was also used in Indian breeding programme [37]. The gene *Sr30* present in Mentana (*Sr8a*) and Festiguay was overcome by new races [66]. The evolution of new races continued and the resistance of *Sr5*, *Sr8b*, *Sr11* and *Sr30* was overcome.

The release of the cultivar Arjun in 1970 carrying *Lr13* [67] provided a high degree of adult plant resistance to leaf rust and led to the decline of the area sown to Sonalika and Kalyansona (both carrying *Lr13*) by 1976. Though, Saini *et al.* [68] identified additional factor for resistance in Arjun, however, the identity of the additional gene(s) could not be established. A variety Kundan, postulated to carry *Lr34* and *Lr23* [69, 70] released in 1985 maintained its level of resistance to leaf rust for a very long period even though several new pathotypes evolved subsequently. Sawhney and Sharma [71] reported that *Lr34* mainly exhibited an infection type 3 to many pathotypes of leaf rust in the seedling, but showed moderate susceptibility (30-60MS) at adult stage [72]. The adult plant resistance gene *Lr34* has been found to be associated with a stripe rust resistance gene *Yr18* [73, 74] and *Sr57* [75]. This gene combination probably was introduced in Indian wheat varieties during 1960s. No systematic work to incorporate race specific resistance to stripe rust has been started in India, though derivatives were identified to possess stripe rust resistance other than that controlled by specific genes [76]. Historically, the introduction of dwarf varieties viz., Kalyansona and Sonalika carrying *Yr2+A* genes provided resistance to the then prevalent races of stripe rust. The genes *Yr2* and *Yr6* have been postulated in a number of Indian varieties [76-78]. However, these genes including *Yr7* have been reported ineffective in north as well in south India [72]. The gene *Yr7* floating in Indian cultivars prior to 1990 was reported to be ineffective against many stripe rust pathotypes previously [79].

Variety HD2329 (developed by V.S. Mathur) released in 1982 was postulated to carry *Lr13*, *Lr10* and *Lr34* and some additional genes for leaf rust resistance, *Sr8b*, *Sr9b* and *Sr11* for stem rust and *Yr2* and *Yr18* providing resistance against stripe rust [27, 80]. The durability to leaf rust in HD2329 may be attributed to the presence of *Lr13* and *Lr34* together. Several workers have reported that *Lr34* interacted favourably with *Lr13* [81, 82]. Variety HD2285 released in 1983 was also equally popular under late sown conditions, which carried a combination of *Lr23*, *Sr9b*, *Sr11* and *Yr2* genes [27]. In Peninsular Zone, a highly adapted genotype named HD2189, carrying the combination of *Lr13*, *Lr34*, *Sr2*, *Sr8a*, *Sr11*, *Yr2*, is still in cultivation occupying a significant area since its release in 1979 [32].

Prior to the release of varieties carrying 1BL.1RS translocation, a few most popular Indian wheat varieties, namely, C306 (*Yr2KS*), NI5439 (*Sr11*), Kalayansona (*Lr13*, *Sr11*, *Yr2KS*), WL711, HUW234 (*Lr14a*, *Sr9b*, *Sr11*, *Yr2Ks*), Sonalika (*Lr13*, *Sr2*, *Sr11*, *Yr2Sk*), HD2285 (*Lr23*, *Sr5*, *Sr9b*, *Sr11* and *Yr2*), HD2329 (*Lr13*, *Lr10*, *Lr34*, *Sr8b*, *Sr9b*, *Sr11*, *Yr2* and *Yr18*), Lok 1 (*Lr13*, *Sr9b*, *Sr11*, *Yr2Ks*) and WH147 (*Lr13*, *Sr7*, *Sr11*, *Yr2Ks*) [83-85] occupied major area across the wheat zones in the country. These genotypes might also have carried unidentified additional resistance genes as indicated by Nayar *et al.* [27, 32]. Two major and relevant changes in stem rust race profile have been the detection of *Sr24* and *Sr25* virulences. A pathotype 40-1 (syn.62G29-1) virulent on *Sr24* was detected in 1990 [86], while *Sr25* became ineffective to a pathotype 40-2 (syn.58G13-3) collected from Karnataka state in 2006 [35]. Similarly, the changes in pattern of leaf rust races have also appeared as virulence(s) against *Lr9*, *Lr19* and *Lr28* have been detected. These pathotypes did not pose a threat to wheat cultivation as they have remained in low frequency and confined to a specific area. In some of the cultivars carrying 1BL.1RS translocation, genes *Sr5* and *Sr2* have also been postulated [27] along with *Sr31*. Since the gene *Sr31* is highly effective in seedling stage against all the prevailing races of stem rust, it obscures the seedling resistance exhibited by *Sr2* and *Sr5*.

The most frequently identified leaf rust resistance genes in the Indian wheats are *Lr13* in bread wheat and *Lr23* in durum genotypes. However, after introduction of 1BL.1RS, *Lr26* and *Lr34* were identified as the most frequent and valuable genes. Many cultivars carried two and three gene combinations and

very few possessed four genes (Fig. 1). The information generated over a period of time reveals that the genes listed here have the potential to provide durable resistance in combination. Sawhney *et al.* [87] suggested that the genes *Lr10* and *Lr23*, when added to the Chinese Spring background provided a good source for durable resistance. After the suitable gene combination, namely, *Lr26+Lr1*, *Lr26+Lr23*, *Lr26+Lr34*, *Lr26+Lr34+Lr1* were suggested, most of the wheats carried these gene combinations and were found very effective for a long time. *Lr34* is an important gene providing resistance to multi-pathogen [75]. It has also been shown to confer resistance to powdery mildew and spot blotch [88, 89] caused by *Bipolaris sorokiniana*. Earlier Singh [73] identified that *Lr34* was

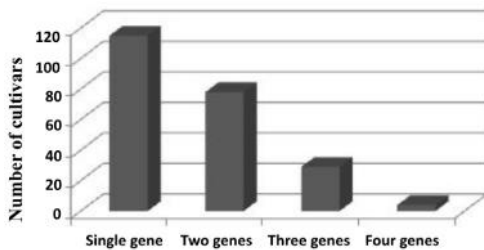


Fig. 1. Frequency of cultivars each carrying one, two, three and four genes for leaf rust resistance

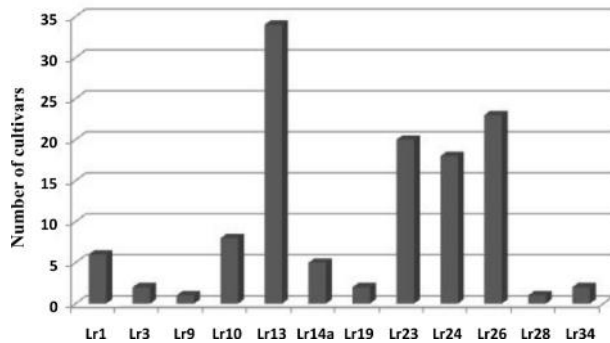


Fig. 2. Frequency of cultivars carrying single leaf rust resistance genes

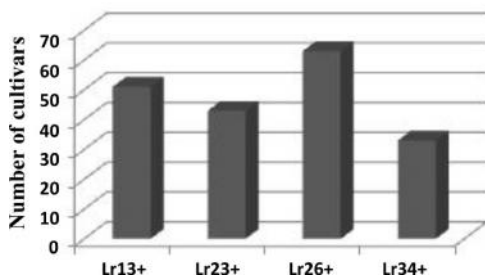


Fig. 3. Frequency of cultivars carrying *Lr13*, *Lr23*, *L26* and *Lr34* genes alone or in combination with other leaf rust resistance genes

associated with leaf tip necrosis (*Ltn1*), a morphological marker. The cultivars carrying *Lr26* have been occupying a major area under cultivation in India.

After the introgression of 1B.1R translocation, many cultivars were released in the wheat growing countries. This translocation was very frequently used in breeding programmes across the world. In India, too, many cultivars like HS240, HUW206 and MACS 2496 were released. One of the selections of this cross (IBL-1RS) was released as PBW343. This cultivar became so popular that it occupied about 7 million hectare [90] area in NWPZ and NEPZ. More than 50 *Sr* genes have been designated so far, but most commonly used in India have been *Sr2*, *Sr11*, *Sr31* and *Sr24* in bread wheat; and *Sr2*, *Sr7b*, *Sr9e*, *Sr11* and *Sr12* among durum wheat [32, 37, 91]. While only a few stripe rust resistance genes such as *Yr2*, *Yr9* and *Yr18* have been the most frequent. Of late, *Yr27* has also been postulated in some of the genotypes e.g. PBW343, PBW373 and HS490 [92].

