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Review Article

Advances in Wheat Rust Resistance: Challenges, and Management Strategies

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ABSTRACT

Breeding wheat for resistance to major rust diseases stem rust (*Puccinia graminis*), stripe rust (*Puccinia striiformis*), and leaf rust (*Puccinia triticina*) is a pivotal strategy for advancing sustainable agronomic systems, safeguarding yield potential, and reducing dependence on fungicides. This effort employs race-specific resistance genes, including Lr47, Lr52, Yr5, Yr10, Yr36, Sr31, and Sr24, which confer high efficacy against specific pathogen races but are vulnerable to evolving virulent strains. To complement this, durable adult plant resistance (APR) genes such as Lr34, Lr46, and Sr57 provide broad-spectrum and long-lasting defense by modulating systemic resistance pathways. These genes trigger mechanisms like enhanced signaling cascades and antimicrobial compound synthesis. Genetic introgression from wild relatives, such as *Triticum turgidum* and *Aegilops* spp., enriches the wheat gene pool with novel resistance alleles. Cutting-edge methodologies, including marker-assisted selection (MAS), genomic selection, and pathogen monitoring, accelerate the incorporation of resistance genes while mitigating risks posed by pathogen adaptation. Through the strategic integration of genetic resistance and molecular precision, this multidimensional approach forms the basis for the creation of durable resistant varieties. These varieties ensure agronomic sustainability and enhance crop defense against biotic stresses, accounting for the complexities of evolving agro-ecological and climatic dynamics.

Keywords: Wheat Breeding, Wheat Rust, *Puccinia*, Genetic Resistance, Pathogen Evolution.

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INTRODUCTION

Wheat accounts for approximately 20% of the global caloric and protein intake by the human population. (Reynolds et al., 2012), making it a cornerstone of food security. Any substantial reduction in wheat production could lead to food shortages, price hikes, and economic instability. The three primary rust diseases leaf rust (*Puccinia triticina*): stem rust (*Puccinia graminis* f. sp. *tritici*): and stripe rust (*Puccinia striiformis* f.sp. *tritici*) have posed persistent threats to wheat yields for centuries, significantly impacting yield stability and grain quality across diverse agro-ecological zones worldwide (Afzal et al., 2018; Khan et al., 2013).

Leaf rust is the most widely spread of these diseases, affecting wheat production across almost all major growing regions (Ijaz et al., 2023). Characterized by orange-brown pustules on leaf surfaces, it compromises photosynthetic efficiency, leading to poor grain filling and yield reductions ranging from 10% to 50% under favorable conditions (Huerta-Espino et al., 2011; Yahya, 2020).

Stripe rust, also known as yellow rust, thrives in cooler, wetter climates, making it particularly problematic in regions such as Europe, the Americas, and parts of Asia,

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including China and the Indian subcontinent (Afzal et al., 2022). This pathogen, which produces yellow streaks on leaves, can infect wheat at any growth stage, resulting in weakened plants and substantial yield loss. Emerging strains of *Puccinia striiformis* f. sp. *tritici* (PST) demonstrated an increased ability to adapt to warmer climates (Milus et al., 2009; Wellings, 2011).These adaptive strains have expanded the disease's range, presenting a major challenge in areas that were previously unaffected (Ali et al., 2017; Afzal et al., 2022).

Stem rust has long been recognized as one of the most destructive wheat diseases (Salotti et al., 2022; Lewis et al., 2024). Pathogen invasion in stem rust affects plant tissues and can lead to lodging, which significantly reduces yields (Laidig et al., 2022). Historical epidemics in the 20th century underscored its impact on food security (Leonard and Szabo, 2005; Bushnell, 2012). The emergence of new virulent races, particularly the Ug99 lineage, which can overcome numerous resistance genes, has reawakened concerns (Singh et al., 2011). Ug99 threatens wheat production in Africa, the Middle East, and other regions (Singh et al., 2011a; Hodson et al., 2012).

