

BREEDING TECHNIQUES FOR RUST RESISTANCE IN WHEAT

Sri Sai Subramanyam Dash^{1,#} and Ankita Mishra^{2,#}

1 Department of Genetics and Plant Breeding, Bidhan Chandra Krishi Viswa Vidyalaya, University in Haringhata, West Bengal, 741252, India.

2 Department of Plant Breeding and Genetics, Odisha University of Agriculture and Technology, Bhubaneswar, Odisha, 751003, India.

Authors with equal contribution

BIOINGENE.COM/PSJ

Article No. : D5MAY21R28

Article type: Review

Received: 1 May 2021

Accepted: 30 June 2021

Online: 21 July 2021

KEYWORDS

Wheat rust, Puccinia, Durable resistance, Plant Breeding, MAS, Genomic selection

Copyright:

Open-access CC BY 4.0.

Conflict of interest: No

Corresponding author:

Mishra, A.

ankitamishra547@gmail.com

ABSTRACT

Wheat is the most important cereal crop, providing carbohydrates to the major world population. In the 1960s, a major breakthrough in global wheat production was brought about by the green revolution. Wheat yield is largely threatened by rust diseases, which occur in three forms: leaf, stem, and yellow stripe rust, leading to severe crop loss. There are two groups of genes used for development of rust-resistant varieties. The first class is all-stage resistance genes (ASR) conferring resistance at only seedling stage and are race-specific. The second class is adult plant resistance genes (APR) characterized by slow rusting and provides long durability. Many rust-resistant varieties are developed till date, but are ruled out of the market due to the fast evolution of rust pathogens. Conventional breeding uses selection and wide hybridization to integrate a desirable resistant trait from alien species. However, due to greater environmental influence, time-consuming nature, and linkage drag, it is replaced by modern breeding tools like Marker-assisted selection (MAS), Genomic selection, TILLING (targeting induced local lesions in genomes), gene pyramiding, reverse breeding, transgenics, and CRISPR technology. These technologies provide immense capabilities to develop rust-resistant varieties conferring broad-spectrum resistance in a short time and accelerate crop improvement to meet global demand.

Citation:

Dash, S. S. S., and Mishra, A. (2021). Breeding techniques for Rust Resistance in Wheat. *Bioingene PSJ*, Issue 1, Volume 2, Article D5MAY21R28, Page 1-11. <http://bioingene.com/wp-content/uploads/2021/07/D5MAY21R28.pdf>

INTRODUCTION

Globally, wheat is the third major food crop, cultivated over about 219 million hectares with an annual production of 763.2 million tonnes (Bhardwaj *et al.*, 2019). The World Bank has projected that an increase in global wheat production by 60% could fulfill the dietary necessities of 9.6 billion people by 2050 (Savadi *et al.*, 2018). Further, India alone will need more than 140 million tonnes of wheat to feed a population of around 1.73 billion (Bhardwaj *et al.*, 2019). The global increase in yield and productivity could only satisfy such a huge demand. Biotic as well as abiotic threats are the major hindrance to wheat production. Amongst biotic stresses, wheat is vulnerable to nearly 80 bacterial, 45 fungal, and 30 viral diseases (Rana *et al.*, 2021). With more than 7800 species worldwide, the rust fungi are the most diversified pathogen and are accountable for significant crop hazard and economic loss (Figueroa *et al.*, 2020). Three wheat diseases, namely stem rust caused by *Puccinia graminis* f. sp. tritici, leaf rust by *P. triticina*, and stripe (or yellow) rust by *P. striiformis* f. sp. tritici, are responsible for significant losses of grain production (Berlin *et al.*, 2015). Leaf rust can cause about 7-30% yield loss, while both stem and stripe rust may lead to 100% loss (Bhardwaj *et al.*, 2019, Rana *et al.*, 2021). However, developing a rust-resistant cultivar remains a challenge because of the continuous emergence of novel races and pathotypes.

The urediniospore excavations from Israel suggest wheat rusts to be the oldest plant pathogens originating around 1300 BC (Bhardwaj *et al.*, 2016). The rust fungus belongs to *Basidiomycota* (phylum), *Urediniomycetes* (class), *Uredinales* (order), *Pucciniaceae* (family), and *Puccinia* (genus) (Bolton *et al.*, 2008). Additionally, the *Puccinia* species are classified as *formae speciales*, that are morphologically -

similar but invade different hosts. *Formae speciales* are further distinguished into physiological races, infection types, or pathotypes, which can parasitize certain cultivars of host species and are identified by differential host cultivars (Gessese, 2019). Rust fungi are biotrophic, obligate parasites with a heteroecious and macrocyclic life cycle (Kolmer, 2013). The rust fungi have a macrocyclic life cycle, with five stages of spore. Among the five spore stages, three (uredinial, telial, and basial) occur on the primary host, while the other two (pycnial and aecial) are on alternate hosts.

