



Tackling a Cereal Killer on the Run: Unending Fight Between Wheat Breeding and Foliar Rusts

10

Achla Sharma, M. Shamshad, Satinder Kaur, Puja Srivastava,
G. S. Mavi, and V. S. Sohu

Abstract

Outbreaks of emerging new pathotypes of wheat rust pathogens, increasing at an alarming rate, are threatening the global food security. Wheat rusts caused by *Puccinia* species are major biotic constraints in efforts to sustain wheat production worldwide. Their quick evolution and capacity to spread over long distances make the resistance breeding in wheat a very challenging task. Pre-emptive or anticipatory breeding and sensible deployment of rust resistant cultivars have proven to be an effective strategy to manage wheat rusts. Efforts are focussed to accelerate rust resistance breeding strategies and explore wheat rust epidemiology. The collaborative role of wheat breeders and pathologists in addressing these threats to plant health is essential. This chapter presents the efforts done for rust resistance breeding at the global level and deployment of resistant cultivars in different geographical areas to combat the effect of stripe rust. 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 of wheat.

Keywords

Anticipatory breeding · Gene deployment · Pathotypes · Physiological specialization · Resistance genes · Virulence · Scouting

A. Sharma (✉) · M. Shamshad · S. Kaur · P. Srivastava · G. S. Mavi · V. S. Sohu
Punjab Agricultural University, Ludhiana, India
e-mail: achla@pau.edu; shamshad-pbg@pau.edu; satinder.biotech@pau.edu;
pujasrivastava@pau.edu; mavig666@pau.edu; sohuvs@pau.edu

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227

10.1 Introduction

Wheat (*Triticum aestivum* L.) is one of the most important cereals consumed worldwide and is an important part of the daily diet of people which along with rice and maize is fulfilling more than half of the calorie demand of the world population. Wheat is the second most important crop following rice in terms of both harvested area and production in India. Since India is the largest wheat-consuming country after China, the increase in wheat production is very important to meet the food demands of increasing population. Wheat yield has increased substantially in the past few years, and this appreciable yield increase may be attributable to the introduction of high-yielding and rust-resistant semi-dwarf varieties developed under the collaborative efforts of the international and national institutions. According to the future projections, India needs to lift its annual food production to 333 million tonnes by 2050 to feed the population (Pingali et al. 2019) from the current level of 296 million tonnes (third advance estimates 2019–2020). India is the second largest producer of wheat worldwide (Sharma and Sendhil 2015, 2016), and the area under wheat cultivation in India is about 30 million hectares (14% of global area) to produce the highest output of 99.70 million tonnes of wheat (13.64% of world production) with a record average productivity of 3371 Kg/ha (Sendhil et al. 2019). There is a limited scope for enhancing the area under wheat in India; therefore, the existing average yield has to increase from 33 to 47 q/ha by 2050 under stable wheat acreage (Sendhil et al. 2019). To meet these projections, wheat breeding programme is principally focussed on productivity and productivity protecting mechanisms which include the possible management strategies to enhance or, at the minimal level, sustain the productivity of wheat.

Many abiotic and biotic challenges come in the way of wheat production. The emergence of new pests and diseases is continuously threatening the food sustainability that is further intensified by the climate change, which might trigger the emergence of new races of the pathogens with wider adaptability to varying environmental conditions. Among the various biotic stresses, rusts are of the foremost importance. Wheat rusts continually pose a threat to global wheat production (Khan et al. 2017). Wheat rusts caused by *Puccinia* species occur in all wheat-growing areas of the world. The ability of *Puccinia* species to spread over long distances and evolve into new virulent isolates makes the management of wheat rusts a very complex task. Currently, 88% of the world's wheat production is prone to wheat stripe rust, leading to global losses of over 5 million tonnes of wheat with an estimated market value of \$USD 1 billion annually (Wellings 2011; Beddow et al. 2015). In India about 10 million hectares in northern states are prone to stripe rust (Bhardwaj and Singh 2019). Outbreaks of rusts in wheat are increasing at an alarming rate and threatening the food security needs of a booming population. The role of wheat breeders in addressing these threats for sustainable wheat production becomes very important. There had been a gradual gain in virulence of rust pathogens, and over the years, many genes have been defeated by newly evolved rust pathogen isolates (Bhardwaj 2012). Very aggressive pathotypes have been identified in the recent past for all rusts. Some of these pathotypes are very