Current status of resistance against wheat rusts

The importance of genetic resistance in controlling rust diseases was initially revealed by Biffen (Biffen, 1905). This innovation laid the foundation for plant disease management through breeding. Since then, breeding for rust resistance has emerged as the most preferred and effective strategy for rust control. Genetic resources are vital for sustaining global wheat production by providing essential genetic diversity for agronomic improvement. This diversity includes wild relatives (Ulukan, 2020), traditional landraces (Adhikari et al., 2022), and ancient wheat varieties (Pietrusińska1 et al., 2018), which serve as sources of alleles for resistance to biotic stresses (such as pests and diseases) and abiotic stresses (like drought and temperature extremes). Conservation methods, including ex situ (seed banks) and in situ (natural environments) preservation, safeguard these genetic resources from erosion, ensuring a steady supply of valuable traits for crop improvement (Pour-Aboughadareh et al., 2021).

Modern wheat breeding programs prioritize the integration of resistance (R-) genes, such as *Sr*, *Yr*, and *Lr*, using advanced molecular breeding techniques (Mapuranga et al., 2022). Organizations like BGRI, ICARDA, and CIMMYT spearhead efforts to distribute rust-resistant germplasm to areas with high inoculum pressure, including South Asia and Sub-Saharan Africa. Despite challenges from evolving pathogen strains and climate-induced stressors, breeding programs are advancing broad-spectrum, durable resistance. This effort is supported by precise phenotyping, real-time pathogen surveillance, and collaborative data-sharing networks, enhancing global wheat resilience against rust outbreaks.

In the field of plant breeding and genetics, rust resistance in wheat is predominantly governed by two major classes of resistance genes: race-specific genes, which confer vertical resistance through gene-for-gene interactions, and race-non-specific genes, which provide horizontal resistance by enhancing durable and broad-spectrum defense mechanisms against pathogenic rusts (Parlevliet, 1985; Dyck and Kerber, 1985).

Race-specific resistance (All-stage resistance, ASR)

Race-specific genes confer a high degree of resistance against specific avirulent pathogen races and are typically inherited in a qualitative, often monogenic, manner (Johnson, 1981). This type of resistance is expressed across all developmental stages of the plant, thus termed as all-stage resistance (ASR). However, ASR genes are susceptible to being overcome by pathogen populations, as rust pathogens can evolve new virulent races through mutation and recombination, leading to rapid resistance breakdown. Deploying ASR genes singularly, therefore, presents a significant epidemiological risk due to the genetic adaptability of rust pathogens (Bariana, 2013).

Race-non-specific resistance (Adult plant resistance, APR)

Race-non-specific genes, in contrast, confer partial yet durable resistance typically observable from the post-seedling stage, thus described as adult plant resistance (APR). APR is quantitatively inherited and generally polygenic, involving multiple minor-effect genes that collectively contribute to moderate but persistent resistance. Since individual APR genes provide only partial resistance, effective and sustainable control of rust diseases usually requires the combination of three to four APR genes to achieve commercially viable resistance thresholds (Singh et al., 2004). The polygenic architecture of disease resistance increases its durability, as the pathogen would need to undergo multiple concurrent mutations to overcome APR, a process that is less likely than adapting to ASR genes. Polygenic architecture refers to a trait being controlled by multiple genes, each contributing a small effect to the overall phenotype. In terms of disease resistance, this means that resistance is governed by several genes, often working together in an additive or synergistic manner. This polygenic resistance is more durable because the pathogen must simultaneously overcome multiple genetic barriers, which is a more complex and less probable process compared to evolving to bypass a single resistance gene, as seen with ASR (allele-specific resistance) genes. As a result, polygenic resistance is more stable and less prone to rapid breakdown by evolving pathogens.

