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Host and Pathogen Factors Determining Yellow Rust Reaction in Wheat- An Overview

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ABSTRACT

Among cereals, wheat is one of the most important crop globally, being a major component of food security. Among rust diseases of wheat, yellow rust is an important which result in considerable losses in normal and colossal losses in epidemic conditions. The disease-causing organism *Puccinia striiformis* is an obligate pathogen with diverse pathotypes which have the ability to invade resistance of the wheat varieties due to prevalence of new pathotypes. It is therefore, important to understand the virulence patterns of pathotypes and host resistant genes to create a mismatch for sustainable production. This review paper examines the losses due to yellow rust, variability in pathogen for virulence, migration of pathogen, meteorological pre-disposing factors, types and number of resistant genes governing yellow rust resistance at various plant growth stages, identification of resistant genes through conventional and molecular markers, conventional and biotechnological methods for developing yellow rust resistant wheat varieties and futuristic outlook to tackle yellow rust epidemic under climate change regime through breeding and management strategies.

Keywords: Wheat, yellow rust, *Puccinia striiformis*, virulence, resistance genes, breeding methods

Introduction

Among cereals, wheat is one of the most important crops worldwide ranking second after rice (Bouvet et al., 2022). Wheat is majorly cultivated since ages to provide caloric and nutritive needs of the people through its biochemical constituents that includes starch, proteins, lipids, fiber and minerals. About 35% people worldwide in developing and developed countries depend on wheat as a staple food besides rice and maize (Pooja et al., 2019). To ensure world food security, sustainably increased wheat production is required. As per FAO, statistic, it is expected that the world population will be around 8 billion by 2025 and around 10 billion by 2050 (Reema et al., 2019). Such a huge increase in population would also result in increase in demand for wheat. Wheat production needs to be increasing sustainability by 50% by 2025 and about 4% annually (Yadav et al., 2017). Wheat production is subjected to risk due to abiotic stresses on account of climate change and biotic stresses on account of prevalence of mutated insect pests and pathotypes. Biotic stresses mainly foliar diseases may reduce wheat yield by 15-20% (Bouvet et al., 2022). Of these foliar diseases, rusts and mildews are more harmful. Among rust diseases, considerable losses are caused in grain yield and quality by yellow rust (*P. striiformis*), stem rust (*P. graminis*) and leaf rust (*P. recondita*) (Ali et al., 2017). Stripe rust also known as yellow rust possess a serious challenge to the wheat growers as well as wheat breeders due to its negative impact both on grain yield and its quality. Several yellow rust epidemics have been documented (Sanders, 2018) from middle East countries and Mediterranean countries during 2009-2010 leading to colossal losses.

Epiphytotic conditions due to yellow rust have been reported from all continents including Americas

(North and South) (Line, 2002), Africa, Asia (Ali et al., 2014a), Australia (Wellings et al., 2003) and Oceania (Chen et al., 2009), the moderate to high losses have been reported due to yellow rust over the years (Ali et al., 2014b). Therefore, yellow rust resistance in wheat has been a cherished goal, both for agronomist and plant breeders (Sharma et al., 2016). As a tangible solution, the resistant varieties are continuously looked upon as cost effective and environment friendly option to cope up with menace caused by yellow rust.

Yellow Rust Losses

Among most important rust diseases of wheat, yellow rust is the cause of concern globally due to losses caused by it as it infects wheat leaves during early growth phases including seedling stage as well as subsequent plant growth stage. The yellow rust infected plants are stunted and weak leading to considerable losses up to 70%. Yellow rust also reduces grain quality including size of the grains and its milling and food product quality. Chen, (2005) reported that development of yellow rust at seedling stage can cause higher or total yield loss in susceptible varieties. Pooja et al., (2021) reported that the yellow rust infection and disease severity is influenced by several plant factors like resistant genes offering host resistance, climatic conditions at initial infection as well as its time, prevailing meteorological conditions before or during infection, duration and progress of development of disease.

Wheat genotypes possessing different *Yr* genes grown in the specific wheat producing regions globally witnessed yield losses over decades of varying intensity ranging from 20-75% leading to huge economic losses subjected to environment during crop growth (Roelfs 1978; Saari et al., 1985; McIntosh et al., 2009; Bouvet et al., 2022). The control of yellow rust using fungicide is environmentally not benign, economically costly and damaging the food safety network (Khanfri et al., 2018). Under such situations, understanding of host pathogen interaction and deployment of resistant genes is the most important management strategy to avoid yield losses. The yellow rust resistant varieties have registered much less yield losses compare to the susceptible varieties as experienced by researchers and farmers in different countries (Sharma et al., 2015). However, the pathogenic races are continuously changing through environmental selection pressure affecting durability of resistance and thus regularly changing the yield loss scenario over the years in different countries (Bouvet et al., 2022).

Pathogen As Causal Organism

Yellow rust causing organism being an obligate parasite necessitate presence of a living host to complete its life cycle. It is caused by a fungal pathogen, *Puccinia striiformis* Westend. f.sp. *tritici* which belongs to order Pucciniales and family Basidiomycota. There has been several nomenclatures for this fungal pathogen since eighteenth century, however Hylander et al., (1953) recoined the name of yellow rust causing pathogen as *Puccinia striiformis* and later reviewed by several researchers over the decades (Rahmatov, 2016). Yellow spots or flecks are evident on wheat leaves after one week of infection as first symptoms of yellow rust. (Fig. 1). Thereafter, disease development progresses and spots or flecks appear in the form of stripes on leaves and sometimes on leaf sheath, awns and glumes. The Incubation period of pathogen ranged from 10-17 days, 11-21 days and 9-19 days whereas yellow rust latent period spanned over 10-23 days, 11-21 days and 11-22 days (Kashyap et al., 2018). As the disease progresses, the small yellow spots become bigger pustules which upon maturity release yellow-orange masses of urediospores. With senescence of wheat plant, the yellow spots and stripes become brown before the maturity of the plant. Yellow rust pathogen reduces plant growth and vigour by removing wheat plant nutrients and water and therefore, reduces grain yield as well (Line, 2002; Chen, 2005; Singh et al., 2017). Poor plant growth is the major reason for loss in grain yield. The other parameters determining yield losses are dry matter, low test weight, reduced kernel number and grain size as evidenced by number of researchers (Wellings, 2011; Mabrouk et al., 2022).