competitive and have become more prevalent and aggressive over the years (Gangwar et al. 2019). The threat of this fungus to wheat breeding is rooted in its tremendous genetic diversity, long-distance dispersal capacity even across the continents and rapid local adaptation via stepwise evolution. All these factors help rust pathogens overcome a single rust resistance gene at a time (Hovmoller et al. 2011). A proactive rust management system facilitated by strong rust surveillance tools makes it possible to identify new pathotypes in initial stages and search for the available resistance sources for newly evolved pathogen isolates. Consequently, corrective breeding efforts in breeding programme are undertaken to mobilize rust resistance into high-yielding wheat germplasm and their deployment at the farmer's field keeping in view the pathogen virulence distribution much before a pathotype reaches epidemic proportions (Bhardwaj and Singh 2019).

In India, the susceptible wheat varieties suffer yield losses of up to 60% or more due to stripe rust. Breeding for resistance to stripe as well as leaf rust constitutes a major objective in the main wheat zone of India which includes Punjab, Haryana, Delhi, Uttar Pradesh, Rajasthan and Uttarakhand. In India the North Western Plain Zone (NWPZ), comprising the Indo-Gangetic Plains of India, is the main wheat-producing region. Punjab, a geographically small state in this region, is known as the food bowl of the country which is testified by the fact that 40–60% of wheat to the national food reserves is contributed by the Punjab state alone. Wheat is the predominant grain crop in Punjab which is grown on an area of around 35 million hectares and occupies about 90% of the total cropped area in the season. Punjab produces about 18% of the wheat produced in the country from 12% of the area under this crop. Development and deployment of cultivars with genetic resistance is the most economical, effective and environment-friendly method to reduce damage and loss caused by leaf rust and stripe rust. To overcome the threat of wheat rusts, efforts are being made to explore rust pathogen diversity and identify newly evolved rust pathogen isolates pathotypes and accordingly undertake anticipatory breeding, evaluation for rust resistance and deployment of rust resistant cultivars. Till now, more than 210 rust resistance genes and the associated markers are available for the use of breeders. Some of the linked gene combinations like *Lr34/Yr18/Sr57/Pm38/Ltn1*, *Lr46/Yr29/Sr58/Pm39/Ltn2*, and *Sr2/Yr30; Lr67/Yr46/Sr55/Ltn3* are known to confer durable resistance to different rusts. Three rusts, stem/black (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. and Henn.), leaf/brown (*P. triticina* Eriks.) and stripe/yellow (*P. striiformis* f. sp. *tritici* Westend.), cause varying degrees of loss worldwide. Masses of dark-red urediniospores on the leaf sheaths, stems, glumes and awns of susceptible plants are typical symptoms of stem rust infection (Kolmer 2005). Breeding for resistance against stem rust was the foundation of Green Revolution in the mid- to the late nineteenth century (Peterson 2001). In India, the stem rust occurs in northern plain regions; however race *U99* could not be detected from India (Global Rust Tracker 2020). Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* has caused severe epidemics since the last decade leading to heavy economic losses (Kumar et al. 2020). Similarly, leaf rust or brown rust caused by the heteroecious basidiomycete *Puccinia triticina*, occurs mostly on the leaf blades, although leaf sheath can also be infected under high epidemic conditions, high

inoculum densities and in case of extremely susceptible cultivars. Losses in grain yield are primarily due to reduced floret set and grain shriveling (Figlan et al. 2020). The rust pathogens continue to evolve new virulences that have led to the exit of important wheat cultivars. For example, the emergence of virulence for *Yr9* in *P. striiformis* in India led to the elimination of mega variety PBW 343. Such quick changes in the virulence patterns of wheat rust pathogens are really alarming for breeders. Considering the impact of wheat rust diseases, the major wheat breeding efforts are diverted towards scouting new genes for resistance and mobilizing this resistance to adapted germplasm after mapping and molecular characterization. This chapter focusses on the efforts done for breeding rust-resistant wheats in recent years and their impact. It consolidates information on the present status of rust diseases and rust-resistant cultivars.