Rust resistance gene inventory

A number of scientists have compiled detailed inventories of rust-resistant genes in wheat, focusing on loci that confer resistance to specific rusts. Here are the references of latest documents (Tong et al., 2024; Shahin et al., 2024; Bhardwaj et al., 2024 ; Khan et al., 2024). Agronomically, these genes serve as critical components in developing rust-resistant wheat varieties through genetic introgression and marker-assisted selection. This genetic resistance mitigates the need for extensive fungicide application, aligning with integrated pest management (IPM) principles and promoting sustainable crop production. Current gene inventories enhance durable resistance, crucial in breeding programs for maintaining yield stability under biotic stress conditions. Combating wheat rusts demands a multifaceted strategy that merges genetics, agronomy, and global disease surveillance. With ongoing research and collaborative efforts, wheat production can keep pace with these evolving biotic threats, securing food supplies and supporting agricultural stability worldwide.

Lr34

The *Lr34* gene is a notable genetic source of durable resistance in wheat (*Triticum aestivum*): widely utilized for its broad-spectrum protection against leaf rust. Unlike race-specific resistance genes, *Lr34* provides non-race-specific, or adult plant resistance (APR), characterized by highly advantageous for global wheat breeding programs (Krattinger et al., 2009).

Mechanism of *Lr34* gene function

The resistance mechanism of *Lr34* is complex and involves a multi-layered defense response. It encodes an ATP-binding cassette (ABC) transporter protein, which is thought to facilitate the transport of antimicrobial compounds to infection sites. This process assists in neutralizing or sequestering pathogenic toxins, thereby hindering the pathogen's ability to invade plant tissues effectively (Krattinger et al., 2011). The gene's activity also influences signaling pathways, particularly those involving salicylic acid and reactive oxygen species (ROS), both integral to plant defense (Krattinger et al., 2009).

Unique among resistance genes, *Lr34* avoids triggering a hypersensitive response (HR): which is often marked by localized cell death. Instead, *Lr34* slows down disease progression in a manner that is less damaging to the plant's tissues, resulting in partial but durable resistance that is compatible with various wheat genetic backgrounds. The gene's ability to protect against multiple pathogens leaf rust, stripe rust, and powdery mildew has significantly reduced fungicide reliance in agriculture, thus promoting sustainable practices.

Incorporation into breeding programs

Lr34's durability has been pivotal in breeding programs worldwide, as it has significantly enhanced the resilience of wheat cultivars without the frequent need for fungicide applications (Bhavani et al., 2016). Nevertheless, the constant evolution of pathogens underscores the necessity of combining *Lr34* with other resistance genes to maintain long-lasting, multi-pathogen resilience. By pyramiding *Lr34* with genes such as *Sr*, *Yr*, and *Lr* genes, breeders strengthen wheat's overall defense. Molecular markers linked to *Lr34* aid in its efficient selection in breeding processes, while field testing ensures the performance of these gene combinations in real farming conditions (Hussain et al., 2015).

Genetic sources of *Lr34*

Initially identified in the Chinese Spring wheat cultivar, *Lr34* represents a significant milestone in breeding for disease resistance. The Thatcher wheat variety is another primary source of *Lr34* and has been invaluable in breeding for leaf rust resistance (McIntosh et al., 1995). Further sources include *Triticum durum* and *Triticum turgidum*, as well as wild relatives like species from the *Aegilops* genus, which offer valuable genetic diversity for broadening the resistance base (Salgotra et al., 2022).

In summary, the *Lr34* gene remains a cornerstone of durable disease resistance in wheat, offering a foundation for breeding cultivars that are resilient in diverse agro-ecological zones and capable of withstanding evolving rust pathogens. Its incorporation with complementary resistance genes ensures an ongoing strategy against wheat rusts, thereby securing wheat productivity and global food stability.

Lr47

The *Lr47* gene is recognized for its effective contribution to leaf rust resistance in wheat across various genetic backgrounds and environmental conditions. Positioned on chromosome 5A, *Lr47* confers resistance against specific leaf rust races, making it a valuable component in wheat breeding (Maccaferri et al., 2015).