STEM RUST OF WHEAT

One of the most devastating winter wheat diseases is stem rust (*Puccinia graminis* f. sp. tritici). The symptoms appear on the stem and leaf sheath after the flowering stage in the form of rust-brown oblong powder of urediniospore pustules. These pustules further coalesce in the form of brown stripes and tear the epidermis (Alabushev *et al.*, 2019). Figueroa *et al.* (2018) suggested that this pathogen also infects leaf sheaths, glume awns, spikes, and grains. The infected plants, as a result, produce a small number of tillers with few kernels per spike. The affected kernels are generally shrunken and small, with an enormous reduction in milling quality (Figueroa *et al.*, 2018). The pathogen is heteroecious in nature with a telial stage on wheat and aecial stage on the *Berberis* spp. It is predominantly found in warm areas with moist conditions. The most typical symptoms include masses of brick-red urediniospores. Chen *et al.* (2014) proposed that the optimum and maximum temperature for spore germination is 15-24°C and 30°C, respectively. The Ug99 stem rust emergence in 1999 was a major setback as many popular cultivars became susceptible. There was an urgent need to find gene sources attributed to resistance against this pathogen (Alabushev *et al.*, 2019). The estimated annual yield loss to wheat stem rust is about 6.12 million

tons, costing about 1.10 billion dollars (Rana *et al.*, 2021). About 7 million hectares of Central and Peninsular India are under the threat of major crop loss due to this pathogen (Bhardwaj *et al.*, 2019).

STRIPE RUST OF WHEAT

The stripe rust pathogen (*P. striiformis* f. sp. *tritici*) is an obligate parasite that uses the photosynthetic machinery of host plants to accomplish its dietary requirements. This pathogen completes its life cycle in two different host species, i.e., wheat and *Berberis* spp. (Zhao *et al.*, 2016). It completes three stages in its life cycle (uredial, telial, and basidial phase) on a primary host (wheat), while the pycnial and aecial phase needs an alternate host (Chen *et al.*, 2020). The optimum conditions for urediniospores growth are rain, followed by a temperature of about 7-12°C (minimum) to 20-26°C (maximum) (Jamil *et al.*, 2020). Elshafei *et al.* (2019) stated that, at 0°C, the symptoms of infection appeared after 5-6 months, but at 15°C, they occurred after 11 days. This pathogen has adapted to high temperatures over time and has also led to severe disease outbreaks, even in subtropical areas. It is an airborne pathogen and can travel thousands of miles to cause sudden disease epidemics (Wang *et al.*, 2017). Presently, about 80% of the world's wheat varieties are susceptible to this pathogen (Rana *et al.*, 2021). It was estimated that an annual loss of about 5 million tons with an estimated cost of ~USD 1 billion occurs every year due to this disease (Jamil *et al.*, 2020). About 51 major stripe rust epidemics have been witnessed globally from 1939 to 2016, with varying intensities from 2% yield losses to total crop failure (Chen *et al.*, 2020). In Northern India, it is a major threat to about 10 million hectares of farm areas (Bhardwaj *et al.*, 2019). More than 78 stripe rust resistance genes have been identified and categorized into diverse classes, i.e., race-specific and adult plant resistance (APR) genes.

LEAF RUST OF WHEAT

Leaf rust caused by *Puccinia triticina* or brown rust is the most prevalent rust of wheat across the globe (Bhardwaj *et al.*, 2019, Gessese, 2019, Rana *et al.*, 2021). Primarily, it infects leaf blades, but under extreme conditions, glumes and leaf sheaths can also get infected (Huerta-Espino *et al.*, 2011). The causal agent is an obligate parasite that can generate infectious urediniospores only on live leaf tissues. It needs primary (telial or uredinal) and secondary (pycnial or aecial) hosts to complete its life cycle. The primary hosts include bread wheat, durum wheat, cultivated, and wild emmer wheat, *Ae. speltoides*, *Ae. cylindrica*, and triticale; and the alternate hosts are *Thalictrum speciosissimum* and *Isopyrum fumaroides* (Bolton *et al.*, 2008). The urediniospores, widely spread through wind and infect host plants, ultimately result in rust epidemics across countries' continents (Gessese, 2019). The spore germinates on leaf surfaces only when there is adequate moisture availability in the form of water with a temperature of about 10-25°C. Its high adaptability to a broad range of climates results in continuous mutations, leading to new virulent pathotypes. This disease occurs in severe form in Asia, North Africa, Europe, North and South America, Australia, and New Zealand (Gessese, 2019). Yield losses caused by brown rust exhibit spatial and temporal variation (Rana *et al.*, 2021).