Centre of Diversity for *Puccinia striiformis*

Rusts are most serious concern in wheat production world over as they can cause colossal losses (Singh et al., 2004). In most wheat production areas globally, yellow rust is prevalent (Chen, 2005). Yellow rust was observed in wheat fields in USA as early as 1915, however it was not a devastating disease and no outbreaks were recorded till 1960's which were first recorded in some states of USA mainly in the western states (Line, 2002). Ali et al., (2014) and Thach et al., (2016) recorded high genetic diversity and recombinant races of *Pst* populations in Himalayan region and its vicinity. They postulated that these regions could be centre of origin and diversity for yellow rust causing pathogen *P. striiformis.* In 1979, yellow rust was reported first time in eastern Australia which subsequently spread to New Zealand in 1980 as reported by Wellings et al., (1987). Yellow rust was reported in the beginning from South Africa and in 2004 in Western Australia. Boyd, (2005) based on phyto-pathological analysis suggested that presumably the new yellow rust pathotype emerged in East

Africa. Singh et al., (2004) summarized that yellow rust appeared in different parts of the world despite diversity in cropping systems, germplasm traits and environmental conditions. A new level of adaptation in rust races is postulated due to outbreak of rusts in countries closer to equators. *Puccinia striiformis* has been witnessed from most of the wheat growing countries from all the continents with an exception of Antarctica. Many countries in north and south America including USA, Canada, Mexico, Bolivia, Cerrebians, Canada, Oceania including Australia, Europe including Germany, France, UK, Asia including India, Pakistan and Africa including south Africa, Kenya have witnessed serious outbreaks of yellow rust over different years.

Pre-disposing Meteorological Factors

Yellow rust occurrence in wheat is mainly governed by prevailing environmental conditions and rust resistance genes in host plant. The observations gathered world over have revealed that both occurrence and severity of rust diseases are associated with changes in major meteorological parameters including maximum and minimum temperature, high and low relative humidity, soil moisture, temperature of soil, photoperiod, velocity of wind, rainfall and cloud cover (Pooja et al., 2021). In general, the temperature ranges from 0-23°C mark the congenial temperature, being minimum at 0°C, optimal at 11-12°C and maximum at 23-24°C (Curtis et al., 2002). The cooler (0-12 °C) and humid nights (RH>70) favour the onset of disease and its progression (Chen et al., 2014). In recent years, yellow rust has predominated the other rusts due to climate change (Jevtić et al., 2017). Pandey et al., (2017) described that the yellow rust severity is determined by favorable pre-disposing meteorological factors and plant water relations along with genetic factors. Therefore, in order to develop pragmatic management strategy for control of yellow rust, it is worthwhile to characterize and modulate key pre-disposing factors governing initiation and progression of disease. In order to develop reliable prediction models for occurrence and severity of yellow rust infection in wheat, it would be necessary to understand meteorological parameters as baseline information to develop disease prediction system. As the wheat can grow in diverse environment, the incidence of yellow rust infection occurs only in cooler and humid environmental conditions. Pooja et al., (2021) elaborated that temperature (max. and min.), relative humidity (morning and evening), rainfall, sunshine hours, cloud cover are associated with infection and progression of yellow rust in wheat. Based on meteorological parameters and using step-wise regression, Pooja et al., (2021) suggested a prediction model that is based on meteorological parameters and their potential contribution in determining disease severity.

In general, the disease progression was slow in cooler months of December and January and faster in moderately cool, February in north-western plain zone of india. As the temperature grows and plant attains senescence in March-April, the pathogen *P. striiformis* is also affected and the disease progression declines due to senescence (Asseng et al., 2011). Also, high temperature, >34°C hampers the growth of *P. striiformis* and hence restrict disease development (Juroszek et al., 2013). Predisposing factors favoring yellow rust incidence are also changing under global climate change regime. In short span of time, the yellow rust occurrence is supposed to be lower in north western plain zone of India as the day and night temperature are rising during and beyond February month which is supposedly the time for progression. However, in longer run, it is expected that new pathotypes of yellow rust adaptable to high temperature conditions will emerge and cause losses due to yellow rust resistance even at higher temperature than the congenial temperature known for yellow rust initiation and progression (Kaur et al., 2008). Yellow rust was reported to be prevalent in wetter and temperate regions with different altitude and latitude Chen et al., (2014).