Mechanism of *Lr47* gene action

Lr47 indeed offers robust resistance to leaf rust in various regions, but its effectiveness might not be long-lasting due to the adaptive nature of the pathogen. The resistance provided by Lr47 relies on nucleotide-binding leucine-rich repeat (NLR) proteins (Eitas et al., 2014), which could be undermined as the rust pathogen *Puccinia triticina* adapts through mutation or gene deletion to evade detection. Similar situations have been observed with the Ug99 race group of *Puccinia graminis f. sp. tritici*, which overcame several major stem rust resistance genes in wheat (Bhardwaj et al., 2014). To address this risk, a promising approach is to combine Lr47 with other multi-pathogen resistance genes, such as Lr34/Sr57/Yr18 and Lr67/Sr55/Yr46 (Moore et al., 2015). These genes are linked to slow-rusting resistance, which provides partial and more durable resistance across multiple pathogens (Mapuranga et al., 2022). Using such a gene combination could create wheat varieties with a more stable defense against rust pathogens, reducing the likelihood of resistance breakdown and helping maintain crop yields in the face of evolving threats (Li et al., 2023a).

Genetic sources of *Lr47*

The *Lr47* gene was initially introduced from *Triticum speltoides*, a wild wheat relative, into bread wheat through genetic transfer (Li et al., 2023). Since its introduction, it has shown consistent and robust resistance to leaf rust in multiple wheat cultivars (Helguera et al., 2000), establishing its importance in broadening the genetic base of resistance in wheat breeding programs (Kthiri, 2017).

A recent study estimated the length of the *Ae. speltoides* 7S#1S segment to range between 157 and 174 Mb, as determined using simple sequence repeat (SSR) markers and referenced to Chinese Spring RefSeq v1.0 coordinates (Xu et al., 2021). The interstitial translocation segment carrying the *Lr47* gene was later backcrossed into several spring wheat cultivars, such as Pavon, Express, Kern, RSI5, Yecora Rojo, and UC104116 (Helguera et al., 2000; Brevis et al., 2008). However, the *Lr47* introgression was linked to several unfavorable agronomic and quality traits, including lower grain yield, reduced flour yield, and higher flour ash content (Brevis et al., 2008). To address these negative effects, further rounds of homoeologous recombination using the *ph1b* mutation are required to reduce the size of the introgressed segment containing *Lr47* and minimize linkage drag. Additionally, cloning the *Lr47* gene and developing transgenic plants could help break the linkage between *Lr47* and the associated detrimental traits. This strategy holds significant promise, as *Lr47* is among the few genes that provide robust resistance to a wide range of *Puccinia triticina* (Pt) isolates and could play a pivotal role in enhancing wheat resistance to leaf rust (Wu et al., 2019; Yuan et al., 2021).

In summary, *Lr47* provides effective race-specific resistance to leaf rust and is a valuable addition to resistance gene pyramiding strategies. Its inclusion in diverse wheat cultivars enhances their resilience to leaf rust, supporting sustainable and effective disease management in wheat production

Lr52

Among the several genes of wheat possessing resistance against leaf rust, Lr52 is a very effective one characterized with broad spectrum resistance (Tar et al., 2008). The *Lr52* gene is known for its role in conferring resistance to leaf rust, making it highly valuable in wheat breeding programs aimed at enhancing leaf rust resilience. Hiebert et al., 2005 identified Lr52, located on the short arm of chromosome 5B, 16.5 cM distal to the microsatellite Xgwm443, through a novel genetic technique called haploid deficiency mapping. The gene was derived from a near-isogenic line of Thatcher (RL6107) and proved effective against 29 diverse isolates of *Puccinia triticina* in North America, showing no virulence. Lr52's effectiveness and unique location make it a valuable resistance source for breeding (Singh Vaibhav et al., .2023)

Mechanism of *Lr52* gene action

The Lr52 gene, identified on chromosome 5BS (Bansal et al., 2011), is notable for its broad-spectrum resistance to multiple *Puccinia triticina* (Pt) pathotypes, providing an important tool for leaf rust management in wheat (Tar et al., 2008). This resistance was mapped through cytogenetic methods, adding to its reliability and precision in genetic studies (Hiebert et al., 2005). These mechanisms make *Lr52* a vital gene in breeding strategies focused on durable resistance to leaf rust.