10.2 History and Status of Wheat Rust Research in India

Wheat is mainly grown under irrigated and rainfed conditions in India. Wheat rust research started in India in around 1922, with the earliest pathotype documented in 1931. With the discovery of the genetic basis of resistance by Biffen (1905), physiological specialization in rust pathogens by Stakman and Levine (1962) and gene-for-gene interaction by Flor (1956), the utilization of the hypersensitive (race-specific) type of resistance has dominated in wheat improvement. Numerous rust resistance genes are now known and have been catalogued (McIntosh et al. 2017). Most of these genes can be detected in seedling evaluations using specific pathotypes. Non-race-specific resistances operate against all the pathotypes or races of a pathogen. The genetic nature of this type of rust resistance is usually complex and based on the additive interaction of several genes having minor to intermediate effects. Slow rusting and partial resistances are almost synonymous terms. As defined by Caldwell (1968), slow rusting is a type of resistance where the disease progresses at a retarded rate, resulting in intermediate to low disease levels against all pathotypes of a pathogen. Partial resistance, as defined by Parlevliet (1975) referring to leaf rust resistance in barley, is a form of incomplete resistance characterized by a reduced rate of epidemic development despite a high or susceptible infection type. The components that cause slow rusting of a cultivar are longer latent, incubation periods, low receptivity or infection frequency, as well as smaller uredial size and reduced viability duration of the spores produced. All these components can affect disease progress in the field. Durable resistance, as defined by Johnson (1988), is that which has remained effective in a cultivar during its widespread cultivation for a long sequence of generations or period of time in an environment favourable to a disease or pest. Since wheat cultivars are grown in a large area, any smart wheat breeding programme uses diverse germplasm sources for rust resistance. Identifying numerous new sources of resistance genes either in wheat or in related species and their transfer to wheat through wide hybridization has been the thrust area of research in wheat breeding for one century.

Indian wheat breeding programme started around 1900, progressed and became one of the most successful programmes in the world achieving self-sufficiency in wheat. It was the multipronged effort focussing on surveillance, identification of pathotypes, understanding the epidemiology of the rust pathogens of wheat and identification of rust resistance sources in wheat which led to the development of rust-resistant cultivars. In the present scenario, research efforts emphasize on the regular monitoring of wheat rust pathogens, the use of specialized mapping populations or panels in the identification of pathotypes, evaluation of germplasm for rust resistance, anticipatory breeding for rust resistance and strategic deployment of wheat cultivars with durable rust resistance. Further, research interests focus on targeting the pyramiding of rust resistance genes using the molecular markers, exploring the genetic variability among the wheat rust pathotypes, genome sequencing of wheat rust pathogens, molecular studies of the host-pathogen interactions and revisiting the epidemiology of wheat rust pathogens.

10.3 Origin of New Pathotypes and Ever-Changing Pathotype Situation

Most of the new pathotypes originate through the mutation and para sexuality. Sexual recombinations, mutation, parasexuality and heterokaryosis could enhance the pathogenic variability in the wheat rusts. In Indian conditions, unavailability of functional alternate hosts eliminates the sexual recombinations. Many of the workers have reported the instances where heterokaryosis or crossing over and mutation have been putatively given rise to new pathotypes (Bhardwaj et al. 1990, 2005, 2010; Nayar et al. 1991; Prashar et al. 2015). Generally, it is believed that mutation is an important way for creating variability in wheat rusts. Gene-for-gene hypothesis suggested that the virulence in rust pathogens is generally recessive and two key genes are necessary for expression of resistance, the *R* gene in the host and the corresponding avirulence (*Avr*) gene in the rust pathogen. The resistance conferred by *R* gene of the host depends on the corresponding *Avr* gene of a pathogen strain. Pathogen overcomes resistance by driving mutation of *Avr* gene, thus leading to loss of recognition by the corresponding *R* gene (Ellis et al. 2014). In case of non-specific interactions, broad-spectrum resistance genes mean that they can recognize *Avr* genes present in all the pathogen isolates. Resistance to rusts can be broadly categorized as all-stage resistance (also called seedling resistance), which can be detected at the seedling stage, but is also expressed at all stages of plant growth, and as adult plant resistance (APR), which is expressed at later stages of plant growth. Most designated yellow rust resistance genes are expressed at seedling growth stages and are usually effective throughout the life of the host. APR is commonly detected at the post-seedling stage and often known as field resistance, although some APR genes can be induced to express in seedlings by varying the growth temperature and light conditions. Genotypes possessing race-specific, all-stage resistance often lose their resistance and become susceptible soon after they are released due to occurrence of more virulent pathotypes. In some instances, adult plant resistance is