BREEDING FOR RUST RESISTANCE IN WHEAT

The production of wheat has always been affected by numerous biotic stresses, among which rust imparts the most serious damage and loss to the crop. There was a breakthrough in wheat production during the green revolution with the release of some Mexican varieties (Penjamo 62, Pitic 62, Lerma Rojo 64, Sanora 64, Siete Cerros, etc.) by CIMMYT, Mexico. However, -

these varieties ruled the market for a short time period before they were attacked by a new strain of stem rust pathogen. Some had longer durability, like Lerma Rojo (11years), Yaqui 50, and Champingo 52, until they were replaced by HYVs (Borlaug, 1968). They conferred long resistance duration due to their strong genetic background as they had a combination of Hope and Thacher type resistance. The durability of wheat rust resistance is still a big challenge for plant breeders due to the faster evolution of rust pathogens. Durable resistance is defined as a source of resistance that remains effective even after a widespread deployment of the disease over a while (Johnson and Law, 1975). The unique features of durable resistance are governed by many genes (quantitative/polygenes), non-race-specific, mostly observed in the adult stage of the plant, and it does not show hypersensitive response. There are two classes of resistance, namely All-Stage Resistance (ASR) and Adult Plant Resistance (APR). The former category of resistance is also called race-specific, major gene resistance, gene-for-gene resistance, or seedling resistance and follows the Flor hypothesis (Flor, 1971). The latter is not observed in the seedling stage but in the adult stage, and it is characterized by slow rusting without any hypersensitive or necrotic reaction (Singh *et al.*, 2011). In the mid-20th century, breeding programs were mostly concentrated on using R genes expressing ASR. However, with the emergence of new strains, their durability and use in agriculture were lost. Nowadays, breeders concentrate on APR, which is less influenced by race-specific pathogen and is more durable (Burdon *et al.*, 2014). It was observed that the APR gene alone could not confer complete resistance, but in combination with other APR genes, it can achieve the goal (Bariana *et al.*, 2007). It was further confirmed by Singh *et al.* (2014) that non-specific APR genes conferred partial resistance to pathogens.

Many breeding approaches have been used to develop rust-resistant varieties in wheat.

The first attempt to breed for rust-resistant wheat was made by Biffen (1905) in Rivet wheat for yellow rust. In the mid-20th century, resistant varieties were mostly developed by selection and wide hybridization, which allowed the introgression of desirable traits from wild species to cultivated crop species. In wheat, many R genes have been used to develop resistant varieties (Olson *et al.*, 2013; Yaniv *et al.*, 2015). According to Rouse *et al.* (2011), rust resistance genes from *Aegilopes tauschii* can be more readily introgressed via synthetic hexaploids developed by a cross between wheat and *Aegilopes*. Even though there was many interspecific hybridization in the past to develop resistant varieties, many were not commercialized due to the presence of negative traits derived from alien species (linkage drag). With the advent of technology, this alien part was minimized by a cytogenetic method of chromosome engineering that allows access to precise DNA markers for proper selection between wheat-alien chromosomes (Olson *et al.*, 2013; Yaniv *et al.*, 2015).

Conventional breeding is time-consuming, environmentally influenced, labor-intensive, and error-prone. Therefore, breeders are more interested in using modern breeding technologies like marker-assisted selection (MAS), genome selection, gene pyramiding, targeting induced local lesions in genomes (TILLING), transgenics, reverse breeding, and CRISPR (Savadi *et al.*, 2018). Marker-assisted selection is the use of tightly linked markers for the selection of particular quantitative traits. The integration of desirable genes for resistance can be achieved by marker-assisted backcrossing (MABC), gene pyramiding, marker-assisted recurrent selection, and genomic selection. Lan *et al.* (2015) investigated the genetic basis of resistance in the 148 F5 RIL population of the cross Avocet × Sujata using DArT and SSR markers. They detected two new co-located resistance loci QLr.cim-1AS/QYr.cim-1AS and QLr.cim7BL/YrSuj, on chromosomes 1AS and 7BL,

respectively, possessed a low level of resistance to yellow stripe rust in both seedling and adult stages. Genes in Sujata, namely, *Lr46/Yr29* and *Lr67/Yr46* exhibited resistance to both the rust. Hence they concluded that the variety Sujata could be used in further breeding programs to transfer multiple resistance genes into a single cultivar. Similar findings were observed by Ren *et al.* (2017) when they studied the genetic basis of resistance in 148 RILs of Avocet × Kundan and constructed a final genetic map with 2937 polymorphic markers with 1.29 cM distance. The three APR genes, namely *Lr46/Yr29*, *QYr.cim-2AL*, and *QYr.cim-5AS* could confer resistance to this population. The gene *Lr46/Yr29* exhibited 49.5 to 65.1% leaf rust resistance and 49.2 to 66.1% resistance to yellow rust.