Genetic sources of *Lr52*

Gene is derived from the wild grass *Dasypyrum villosum* (L.) (Qi et al., 2011). The *Lr52* gene has been identified in the wheat variety Harrington, where it has shown strong resistance against leaf rust. Its presence in Harrington supports its potential for developing resistant wheat cultivars, as it provides a robust defense mechanism suitable for various breeding programs (Khan et al., 2020).

Stripe rust

Recent research has identified several effective resistance genes against stripe rust (*Puccinia striiformis* f. sp. *tritici*) in wheat. Notable genes include:

Yr5

The *Yr5* gene is well-regarded in wheat breeding for its race-specific resistance against stripe rust, particularly due to its durability across various wheat genetic backgrounds (Yan et al., 2003). A study conducted by Zong et al. (2009) provided compelling evidence indicating allelism or extremely tight genetic linkage between the stripe rust resistance loci Yr5 and Yr7. The research integrated phenotypic evaluations under controlled and field conditions with molecular marker analysis to validate this association. The close genetic relationship between these loci highlights their potential utility in breeding programs (Zhang et al., 2005). By pyramiding Yr5 and Yr7 or leveraging their derivatives, wheat breeders can develop cultivars with more durable resistance to the evolving races of *Puccinia striiformis*, ensuring enhanced resilience against stripe rust in diverse agro-ecological environments (Rehman et al., 2024).

Located on the long arm of chromosome 2B (McGrann et al., 2014), *Yr5* provides strong resistance to multiple virulent strains of *Puccinia striiformis* f. sp*. tritici* (stripe rust), especially those that have evolved to overcome other resistance genes (McIntosh et al., 1995; Chen, 2005).

Mechanism of *Yr5* gene action

Yr5 operates through a hypersensitive response (HR) mechanism, activating localized cell death upon detecting specific avirulence (Avr) proteins from the pathogen. This prevents the spread of infection, limiting pathogen growth and aiding in the plant's overall defense. The gene follows a gene-for-gene mechanism, which means its effectiveness depends on recognizing specific pathogen proteins. Unlike some temperature-sensitive resistance genes, *Yr5* maintains stable resistance across a wide range of environmental conditions, making it highly valuable in diverse wheat-growing regions, particularly those with high stripe rust pressure (Ellis et al., 2014; Chen, 2005).

Although *Yr5* has shown effectiveness against many virulent races of stripe rust, the pathogen's adaptability suggests combining *Yr5* with other resistance genes to strengthen and prolong its efficacy. This practice, known as gene pyramiding, builds layered resistance within wheat cultivars, helping manage stripe rust over time and reducing reliance on fungicides (Wan et al., 2004).

Genetic sources of *Yr5*

The *Yr5* gene originates from *Triticum dicoccoides* (wild emmer wheat) where it was identified and subsequently introduced into modern wheat varieties. Notable wheat cultivars incorporating *Yr5* include 'Thatcher' and 'Lerma Rojo 64,' both recognized for their significant resistance to stripe rust, making them valuable sources in breeding programs (Roelfs et al., 1992; McIntosh et al.1995). Additionally, wild relatives such as *Aegilops tauschii* and other lines of *Triticum dicoccoides* serve as critical sources for introducing *Yr5* and other resistance genes into cultivated wheat, enhancing the potential for more resilient, disease-resistant wheat varieties (Zhang et al., 2017).