controlled by temperature and known as high-temperature adult plant (HTAP) resistance or temperature-sensitive resistance (Roelfs et al. 1992). HTAP is race-non-specific, durable resistance and one of the most effective types of adult plant resistance. Cultivars with only HTAP resistance are susceptible to all races at the seedling stage, and as the temperature increases during the growing season, resistance is triggered, and plant becomes more resistant (Chen 2005). Unlike the seedling resistance genes, the adult plant resistance expresses only when the wheat plants enter into reproductive phase, thus sustaining the pathogen races even when the resistance shown by the carrier wheat is very high at adult plant stage. *Sr2*, a stem rust resistance gene, and *Lr34*, a disease gene complex that provides resistance against leaf rust, stripe rust and powdery mildew, are the best-known APR genes which have been used in commercial wheat varieties for almost 100 years (Ellis et al. 2014). Importantly neither APR genes on their own provides adequate levels of resistance under high disease pressure, nor the APR expression sometimes protect the crop yield in the field completely. The slow rusting and quantitative nature of their phenotypes have incorrectly led to misinterpretation of their effectiveness and in some instances have been reported as having lost effectiveness (Yildirim et al. 2012; Krattinger et al. 2013).

10.4 Current Strategies to Combat the Rusts

Host resistance is the most efficient, cheap and environmentally most secure means of rust management. When adequate genetic resistance is available in a cultivar, no other measures are necessary. The systematic breeding for rust resistance in wheat in India began in the early 1950s. Wheat variety NP 809, resistant to all the three rusts, was the first resistant cultivar to be developed by the Indian Agricultural Research Institute (Tomar et al. 2014). Much has been achieved through these years in controlling rusts by developing resistant wheat cultivars. Such genetic diversity has not only proved critical in developing rust-resistant cultivars but also in understanding rust epidemiology and has gradually reduced the quantum and frequency of wheat rust epidemics. The resistance gene *Lr26* in combination with *Lr13*, *Lr23*, and *Lr34* and the Agropyron segment carrying genes *Lr24* and *Sr24* have played a crucial role in providing field resistance and protecting wheat from any leaf rust epidemic threat to sustained wheat production. Likewise, *Sr31* in combination with *Sr2*, *Sr24*, *Sr5* and *Sr8* has provided protection against stem rust, whereas *Yr9* in combination with *Yr2*, *Yr18* and some unknown adult plant resistance genes conferred protection from stripe rust (Bhardwaj and Singh 2019). In recent years, wheat production has been observed to be stable due to development and deployment of resistant cultivars. Detailed accounts of Indian efforts in breeding wheat for disease resistance are available (Tomar et al. 2014). Marker-assisted backcross breeding has become an integral part of Indian wheat breeding programmes (Bhardwaj 2011; Bhardwaj et al. 2016a, b).