Wheat cultivation in India

Wheat is being grown in India from 2300-1750 B.C. [93] as evidenced from the cultivation in Sind and Punjab during the Harappan period. The excavations at the ancient site of Mohan-Jo-Daro (the remains of Indus Civilization) revealed the carbonized grains belonging to a sub-species of *Triticum aestivum* L. i.e. *Triticum compactum* [94, 95] or/and *Triticum sphaerococcum* (Indian shot wheat) which were in cultivation in that area about 5000 years back [96]. This indigenous wheat has now practically gone out of cultivation. India is admirably suited for cultivation of the finest quality of both soft and hard wheat. Indian landraces and improved cultivars have been used in several countries as source of useful traits contributing towards earliness, tolerance to abiotic stresses and grain quality. Genetic improvement in respect of grain quality, particularly hardness of grain in soft wheat grown in western nations was brought in by introducing genes from Indian landrace Hard Red Calcutta which was also involved in the pedigree of Canadian wheat Marquis [96].

Early introductions

To enhance wheat production in India, introduction of exotic wheats had taken place towards the end of 19th and beginning of 20th century. Testing of material was started at Kanpur (1880-81), Nagpur (1887) and Lyallpur (1901) followed by Pune (1903-04) [97]. Australian wheat No. 27 was introduced during 1905-

06 followed by cultivar Bena, Federation, Gabo and Ridley. Later, Padova I and Padova II were introduced from Italy during Mid 1930s [98]. Ridley was superior or equal in yield in comparison to some Australian (Yalta, Seewari etc.) and Indian wheat varieties. Therefore, Ridley was recommended for cultivation after testing during 1948-51 at multi-locations in Himachal Pradesh, Uttar Pradesh, Punjab and West Bengal. Both these varieties showed resistance to black, brown and yellow rusts during the trials conducted at Wheat Breeding Sub-station, Shimla in 1951-52 [99]. The early wheat breeders were conscious enough to protect their wheat varieties from fungal diseases. All these wheats were tall as the concept of dwarf wheats was not conceived prior to the introduction of Mexican dwarf wheats such as Lerma Rojo 64 and Sonora 64 during early 1960 in India.

Early work on breeding in India

Plant breeding in India started in response to British Industrialists rather than from any initiative by the Govt. of India or by the Indians [100]. Systematic work on wheat improvement in India started only during the first decade of 20th century when the Agricultural Research Institute was established by Albert Howard and GLC Howard in 1905 at Pusa Bihar. Howard and Howard [101] had developed some improved varieties. Subsequently, the research on wheat started at Niphad, Shimla, Gurdaspur, Durgapura, Kalyani and Indore. During the early phase, the varieties were developed through pure line selection from landraces. At Pusa, four varieties were first isolated viz., Pusa 20, Pusa 21, Pusa 22 and Pusa 23 and later Pusa 4 and Pusa 12 [100]. In this effort, the varieties Pusa 4, Pusa 12, Type 9, Type 8a, C13, C46, AO13, Ekdania 69, Motia, Gulab, Arnej 206 etc. were developed. Ch. Ram Dhan Singh, who worked closely with Albert Howard developed C518 and C591 after 1926.

Rust resistance breeding

A breeding programme to develop rust resistant varieties was initiated in 1934. After 18 years of work at IARI, the variety NP 809 resistant to all the three rusts was evolved under a planned programme. Due to the lack of knowledge about causal organisms and their physiological races and requisite information regarding the rust epidemiology in India, the breeding of rust resistant varieties had little value. The problem of breeding superior rust resistant varieties by incorporating resistance available only from otherwise agronomically unsuitable exotic wheats was a very complex and long term project [102].

Systematic work on race analysis and testing of varieties against wheat rusts in India had started in 1931 [18, 19] and has continued since then [24]. Simultaneously, screening of varieties in seedling stage in glass house had also taken place to identify resistant ones that led to the selection of NP790, NP796, NP797 and NP846. With a view to test the varieties against multiple diseases, plant pathological screening nurseries were started in 1969 in hot spot locations [22]. Since 1967, disease surveillance has been conducted by the All India Co-ordinated Wheat Improvement Programme at Indian Agricultural Research Institute, New Delhi [23], using mobile and trap plot nurseries. The work on rust resistance was started in three stages. In the first stage, when no suitable resistant stocks were available for hybridization, rust losses were sought to be minimized by introducing rust tolerant varieties. In the second stage, the attention was devoted to the production of strains possessing resistance to individual rust and in third stage attempts were made to achieve a combination of resistance to all the three rusts. Rust resistant sources such as, Khapli, Kenya 184, Kenya Ploughman for black rust, Frontiera, Frontana, Bowie Texas, Mentana and Tremez Molle for brown rust and Ceres Klein, Klein Cometa, Frondosa and Spalding's Prolific for yellow rust and exotics like Gabo, Gaza, Yaqui 53, Timstein (*Lr23*) (resistant to black and brown rusts), Rio Negro, La Prevision (for brown and yellow rusts) from other countries were also used in hybridization programme to introduce rust resistance in Indian varieties. In the first attempt, rust tolerant varieties like NP710, NP718 and NP761 were developed and released. Breeding for rust resistance continued which led to the evolution of genotypes such as NP783 and NP784 (Democrat x PbC518). Later on the efforts were concentrated to develop genotypes with diverse resistance involving more than two parents. NP809 was released from a cross [(Democrat x PbC518)-F9 x (Spalding's Prolific x NP114)-F9] x E220, which combined resistance to rusts and loose smut [103]. With the available knowledge of different types of resistance, Indian wheat breeders were using these sources and were successful in developing suitable varieties.

Types of resistance

Amongst various types of resistance described in literature, majority belongs to race-specific major genes. A large number of resistance genes have been identified (>55 of stem rust, > 70 of leaf rust, >48 of stripe rust) and catalogued [104] and most of these

have been shown as race specific resistance genes associated with hypersensitive reaction in the host. This type of resistance has been commonly utilized in breeding programmes. It is observed that this type of resistance is short lived due to evolution of new races [105]. Flor [106] described that race-specific resistance is conditioned by the interaction of specific genes in the host with those of the pathogens. Stakman *et al.* [107] described immunity as the absence of visible lesions on the host plant. Robinson [108] observed lesions on leaves after the pathogen infection but no colonization of pustules on host could be recorded. It is generally agreed that plants immune to diseases are immune to infection by the pathogen. Gene *Lr28* showed immunity in India over a very long period, even flecks were not observed on the host leaves. Many of the genes for hypersensitive reaction can produce an immune response to some rust races and visible fleck infection types to other cultures. Van der Plank [109] put forward the concept of vertical (race specific) and horizontal resistance (race nonspecific). Vertical resistance in wheat is effective from seedling stage onwards while horizontal resistance is often effective at adult plant stage [108] and effective against a wide spectrum of rust races. Parlevliet [110] described it as partial resistance or slow rusting, associated with race non-specificity and is often referred as adult plant resistance (APR). Slowing effect on disease development may be attributed to resistance controlled by minor genes [111].

Some of the genes exhibit moderate or intermediate type of resistance, when the seedling produces 1 to 3 type of reaction. Such genes minimize the intensity and sporulation at adult plant stage. It has also been observed that genes governing resistance can also be suppressed by non-allelic genes e.g., the resistance of *Lr23* is inhibited by a gene present in Thatcher [112] and powdery mildew resistance gene *Pm8* is suppressed by *Su-Pm8* located in 1A chromosome of wheat [113]. Genes for resistance, when introgressed from alien species frequently show diluted effectiveness in the hexaploid wheat background or completely suppressed [114].