Introduction and Migration of *Puccinia striiformis*

Since, the inoculum of yellow rust resistance needs an obligate host for its perpetuation over seasons, after wheat season, it grows on its alternative collateral host, *i.e.*, grasses growing in cooler areas of hills. The spores migrate from the centre of origin to new localities with monsoon clouds and rains and are distributed over different geographical regions through rains. This fact can be ascertained through spore trap methods (Rogers et al., 2009). After falling on growing wheat plants in winter season, the yellow rust spores can have one of the following consequences: It may germinate on leaf sheath of wheat plant (Jin et al., 2010), form conidia, puncture leaf tissue and establish itself and draw nutrition from wheat leaves through formation of haustoria (Ma et al., 2009; Sorensen, 2012) and finally establish full grown mycelia from which urediospores will be produced and released in the air for secondary infection (Chen, 2005; Sorensen, 2012). During wheat growth, 2-3 such cycles may happen which is responsible for disease progression and in some cases epiphytotic conditions. The congeniality of climatic conditions, virulence of the pathotypes and resistance of the host will determine the number of reproductive cycles of fungal pathogen and hence disease severity.

Variability in Pathogen Virulence

The mother nature gives mechanisms to all living beings to adapt to changed habitat, natural selection pressures particularly to lower organisms through mutations which are building blocks of variations and recombination can further expand such variations. Yellow rust pathogen, being an obligate parasite, thrives on living host of crop plants and collateral host in off-season mostly weeds. During this phase, the rust causing pathotypes acquire variations. The awareness about the variations in yellow rust races were experienced in early fourtees when the yellow rust races 31,13 and 20 were identified from northern and southern hills. Likewise, race A was identified from Punjab (Gurdaspur) (Bhardwaj, 2011). Since then, about 28 pathotypes are known to occur from India (Bhardwaj et al., 2012). Tracing the variation in rust races revealed that Kalyansona, the first green revolution wheat variety sown in 1967 first time as rust resistant variety became susceptible to yellow rust races 14A, 20A and 38A within a span of three years by 1970 (Sharma et al., 1972). It is presumed that widespread cultivation of two green revolution varieties; Kalyansona (*Yr2*) and Sonalika (*Yr2*) were exposed to new races I, K, N which might have evolved in the region or migrated from other adjacent regions (Nagarajan et al., 1984). Since then, many evidences have been documented to register occurrence of new pathotypes like race L, P-1 and CIII-1 virulent to *Yr9* (Kumar et al., 1994; Nayar et al., 1996). In the same analogy, popular wheat cultivars PBW343 and PBW-373 possessing *Yr27* became susceptible to stripe rust as its resistance was overcome by virulent race 78S84 (Prasher et al., 2007).

Somatic recombination, sexual recombination and mutations during natural reproduction have been suggested as possible mechanisms for emergence of new pathotypes. Genomic diversification of pathogenic races has been attributed to genetic recombination in recent studies. Zheng et al., (2013) reported high levels of genetic recombination which were consequently found in *Pst* population in countries where *Berbery* species are widely distributed, for example, Western China and Central Asia. Variation in yellow rust pathogen should be correctly accessed for effective deployment of resistant genes to develop rust resistant wheat cultivars. It is therefore essential to identify virulent and avirulent races of *P. striiformis* as part of the management strategy of maximizing wheat production. In recent years, emergence of new virulent races of yellow rust have been identified which have caused yellow rust disease; these virulent races are identified as *PstS1, PstS2*, *PstS4*, *PstS5*, *PstS6 PstS7, PstS8*, *PstS9* and *PstS10* (Ali et al., 2017). The characteristic differences between virulence and avirulent race are related to initial inoculum, rate and time of reproduction. In virulent races, the rate as well as time of reproduction is high where as in avirulent strains, initial inoculum may be high but it does not explode due to low reproduction rate. The virulent races cause losses due to the fungal growth on wheat host depriving it for nutrients and water. Moreover, leaf area covered with fungal spores hampers photosynthesis and hence biomass in sink and source affecting grain yield adversely. These diverse races have been identified by differential host methods (Bhardwaj et al., 2012), morpho-pathotypes and molecular markers (Pooja et al., 2019). Molecular markers offer potential approach to tag genes for pathogenicity in pathogen and genes for resistance in plant host.

DNA /gene markers are DNA polypeptides coding for the particular trait like virulence and can be easily accessed for much higher reliable results both about number of genes and type of genes governing virulence in yellow rust pathotypes, with much higher reliability than conventional methods (Aktar-Uz-Zaman et al., 2017). Molecular markers like RFLP, AFLP, RAPD, SSR, SNPs etc. have been used for characterization of virulent pathotypes for yellow rust (Chen, 2005). Randhawa et al., (2019) reported the molecular markers are available to tag various *Yr* genes including *Yr5, Yr9, Yr10, Yr15, Yr18, Yr24, Yr26, Yr28, Yr32-Yr36, YrH52* and *Yrns-B1* as well as gene analog for *Yr17*. According to Wan et al., (2017) a *Pst* is a highly variable pathogen due to its unique attributes including high reproduction rate, ability to disseminate and its adaptation in various environments and to different host species. Liu et al., (2012) and Zheng et al., (2013) opined that sequencing technologies can facilitate to study variation in virulence and evolution of emerging pathotypes in yellow rust. Waqar et al., (2018) suggested that different mechanisms are involved in evolution of new virulent races, of which mutations are most important. In Turkey, the *Pst* named as "Warrior" was reported from RRS, Izmir and CRI, Ankara in 2014. This race became widespread in subsequent years as the resistant varieties in Turkey became susceptible to this *Pst* race (Warrior). Prevalence of Warrior race in high frequency in Morocco and Algeria (Rust Tracker, 2011) as well as North Africa and many European countries was reported by Mert et al., (2016). This new race was grossly different from the previously existing races in Europe and exhibited high diversity in pathogenesis (Hovmøller et al., 2016). Pooja et al., 2018 reported variability for rust infection among 210 RILs, of which 156 RILs showed 0-traces infection, 10 RILs depicted

0-5% infection, 6 RILs showed 5.1-10% infection, 15 RILs showed 10.1-20% infection, 6 RILs showed 20.1- 30% infection, 14 showed 30.1- 40% and 4 RILs showed 60% severity.