10.5 Case of Stripe Rust Epidemics and Effect on Breeding Programs

First described in Europe in 1777, stripe rust is one of the most important and destructive diseases of wheat. This rust was mainly endemic to cooler regions until a decade ago, but now the new aggressive strains have emerged and spread globally causing severe epidemics in warmer regions across the world. This has rendered stripe rust as an economically most important disease that poses a threat to the world food security. The semi-dwarf and rust-resistant varieties developed at the International Maize and Wheat Improvement Centre (CIMMYT), Mexico, in the early days of 'Green Revolution' had been responsible for yield breakthrough in India and many other countries of the world. After the introduction of these Mexican wheats, Kalyansona and Sonalika maintained resistance to stripe rust until 1970. Thereafter, Kalyansona became susceptible followed by emergence of another pathotype (46S102), which rendered Sonalika susceptible. The next source of resistance in wheat was from a block of genes, *Sr31/Lr26/Yr9/Pm8*, reported from rye chromosome 1R, in cultivars Salzmunde Batweizen and Weieue, released in 1960 in Czechoslovakia. These cultivars are believed to have originated from the crosses Ciewene 104 × Petkus rye and *Triticum dicoccum* × *Agropyron intermedium*, respectively (Bartos and Bares 1971). A sister line of these, 'Neuzutch' was used for breeding in the Soviet Union and gave rise to Russian cultivars Kavkaz, Aurora, Besostaya 2, Skorospelka, etc. Neuzutch possessed a complete 1R chromosome, whereas Kavkaz and Aroura were the first lines to have interchanged chromosome having wheat chromosome 1B and rye chromosome 1R segment. Kavkaz was introduced to CIMMYT germplasm from Russia, leading to the development and release of high-yielding wheat cultivar, 'Veery'. This translocation became widespread in wheat cultivars released in major wheat-growing regions of the world including India and showed significant grain yield advantage, wide adaptation over range of environments and superior disease resistance attributes due to the presence of the 1B.1R translocation. This led to another significant yield jump as well as disease resistance, specifically rusts. Mega cultivars PBW343 and Inqalab 91 in India and Pakistan, respectively, were extracted from this material from CIMMYT. A race of *P. striiformis*, having virulence for gene *Yr9*, was first observed in East Africa in 1986 and subsequently in North Africa and South Asia. Once it appeared in Yemen in 1991, it took just 4 years to appear in the wheat fields of South Asia (Singh et al. 2000). Most of the cultivars grown at that time were susceptible to *Yr9* virulence and consequently considerable losses in wheat production incurred in almost all major wheat-growing regions of North Africa, Central and Western Asia and South Asia. By virtue of stripe rust resistance gene *Yr27*, derived from Selkirk, PBW 343 withstood the spread of *Yr9* virulence, to which many other Veery derivatives succumbed (McDonald et al. 2004; McIntosh et al. 2003). This widespread popularity of PBW 343 with 1B-1R translocation led to monoculture, finally resulting in evolution of devastating rust virulences. Similarly, *Yr27* virulence (pathotype 78S84) emergence and its movement following the pathway of *Yr9* gene ruined the wheat production in India. The breeding pipeline was being majorly

fed by germplasm having the same resistance base. In 2005, the wheat crop in Northern India was severely hit by this super aggressive race of yellow rust where most of the area was under PBW343 which constituted almost 80% of the grain output of Punjab, Haryana and Western Uttar Pradesh. These top three wheat producers in India were under the stripe rust havoc. The evolution of the stripe rust pathogen in case of 78S84 pathotype not only rendered PBW343 susceptible to stripe rust but also slowly wrapped up all the newly released varieties in the wrath of susceptibility which included DBW17 (2007), PBW550 (2008), PBW621 (2011) and HD2967 (2011). The resistance of these varieties was so short lived which continues till now and has sparked up a continuous unending battle between the newly evolving rust pathotypes and wheat breeders.

The single most important innovation in rust resistance breeding in recent years has been the advent of molecular markers. Initial work on marker-assisted breeding for rust resistance was typically associated with several problems. Known, marked genes were available in inferior/unadapted genetic backgrounds, seriously undermining their utility for breeding purposes. Marker work was generally conducted outside or on the periphery of the breeding programme. Access to the future varietal candidates for use as recipients was mostly lacking. Limited resources/low-throughput technology limited the number of recipient genotypes. The situation often resulted in putting one's bets on the wrong horse, and the products had a little scope for breaking into the commercial arena. In spite of these initial problems, the use of molecular markers has brought about significant improvements in breeding for rust resistance. Several major genes, viz. *Yr5*, *Yr10*, *Yr15*, *Yr36*, *Yr47*, *Yr51*, *Yr57* and *Yr63* known to provide resistance to currently prevalent races of stripe rust, are available to be stacked in combinations using molecular markers. Gene *Yr5* identified in *Triticum aestivum* subsp. *spelta*, located on chromosome 2BL, confers resistance to almost all pathotypes of stripe rust but has not been commercially utilized (McIntosh et al. 1995). Gene *Yr15* originated from *Triticum dicoccoides* and molecular markers linked to this gene are available (Peng et al. 2000). The linked rust resistance gene complex, viz. *Yr17*, *Lr37* and *Sr38*, which confer resistance to stripe rust, leaf rust and stem rust, respectively, has its origin in *Triticum ventricosum* Ces. (syn. *Aegilops ventricosa*) and has been used by breeders in many parts of the world (Robert et al. 1999). The 2NS chromosome segment (*Yr17/Lr37/Sr38*) has also been reported to be associated with significant reductions in head blast incidence in wheat under natural epidemic conditions in the field. But, not all cultivars and lines with 2NS showed resistance under controlled inoculations in the greenhouse (Cruz Alcantara-de la et al. 2016). The CIMMYT cultivar KACHU (Kohli et al. 2011) possesses the 2NS translocation, and Milan-based resistant wheat cultivars released in South America appear to contain high levels of resistance to wheat head blast under field conditions (Kohli et al. 2011). This resistance is present in most of the germplasm in India through KACHU sourced from CIMMYT. In addition to effective rust and blast resistance, the 2NS/2AS translocation brings additional value to the wheat breeding programme as it also carries resistance genes *Rkn3* and *Cre5* against root-knot nematodes

(*Meloidogyne* spp.; Williamson et al. 2013) and the cereal cyst nematode (*Heterodera avenae* Wollenweber; Jahier et al. 2001), respectively.