The widely used gene for resistance of wheat leaf rust, *Lr16* was mapped using 43 SNPs markers in a set of 133 cultivars and breeding lines by Kassa *et al.* (2017). They designed Kompetitive Allele Specific PCR (KSAP) assay for all SNPs and spotted that only 6 SNPs showed high clustering with KSAP assay i.e they were consistent with *Lr16* phenotype. Thus, these six SNPs are suitable for future MAS for the *Lr16* gene in wheat cultivars. Two closely linked markers *QLr.hbau-2AS* were identified by Wang *et al.* (2015) from the cross of Weimai 8 and Zhengzhou 5389 using SSR markers, and this marker location was close to the resistance gene *Lr37* of wheat.

There have been serious issues due to the emergence of a new variant of stem rust (*Pgt/Puccinia graminis* f. sp. *tritici*; *Pgt*), along with Ug99 race, which has enhanced the search for new *Sr* resistance gene in wheat. Hiebert *et al.* (2016) studied the genetic map of *SrTmp* (gene that confers resistance to Ug99 in Triumph 64 cultivar) and examined the relationship of other *Sr* genes in the same chromosomal location. Genetic mapping done with SSR markers placed the *SrTmp* gene in the same location as *SrCad*

and *Sr42*, but all three showed different levels of resistance to stem rust. The SNP markers showed no difference in these three genes, concluding that the markers near to *SrTmp* can be used for MAS for stem rust resistance. Sharma *et al.* (2019) also identified two resistant QTLs (*QSr.fcu-2B*) and *6AL* (*QSr.fcu-6A*) in chromosome 2BL in durum wheat cultivar PI193883 that confers stem rust resistance.

Five QTLs were developed for stripe rust resistance of popular spring wheat rust resistant cultivar PI182103 by Feng *et al.* (2018) when they examined the map developed from RILs using SSR marker. A new gene was identified from the QTL map, namely *Yr79*, which was highly polymorphic for SSR markers for resistance and can be a potential gene for durable stripe rust resistance. The novel gene responsible for resistance to stripe rust is *Yr15* derived from wild emmer wheat *Triticum dicoccoides*. Yaniv *et al.* (2015) validated some SSR markers for *Yr15* region and found that markers *Xbarc8* and *Xgwm493* were polymorphic for all 34 introgressions, making it an efficient tool for MAS for transfer of *Yr15* gene in wheat lines. Some successful examples of MAS are pyramiding of *Lr24* and *Lr28* from NIL PBW-343 into MP3299 Savitha *et al.* (2016), *Lr75* from Forno to Ariana by MABC Singla *et al.* (2017), *Sr36* from *Triticum timopheevii* to HI8498 Sai Prasad *et al.* (2014), *Yr15* from Avocet and *Lr19/Sr25* and *Lr24/Sr24* from FLW 8 and FLW 2 to UP2338 Singh *et al.* (2018) and many more.

In the recent breeding era, instead of MAS, genomic selection is being used by many researchers for the selection of particular traits in selected crops. Genomic selection (GS) is a selection based on a large number of molecular markers distributed across the whole genome instead of specific markers used in MAS. The traditional MAS method is used to identify some QTLs showing large effects, but GS is used to identify large numbers of QTLs with large or -

small effects and increased accuracy (Desta and Ortiz, 2014). Advantages of GS include, it can combine many resistant genes from different sources without mapping Rutkoski *et al.* (2011), and testing is based only on genotypic data, which speeds up the selection cycles and increased selection gain (Heslot *et al.*, 2014; Bassi *et al.*, 2016). It is an efficient tool for developing resistant varieties in a short time for diseases like wheat rust strain Ug99, which evolves very fast. Rutkoski *et al.* (2011) were the first to use GS for wheat rust resistance. Juliana *et al.* (2017) compared different models of genomic prediction for seedling and adult plant resistance to wheat rust and deduced that the mean predictions for seedling resistance of leaf rust and yellow rust ranged from 0.31-0.74 and 0.70-0.78, respectively. The prediction for adult rust resistance for leaf rust, stem rust, and stripe rust was 0.12-0.56, 0.31-0.65, and 0.34-0.71. A similar experiment was conducted by Azizinia *et al.* (2020) and resulted in prediction accuracy of 0.56-0.71 for leaf rust and 0.51-0.56 for yellow rust. However, stem rust had variable accuracy rate due to higher GE effects. Genetic gain is increased in genomic selection due to the accumulation of positive alleles, and the comparison for genetic gain from GS and PS (Phenotypic selection) for quantitative wheat stem rust resistance (QSRR) was done by Rutkosi *et al.* (2015). They found that the overall gain from GS and PS in QSRR was 31 ± 11 and $42 \pm 12\%$ and 138 ± 22 and $180 \pm 70\%$ for PBC (pseudo-black chaff- a correlated trait), respectively. It was concluded that both GS and PS could have equal genetic gain for a short time whereas GS can reduce the genetic variability in further generations.