In summary, *Yr5* is a powerful gene for stripe rust resistance, with its origins in wild wheat relatives contributing to its value in breeding programs. Its incorporation into wheat varieties offers a robust defense mechanism that is strengthened through gene pyramiding, which is crucial for sustainable management of stripe rust in agriculture.

Yr 10

Yr10 is a key race-specific resistance gene used in wheat breeding programs for protection against stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (Pst). Known for its effectiveness against certain races, *Yr10* is appreciated in developing resistant wheat cultivars. The observation that resistance genes like Yr10 do not carry a yield penalty is significant for breeding disease-resistant crops, especially wheat, which is vulnerable to destructive diseases like stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (Pst). Yield penalty refers to the decrease in crop yield due to the metabolic and resource costs of retaining resistance mechanisms. In some cases, plants that transmit resistance genes can experience reduced development or produce under non-stress circumstances, as energy and resources are directed towards defense pathways instead of development or reproduction. However, investigation advocates that Yr10 and similar resistance genes do not impose this cost on wheat, sanctioning plants to maintain productivity while being threatened against stripe rust (Kaur et al., 2016)

Mechanism of *Yr10* gene action

The study by Wu et al. (2023) investigated the resistance mechanisms associated with the Yr10 gene in wheat, which confers race-specific, all-stage resistance against stripe rust caused by Puccinia striiformis f. sp. tritici (Pst). Utilizing transcriptomic sequencing, the research analyzed differentially expressed genes (DEGs) at 0, 18, and 48 hours post-inoculation in compatible (Avocet S) and incompatible (Yr10-carrying) wheat lines when challenged with the Pst race CYR32.

Genetic sources of *Yr10*

Originally identified in the *Triticum aestivum* line PI 178383 (Temel et al., 2008): *Yr10* has been incorporated into numerous wheat breeding programs to enhance rust resistance. Cultivars such as 'Avocet S' are prominent sources of *Yr10*, known for their strong resistance to stripe rust, making them highly desirable in breeding (McIntosh et al., 1995). Another cultivar, 'Kauz,' also contains *Yr10* and has been widely used to improve resistance across diverse wheat varieties (Nazari et al., 2009; Boros et al., 2020).

Wild relatives of wheat provide additional sources of *Yr10*, such as *Aegilops tauschii*, which offers valuable genetic diversity for introducing resistance traits into cultivated wheat. *Triticum dicoccoides* (wild emmer wheat) also serves as an important genetic source, contributing traits that support the development of disease-resistant wheat varieties (Gill et al., 2011) .Further research by various breeding programs has mapped and incorporated *Yr10* into numerous wheat lines, allowing breeders to assess its effectiveness against different Pst races (Yuan et al., 2018;Liu et al., 2014). This work is essential for maintaining resistance durability as pathogen populations evolve, guiding the strategic use of *Yr10* in wheat breeding for sustainable disease management.

Yr36

Yr36 is a significant gene in wheat breeding for providing durable resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*). Its effectiveness has led to its incorporation into numerous modern wheat cultivars, enhancing resilience in varied environments. A unique feature of *Yr36* is its temperature-sensitive resistance, which functions optimally at temperatures above 15°C. This quality makes *Yr36* especially valuable in regions where warmer temperatures coincide with stripe rust outbreaks, increasing its durability and global applicability in breeding programs (Fu et al., 2009).

Mechanism of *Yr36* gene action

The *Yr36* gene encodes a protein with two distinct domains: a kinase and a START (steroidogenic acute regulatory protein-related lipid transfer) domain. Together, these domains enable the gene to detect stripe rust and respond with a defense mechanism that includes programmed cell death (PCD) at infection sites, preventing the spread of the pathogen. This gene operates through a hypersensitive response, a mechanism that is often associated with durable, broad-spectrum resistance (Fu et al., 2009). Unlike many single-gene resistances that pathogens can quickly overcome, *Yr36* provides protection against a broad range of stripe rust strains, including some that have developed virulence against other resistance genes (Uauy et al., 2005).