Adult plant resistance/durable resistance

While studying stripe rust of wheat, Johnson [115, 116] introduced the term durable resistance, which refers to resistance that has remained effective in cultivars for a very long period. In other terms, this resistance remains effective during the prolonged and widespread use in an environment favourable to

disease [117]. A combination of several genes may confer durability of resistance on the premise that components such as increased latent period, smaller pustule size, reduced number of uredia per unit area etc. may contribute towards slow development of rust. Cultivars namely, HP1102, HP1209, HW741, HW971 carrying *Lr13* in combination with *Lr34* or *Lr23* were slow rusters and produced moderate infection type against 77-1, 77-2 and 104 races of leaf rust [118, 119]. HD2189 showing adult plant resistance for more than 30 years in peninsular India carries race-specific genes *Lr13*, *Lr17*, *Lr23* and a race non-specific gene *Lr34*. In response against different leaf rust races, genes *Lr12*, *Lr13*, *Lr22* and *Lr22b* showed race specificity but also provided adult plant resistance to cultivars throughout the world including India [72, 120-122]. Race-specific genes *viz.*, *Lr1*, *Lr3*, *Lr10*, *Lr13*, *Lr23*, and *Lr26* are commonly found alone or in combination among Indian cultivars (Figs. 2 and 3) e.g., GW322, NIAW34, HD2329, HS420, VL832 (all bread wheats) and A-9-30-1, PDW233, PBW34 and GW1189 (all durums) etc. show adult plant resistance against one or more virulent and widely prevalent pathotypes 12-2, 77-5 and 104-2 [123]. These cultivars carried *Lr13+* or *Lr13+Lr34+* combination and showed adequate level of APR.

We need to acknowledge and appreciate the success of the slow rusting, minor gene based adult plant resistance approach. Tomar and Menon [124] identified some Indian cultivars expressing slow development of rust at adult plant stage. Besides many exotic stocks showing resistance at adult plant stage include the Australian cultivar CSP44 and Indian genotype VL404 exhibited low reactions (40MSS and 30S) to leaf rust in adult stage [72] which was later attributed to presence of genes *Lr48* and *Lr49*, respectively [125]. Bansal *et al.* [126] confirmed the presence of durable leaf rust resistance gene *Lr34* in CSP44 and VL404 using tightly linked marker *csLV34*. A recessive gene *Lr48* has displayed adult plant resistance against the leaf rust pathotypes of sub-continent. This recessive gene has been combined with a race-specific gene *Lr24* in the background of popular cultivar PBW343 to enhance durability of resistance [127]. Indian wheat cultivars and some derivatives from wheat x *T. timopheevi* were identified with APR against virulent pathotypes of leaf rust resistance. Test of allelism demonstrated that cv. WR544 and a *T. timopheevi* derivative Sel. T3073 possessed APR genes different from that of *Lr13* and *Lr34* present in Kundan and Thatcher [128]. The slow

rusting is observed in other than *Lr34* genotypes such as Pavon76, which carries *Lr46* [129]. This gene also functions similar to *Lr34* [130]. Nayar *et al.* [32] analysed that about 20% genotypes from India possesses *Lr34*. Independent loci conferring APR or slow rusting against leaf and stripe rusts were identified distributed over 5 chromosomes in a population derived from Avocet S/Pavon [131]. Our observations at Wellington (India) are that the linked APR genes *Lr46*/*Yr29* present in Pavon76 and Diamond Bird produced 10MR-20MS and 10S reactions at adult plant stage to leaf and stripe rusts, respectively. Similarly, RL6077 carrying *Lr67*/*Yr46* exhibited 30MRMS reaction to leaf rust and 20S to stripe rust. The genotype Parula carrying *Lr34*, *Lr46* and *Lr68* [132] showed 20 MR to leaf, 20S to stripe and 40MSS to stem rust against prevailing pathotypes in the Nilgiris. Sivasamy *et al* [133] identified 36 Indian germplasm lines of which five carried *Lr46*, another five possessed *Lr67* and seven lines carried the combination of *Lr34* and *Lr67*. The 77-5 of leaf rust and I of stripe rust are dominant races at this hot spot location. The genes *Lr46* and *Lr67* have not yet been postulated among Indian cultivars. Many breeding programs are using these genes in developing cultivars with slow rusting resistance for all three rusts. Stripe rust resistance genes *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr16* and *Yr18* have been characterized as APR genes [134-137]. Stocks carrying these genes showed APR against stripe rust flora present in the Nilgiris [72]. Except *Yr18*, all are widely distributed among European winter and spring wheats. An incompletely dominant gene *YrA* in Avocet has also shown APR against Mexican race Mex96-11[138].

Gene interaction for durable resistance

It is presumed that the durable resistance is a result few gene combinations acting in manner of novel association. The genes *Lr13* and *Lr34* providing leaf rust resistance might have come in Indian germplasm from Frontana, an American variety. The gene *Lr34* has been reported to interact in a complementary manner with other resistance genes [70, 139]. The genotype Chinese Spring showed partial resistance under field conditions, which is ascribed to the presence of *Lr34*, *Lr12* and *Lr31*. The resistance in cultivar Gatcher was reported to be due to complementary interaction between seedling genes *Lr27* and *Lr31* [140]. These genes also showed enhanced resistance at adult plant stage possibly due to interaction [87]. The seedling gene *Lr13* has been shown interactive with other genes such as *Lr16* and *Lr34* [82, 141] and the combination has shown durability

in resistance in some cultivars [142]. The gene *Yr18* is inseparable with *Lr34* and it interacts favourably with *YrA* [138]. Stem rust resistance gene *Sr2* is another such gene which is widely present among wheat varieties and provides enhanced durable resistance in combination with other resistance genes possibly due to interaction between them [143]. Interactions between race specific resistance genes with minor undesigned genes are also reported [144]. Many gene interactions have also been reported to suppress the resistance [114, 145-147].

Genetic linkages

The linkage between useful genes has come handy to the breeders in that attempts to incorporate a particular gene automatically brings along another useful gene. It is happening because more than one desirable genes are linked to have pleiotropic properties. One of the most popular and perhaps most widely used linked gene segment is that transferred from *Secale cereale* spontaneously. The rye segment carries genes for resistance to stem, leaf and stripe rusts and powdery mildew (*Sr31* *Lr26* *Yr9* *Pm8*). This alien segment is presumed to have genes influencing physiological traits leading to higher yield as evidenced by the number of varieties being cultivated world over including India. The other useful linked gene complexes, namely, *Lr34*/*Sr57*/*Yr18*/*Pm38*/*Ltn*, *Lr24*/*Sr24*, *Lr37*/*Sr38*/*Yr17*, *Lr25*/*Pm7*, *Lr16*/*Sr23*, *Lr20*/*Sr15*, *Lr46*/*Yr29*, *Lr21*/*Sr33*, *Sr2*/*Lr27*, *Sr31*/*Lr26*/*Yr9*/*Pm8*, *Lr13*/*Yr27*, *Sr9g*/*Yr7*, *Sr17*/*Pm5*, *Sr15*/*Lr20*/*Pm1*, *Sr38*/*Lr37*/*Yr17*, *Sr33*/*Lr21*, *Sr34*/*Yr8*, *Sr36*/*Pm6*, *Lr57*/*Yr40*, *Lr67*/*Yr46* are known. Out of these, only *Lr34*/*Yr18*/*Pm38*/*Ltn*, *Lr24*/*Sr24*, *Sr2*/*Lr2*/*Pbc*, *Sr31*/*Lr26*/*Yr9*/*Pm8* and *Lr13*/*Yr27* have been successfully and commercially exploited in India. Several cultivars (Table 1) carrying an useful alien segment with *Lr24*/*Sr24* occupied a total of about 15 million ha (Table 2) over a period of 20 years. Another block of genetically linked genes *Lr34*/*Yr18* providing durable resistance has been in use in commercial cultivars in India. Stable linked genes *Lr19*/*Sr25*, *Sr36* and *Pm6* have been utilized in a few Indian cultivars [148]. The association of *Lr34* with adult plant stem rust resistance in Canada [149] and India [71] and also with stripe rust resistance gene *Yr18* [73, 74] has not only aided wheat breeding but assisted the identification of genetic diversity in wheat. The *Lr34* is also associated with a gene manifesting leaf tip necrosis (*Ltn*) [73]. Segments carrying *Sr2*, *Lr34* and *Lr46* have been identified to have linkage with many other genes *viz.*, *Sr2*/*Yr30*/*Lr27*/*Pbc1*, *Lr34*/*Yr18*/*Sr57*/*Pm38*/*Sb1*/*Ltn1* and *Lr46*/*Yr29*/*Sr58*/*Pm39*/*Ltn2*

Table 1. List of released varieties carrying specific leaf rust resistance gene(s) *Lr24/Sr24* based on gene postulation and pedigree and their breeders seed production over the years