Morpho-Pathological Symptoms, Disease Severity and Incidence of Progression

Flor (1964 and 1971) propounded gene-for-gene hypothesis which elaborates that for each resistant gene (R) in host whereas corresponding gene for virulence/ avirulence (vr/avr) in pathogen. This hypothesis warrants a basic compatibility between host for *Yr* genes and pathogen for virulent genes is required for development of disease. In incompatible systems of *Yr* genes offering resistance is not overcome by virulence of pathogenic race and host expresses resistance to yellow rust. The severity as well as pattern of disease also varies depending on *Yr* gene (s) and virulence genes (vr). Some races of pathogen cause enormous number of pustules while in other races the number of pustules is less but the size of pustule is large and yet in other types the number of stripes is more covering major area of leaves. Some races show symptoms on glumes (Marsalis and Goldberg et al., 2016) while the others confined to leaves only.

There are some genes in pathogen which can set infection but not the disease, such genes are known as avirulent races (Surico, 2013). There are some races which lead to hypersensitive reaction in which the host cell immediately dies upon interaction which leads to incompatibility (Higgins et al., 1998; Hysing, 2007).

Plant Resistance to Yellow Rust

Resistance against fungal diseases is generally defined as plants ability to resist invasion by pathogen that includes infection by pathogen, its entry into plant tissues, development of haustoria for driving nutrition and water by pathogen and development of mycelia for further reproduction and uredospore production. This implies that development of disease is less in resistant genotypes possessing *Yr* genes in case of yellow rust than the susceptible genotypes.

Vertical or horizontal resistance or combination of both governs resistance against pathogen in plant host (Vander Plank, 1963; Miedaner, 2016). Vertical resistance is governed by one or more genes which are race specific and the resistance is qualitative meaning either the genotype is resistant or susceptible. Vertical resistance offers resistance against pathogen species-specific or pathogen strain-specific causal organisms whereas it is susceptible against matching races of pathogen. Several workers have reported race specific resistance by *Yr* genes in wheat. Also, it has been observed that low infection rate characterizes vertical resistance (Rajaram et al., 2002). Vertical resistance may be operative during all plant growth stages spanning from seedling to successive plant growth stages and thus may offer holistic durable resistance for some time. It is subjected to boom (resistance) and bust (breakdown of resistance) cycles with the occurrence of new pathotypes either through mutation or recombination (McDonald et al., 2002; Knott, 2008). When differential interaction is absent, it is called as horizontal resistance (Brar, 2015).

Horizontal resistance is governed by polygenes with small to intermediate additive effects. This is also known as race non-specific resistance as HR offers some resistance to all races of the pathogen. Inheritance of HR is usually complex as environmental factors have greater influence on HR than VR (Francisco., 2001). Sometimes the plant host possess both vertical and horizontal resistance combining synergy of both the systems in case of rusts which results in 'slow rusting'. In such a system of slow rusting, disease develop slowly against all pathotypes resulting into low levels of disease over longer period due to longer latent period of pathogen, low initial inoculum as well as low reproduction. Horizontal resistance slows down the disease progression due to smaller spore and uredial size and longer duration for sporulation (Kumar et al., 2015; Ellis et al., 2014).

Johnson (1988) described durable resistance as long lasting which remains effective over a longer period in environments favoring the disease development. This type of resistance is characterized by known race specific resistance operative at seedling and adult plant stages where resistant polygenes are effective additively to determine non-hypersensitive reaction. Race specific partial resistance against pathotypes is offered by some APR genes but offers tangible resistance over longer period. One such example is reported by Mallard et al., (2005) regarding resistance offered by APR genes in bread wheat variety "Camp remy" in France for more than 20 years.

'Vertfolia effect' (Vander Plank, 1963) is a condition where the oligogenes mask the expression of HR genes and/or VR genes are combined with low levels of HR offering low levels of resistance and the strong resistance offered by VR is overcome by virulent pathotypes leading to higher susceptibility of a genotype to rust pathotypes.

Resistance to yellow rust is also named as per the stage of plant at which it is expressed under controlled inoculated experiments. Chen (2005) and Bulli et al., (2016) opined that such resistance against specific races may be operative at seedling as well as Adult Plant stages as per expression of resistant stages. Some researchers like Chen (2005); Jin et al., (2010) and

Wellings (2011) reported that mostly, the seedling and in some cases adult plant resistance is race-specific which are subjected to emergence of new pathotypes due to natural selection pressure in favor of pathogen. In some genotypes, the adult plant resistance remains operative even at higher temperature particularly when plant grow old and progresses towards maturity. (Chen (2005) reported that high temperature adult plant resistance (HTAP) is durable against non-specific races and therefore, durable than seedling resistance, even though HTAP resistance is susceptible to all races of *Pst* at seedling stages.