For the durability of resistance, molecular marker-assisted gene pyramiding is considered to be essential. Besides aiding in gene pyramiding, these markers help in understanding the relationships among different genes. The gene pyramiding strategy, combining several resistance genes into one cultivar, has been proposed to enhance the durability of resistances. Combining two or more resistant genes using classical host-parasite infection methods is highly time-consuming and needs specific virulent pathotypes that are often not available or too risky to use. Molecular biology and marker-assisted selection (MAS) offer the possibility to stack resistance genes in cultivars in an easier and more efficient way. With the advent of genetic engineering and biotechnology, plant breeding has got a new dimension to produce crop varieties with more desirable characters. Marker-assisted selection (MAS) which involves indirect selection of traits by selecting the marker linked to the gene of interest has become a reality with development and availability of an array of molecular markers and dense molecular genetic maps in crop plants. Molecular markers are especially advantageous for agronomic traits that are otherwise difficult to tag such as resistance to pathogens, insects and nematodes, tolerance to abiotic stresses, quality parameters and quantitative traits. Molecular marker studies using different mapping populations like near isogenic lines (NILs), MAGIC population or recombinant inbred lines (RILs) have accelerated the mapping of many genes in different plant species. In a gene pyramiding scheme, strategy is to stack genes into a single genotype using DNA markers, which permits complete gene identification of the progeny at each generation and hence increases the speed of pyramiding process. In general, the gene pyramiding aims at the derivation of an ideal genotype that is homozygous for the favourable alleles at all loci. The gene pyramiding scheme can be divided into two parts. The first part aims at cumulating all target genes in a single genotype called the root genotype. The second part is called the fixation step which aims at fixing the target genes into a homozygous state, i.e. to derive the ideal genotype from the one single genotype. Although the pedigree step may be common, several different procedures can be used to undergo fixation in gene pyramiding.

Another alternate, most promising, long-term control strategy is to breed and deploy cultivars carrying durable resistance based on minor, slow rusting genes with additive effects. The sources of durable resistance to stripe rust mostly carry *Yr18* and *Yr29* (Singh et al. 2004). These genes confer a very low level of resistance requiring at least two to three additional minor genes to be effective under high disease pressure. Hence, they cannot be deployed independently in breeding programs. The preferred strategy would include at least one major gene in combination with minor genes, and moreover the major selected major gene for stripe rust resistance should be preferably linked to leaf rust resistance. Many such genes are available including stripe rust resistance gene, *Yr18* (linked with *Lr34*) and gene *ltn* (McIntosh 1992; Singh and Rajaram 1992). It is characterized morphologically by a distinctive leaf tip necrosis (Dyck and Lukow 1988; Singh and Rajaram 1992). The other minor gene, *Yr29*, confers moderate levels of adult plant resistance, is closely linked with gene *Lr46* and is located at the distal end of the long arm of wheat

chromosome 1B. In the recent past, stripe rust resistance genes linked to leaf rust resistance genes, namely, *Lr57/Yr40* and *Lr70/Yr76*, have been derived from *Aegilops geniculata* and *Aegilops umbellulata*, respectively (Kuraparthy et al. 2009; Bansal et al. 2020).