Name of the variety	Year and the zone for which released	Adaptation	Pedigree	Yield potential (q/ha)	Total breeders seed production over the years from 1993-2012
DL784-3 (Vidisha)	1993, NEPZ	LS, IR	Kalyansona*4/TR380-27* 4/3 #Ag/3/	59.8	275.1
HW2004 (Amar)	1995, CZ	TS, RF	C306*7/TR380-14*7/3 Ag #14	28.3	3340.4
DL788-2 (Vaishali)	1996, CZ	TS, IR	K7537/HD2160//HD2278/Lr24//K4-14	56.0	1707.8
HW2045 (Kausambi)	2002, NEPZ	LS, IR	HD2402*6/Sunstar*6/C80-1	55.3	236.5
HD2781 (Aditya)	2002, PZ	TS, RF	BOW/C306//C591/HW2004	23.6	13.6
HI1500 (Amrita)	2002, CZ	TS, RF	HW2002*2/HW1042/Strampalli/PNC5	30.3	1278.5
MP4010	2002, CZ	LS, IR	Angostura 88	53.6	1566.6
Raj4037	2003, PZ	TS, IR	DL788-2/Raj3717	59.3	5417.0
HD2851 (Pusa Vishesh)	2003, Delhi	TS, IR	CPAN3004/WR426//HW2007	64.1	1342.7
HD2833 (Tripti)	2004, PZ	LS, IR	PBW226/HW1042//HD2285	59.3	223.0
NW1067	2004, UP	TS, IR, AST	TR380-16-30614/CHAT 'S'	49.8	90.0
HI1531	2005 CZ	TS, RF, LIR	HI1182/CPAN1990	39.8 [#] , 40.0 [@]	974.5
COW(W)-1	2005, TN	TS, RIR	HD2646/HW2002A/CPAN3057	44.5	170.0
HD2888 (Pusa Wheat)	2005, NEPZ	TS, RF	C306/ <i>T. shpaerococcum</i> //HW2004	38.3	111.3
AKAW3722 (Vimal)	2005, Vidarbha (MH)	TS, IR	WH147/ Sunstar*6/C80-1	57.3	94.5
AKAW4627	2011, PZ	LS, IR	WH147/ Sunstar*6/C80-1	60.9	18.0

NEPZ= North Eastern Plains Zone; CZ= Central Zone; PZ= Peninsular Zone; SHZ= Southern Hills Zone; NCR= National Capital Region; U.P.= Uttar Pradesh; Mah.= Maharashtra; Vid.= Vidharbh; PTN= Plains of Tamil Nadu; TS= Timely Sown; LS= Late Sown; IR= Irrigated; RF= Rainfed; RIR= Restricted Irrigated; LIR=Late Restricted Irrigation, [#] = Under rainfed conditions, [@] = Under limited irrigation condition

providing resistance against multiple diseases [150-152]. The genes *Lr34/Yr18/Sr57* conditioned resistance to leaf rust, stripe rust and stem rust along with other diseases such as powdery mildew for a long period in Canada also [153]. The genotypes carrying *Lr67/Yr46* showed 20% reduction in mean powdery mildew severity [154]. The phenomenon of linkage facilitates simultaneous introgression of genes, permitting postulation of genes in case the matching virulence for other linked gene is not available.

Ecology and pattern of varieties in different wheat zones

A large number of improved wheat cultivars suited to different agro-ecological conditions have been released in India since the inception of systematic research in the early 1900. In the first era, the emphasis was given

on traditionally developed wheat varieties mainly for subsistence agriculture, which continued till early 1960s. The official system of variety testing, release and notification of new varieties started in the 1960s. The All India Coordinated Wheat Improvement Project (AICWIP) was established in 1961. The Central Varietal Release Committee (CVRC) and State Variety Release Committees (SVRC) were also established simultaneously. Multi-locational testing was also adopted in wheat breeding with the aim to identify diverse sources of resistance. Though multi-locational testing may not be the perfect system for identifying diverse sources but in India, this kind of testing has shown great promise in Indian wheat breeding programme. The lines that exhibited resistance at multi-locations indicated low average coefficient of infection and often possessed major and minor genes

Table 2. Estimation of area covered by the varieties carrying *Lr24*

Variety	Total breeder seed production (q)	Certified seed (q)	Area covered (ha)	Remarks
HD2781	13.60	12240	12240	
AKAW4627	18.00	16200	16200	
NW1067	90.00	81000	81000	
AKAW3722	94.48	85032	85032	Certified seed :
HD2888	111.25	100125	100125	Ratio of breeder seed to Foundation seed is 1: 30 and from foundation seed to certified seed is 1: 30.
COW(W)1	170.00	153000	153000	Thus breeder seed x 30x 30 = Certified seed quantity.
HD2833	223.00	200700	200700	Area covered:
HW2045	236.45	212805	212805	Assumption that 100 kg seed is needed for 1 ha.
DL784-3	275.10	247590	247590	1q certified seed for =1 ha
HI1531	974.50	877050	877050	Thus
HI1500	1278.50	1150650	1150650	Total estimated area that can be covered by BSP of above varieties = 15.2 m ha
HD2851	1342.70	1208430	1208430	
MP4010	1566.62	1409958	1409958	
DL788-2	1707.80	1537020	1537020	
HW2004	3340.40	3006360	3006360	
Raj4037	5417.00	4875300	4875300	
Total	16859.40	15173460	15173460	

Source: DWR, Karnal

for resistance. The era of modern agriculture started with the introduction of short statured, high yielding, photo-insensitive cultivars that transformed agriculture and led to the "Green Revolution" and also enabled the wheat revolution to be sustained over the years.

Agro-ecological zones of wheat in India

After analyzing a number of factors such as physiography, climate, geology, vegetation, soils, land use and cropping patterns, India was initially divided into 9 agro-climatic regions for wheat cultivation, namely, northern hills, northern, north-western, north-eastern, eastern, central, south eastern, peninsular and southern hills zones (Murthy and Pandey, 1978). However, looking at the regional peculiarities of some areas and the need, later on six zones namely viz., Northern Hills Zone (NHZ), North-Western Plains Zone (NWPZ), North-Eastern Plains Zone (NEPZ), Central Zone (CZ), Peninsular Zone (PZ) and Southern Hills Zone (SHZ) were recognized [155].

Northern Hills Zone

The zone is constituted mainly of the areas of higher

and lower altitude hills in Jammu and Kashmir, Himachal Pradesh, Uttarakhand (excluding Terai region), Sikkim, West Bengal and Manipur. Yellow rust, leaf rust, and powdery mildew are the prevailing diseases, hill bunt and BYDV may also appear. However, stem rust is also observed sporadically. After Ridley and different NP varieties, Sonalika was highly adapted variety occupying a major area. The varieties, Girija (HS1097-17) and Shailaja (HS1138-6-4) were released as early as 1973. Improved varieties namely, HS420, HS295, HS375, VL738, HS251, HS240, HS490 and VL892 are being cultivated in the zone. Some varieties viz., SKW196, HS365 and VL832 are being suitably grown in higher altitudes. Resistance genes *Lr10*, *Lr13*, *Lr23*, *Lr26* and *Lr34* for leaf rust and *Yr2*, *Yr9* and *Yr18* for stripe rust are postulated in the cultivars grown in this zone. Although, stem rust is not a problem of this zone due to low temperatures and non congenial environments for the sporulation, the genotypes grown in this zone carry resistance genes *Sr2*, *Sr5*, *Sr8b*, *Sr11* and *Sr31* genes. In recent years the prevailing pathotypes of stripe rust in this zone are 78S84, 46S119 and 67S64, while 104-2 and 104-3 of leaf rust occur.

North Western Plains Zone

This agro-ecological zone is comprised of states of Punjab, Haryana, Western Uttar Pradesh, (excluding Jhansi division), Rajasthan (excluding Kota and Udaipur divisions), Delhi, Tarai region of Uttarakhand, Jammu and Kathua districts of J & K, Paonta Valley and Una district of Himachal Pradesh. Cultivars grown in this zone are of dwarf stature carrying both *Rht1* and *Rht2*. After the Green Revolution, the prominent cultivars grown in this zone are Sonora64, PV18, Kalyansona, Sonalika, HD2329, HD2285, WL711, PBW343, HD2687, PBW550, PBW373, PBW502, UP2338, WH542, DBW17, Raj3765, DBW16, C306, PBW175, PBW396 and HD2851. Currently, varieties viz., HD2967, HD3059, PBW590, DPW621-50, UP2425, WH291, WH1021 and PDW314 (durum) are in cultivation. The prevalent races of leaf rust are 12-4, 12-7, 77-1, 77-5, 104-2 and 104-3, while that of stripe rust are 46S119 and 78S84. Stem rust rarely appears and that too at very late stage or does not appear at all in this zone. Before the deployment of commercial cultivars involving Veery (1BL.1RS translocation possessing genes *Sr31/Lr26/Yr9/Pm8*) in 1992, the cultivars were mostly carrying the genes *Sr2*, *Sr5*, *Sr9e*, *Sr11* for stem rust, *Lr1*, *Lr13*, *Lr23*, *Lr34* for leaf rust and *Yr2*, *Yr2KS*, and *Yr18* for stripe rust. Although, the cultivar HUW206 carrying 1BL.1RS translocation was deployed in NEPZ in 1983, the cultivars carrying this translocation were continuously released since 1992 in this zone. The zone is vulnerable to stripe and leaf rusts. The rust resistance genes *Lr13*, *Lr26* and *Yr9* became ineffective in 1972, 1983 and 1996, respectively. However, the varieties released after this period carried diverse resistance genes. The gene *Lr24* transferred from a backcross line HD2329*6/TR380-14*7/3Ag#14 was first deployed in 2004 in variety HD2851 developed indigenously from a cross CPAN3004/Hy65//HW840/ HD2329*6/TR380-14*7/3Ag#14. HD 2851 (Pusa Vishesh) is a quality wheat producing fine lustrous grains suitable for both chapati and bread making.