In monocropping system, high yielding yellow rust resistant wheat varieties are grown over large areas year after year, this situation leads to enormous selection pressure on pathotypes for survival. Due to this reason, the prevailing pathotypes, both avirulent as well as virulent not able to cause disease due to host resistance undergo mutation to develop new pathotypes capable of overcoming host resistance. This determines potential of host resistant genes to offer resistance against race-specific pathogens for a specific period only. Pooja et al., (2019) investigated 210 recombinant inbred lines to conduct diversity and spatial analysis for different *Yr* genes for example 4 *Yr* genes in RILs *Yr7, Yr36, Yr47, Yr53* and 2 *Yr* genes in RILs *Yr18, Yr26* and *Yr7, Yr47* and 1 *Yr* gene in RILs *Yr26, Yr29, Yr26, Yr29, Yr18, Yr36, Yr7, Yr47.*

Genetic Variability for Plant Resistance Against Yellow Rust

Aktar-Uz-Zaman et al., (2017) reported more than 187 rust resistance putative genes were described of which 78 yellow rust resistance genes (*Yr1-Yr78*) were catalogued (This number of *Yr* genes is increasing with intensification of research on yellow rust resistance genes and about 83 yellow rust resistance genes have been described). The acronym '*Yr*' is used to specify strains for specific yellow rust resistance genes. In wheat germplasm these *Yr* genes have been introduced either from primary gene pool, *i.e.*, extant varieties of wheat through recombination or through secondary and tertiary gene pools through introgression. Sharma (2012) found that *Yr9* is linked to *Lr26* offering resistance to leaf rust, *Sr31* offering resistance to stem rust and *Pm8* offering resistance to powdery mildew. likewise *Yr17* was found to be linked to *Lr37* as well as *Sr38* offering resistance to leaf rust and stem rust respectively. Aktar-Uz-Zaman et al., (2017) suggested that *Yr* genes in *Triticum aestivum* were introgressed from its cultivated and wild relative species and genera namely, *T. spelta, T. album*, *T. dicoccoides, T. tauschii, Aegilops comosa, Aegilops ventricosa, Secale cereale* and *Haynaldia villosa.*

Wheat Breeding for Resistance to Yellow Rust

Wheat, being a predominantly self-pollinated hexaploid species have relatives in primary, secondary and tertiary gene pool. On the other hand, genes of interest like yellow rust resistance in present case are scattered over a number of purelines. Keeping in view, the prevalence of virulent pathotypes, a wheat breeder has to deploy yellow rust resistant genes in good agronomic backgrounds for sustainable wheat production. Several breeding techniques like pedigree, back cross, and single seed descent and biotechnological approaches like Marker Assisted Selection in segregating populations through genomic characterization of *Yr* genes and transgenics are effective to achieve tangible improvement in wheat for yellow rust resistance. Therefore, selection of purelines possessing different *Yr* genes is a pre-requisite for recombination breeding. Normally, good agronomic background purelines susceptible to yellow rust are crossed to donors of resistance '*Yr*' genes and then from segregating populations, high yielding stripe rust resistant plants are selected in each segregating generation of self-plants/lines till they become homozygous/pure line to be a new high yielding yellow rust resistant variety.

Disease resistance is mainly governed by one or more oligogenes in case of race-specific resistance. In such cases, gene deployment over space and time of major genes is important strategy to breed high yielding rust resistant variety for different wheat growing regions. Marker Assisted Selection (MAS) could also be effective in breeding yellow rust resistant wheat genotypes (Reema et al., 2019). Sometimes, more number of resistant genes are involved in determining resistance along with a threshold level. Under such situation, gene pyramiding is required approach in conventional plant breeding and accumulation of QTLs in biotechnological approaches.

In horizontal resistance, each gene of polygenic system contributes to rust resistance and sum total of polygenes are thus responsible for expression of yellow rust resistance. Such genes are highly sensitive to environmental effects and therefore exhibit low heritability, the judicious approaches to accumulate polygenes governing resistance through selection over generations in a selfing and selection series experiments in different environments. In view of these peculiarities, following breeding approaches may be explored to develop yellow rust resistant varieties.

Conventional Plant Breeding Methods

Recombination breeding including pedigree method for transgressive segregants and pyramiding

of genes through gene transfer and backcross method for transferring resistance gene only without disturbing genetic architecture of recipient parent as well as for breaking negative linkages. While pedigree method is a progressive method to expand genetic variability, the backcross method is genetically conservative as it allows transfer of donor genes. The conventional breeding includes initial wheat germplasm screening for yellow rust resistance under epiphytotic conditions created artificially followed by selection of resistant genotypes expressing resistant at seedling stage or adult plant stage or both. Such lines are involved in hybridization programme as one of the parents in pedigree, single seed descent and backcross to transfer genes as per breeding objective. Combining grain yield potential and resistance to yellow rust have been developed using these methods. However, the shuttle breeding method may nicely complement these conventional methods to select the potential resistant and high yielding lines in different environments by growing segregating generations in off-season nursery differing in environmental conditions and prevalence of virulent pathotypes of yellow rust. This will enable identification of wheat genotypes resistant to a mixture of yellow rust races across the years and locations. Both the nature of plant resistance against yellow rust (seedling or adult) and mode of inheritance of rust resistance genes (qualitative or quantitative) will determine the breeding strategy to be employed for desired improvement. Pureline selection in pedigree and modified pedigree method, bulk breeding, recurrent selection, single seed descent method and back cross breeding methods have been most sought-after method to develop high yielding yellow rust resistance cultivars. However, in some cases, gene mutations have also paid dividend. Earlier studies provide adequate evidence that these methods were used in red to amber color wheat namely, *Chandausi, White Pissi*, *Sharbati* and *Lal Kanak* in India. A cross between Indian wheat variety Hard Red Calcutta X Common Fife followed by pedigree selection led to the development of famous wheat variety 'Marquis' in 1909 which offered effective resistance against yellow. Marquis, being an early maturing escaped abiotic and biotic stress and become a prominent variety in yellow rust in the region of Western North Dakota (Stoa, 1945). When the major genes govern the yellow rust resistance, usually modified pedigree method is more effective in breeding yellow rust resistance cultivar. Back cross breeding method is more successful either to transfer single dominant gene (dominant and recessive) through crossing back F_1 with recipient parents recurrently followed by selection of homozygous phenotype. In case of resistance governed by recessive alleles, each backcross population needs to be selfed and selection is made in selfed population so that resistant types are phenotypically recognizable. Bulk breeding method is useful in both major and minor genes which are involved in governing yellow rust resistance (Singh and Trethowan, 2007; Singh *et al*., 2014).