Breeders transfer a target allele from a donor variety to a popular cultivar by a repetitive process called backcrossing, which, unfortunately, is slow and uncertain. Breeding a plant that has the desired donor allele but otherwise looks just like the popular cultivar usually takes 6–7 years or longer. Worse, the improved variety may look just like the popular cultivar, but it inevitably retains stray chromosome segments from the donor. Consequently, to a greater or lesser extent, it will fail to perform exactly like the popular cultivar, thus limiting its appeal to farmers. Marker-assisted breeding tackles both problems by allowing breeders to identify young plants with the desired trait and by facilitating the removal of stray donor genes from intermediate backcrosses. The result, in about 2 years, is an improved variety exactly like the popular cultivar except that it possesses the transferred advantageous gene. Markers are effective aids to selection in backcrossing as they can aid selection on target alleles whose effects are difficult to observe phenotypically. Examples include recessive genes, multiple disease resistance gene pyramids combined in one genotype (where they can epistatically mask each other's effects), alleles that are not expressed in the selection environments (e.g. genes conferring resistance to a disease that is not regularly present in environments), etc. Also, markers can be used to select for rare progeny in which recombination near the target gene has produced chromosomes that contain the target allele and as little possible surrounding DNA from the donor parent. Further, markers can be used to select rare progeny that are the result of recombination near the target gene, thus minimizing the effects of linkage drag. In general, the marker-assisted backcross-based gene pyramiding can be performed in three strategies. In the first method, the recurrent parent (RP1) is crossed with donor parent (DP1) to produce the F₁ hybrid and backcrossed up to the third backcross generation (BC₃) to produce the improved recurrent parent (IRP1). This improved recurrent parent is then crossed with other donor parent (DP2) to pyramid multiple genes. This strategy is less acceptable as it is time-taking, but pyramiding is very precise as it involves one gene at one time. In the second strategy, the recurrent parent (RP1) is crossed with donor parents (DP1, DP2, etc.) to get the F₁ crossed with donor parents (DP1, DP2, etc.) to get the F₁ (IF₁). This improved F₁ is then backcrossed with the recurrent parent to get the improved recurrent parent (IRP1). As such, the pyramiding is done in the pedigree step itself. However, when the donor parents are different, this method is less likely to be used because there is a chance that the pyramided gene may be lost in the process. The third strategy is the mixture of the first two which involve simultaneous crossing of recurrent parent (RP1) with many donor parents and then backcrossing them up to the BC₃ generation. The backcross populations with the individual gene are then intercrossed with each other to get the pyramided lines. This is the most acceptable way as in this method not only time is reduced, but also fixation of genes is fully assured. Marker-assisted backcrossing to be effective depends upon several factors, including the distance between the closest markers and the target gene, the number of target genes

to be transferred, the genetic base of the trait, the number of individuals that can be analysed and the genetic background in which the target gene has to be transferred, the type of molecular marker(s) used and available technical facilities. When these entire selection criteria are maintained properly, only then a well acceptable MAS or MABB-based gene pyramiding scheme can lead to durable crop improvement.

10.6 Resistance Breeding: Development and Deployment of Resistant Wheat Varieties

Rust-resistant cultivars are the most economic, ecologically safe and effective way to manage wheat rusts. Wheat breeding in combination with developments in biotechnology such as high-throughput molecular markers has made a remarkable progress in increasing crop yields since the recent past. There are always regional differences in the distribution of rust pathogens, as well as of the pathotypes of each rust pathogen (Prashar et al. 2007). Based on the distribution of pathotypes of the different *Puccinia* species on wheat and the rust resistance of wheat varieties, deployment of rust-resistant wheat varieties is undertaken tactfully in different wheat-growing areas. The racial evolution for stripe rust has not only worked against the released varieties, but also observations on a set of diverse and initially resistant stocks showed subsequent breakdowns. The stocks that succumbed completely or partially included so-called durable-resistant stocks with genes from Tukuru, Kukuna, DBW18 and C591 and major gene stocks *Lr57/Yr40*, *Lr76/Yr70*, and *Lr37/Yr17* when introgressed individually.

Punjab Agriculture University, Ludhiana, Punjab, is first in the country to develop a variety using modified marker-assisted backcross breeding (MABB) and release at the national level. PBW723 (*Unnat* PBW343) is the improved version of PBW343 and has five resistant genes introgressed into it. It has seedling resistance to all the four isolates (two of stripe rust and two of leaf rust), while PBW343 is susceptible to all, and other checks showed susceptibility to two or three of the isolates. Based on APR against individual pathotypes, PBW723 possesses resistance against all predominant pathotypes of yellow and brown rusts. PBW723 also has enhanced resistance to Karnal bunt compared to recipient variety PBW343 as well as other check varieties (HD2967, DPW621-50 and WH1105). Post release, the variety PBW723 has made its way to the farmer's field and is being grown in Punjab at an average yield of 55–60 qtls/ha. More than 11,000 quintals of seed have been produced since the last 2 years (Sharma et al. 2021). Another variety, *Unnat* PBW550, possesses gene *Yr15* in PBW550 background and provides complete foliage resistance to rusts. Rust-resistant genes have also been incorporated into other backgrounds. Gene *Lr57/Yr40* has been introgressed in DBW17 background, and variety PBW771 has been released and recommended for cultivation under late-sown conditions of Indo-Gangetic Plains. Similarly, another cultivar, PBW752, having *Yr10* gene has been released and recommended for NWPZ for late-sown irrigated conditions. PBW757, a short-duration cultivar released by PAU for cultivation under very-late-sown conditions, has gene *Yr36* in PBW550 background.