Because *Yr36* works best in warmer climates, it is often combined with other resistance genes to provide robust defense mechanisms across various climatic conditions (Bryant et al., 2014). This gene-stacking strategy is essential for reducing pathogen adaptation, promoting sustainable rust management, and minimizing reliance on fungicides.

Genetic sources of *Yr36*

Stripe rust, caused by the biotrophic fungal pathogen *Puccinia striiformis f. sp. tritici* (Pst), is a severe disease affecting wheat (*Triticum aestivum*) production globally. The emergence of virulent races of Pst has rendered most race-specific resistance (R) genes ineffective, posing a significant challenge to sustainable wheat cultivation.

The resistance gene *Yr36* (WKS1), identified through map-based cloning, offers broad-spectrum resistance to stripe rust under high-temperature conditions (25°C to 35°C). This gene comprises two critical domains: a kinase domain and a putative START lipid-binding domain. Functional analyses, including five independent mutations and transgenic complementation assays, have demonstrated that both domains are essential for mediating resistance (Fu et al., 2009). Interestingly, *Yr36* originates from wild wheat species but is absent in the germplasm of modern durum and bread wheat cultivars. Its introgression into elite breeding lines holds significant potential for enhancing genetic resistance to stripe rust, contributing to durable disease management strategies and improving wheat productivity across diverse agro-ecological zones. The gene offering a valuable source of resistance that has been successfully integrated into cultivated wheat lines (Uauy et al., 2006). Advances in genomics have facilitated the identification and transfer of *Yr36* into various wheat varieties, enhancing the genetic diversity for stripe rust resistance in global wheat production (Chen et al., 2024; Afzal et al., 2024).

Ongoing research continues to focus on discovering and incorporating additional resistance genes like *Yr36* to combat the evolving stripe rust pathogen, aiming for even more resilient wheat cultivars in the future.

Stem Rust

Recent research highlights several effective genes against stem rust (*Puccinia graminis* f.sp. *tritici*) in wheat, critical for breeding durable resistance. Key genes include Sr31, known for its strong resistance against specific stem rust strains and widely used in global wheat breeding (De Groot, 2012), though it has been overcome by the virulent race TTKSK (Ug99) in some regions (Pretorius et al., 2000). Despite this limitation, it remains valuable in managing non-Ug99 races. Sr36 offers broad-spectrum resistance, proving highly effective against a range of stem rust races, including some that have overcome Sr31. Its versatility across different environmental conditions enhances its value in breeding programs (Odemba 2018).

Sr24, widely used for its durable resistance against multiple races, has remained effective even against certain aggressive Ug99 lineage races, making it a critical gene for resistance management (Xu et al., 2017). Sr50, derived from *Secale cereale* (rye), provides strong resistance to various stem rust races, including those that impact other resistance genes, reinforcing its importance in resistant cultivar development (Ortiz et al.,2022). Researchers are actively working on combining these resistance genes to build multi-layered protection against stem rust. By incorporating combinations of these genes, breeders aim to enhance resistance durability, safeguard yield, and contribute to food security.

Sr31

The Sr31 gene is a significant source of resistance to stem rust (*Puccinia graminis* f.sp. *tritici*) in wheat (Afzal et al., 2021). It provides resistance to multiple races of the stem rust pathogen, offering protection against various strains. Sr31 has been successfully incorporated into numerous wheat breeding programs and has contributed to developing resistant wheat varieties globally. Despite its effectiveness, the Sr31 gene has faced challenges due to the emergence of the virulent race TTKSK (Ug99) which has overcome this resistance in some regions (Cao et al., 2019). However, Sr31 remains valuable in areas where non-Ug99 races of stem rust are prevalent (Li et al., 2016). Efforts continue to incorporate Sr31 alongside other resistance genes to enhance the durability and breadth of resistance against stem rust in wheat (Xu et al., 2017).