North Eastern Plains Zone

The agro-ecological zone with diverse ecological, hot and humid conditions is constituted of Bihar, eastern Uttar Pradesh, Jharkhand, West Bengal (excluding the hills) and Assam. Cultivars of semi-dwarf stature carrying dwarfing genes are grown. Resistance to foliar blights like *Alternaria*, *Helminthosporium*, [*Cochliobolus sativus* (anamorph, *Bipolaris sorokiniana*

Sacc. (Shoem)] and leaf rust are the major thrust areas. Spot blotch (*Bipolaris sorokiniana*) is a serious problem of this zone. Short winter, early monsoon, high humidity and pre-harvest sprouting of grains are some of the characteristic features of this zone. The prominent varieties grown in this zone are: HUW206, K8027, HUW234, HP1633 (Sonalika), DL784-3 (Vaishali), K9107, DBW39, NW2036, HD2733, DBW14, MACS6145 (HW2034), and HD2888. Recently, varieties viz., CBW38, DBW39, HD2985, K307, Raj4120 and HI1563 are being cultivated. Leaf rust pathotypes 104-2, 104-3 and 77-5 are prominent, whereas stem rust is sporadically identified from this zone. This zone is also not affected by yellow rust but recently 46S119 race of stripe rust has been identified with insignificant impact on wheat crop. The genes postulated in the varieties of this zone are: *Lr10*, *Lr13*, *Lr23* and *Lr26*, which are providing effective resistance to leaf rust, whereas for stem rust the genes *Sr2*, *Sr5*, *Sr7a*, *Sr11*, and *Sr31* have been identified. After the introduction of Veery derivatives in this zone during the year 1983 (HUW206), at present many varieties carry 1BL.1RS translocation. Prior to introduction of *Secale cereale* derived gene *Lr26*, the gene *Lr9* was deployed in 1992 through the release of a variety Sonalika (HP1633). It provided effective resistance for a brief period till a virulence 77-7 (biotype of race 77) of leaf rust was identified.

Central Zone

Considerable agro-ecological diversity exists in this zone comprising states of Madhya Pradesh, Gujarat, Chhattisgarh, Rajasthan (Kota & Udaipur Divisions) and Bundelkhand region (Jhansi Division) of Uttar Pradesh and parts of Rajasthan, which is characterized with tall and dwarf wheats (*Rht1*, *Rht2*), combination of input responsiveness, efficiency (high fertility irrigated) medium input responsiveness (low fertility and rainfed) and recently limited irrigation area has also been identified. Stem rust resistance genes, *Sr2*, *Sr5*, *Sr9e*, and *Sr11* along with the combination of *Sr2+* *Sr24* prevail, while for leaf rust, the genes, *Lr10*, *Lr13*, *Lr23*, *Lr34* and *Lr24* are commonly present. The durum wheats carry unique resistance to leaf rust [156]. Two genes viz., *Lr14a* and *Lr23* have originated from *T. durum* but other genes such as *Lr3*, *Lr53*, *Lr61* and *Lr64* occur among both common and durum wheats. The leaf rust races, namely, 12-4, 12-7, 77-1, 77-2, 104A, 104-2, 104-3 162A, 162-1 and 162-2 and stem rust races 40A and 117-6 are prominently occurring in this zone. The zone is free of stripe rust

as no pathotype has been identified so far. Prominent varieties in cultivation are: HI365, Sujata, C306, WH147, Lok-1, HI977, HI1077, HI8381(d), HI8498(d), HI8663 (d), MPO1215 (d), GW322, GW366, HI1418, HI1454, HI1544, DL788-2, HW2004, HI1500, HI1531, MP4010, MP1203, MP1215 and HD2932.

Peninsular Zone

This agro-ecological zone comprising Karnataka and Maharashtra states where hot and dry climate and comparatively short duration winter prevails, early maturing and thermo-tolerant varieties are most suitable for cultivation. *T. dicoccum* is also being cultivated in sizeable area (mainly in Karnataka state). Stem rust and leaf rust resistance is of prime importance in this zone; leaf blight appears occasionally. The leaf rust races prevailing during the last few years are: 12-4, 12-5, 12-7, 77-1, 77-2, 77-5, 77-9, 104-2, 104-3, 162, 162A and 162-2, while among stem rust races only 40A is prominent. Stripe rust does not occur in this zone. The glutenin sub-unit composition of wheat commonly cultivated in this zone is 2*, 2+5, 17+18 (i.e., *glu-1* score 8/10). This zone is important from epidemiological point of view, as the spores of stem rust and leaf rust from main foci are disseminated here for further movements to the central plains and beyond. Presently the varieties NI5439, HD2833, HD2781, HD2932, HD2987, AKAW4627, HI8663, MACS6222, MACS6273, NIAW34, NIAW917, NIDW295, PBW596, RAJ4037, RAJ4083, UAS304 and UAS415 are grown in this zone. The varieties predominantly carry stem rust resistance genes *Sr2*, *Sr9e*, *Sr11* and recently *Sr24* and *Sr31*.

Southern Hills zone

This small zone is comprised of Nilgiri and Palani Hills, plains of Coimbatore, Salem and Erode districts of Tamil Nadu. This zone has insignificant contribution to total wheat production. However, the zone attains a paramount importance as the Nilgiri and Palney hills constitute the main foci for stem rust and leaf rust that spread to the neighbouring wheat growing areas in Karnataka. All the three rusts, powdery mildew, leaf and glume blotch are the major problems. A large number of races of all the rusts evolved here knocking down the resistance genes. Wheat is cultivated under both irrigated and rainfed conditions. In the hills, *T. dicoccum* (Samba/khapli wheat) and bread wheat varieties are cultivated, while in the plains only *T. aestivum* varieties are grown. Although, a number of wheat varieties have been released but only HW1985,

HW2044 (*Lr24*) and Co W(W)-1 are being grown presently. For a long time, Khapli wheats and the improved varieties of *T. dicoccum* such as NP200, NP201 and NP202 were grown. To contain the rust inoculum multiplication, some of the prominent varieties, namely, Safed Lerma, Chhoti Lerma, HW517, HW741, HW978 and HD2135 were recommended for cultivation in these hills.

Gene Deployment

It is expected that by increasing genetic diversity in the field the losses due to rusts are likely to be curtailed. While detailed knowledge of the genetic basis is not essential for an effective resistance breeding [157], much can be gained if the genetics of resistance is known. Browning *et al.* [158] proposed the use of vertical resistance gene(s) of crown rust for deployment in different geographical areas to minimize the risk of epidemic in United States. McIntosh [159] advocated the use of overlapping oligogenic resistance or the combinations of oligogenes which exhibited low coefficient of rust infection. Gene deployment is a promising and effective strategy to curtail the rust epidemics. Like other countries, the existence of a *Puccinia* path in the Indian subcontinent was established [160]. It was earlier suggested to deploy specific gene or gene combinations in each zone [161]. Therefore, strategically devised gene deployment can be followed in central and peninsular India against stem rust of wheat. Similar possibilities exist in the Indo-Gangetic Plain for managing leaf rust also [162].