This cultivar targets the farmer community who grows turmeric, sugarcane or potato, and the fields are vacated in the first week of January. A spectrum of wheat varieties having one or more resistant genes are available for cultivation under almost all target environments of the region and are the outcomes of systematic resistance breeding efforts.

Similarly, pyramiding disease resistance in elite genetic backgrounds is the strategy used globally for wheat breeding. Resistance to different diseases, namely, common bunt, rusts (leaf, stem and stripe) and *Fusarium* head blight caused by fungal pathogens, has been combined in Canadian winter wheat germplasm based on available DNA markers and gene sequences (Toth et al. 2019; Laroche et al. 2019). A panel of *Yr* gene pyramiding lines (consisting of 3–8 *Yr* genes) with cv. Chuanyu12 as background parent were constructed by using marker-assisted selection and evaluated under currently epidemic *Pst* races in China with an aim to develop gene pyramided lines in wheat (Liu et al. 2020). They showed that the number of pyramided *Yr* genes was significantly correlated with stripe rust resistance ($p < 0.001$), and pyramiding more than four effective or partially effective *Yr* genes can provide enough resistance to stripe rust.

10.7 Future Strategies to Breed Rust-Resistant Wheat Varieties

The pipeline of any breeding programme needs to be well fed by the germplasm developed using marker-assisted selection (MAS) for gene(s) of interest in diverse backgrounds and MABB for reviving the promising varieties. Information on emergence and global dissemination of new virulences has to be matched with specific and urgent genetic amelioration. Indian breeding program, specifically in the North Western Plain Zone, the wheat basket of the country, has faced this situation since more than one decade, first for *Yr 9* virulence coming from East Africa via Turkey and Iran, followed by 78S84 race of yellow rust which overcomes *Yr 27* gene responsible for resistance in PBW343. Rather than providing deeper insights into the stripe rust phenomenon, the events of the last few seasons have made the wheat scientific community actually aware of the gaps in understanding the wheat foliar rusts. The stripe rust race 78S84 had been detected as early as 2000 from Gurdaspur. By that time PBW 343 monoculture was already in place. Yet, the race failed to establish itself. Over the next 6–7 years, it kept on occurring on a miniscule scale in an extremely scattered pattern over the Punjab state. It was only in 2008–2009 that the race made a devastating impact on farmers' fields. Did critical evolutionary changes occur during this period? Or the race that finally caused the epidemic was unrelated to the one originally detected in 2000. There is an urgent need to solve these riddles in the future. The next important question is that what is the scope of evolutionary change in stripe rust in this region? If locally evolved virulence is not critical, is locally evolved environmental adaptation critical for the spread of a new race? Perception of differential environmental adaptation on the one hand and apprehension of climate change on the other call for a fine race-specific

analysis of environmental adaptation. The race identity needs to be tracked with precision and studied under different environmental regimes.

Before any of these questions are resolved, the larger picture concerning stripe rust perpetuation and evolution in the region needs to become clearer as a pre-requisite to further breeding efforts. The spore bank and green bridge need to be mapped precisely in terms of space and time. Besides local events, long-distance dispersal may be of critical importance. While spore movement from Turkey and adjoining region is often implicated, the role of Central Asian wheat-growing regions and Caucasian mountains as a source of new virulences is poorly understood. The exact role of high-altitude zone in the Himalayas and Hindukush mountains, which can support wheat cultivation in the off-season, also remains unknown. Important tools have now become available to address many of these questions. The geographical monitoring has undergone revolutionary developments. The weather patterns and wind currents are now under close scrutiny. It is probably time to uncover the riddle of stripe rust in this important wheat-growing region responsible for more than 90% of the national wheat reserves which will certainly give a strong push to efforts towards resistance breeding.

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