Mutation is the ultimate source of genetic variation. Whether natural or induced, mutation can produce beneficial phenotypic variation that can be used for breeding programmes. Polyploid crops like wheat can tolerate high frequency of mutation (Kurowska *et al.*, 2011). However,

detection of mutation can be difficult. One of the best methods for detecting mutation of a specific gene is TILLING (Targeting Induced Local Lesions in Genomes). This method identifies a single base mutation by combining chemical mutagen (EMS) with a DNA screening technique. Fu *et al.* (2009) used mutagen EMS (ethyl methyl sulphonate) lines to clone yellow rust resistance gene Yr36 in wheat. This gene was present within 0.02 cM distance from two markers, namely, Xucw129 and Xucw148. They also found two other genes *IBR* and *WKS*, in the same region, which later was confirmed by TILLING studies that the *WKS* gene is nothing but the *Yr36* gene (Fu *et al.*, 2009). Furthermore, TILLING allows direct induction of variation in the desired cultivar, thus, avoiding introgression through numerous intensive crossing programs (Sestili *et al.*, 2010). Apart from breeding techniques, transgenic technology has also been used to achieve rust resistance in wheat (Savdhi *et al.*, 2018; Eissa *et al.*, 2017; Kaur *et al.*, 2017).

CONCLUSION

Biotic stress like rust has the potentiality to turn into an epidemic and is a threat to food security around the globe. Amongst the three rusts, stem rust is the most devastating as compared to leaf and stripe rust. The rust pathogen is an obligate macrocyclic fungi that produces three types of spores (uredia, telia, basidia) in the primary host and other two (pycnidia and aecia) in the alternate host. Since the rust pathogen mutates faster to form new strains, breeding for rust resistance is complex and resource-consuming. Plant breeding tools for developing rust-resistant varieties have advanced from simple selection to modern breeding techniques like MAS, genomic selection, reverse breeding, transgenics, and genome editing. Genomic selection uses a wide range of markers distributed all over the genome compared to specific markers in MAS, which allows GS to be an efficient tool for selection with precision along with short selection cycles.

TILLING is generally used to detect the desirable genetic variation created by mutation in the crop genome and helps in sorting suitable rust-resistant mutants from a population. Moreover, researchers should target towards discovery and introgression of APR genes for durable resistance. These technologies, thereby, can boost the production of wheat around the world as well as maintain sustainable food security.

DOI: <https://doi.org/10.1007/s10658-014-0534-2>

REFERENCES

Alabushev, A. V., Vozhzhova, N. N., Kupreyshvili, N. T., Shishkin, N. V., Marchenko, D. M., and Ionova, E. V. (2019). Identification of Stem Rust Resistance Genes in the Winter Wheat Collection from Southern Russia. *Plants*, 8(12), 559.

DOI: <https://doi.org/10.3390/plants8120559>

Azizinia, S., Bariana, H., Kolmer, J., Pasam, R., Bhavani, S., Chhetri, M., *et al.*, (2020). Genomic Prediction of Rust Resistance in Tetraploid Wheat under Field and Controlled Environment Conditions. *Agronomy*, 10(11), 1843.

DOI: <https://doi.org/10.3390/agronomy10111843>

Bariana, H. S., Brown, G. N., Bansal, U. K., Miah, H., Standen, G. E., and Lu, M. (2007). Breeding triple rust resistant wheat cultivars for Australia using conventional and marker-assisted selection technologies. *Australian Journal of Agricultural Research*, 58(6), 576-587.

DOI: <https://doi.org/10.1071/AR07124>

Bassi, F. M., Bentley, A. R., Charmet, G., Ortiz, R., and Crossa, J. (2016). Breeding schemes for the implementation of genomic selection in wheat (*Triticum* spp.). *Plant Science*, 242, 23-36.

DOI: <https://doi.org/10.1016/j.plantsci.2015.08.021>

Berlin, A., Rahmatov, M., Muminjanov, H., and Yuen, J. (2015). Sexual reproduction contributes to genotypic variation in the population of *Puccinia graminis* in Tajikistan. *European journal of plant pathology*, 141(1), 159-168.

Bhardwaj, S. C., Prasad, P., Gangwar, O. P., Khan, H., and Kumar, S. (2016). Wheat rust research-then and now. *Indian J Agric Sci*, 86(10), 1231-1244.

Bhardwaj, S. C., Singh, G. P., Gangwar, O. P., Prasad, P., and Kumar, S. (2019). Status of wheat rust research and progress in rust management-indian context. *Agronomy*, 9(12), 892.

DOI: <https://doi.org/10.3390/agronomy9120892>

Mendel's laws of inheritance and wheat breeding. *The Journal of Agricultural Science*, 1(1), 4-48.

DOI: <https://doi.org/10.1017/S0021859600000137>

Bolton, M. D., Kolmer, J. A., and Garvin, D. F. (2008). Wheat leaf rust caused by *Puccinia triticina*. *Molecular plant pathology*, 9(5), 563-575.

DOI: <https://doi.org/10.1111/j.1364-3703.2008.00487.x>

Borlaug, N.E. (1968). Wheat breeding and its impact on world food supply. *Proceedings of the 3rd International Wheat Genetics Symposium, Canberra, 5-9 August 1968*, 1-36.