The strategy for gene deployment along the "Puccinia path" for managing stem and leaf rust of wheat has been proposed by Nagarajan *et al.* [41] and Bahadur and Nagarajan [163] following the effectiveness of resistance genes and the distribution of pathotypes. Bahadur *et al.* [164] advocated the use of resistance genes, namely, *Sr24*, *Sr31* and *Sr36* for stem rust and *Lr9*, *Lr19*, *Lr24* and *Lr34* for the management of leaf rust. Stripe rust resistance gene *Yr9* provided resistance for a very long period in India but now has become ineffective due to evolution of new virulences. Deployment of genes such as *Yr5*, *Yr10* and *Yr15*, which are individually as well as collectively effective against the prevailing races would be an appropriate strategy to check the losses due to stripe rust. Virulence against *Yr5* was reported in Australia [165] and India [80]. The gene *Yr10* originating from Turkish bread wheat has also been defeated due to emergence of a new virulence in Canada [166] but no virulence has been detected yet in India.

Rust resistant Mexican wheats Lerma Rojo and Sonora 64 were introduced after 1962 and the cultivars, Sonalika and Kalayansona selected from segregating materials were grown on large scale shaping the Green Revolution. Through these varieties, rust resistance genes *Lr1*, *Lr3*, *Lr10* and *Lr13*; *Sr2*, *Sr5*, *Sr11* and *Yr2* were deployed [27, 167]. The susceptible cultivars were replaced rapidly by new releases. A successful, though unintentional, deployment for stem rust resistance is the large scale cultivation of HD2189 in Peninsular India which is known to carry *Sr57/Lr34/Yr18* along with *Sr2* and *Sr11*. HD2189 also carried *Lr13*. Presently, this cultivar is resistant to Indian stem rust pathotypes. Another cultivar DWR162 carrying *Sr31* was released in 1993 in PZ. So, the inoculum which spreads from Karnataka or Nilgiris is not able to multiply as it lands on the resistant cultivars. Consequently, three popular cultivars of Central Zone, namely, Lok-1, Sujata and WH147, though susceptible, are protected due to lack of transported inoculum. In addition resistant cultivars, HW2004, HI1500 (both rainfed wheats sown early) and DL788-2 (timely sown) carrying *Lr24/Sr24* are being cultivated on large scale in the central zone. To avoid any expected rust epidemic, wheat breeders need to diversify *Lr24* based leaf rust resistance in central zone as presence of *Lr24* in early sown varieties HW2004, HI1500 and HI1531 and timely sown variety HI1544; and in DL788-2 and MP4010 (late sown) poses a potential threat due to its continuity in time and space; particularly in view of occurrence of *Lr24* virulence in neighbouring Nepal [168].

***Lr26/Sr31/Yr9/Pm8* (1BL.1RS translocation)**

Spontaneous centric fusion translocation between wheat and rye was identified by Zeller [169] conferring spectacular resistance to multiple diseases (Bluthner and Weinrich, 1978 cited by Gale and Miller [170], such as leaf rust, stem rust, stripe rust and powdery mildew. Earlier, Bartos and Bares [171] identified cultivars Salzmunder, Bartweizen and Weique which carried the linked genes. A sister line of these cultivars Neuzutch (carried complete 1R chromosome) was involved in the evolution of Russian winter wheat cultivars, Kavkaz, Aurora, Besostaya2 and Skorospelka carrying 1BL.1RS interchange chromosome. Although in Europe the gene *Lr26* derived from *Secale cereale* L. was an important source of resistance, but virulent strains of leaf rust appeared soon after cultivars with this gene were released [172]. The genetic stocks, namely, Benno, Kavkaz, Aurora, Clement, Skorospelka 35 carrying 1BL.1RS translocation (*Sr31/Lr26/Yr9/Pm8*) were received in

India during late 1970s. These genes were observed to be very effective against the virulences of respective rust and powdery mildew pathogens hence their utilization in breeding programme began. Since they were late in flowering (winter wheats) and produced red kernel, their use was restricted. Even before the deployment of *Lr26+* combination of genes, a virulence matching it was observed at Wellington (India) in the beginning of 1980s and later confirmed in 1987 [62]. Changes in the population of *Puccinia triticina* have been recorded regularly in India and therefore, a number of pathotypes with different avirulence/virulence combinations have evolved since the deployment of *Lr26*. All the cultivars released had shown differential reaction to leaf rust, which may be due to the presence of additional resistance genes in them. Benno gave low coefficient of infection at multi-location [173]; the low level of resistance was perhaps due to the presence of a new virulent pathotype 77-1 in the natural population [62]. Subsequently, four new pathotypes viz., 12-1, 12-3, 77-3 and 107-1 virulent on *Lr26* were identified [28, 29, 174] from 1983 to 1986. In spite of virulences identified for *Lr26*, the utility of this translocation was not lowered by its ineffectiveness. The wheat-rye 1BL.1RS translocation has been most extensively exploited for the development of cultivars in India and other parts of the world. The first variety HUW206 carrying these genes was released for general cultivation in 1983 in the North Eastern Plains Zone, where both stem rust and stripe rust were not a problem. A cultivar DWR162 carrying *Lr26* released in 1993 for PZ was resistant to leaf rust for many years. This is not unique but perhaps may be the first example when an alien gene deployed in 1993 on a large scale was rendered ineffective in India prior to its adaptation. No doubt that the gene *Lr26* has played a very crucial role in providing durable resistance and protecting wheat from any epidemic threat to stable wheat production. Although, the resistance was overcome shortly after its deployment, the gene still provided effective resistance in combination with other genes viz., *Lr1*, *Lr3*, *Lr10*, *Lr23* and *Lr34*. Out of about 60 varieties released so far, 19 varieties carry *Lr26+Lr23* combination. This spontaneous beneficial translocation exhibited superior agronomic properties and heterotic effect and therefore, increased yield, stability and wider adaptability not only in India but elsewhere too [175]. The breeding of 1BL.1RS translocation was easy without any cytological problem associated with it [176]. Therefore, the incorporation of these genes through breeding was done on the basis of resistance during selection and not that these genes

were deliberately pyramided. But these genes were deployed because these seem to be associated (particularly, 1RS) with increased yield [177].

Stem rust resistance in wheat cultivars carrying *Sr31* remained effective globally for more than 30 years, but an isolate of *Puccinia graminis tritici* virulent on this gene was first identified in Uganda in 1999 [178]. Later on it was named as TTKSK (Ug99) and its variant TTKST was virulent to *Sr24* [179]. The wide spread cultivation of cultivars with 1BL.1RS translocation led to the evolution of new races of *P. striiformis* also.

A stripe rust race overcoming *Yr9* was first identified in east Africa in 1986 and subsequently migrated to South Asia [180]. However, Li *et al.* [181] reported breakdown of *Yr9* in the cultivar Lovrin in China before 1986. The gene *Yr9* provided durable resistance for a long period of time in spite of the migration of virulence from across the northern border in the 1990s. It was a significant development and a major concern of the breeders because the *Yr9* resistance was deployed on large area. The resistance to powdery mildew associated with 1BL.1RS was rapidly overcome by new races at very early stage of deployment [182, 183]. In UK, the combination of *Yr6* and *Yr9* gave resistance to all the races before 1987, however, a combined virulence occurred on these two genes on a cultivar Hornet resulting in a small scale epidemic [184]. Another combination of *Yr7* and *Yr9* present in several CIMMYT cultivars showed resistance in several countries but later on, virulence developed independently in more than one place. Heavy infection of *Yr9* virulence was observed in some of the adjoining countries, where replacement of this gene variety could not be practiced. In India, the release of PBW343 at the time of prevalence of *Yr9* virulence proved very useful as it was found resistant due to presence of additional gene *Yr27*. Presently, three *Yr9* virulence(s) have been identified which are spreading in the North and North western parts of the country as a large number of genotypes with *Yr9* released during the past 20 years (PBW343, HD2687, UP2338) have become susceptible and so are the other genotypes carrying *Yr9*. Recently, timely sown wheat variety HD2967 carrying minor gene based resistance is replacing varieties carrying *Yr9* in NWPZ. Late sown variety HD3059 released for NWPZ also showed low average coefficient of infection against yellow rust.

Lr24/Sr24

The *Agropyron elongatum* derived rust resistance genes *Lr24/Sr24* conferred effective resistance to leaf and stem rusts for many years [72, 185, 186] against the prevailing race flora in the Nilgiris, India. The resistance of *Lr24/Sr24* has been extensively exploited to develop commercial cultivars in the USA and South Africa [187]. The linked genes *Lr24/Sr24* have been reported ineffective to some of the races of leaf and stem rust in South Africa, South America and North America [111, 188-191] but the resistance exhibited by *Lr24* continues to be very effective against Indian leaf rust races in seedling as well as adult stage [72, 124, 192]. Although, Samborski, [193] expressed his opinion that exotic genes for resistance are not better than other genes if they are used singly.