Gene Deployment:

In order to ensure a mis-match between *Yr* resistant genes in wheat host and *Pst* effectors in field conditions, it is priori consideration to deploy resistant gene in wheat variety against specific races of yellow rust in different wheat growing regions to develop a mosaic canvass of resistance. Therefore, allocating wheat varieties possessing resistance against specific races in specific region is an effective approach of gene deployment to thwart yellow rust epidemics. In Indian sub-continent, the existence of *Puccinia* path is different in agro-ecological zones. The diversity of prevalence of races for yellow rust pathogen and the genes offering resistance to such races need a coherent strategy to deploy specific gene or gene combination in each agro-ecological zone. Therefore, strategy for the gene deployment would also differ from one region to the other (Nagarajan and Joshi, 1980). Nagarajan et al., (1986) and Bahadur and Nagarajan (1984) have suggested strategy for gene deployment in view of effectiveness of rust resistance genes and distribution of pathotypes and yellow rust races. Bahadur et al., (1985) reported that the deployment of *Yr*9 remain effective against stripe rust for many years which now has been ineffective whereas deployment of *Yr5*, *Yr10* and *Yr15* are still effective collectively or individually against prevailing races of yellow rust. They advocated that gene deployment is an effective strategy to avoid epidemics and hence losses. *Yr5* deployed in Australia (Wellings and McIntosh 1990) and *Yr10* have been defeated by a virulent strain emerged in Canada (Randhawa et al., 2011) but no virulence against *Yr5* was detected in india (Nagarajan et al., 1986). In some instances, unintentional deployment for *Sr* genes also resulted in a deployment of gene complex carrying *Sr57*/*Lr34*/*Yr18* besides other *Sr* genes. Diversity for oligogenes conferring resistance against yellow rust (*Yr*) in any geographical region or even in a wheat field is an effective strategy for resistance breeding in wheat (Simmonds, 1985). McIntosh, (1985) suggested that deployment of overlapping oligo-genes or combination of oligogenes resulted in low severity of rust infection coefficient. It could be pertinent to know as to which *Yr* genes are effective for rust resistance at what stage of plant growth whether it is seedling stage or adult plant stage. The deployment strategy should be judiciously

planned to ensure that at least one or more oligo-genes have been deployed for an effective resistance level at each stage of plant growth to minimize yield losses.

Gene Pyramiding:

In gene pyramiding, the objective is to assemble and reassemble multiple yellow rust resistant genes with additive effects in a certain genetic background of proven agronomic superiority. The care must be taken that all the multiple resistant genes are complementing each other and not antagonizing their effects to prevent breakdown of resistance in host against *Pst* strains under field conditions. Normally gene pyramiding is achieved by pair-wise crosses among various pure lines possessing different *Yr* genes followed by crossing of F_1 obtained from single crosses, double crosses and multiple crosses to pyramid all *Yr* genes in a pure line achieved through selection from segregating population of multiple crosses. However, this approach is time consuming which calls for employing speed breeding techniques (Watson et al., 2018) or growing segregating population in offseason nursery to advance generation. The first gene pyramiding experiments were conducted at CIMMYT where *Yr8* complex providing durable resistance was explored (Singh et al., 2005). Gene pyramiding can involve primary gene pool through intervarietal crosses for transfer of *Yr* genes to different genetic backgrounds or secondary or tertiary gene pool through interspecific and inter-generic crosses for achieving introgression of *Yr* genes present in associated progenitors, wild or cultivated relatives of bread wheat (Aktar-Uz-Zaman et al., 2017). However, it is difficult and time consuming to pyramid unlinked genes *via* crossing without their proper identification and characterization. In fact, linkage of *Yr* genes may create problems associated with 'linkage drag'. Hafeez et al., (2021) reported that incorporation of 12 resistant genes *via* crossing in a single recipient background needed 20 generation. This holds true even in interspecific and intergeneric crosses where the introgressed genes may also carry linked genes with deleterious effects on grain quality for grain size and texture through production of PUROINDOLINE genes and other genes for different rust diseases like *Sr*60 from *T. monococcum* in to bread wheat (Chen et al., 2020). Further, it is tedious to maintain different resistant genes together under selection, in fact some of the genes due to their over-expression may be selected preferably and such genes may be exposed to new pathotypes which can overcome the resistance of such genes. Therefore, it is important to identify natural occurring multigenic resistant varieties to mimic gene cassette for faster gene flow and quick incorporation of resistant genes (Luo et al., 2021). Gene pyramiding approach is not without challenges, though it offers tangible solution for durable resistance. Effects of different *Yr* genes incorporation through linkage drag may create new problems of consumer acceptance which need to be minimized by transfer of single resistant genes through back crosses to break negative linkages and then reassemble *Yr* genes to multiple crosses. Hafeez et al., (2021) has suggested some solutions to tackle such problems by generating R gene atlas for major wheat diseases and genes offering resistance. Corredor Moreno et al., (2021) suggested that gene identification will help in achieving *Yr* resistant genes *vis-à-vis Pst* effectors over different environments to eliminate *Yr* susceptibility increasing genes and eliminate other unwanted genes.