Burdon, J. J., Barrett, L. G., Rebetzke, G., & Thrall, P. H. (2014). Guiding deployment of resistance in cereals using evolutionary principles. *Evolutionary Applications*, 7(6), 609-624.

DOI: <https://doi.org/10.1111/eva.12175>

Chen, W., Wellings, C., Chen, X., Kang, Z., and Liu, T. (2014). Wheat stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici*. *Molecular plant pathology*, 15(5), 433-446.

Chen, X. (2020). Pathogens which threaten food security: *Puccinia striiformis*, the wheat stripe rust pathogen. *Food Security*, 12(2), 239-251.

DOI: <https://doi.org/10.1007/s12571-020-01016-z>

- Desta, Z. A., and Ortiz, R. (2014). Genomic selection: genome-wide prediction in plant improvement. *Trends in plant science*, 19(9), 592-601. DOI: <https://doi.org/10.1016/j.tplants.2014.05.006>
- Eissa, H. F., Hassanien, S. E., Ramadan, A. M., El-Shamy, M. M., Saleh, O. M., Shokry, A. M., *et al.*, (2017). Developing transgenic wheat to encounter rusts and powdery mildew by overexpressing barley chi26 gene for fungal resistance. *Plant methods*, 13(1), 1-13. DOI: <https://doi.org/10.1186/s13007-017-0191-5>
- Elshafei, A. A., Afiah, S. A. E. A., Al-Doss, A. A., and Ibrahim, E. I. (2019). Morphological variability and genetic diversity of wheat genotypes grown on saline soil and identification of new promising molecular markers associated with salinity tolerance. *Journal of Plant Interactions*, 14(1), 564-571. DOI: <https://doi.org/10.1080/17429145.2019.1672815>
- Feng, J., Wang, M., See, D. R., Chao, S., Zheng, Y., and Chen, X. (2018). Characterization of novel gene Yr79 and four additional quantitative trait loci for all-stage and high-temperature adult-plant resistance to stripe rust in spring wheat PI 182103. *Phytopathology*, 108(6), 737-747. DOI: <https://doi.org/10.1094/PHYTO-11-17-0375-R>
- Figuroa, M., Dodds, P. N., and Henningsen, E. C. (2020). Evolution of virulence in rust fungi—multiple solutions to one problem. *Current opinion in plant biology*, 56, 20-27. DOI: <https://doi.org/10.1016/j.pbi.2020.02.007>
- Figuroa, M., Hammond-Kosack, K. E., and Solomon, P. S. (2018). A review of wheat diseases—a field perspective. *Molecular plant pathology*, 19(6), 1523-1536. DOI: <https://doi.org/10.1111/mpp.12618>
- Flor, H.H. (1971). Current status of the gene-for-gene concept. *Annu. Rev. Phytopathol.* 9, 275-296. DOI: [10.1146/annurev.py.09.090171.001423](https://doi.org/10.1146/annurev.py.09.090171.001423)
- Fu, D., Uauy, C., Distelfeld, A., Blechl, A., Epstein, L., Chen, X., *et al.*, (2009). A kinase-START gene confers temperature-dependent resistance to wheat stripe rust. *Science*, 323(5919), 1357-1360. DOI: [10.1126/science.1166289](https://doi.org/10.1126/science.1166289)
- Gessese, M. K. (2019). Description of Wheat Rusts and Their Virulence Variations Determined through Annual Pathotype Surveys and Controlled Multi-Pathotype Tests. *Advances in Agriculture*, 2019. DOI: <https://doi.org/10.1155/2019/2673706>
- Heslot, N., Akdemir, D., Sorrells, M. E., and Jannink, J. L. (2014). Integrating environmental covariates and crop modeling into the genomic selection framework to predict genotype by environment interactions. *Theoretical and applied genetics*, 127(2), 463-480. DOI: <https://doi.org/10.1007/s00122-013-2231-5>
- Hiebert, C. W., Kassa, M. T., McCartney, C. A., You, F. M., Rouse, M. N., Fobert, P., and Fetch, T. G. (2016). Genetics and mapping of seedling resistance to Ug99 stem rust in winter wheat cultivar Triumph 64 and differentiation of SrTmp, SrCad, and Sr42. *Theoretical and Applied Genetics*, 129(11), 2171-2177. DOI: <https://doi.org/10.1007/s00122-016-2765-4>
- Huerta-Espino, J., Singh, R. P., German, S., McCallum, B. D., Park, R. F., Chen, W. Q., *et al.*, (2011). Global status of wheat leaf rust caused by *Puccinia triticina*. *Euphytica*, 179(1), 143-160. DOI: <https://doi.org/10.1007/s10681-011-0361-x>
- Jamil, S., Shahzad, R., Ahmad, S., Fatima, R., Zahid, R., Anwar, M., *et al.*, (2020). Role of Genetics, Genomics and Breeding approaches to combat stripe rust of wheat. *Frontiers in Nutrition*, 7, 173.