A vigorous programme of transferring the effective alien genes was undertaken at IARI Regional Station, Wellington in 1980. However, DL784-3 (Vaishali) was the first variety carrying *Lr24/Sr24* using donor TR380-27*4/3Ag#14 and released in 1993 for timely sown, irrigated conditions in the NWPZ. With a different donor TR380-14*7/7/3 Ag#14 another variety HW2004 was released in 1995 [194] for moisture stress conditions in CZ, which became most favoured genotype with the farmers. Since then, about 18 varieties having *Lr24/Sr24* for different ecological conditions ranging from moisture stress environments to irrigated, and timely sown to late sown conditions have been released and notified in different zones and states (Table 1). Tomar and Menon [186, 192] transferred *Lr24* into 19 Indian cultivars using backcross breeding and a few of them were released as cultivars. It is evident that the release of a large number of varieties with *Lr24* indicate that alien race specific gene *Lr24* has no impediment on yield. The popular belief that alien genes reduce the yield potential of a genotype [195] is not tenable, if the selection in segregating populations is carefully made.

The plains of central India are the route of migration of stem and leaf rust uredospores to the main wheat growing areas of northern India. Since, the rainfed crop in central India is early sown, the inoculum built up on susceptible cultivars poses a major threat to the timely sown crop of central and northern plains. To check the rust infection in this secondary source, cultivation of HW2004 is economic and effective answer. So far 18 varieties carrying *Lr24* have been released in India since 1995 and hitherto, approximately 15 m ha area has been occupied by these cultivars (Tables 1 & 2, Fig. 4) as per the Breeder

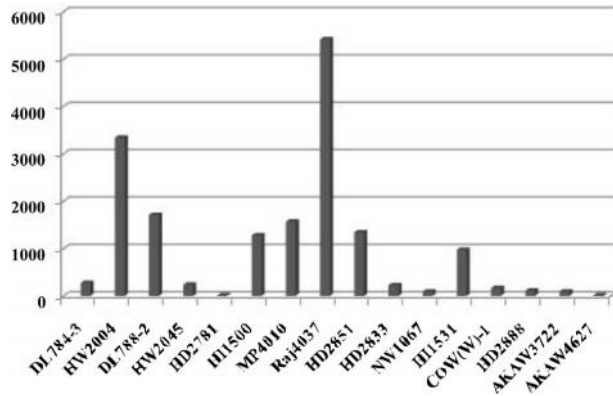


Fig. 4. Breeder seed production of wheat varieties carrying *Lr24* (1993-2011)

seed indent records. In addition to this, the area covered by cultivars carrying *Lr24/Sr24* could be more as there is always a possibility of informal movement of seeds among/between the farmers. Till date, no virulence against *Lr24* has been reported from India.

In India, a virulent biotype 40-1 of stem rust was isolated from the Nilgiris in 1989 [86], well before its deployment of *Sr24* in 1993. *Sr24*-virulent culture detected from Wellington has remained confined to this area for more than 20 years. Even within Nilgiris this virulence is not predominant even though present. Therefore, it is not necessary that the evolution of a new rust race occurs under selection pressure only, as it is evident from the ineffectiveness of *Lr26* and *Sr24* when both these genes were overcome by new virulence(s) before they were deployed.

Lr9

Gene *Lr9* (from *Aegilops umbellulata* Zhuk.) conferred seedling resistance to a number of Indian leaf rust pathotypes and was also effective in adult stage [124, 196]. India released a cultivar Sonali (HP1633) with *Lr9* in north eastern region for late sown irrigated conditions in 1992. Sonali has been postulated to carry stem rust resistance genes, *Sr2*, *Sr7a*, *Sr11+* and *Yr2+* for stripe rust. The resistance conferred by Transfer (*Lr9*) was overcome by a virulence in 1972 [197] in United States of America. In India also, a new pathotype virulent on *Lr9* was identified after deploying it in 1992 [198] and the variety could not spread. More over this gene unlike *Lr24* does not combine with yield and hence was not utilized on large scale in Indian wheat breeding programme.

Lr19/Sr25

The gene *Lr19* (Agatha) transferred from *Agropyron*

elongatum conferred total immunity to Indian leaf rust races at seedling stage [196] and also exhibited resistance at adult plant stage [72] for a long time at hot spot location, Wellington in the Nilgiris south India. The virulence(s) on *Lr19* were detected in Mexico [199] and Russia [200]. Two cultivars viz., PBN142 (HD2189/NI917//Agatha) and WH533 (Agatha/Yacora17) were released for general cultivation in 1989 (Maharashtra state) and 1993 (Haryana state), respectively. The presence of *Lr19* in PBN142 and WH533 is indicated from their pedigree as one of the parents involved is Agatha. Detection of a stem rust virulence against linked gene *Sr25* raised concerns about its usefulness but the virulence has remained confined to a very small area. Singh *et al.* [201] observed that 7D.7Ag segment with *Lr19/Sr25* increased grain yield potential by 10-15% in a range of genotypes. India remained free from virulence attacking *Lr19* till 2005, when a new virulence 77-8 (253R31) appearing close to the pathotype 109R31 [62] was detected [202] from Karnataka and Gujarat states. However, pathotype 77-8 is avirulent to *Lr9*, *Lr23*, *Lr24* and *Lr26* and is not commonly occurring in India, hence the gene still may provide effective resistance.

Lr28

The gene *Lr28* transferred from *Aegilops speltoides* Tausch. has not been used on a large scale, although it exhibited a high degree of resistance in seedling and adult stage for many decades in India [124] and in Europe [203, 204] and other ecological zones. Although, no detrimental effects appear associated with the presence of *Lr28*, the durability of resistance is likely to be low [205]. A variety MACS 6145 (HW2034) with *Lr28* utilizing a translocation CS 2A/2M #4/2 was released in India for rainfed conditions in NEPZ [206]. Kumar and Raghavaiah [207] reported that the gene *Lr28* as integrated in the backcross lines [72, 192] neither carried any undesirable linkage drags nor affected yield of the lines. It does not show any disadvantage in yield. However, a new virulent pathotype 121R60-1 overcoming the resistance of *Lr28*, which appears closely related to the most prevalent pathotype 121R63-1 (77-5) has been reported by Bhardwaj *et al.* [208]. The *Lr28* is still a potential gene which can be utilized in combination of other genes which are effective against this particular race.

Current status of resistance breeding

If India had not experienced frequent rust epidemics, it is because of the cultivation of diverse genotypes

carrying different resistance genes. The current status of rust resistance breeding involves both conventional and molecular breeding approaches including QTL mapping. Efforts are being made since long time to utilize wild relatives to develop novel germplasm. Wild species viz., *Triticum timopheevii* and its mutant species *T. militinae* [209, 210], *Ae. speltooides* [210, 211], *Ae. markgrafii* [212], *Ae. triuncialis* [213], *Ae. ovata* [214, 215], and *Ae. umbellulata* [216, 217] have been exploited for leaf rust resistance. Useful genetic diversity is being continuously harnessed from wild relatives of wheat to diversify diseases resistance in wheat [218-221]. Kuraparthy *et al.* [222] transferred leaf rust and stripe rusts resistance *Lr57/Yr40* from *Aegilops geniculata* into common wheat and mapped them on specific chromosome 5DL [223]. Another major gene *Lr58* conditioning resistance to leaf rust was transferred from *Aegilops triuncialis* into common wheat and has been mapped on 2BL chromosome [224]. Some QTLs conferring adult plant resistance to stripe rust were introgressed from *T. monococcum* and *T. boeoticum* [225] which have been mapped on specific chromosomes [216]. Quantitative trait loci governing broad spectrum resistance to rust are also being identified and mapped [218, 226]. Bhojaraja [227] mapped the *Secale cereale* - derived gene *Lr45* on 2A and developed PCR based co-dominant markers. Codominant microsatellite markers linked to *Lr25* have also been identified on 4BL chromosome [228]. A gene for leaf rust resistance in *Triticum durum* var. Trinakria has been identified and mapped on 5BS chromosome [229]. Similarly, stem rust resistance genes have been mapped on chromosomes 5DL and 2BL in a bread wheat stock WR95 [230]. Pyramiding of major genes using marker assisted selection in agronomically suitable cultivars is also being pursued [127, 231-234] to prevent the breakdown of resistance and the pyramided lines are being tested at multi-locations for their yield potential. Resistance genes have also been incorporated through conventional breeding methods, which have later been confirmed molecularly [235]. Leaf rust resistance genes *Lr19/Sr25* and *Lr28* are pyramided in the background of cv. HD2687 carrying 1BL.1RS translocation using marker assisted breeding [232]. Cook*6/C80-1, an Australian line carries *Lr19/Sr25* plus a DNA segment carrying *Sr36/Pm6* from *Triticum timopheevi* was used as donor for *Lr19*. The pyramided line showed more than 90% genomic similarity with recurrent parent, HD2687. Another popular cultivar HD2932 has been improved for multiple rust resistance by marker assisted transfer of gens *Lr19*, *Sr26* and *Yr10* [236]. Similarly, popular

cultivars HD2733 and HD2967 are being improved by transferring multiple rust resistance genes utilizing MAS. Effective gene for stripe rust resistance (*Yr15*) has been introgressed into a popular but rust susceptible cultivar HD2329 [237].