Introgression for yellow rust resistance

Identification and transfer of novel genes from interspecific crosses is also important to thwart the chances of moving and spreading races of yellow rust in wheat growing regions worldwide to cause disease epidemics. Yellow rust resistant wheat lines from inters-generic crosses such as wheat, *wheat-leymus,* rye and *wheat-thinopyrum* have been developed through transferred genetic material in the form of translocations/substitutions (Chen et al., 2020). The incorporation of resistance to yellow rust from associated species and genera growing in different environments also infuse environmental resilience in wheat variety developed in this way.

Multiline varieties:

Multiline varieties are a group of isogenic lines developed by convergence of donor genes in a common genetic background (pureline variety) through backcrossing to different donor varieties for resistance genes. Individual back crosses are needed to transfer one resistant gene each time. Therefore, multiline varieties involved simultaneous backcrossing programme to transfer rust resistant genes from different sources. The multilines are agronomically same except they differ for rust resistant genes. Collectively, these multilines mimic multigenic lines. The advantage of multiline is that various components are showing different pathogen host interaction and if one component line become susceptible to a new pathotype, all other components remain resistant. Therefore, different component lines preclude the possibility of epiphytotic conditions and allows sustainable wheat production. Several researchers have developed multilines like KSML3, (Gill et al., 1980) MLKS 11 and KML 7404 (Rao et al., 1981). There are two approaches for developing multilines, one is known as clean cut approach where dominant race-specific resistant genes are involved in transfer through series of backcrosses, allowing no

disease development till the resistance offered by genes is effective. In dirty approach, the component carrying major and minor genes offering partial resistance are transferred through backcross and in such lines some disease always prevails. Both types have their own advantages and limitations, the first approach multilines are subjected to emergence of new pathotypes and therefore, boom and bust cycle (Priestly, 1978) whereas in dirty approach, possibility of emergence of new races is low.

Biotechnological/Genomic approaches

The conventional plant breeding approaches for developing yellow rust resistant variety are time consuming and sometimes the environmental effects on expression of resistance gene may jeopardize whole hybridization and selection programmes. Moreover, gene transfer from interspecific and intergeneric gene pool is cumbersome and seldom possible. Due to these reasons, use of biotechnological methods called for. The new genomic techniques are more quick, reliable, targeted, independent of environmental effects and offer effective tool for characterizing wheat germplasm for rust resistant genes effective against different pathotypes as well as their transfer to desired wheat genotypes through complementing classical map-based technologies (Adamski et al., 2020).

Pooja, (2018) embarked on use of SSR markers for characterizing parental stocks for polymorphism to identify presence of *Yr* genes (Fig.2).

DNA molecular marker associated with rust resistant genes can be identified through association mapping and thus can be selectively identified in segregating populations of wheat crosses involving susceptible and resistant parents. In this analogy, 'RenSeq' method (Jupe et. al., 2013) for identification of stem rust resistance can also be used for detection of yellow rust resistant genes (Arora et al., 2019). Gardiner et al., (2019) and Walkowiak et al., (2021) reported More technology variants for association mapping such as capture arrays or whole genome sequencing, haplotyping, SNPs and use of reference genome assemblies which can be can be employed for identification of yellow rust resistant gene in wheat. Pooja et al., (2021) identified several *Yr* genes using SSR markers in recombinant inbred lines (F_6) obtained from cross between WH542 (resistant) X WH711 (susceptible) and developed using Single Seed Descent method. SSR markers were effective in deciphering *Yr5, Yr10, Yr13, Yr14Yr15, Yr17, Yr26, Yr28, Yr29, Yr34, YrH52, YrSp, YrSk* and *Yrns-B1* genes conferring resistance against yellow rust. In recombinant inbred lines and thus identified resistant stocks within a population. Likewise, molecular markers are also effective in identifying the *Pst* genome assemblies in pathotypes (Cantu *et al*., 2013; Zheng *et al*., 2013; Schwessinger et al., 2020). These molecular markers tools are effective in tracing pathogen effectors based on pathotype in to varietal interactions (Adams et al., 2021). For example, knowledge about the interactions between R genes (host) and corresponding *Pst* effectors (pathogen) can be precisely recognized to determine the contribution of each component. This will help in designing synthetic R genes which would offer resistance against multiple races of pathogen. Marker assisted selection also effective in allowing selection of *Yr* genes offering resistance and elimination of genes which are non-effective for rust resistance. Based on molecular markers and marker assisted selection, many resistant genes have been cloned and listed (Reema et al., 2019). Pooja et al., (2019) reported that out of 70 SSR markers, only 8 were found polymorphic (*Xgwm46*, *Xgwm95, Xgwm146, Xgwm296, Xgwm302, Xgwm334, Xgwm408, Xgwm68)* on parents and RILs. Out of these, seven *Yr* specific markers *Xgwm130* linked to *Yr7, Xbarc 352* linked to *Yr18, Xgwm 11* linked to *Yr26, Xwmc 44* linked to *Yr29, Xwmc 149* linked to *Yr53, WKS1_I* linked to *Yr36 and Xcfb309* linked to *Yr47* were evident and linked to yellow rust resistance in bread wheat (Table.1).

Therefore, attempt should be made to use disease resistance specific markers to save time, material and cost.