- Johnson, R., and LAW, C. N. (1975). Genetic control of durable resistance to yellow rust (*Puccinia striiformis*) in the wheat cultivar Hybride de Bersee. *Annals of Applied Biology*, 81(3), 385-391. DOI: <https://doi.org/10.1111/j.1744-7348.1975.tb01654.x>
- Juliana, P., Singh, R. P., Singh, P. K., Crossa, J., Huerta-Espino, J., Lan, C., *et al.*, (2017). Genomic and pedigree-based prediction for leaf, stem, and stripe rust resistance in wheat. *Theoretical and Applied Genetics*, 130(7), 1415-1430. DOI: <https://doi.org/10.1007/s00122-017-2897-1>
- Kassa, M. T., You, F. M., Hiebert, C. W., Pozniak, C. J., Fobert, P. R., Sharpe, A. G., *et al.*, (2017). Highly predictive SNP markers for efficient selection of the wheat leaf rust resistance gene Lr16. *BMC plant biology*, 17(1), 1-9. DOI: <https://doi.org/10.1186/s12870-017-0993-7>
- Kaur, J., Fellers, J., Adholeya, A., Velivelli, S. L., El-Mounadi, K., Nersesian, N., *et al.*, (2017). Expression of apoplast-targeted plant defensin MtDef4. 2 confers resistance to leaf rust pathogen *Puccinia triticina* but does not affect mycorrhizal symbiosis in transgenic wheat. *Transgenic research*, 26(1), 37-49. DOI: [10.1007/s11248-016-9978-9](https://doi.org/10.1007/s11248-016-9978-9)
- Khan, M. H., Bukhari, A., Dar, Z. A., and Rizvi, S. M. (2013). Status and strategies in breeding for rust resistance in wheat. *Agricultural Sciences*, 4(06), 292. DOI: <http://dx.doi.org/10.4236/as.2013.46042>
- Kolmer, J. (2013). Leaf rust of wheat: pathogen biology, variation and host resistance. *Forests*, 4(1), 70-84. DOI: <https://doi.org/10.3390/f4010070>
- Kurowska, M., Daszkowska-Golec, A., Gruszka, D., Marzec, M., Szurman, M., Szarejko, I., and Maluszynski, M. (2011). TILLING-a shortcut in functional genomics. *Journal of applied genetics*, 52(4), 371-390. DOI: <https://doi.org/10.1007/s13353-011-0061-1>
- Lan, C., Zhang, Y., Herrera-Foessel, S. A., Basnet, B. R., Huerta-Espino, J., Lagudah, E. S., and Singh, R. P. (2015). Identification and characterization of pleiotropic and co-located resistance loci to leaf rust and stripe rust in bread wheat cultivar Sujata. *Theoretical and Applied Genetics*, 128(3), 549-561. DOI: <https://doi.org/10.1007/s00122-015-2454-8>
- Olson, E. L., Rouse, M. N., Pumphrey, M. O., Bowden, R. L., Gill, B. S., and Poland, J. A. (2013). Introgression of stem rust resistance genes SrTA10187 and SrTA10171 from *Aegilops tauschii* to wheat. *Theoretical and applied genetics*, 126(10), 2477-2484. DOI: <https://doi.org/10.1007/s00122-013-2148-z>
- Rana, M., Kaldate, R., Nabi, S. U., Wani, S. H., and Khan, H. (2021). Marker-Assisted Breeding for Resistance Against Wheat Rusts. In *Physiological, Molecular, and Genetic Perspectives of Wheat Improvement* (pp. 229-262). Springer, Cham. DOI: https://doi.org/10.1007/978-3-030-59577-7_11
- Ren, Y., Singh, R. P., Basnet, B. R., Lan, C. X., Huerta-Espino, J., Lagudah, E. S., and Ponce-Molina, L. J. (2017). Identification and mapping of adult plant resistance loci to leaf rust and stripe rust in common wheat cultivar Kundan. *Plant disease*, 101(3), 456-463. DOI: <https://doi.org/10.1094/PDIS-06-16-0890-RE>
- Rouse, M. N., Olson, E. L., Gill, B. S., Pumphrey, M. O., and Jin, Y. (2011). Stem rust resistance in germplasm. *Crop Sci.* 51, 2074-2078. DOI: [10.2135/cropsci2010.12.0719](https://doi.org/10.2135/cropsci2010.12.0719)
- Rutkoski, J. E., Heffner, E. L., and Sorrells, M. E. (2011). Genomic selection for durable stem rust resistance in wheat. *Euphytica*, 179(1), 161-173. DOI: <https://doi.org/10.1007/s10681-010-0301-1>
- Rutkoski, J., Singh, R. P., Huerta-Espino, J., Bhavani, S., Poland, J., Jannink, J. L., and Sorrells, M. E. (2015). Genetic gain from phenotypic and