Currently, the cultivar HD2967 is occupying a large area in NWPZ. It exhibits resistance to all the three rusts at adult plant stage. A high degree of APR against most virulent and prevalent races 77-5 and 104-2 is ascribed to minor gene based durable resistance [238], although it has been postulated to carry *Lr13+* which alone is not effective against above mentioned races of leaf rust. Identification and mapping of rust resistance genes is crucial for development of effective and durable resistance in wheat. The apparent effectiveness of these genes is observed in Indian bread wheat genotypes, hence the search for this type of novel or similar type of resistance in the durum or hexaploid state should be intensified.

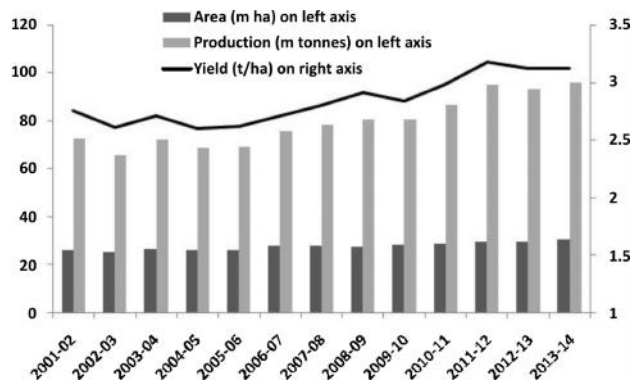
Impact of gene deployment on wheat production in India

India has touched record production levels continuously from 2006-07 to 2011-12 (Table 3 and Fig. 5) crop season and after marginal decrease in total wheat production in 2012-13 [239], it is expected to touch new record of 95.85 mt during 2013-14 (3rd Advance estimates, DAC, GOI). In recent years, wheat has achieved relatively higher production stability as compared to other cereal crops. Only marginal increase in wheat area is recorded but the strategic deployment of rust resistance genes is crucial in sustaining the production levels. Further, enhancing productivity and production of wheat could be achieved if the minimum enabling production environment is provided to bridge the yield gap. Besides, several other factors such as increasing irrigation, developing short duration varieties application of balanced fertilizer and nutrients, etc., cultivation of rust resistant varieties may be most protective of crop production avoiding rust epidemics. The North Western Plains Zone, the wheat bowl of the country, has been given more emphasis by release of number of latest wheat genotypes having diversified gene combinations for rust resistance specifically for stripe rust. Among these, promising cultivars are HD 2967, HD3059, DPW 621-50 and WH 1105 which carries minor gene based resistance to all the rusts. The strategic planning to control stripe rust in the NWPZ through deployment of resistant cultivars and chemical control has been crucial in sustaining the productivity levels. As wheat productivity depends on the

Table 3. Recent wheat production trends in India

Year	Area (m ha)	Yield (t/ha)	Production (m t)
2001-02	26.34	2.76	72.8
2002-03	25.2	2.61	65.8
2003-04	26.59	2.71	72.2
2004-05	26.38	2.6	68.6
2005-06	26.48	2.62	69.4
2006-07	27.99	2.71	75.8
2007-08	28.04	2.8	78.6
2008-09	27.75	2.91	80.7
2009-10	28.46	2.84	80.8
2010-11	29.07	2.99	86.9
2011-12	29.87	3.18	94.9
2012-13	30	3.12	93.5
2013-14	30.61	3.12	95.9

*3rd advance estimates of GOI

**Fig. 5.** Recent wheat production trends in India

competition of new emerging rust pathotypes and the rate of deployment of rust resistance genes, the judicious gene deployment singly or in combination has checked the spread of stem and leaf rust inoculums to the wheat belt of the country, particularly in Indo-Gangetic plains occupying more than 20 million ha area under wheat crop. The Indian wheat programme has efficiently addressed the strategy to deploy rust resistance genes and the success of such strategies can be envisaged from the fact that there were no major wheat losses due to rusts in India for last 40 years when neighboring countries (1994-96) and countries like United States of America (1998) faced rust epidemics. Presently, major genes deployed in Indian wheat cultivars are *Lr1*, *Lr3*, *Lr10*, *Lr13*, *Lr14a*, *Lr23*, *Lr24*, *Lr26*, *Lr34* for leaf rust

resistance; *YrA*, *Yr2*, *Yr2KS*, *Yr2 (SKA)*, *Yr9*, *Yr18*, *Yr27* for stripe rust and *Sr2*, *Sr 5*, *Sr7b*, *Sr8a*, *Sr9e*, *Sr11*, *Sr 24*, *Sr 31* for stem rust resistance are commonly occurring.

Conclusion

In the past four decades, much has been accomplished in controlling the wheat rusts in India. A principal reason for the progress has been the number of trained individuals working on the problem in each wheat zone. This collective effort of plant pathologists and plant breeders in developing resistant cultivars and understanding disease epidemiology has gradually reduced the magnitude and frequency of epidemics. Use of knowledge of pathogen variability generated thus far, formed the basis of strategy for deployment of resistance genes in the field. The emergence of new races of rusts require continued efforts to deploy new resistance genes. It is obvious that gene management in field has considerable promise for sustained control of rusts. The popular Indian wheat cultivars Kalyansona, Sonalika, HD2329, Lok1, HD2285, HD2189, PBW343, PBW373 and recently HD2967 have diverse genes for rust resistance. Mega varieties dominated in India despite release of a large number of varieties. In India the resistance genes have been fairly and properly managed. The diversification of cultivars in a mosaic pattern in each zone, intentionally or unintentionally, resulted in strategic deployment of resistance genes which contained rust infection. It has often been difficult to withdraw popular susceptible cultivars over an entire epidemiological area because of market demand and economic benefits. The cooperation between pathologists and breeders is to be maintained so that the rusts do not pose a major threat to wheat production in India. India has the potential to produce >100 million tonnes in the absence of a rust epidemics, however, some apprehensions have been expressed in the world [240-242] against achieving such a target due to races of rusts acquiring more virulence. However, synergy between pathologists and breeders can overcome this hurdle and achieve this projection..

Future prospects

Breeding program for disease resistance still requires strengthening in the perspective of climate change. The effective control of the wheat rusts has been largely due to the exchange of improved germplasm, which provides a vital source of genetic variation. The major contributor to Indian wheat programme is International

Maize and Wheat Improvement Center (CIMMYT) which is sharing the advanced material. The impetus on the high yielding cultivars must continue and the emphasis on disease resistance may be even higher. Appropriate management of the host resistance genes through deployment of resistant cultivars in different geographical regions and gene pyramiding are the suitable strategies to increase the durability of resistance. Use of durable resistance will be a good strategy for providing agronomically acceptable option to farmers. Wider application of the genes having minor phenotypic effect is advocated. Migration of rust strains from adjoining areas is important. Hence, constant vigil and monitoring of rust is to be continuously done. Also monitoring crop health and management of the food resources is likely to get greater emphasis as the pressure on land increases.

The use of race-specific rust resistance in development of cultivars can routinely be followed with cautious approach in wheat breeding, keeping in mind the continual evolution of new races or biotypes of the pathogen. There are a number of examples of cultivars with single gene, race-specific resistance became susceptible in a short span of time. At the same time, these major genes have provided long lasting resistance and therefore, the use of the race-specific resistance should not be discouraged and these genes need not be dumped. In this endeavour both race-specific and non race-specific resistance could be combined. The basic objective should be to reduce the selection pressure for virulence in the pathogen. Search for new resistance genes from across the genera and species must be intensified. A lot remains to be learned in the areas of both applied and basic research.

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