Future Outlook and Conclusion

Cultivation of yellow rust resistant cultivars has been the most commonly adopted strategy to manage successful wheat production globally. However, emergence of new pathogen races necessitates to continuously monitor for shifts in pathogenic races due to mutations on account of selection pressure to develop resistant wheat genotypes which would offer resistance against emerging pathotypes. Several approaches like pedigree, backcross, single seed descent, recurrent selection, gene pyramiding, gene deployment have been used to accumulate yellow rust resistance gene in good agronomic background. Both race specific, host resistant major genes as well as race-nonspecific polygenes have been capitalized to incorporate durable resistance. however, emergence of new pathotypes against race specific host resistance have caused disease problems and even epidemics in many instances world over. This would call for regular monitoring of emergence of new virulent races in the region or migration of virulent races from across the borders of other regions. The incorporation of resistant genes from primary gene pool is easier provided the

genes of interest offering yellow rust resistance are available in diversified varieties. The transfer of genes from allied wild progenitors or genera is cumbersome, yet it is bit feasible through embryo rescue technology followed by chromosome doubling. Many effective rust resistant genes have been transferred this way in to cultivated varieties of wheat. Climate change in relation to new pathotypes possessing virulence under high temperature and low humidity conditions have further cause complexity for developing yellow rust resistant varieties. Climate change is associated with shifts in meteorological parameters and also evolution of new races which are more virulent and can persist in diverse environment.

Breeding for yellow rust resistance in climate change regime requires further strengthening. The germplasm exchange among various countries should be encouraged to expand the genetic variability which would enable selection of potential resistant genes among accessions. In view of climate change, emphasis should be there on selection of high yielding genotypes possessing high level of yellow rust resistance. For that matter, diverse wheat genotypes possessing different *Yr* should be deployed in different agro-ecological zones and development of multigenic resistant varieties through gene pyramiding are promising strategy to increase the durability of resistance. In turn, cultivation of yellow resistant high yielding cultivars would offer more favourable option to the farmers. Both HR (Horizontal Resistance) and VR (Vertical Resistance) resistance genes should be combined to accomplish minimum selection pressure against pathotypes for durable resistance. Also, continuous search for resistant genes in gene pools should be continued and intensified.

The change in climate and consequent emergence of new pathotypes would need to employ biotechnological tools for diagnostics of pathogenic races, resistant gene, interaction between pathogen race and wheat variety using molecular markers. The use of genomics will help in tracing new pathotypes as well as new resistant genes across varieties, species, genera and also the incorporation of resistant genes through marker assisted selection (MAS). Molecular markers will also facilitate speed breeding to cut short time period either in selecting resistant genotype or designing of genes. Biotechnological tools would pay dividend in developing double haploid from high yielding rust resistant crosses to establish homozygous lines in quick succession. Molecular markers can be employed in identifying rust resistant genes from different genera and species for selective transfer as transgenes or through appropriate breeding methods assisted by biotechnological methods.

Finally, it is important to share data about emergence of new virulence globally so that appropriate strategy could be in place to control yellow rust and manage sustainable wheat production through international cooperation research and development.

Figure 1. Yellow rust symptoms in wheat. (Original)

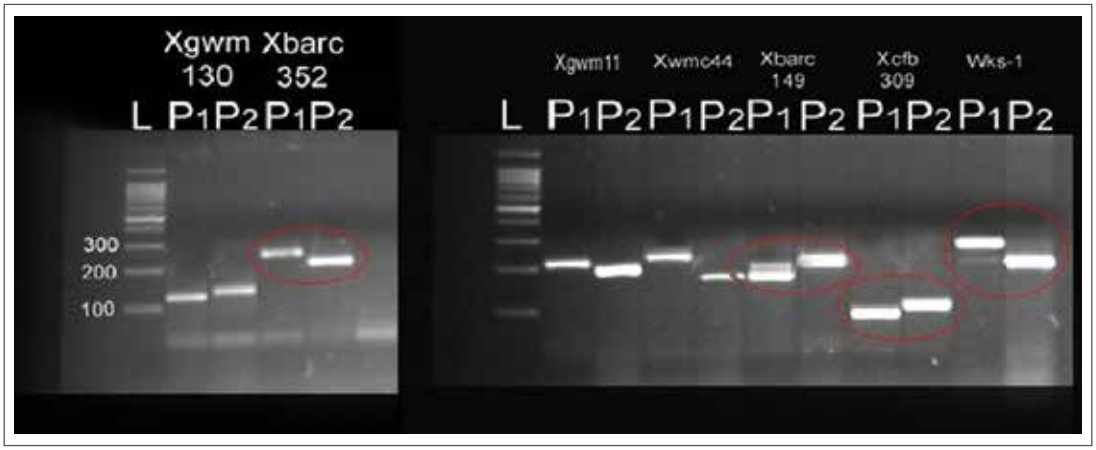

Figure 2. Parental polymorphism for seven *Yr* specific SSRs (Pooja et al., 2019).

Table 1. Identification of *Yr* genes in Recombinant inbred lines of bread wheat .

Recombinant Inbred Lines-210	
60 RILs (6, 8, 9, 10, 13, 17, 22, 26, 28, 30, 31, 32, 33, 35, 38, 43, 45, 48, 54, 56, 62, 65, 70, 71, 72, 75, 76, 79, 85, 89, 91, 92, 94, 103, 107, 110, 112, 113,114, 118, 119, 120, 123, 126, 128, 134, 140, 141, 170, 171, 180, 183, 190, 191, 195, 196, 198, 201, 207, 208)	RILs with 1 *Yr* gene
25 RILs (3, 7, 12, 15, 18, 19, 24, 25, 27, 40, 46, 63, 64, 66, 67, 73, 74, 82, 93, 115, 117, 121, 124, 133, 135)	RILs with 2 *Yr* gene
6 RILs (20, 21, 23, 29, 39, 53)	RILs with 3 *Yr* gene
3 RILs (51, 52, 55)	RILs with 4 *Yr* gene

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