- genomic selection for quantitative resistance to stem rust of wheat. *The Plant Genome*, 8(2), plant genome 2014-10. DOI: <https://doi.org/10.3835/plantgenome2014.10.0074>
- Sai Prasad, S. V., Singh, S. K., Ambati, V. D., Prakasha, T. L., Singh, J. B., Dubey, V. G., ... and Mishra, A. N. (2014). Introgression of stem rust resistance gene Sr36 into durum wheat background using marker assisted backcross breeding. *J Wheat Res*, 6(1), 21-24.
- Savadi, S., Prasad, P., Kashyap, P. L., and Bhardwaj, S. C. (2018). Molecular breeding technologies and strategies for rust resistance in wheat (*Triticum aestivum*) for sustained food security. *Plant pathology*, 67(4), 771-791. DOI: <https://doi.org/10.1111/ppa.12802>
- Savitha, B. S., Desai, S. A., Biradar, S. S., Naik, R., and Lohithaswa, H. C. (2016). Identification of SSR Marker Linked to Leaf Rust Resistant Gene Lr24 and Marker Assisted Transfer of Leaf Rust Resistance Genes into Bread Wheat. *Journal of Agricultural Science and Technology (JAST)*, 18(2), 545-552.
- Sestili, F., Botticella, E., Bedo, Z., Phillips, A., and Lafiandra, D. (2010). Production of novel allelic variation for genes involved in starch biosynthesis through mutagenesis. *Molecular Breeding*, 25(1), 145-154. DOI: <https://doi.org/10.1007/s11032-009-9314-7>
- Sharma, J. S., Zhang, Q., Rouse, M. N., Klindworth, D. L., Friesen, T. L., Long, Y., *et al.*, (2019). Mapping and characterization of two stem rust resistance genes derived from cultivated emmer wheat accession PI 193883. *Theoretical and Applied Genetics*, 132(11), 3177-3189. DOI: <https://doi.org/10.1007/s00122-019-03417-x>
- Singh, A., Jaiswal, J. P., and Badoni, S. (2018). Enhancing rust resistance in wheat through marker assisted backcross breeding. *Indian J. Genet*, 78(1), 19-25. DOI: 10.5958/0975-6906.2018.00003.2
- Singh, R. P., Herrera-Foessel, S., Huerta-Espino, J., Singh, S., Bhavani, S., Lan, C., and Basnet, B. R. (2014). Progress towards genetics and breeding for minor genes based resistance to Ug99 and other rusts in CIMMYT high-yielding spring wheat. *Journal of Integrative Agriculture*, 13(2), 255-261. DOI: [https://doi.org/10.1016/S2095-3119\(13\)60649-8](https://doi.org/10.1016/S2095-3119(13)60649-8)
- Singh, R. P., Huerta-Espino, J., Bhavani, S., Herrera-Foessel, S. A., Singh, D., Singh, P. K., and Crossa, J. (2011). Race non-specific resistance to rust diseases in CIMMYT spring wheats. *Euphytica*, 179(1), 175-186. DOI: <https://doi.org/10.1007/s10681-010-0322-9>
- Singla, J., Lüthi, L., Wicker, T., Bansal, U., Krattinger, S. G., and Keller, B. (2017). Characterization of Lr75: a partial, broad-spectrum leaf rust resistance gene in wheat. *Theoretical and Applied Genetics*, 130(1), 1-12. DOI: <https://doi.org/10.1007/s00122-016-2784-1>
- Wang M., and Chen X. (2017). Stripe rust resistance. In: Chen X and Kang Z, editors. *Stripe Rust*. Dordrecht: Springer (2017). p. 353-558. DOI: 10.1007/978-94-024-1111-9_5
- Wang, J., Li, Z., Shi, L., Zhu, L., Ren, Z., Li, X., ... and Shah, S. J. A. (2015). QTL mapping for adult-plant leaf rust resistance genes in Chinese wheat cultivar Weimai 8. *Czech Journal of Genetics and Plant Breeding*, 51(3), 79-85. DOI: <https://doi.org/10.17221/51/2015-CJGPB>
- Yaniv, E., Raats, D., Ronin, Y., Korol, A. B., Grama, A., Bariana, H., *et al.*, (2015). Evaluation of marker-assisted selection for the stripe rust resistance gene Yr15, introgressed from wild emmer wheat. *Molecular breeding*, 35(1), 1-12. DOI: <https://doi.org/10.1007/s11032-015-0238-0>

Zhao, J., Wang, M., Chen, X., and Kang, Z. (2016).
Role of alternate hosts in epidemiology and
pathogen variation of cereal rusts. *Annual
Review of Phytopathology*. 54, 207-228.
DOI: <https://doi.org/10.1146/annurev-phyto-080615-095851>

FUNDING

None