Mode of action of gene

The Sr31 gene provides resistance to stem rust (*Puccinia graminis f. sp. tritici*) in wheat through a mechanism that involves pathogen recognition and a hypersensitive response (HR). As an R (resistance) gene, Sr31 encodes proteins that recognize specific avirulence (Avr) factors from the stem rust pathogen. This recognition triggers a localized HR at the infection site, leading to rapid cell death in the affected area. This process limits the pathogen's access to nutrients and prevents further spread within the plant. Additionally, Sr31 activates signal transduction pathways that produce reactive oxygen species (ROS) and antimicrobial compounds, further enhancing the plant’s defense mechanisms.

Despite its historical success in conferring resistance, Sr31's effectiveness has been compromised with the emergence of the Ug99 race of stem rust, which can bypass this resistance. As a result, integrating Sr31 with other resistance genes has become crucial for maintaining durable resistance. This gene-stacking approach strengthens the plant’s defense system, reducing the likelihood of pathogen adaptation and ensuring ongoing protection against stem rust across various regions. By combining Sr31 with other resistance genes, breeders can create wheat varieties with broader and more sustainable resistance to stem rust, securing wheat yields and contributing to global food security.

Emergence of Ug99

The Sr31 gene was once a cornerstone in defending wheat against stem rust (*Puccinia graminis* f. sp. *tritici*): offering broad-spectrum resistance that protected crops worldwide. However, the emergence of a highly virulent strain of stem rust, Ug99, first identified in Uganda in 1999, posed a major challenge. Ug99 has the ability to bypass Sr31 and several other key resistance genes, making it particularly dangerous for global wheat production. The emergence of Ug99 highlighted the adaptability of the stem rust pathogen and emphasized the need for new, durable resistance strategies to safeguard future wheat crops (Singh et al., 2011). Severe grain losses were reported globally due to the emergence and spread of the Ug99 race of *Puccinia graminis f. sp. tritici*, the causal agent of stem rust, which was first identified in Uganda in 1998. The agronomic impact of Ug99 was so profound that, in 2005, it was recognized as a global threat to food security. The pathogenicity of Ug99 is largely attributed to its virulence against the *Sr31* and *Sr38* resistance genes, derived from *Secale cereale* and *Triticum ventricosum*, respectively. These genes had previously provided effective protection against the prevailing stem rust races until the advent of Ug99. The emergence of Ug99 highlighted the adaptability of the stem rust pathogen and emphasized the need for new, durable resistance strategies to safeguard future wheat crops (Singh et al., 2011).

In response to Ug99, there has been a vital shift toward developing wheat varieties with durable resistance. One of the key strategies is gene pyramiding, or stacking multiple resistance genes, which helps plants withstand evolving pathogens over time. By combining different genes, breeders can build a more robust defense against Ug99 and other rust threats, reducing the risk of resistance breakdown. In addition, real-time pathogen surveillance has become an essential tool. Monitoring rust variants like Ug99 enables researchers to quickly respond to new threats, adjusting breeding programs and fine-tuning resistance genes based on pathogen evolution (Afzal et al, 2015; 2022). This proactive approach has been instrumental in managing stripe and leaf rust, an area where Dr. Amir Afzal's work (Afzal et al, 2018; 2021[b]; 2022; 2024; Ijaz et al., 2023) aligns with global efforts, particularly in regions like Pothohar, where environmental challenges and increasing rust pressure make wheat crops particularly vulnerable.

Historically, Sr31 was widely used in wheat breeding programs due to its consistent performance and broad-spectrum resistance, playing a significant role in global food security for decades (Singh et al., 1998). However, with the identification of Ug99, it became clear that relying on single-gene resistance was risky, as the pathogen could evolve to bypass it. This underscores the importance of genetic diversity in resistance sources to avoid over-reliance on any one gene (Pretorius et al., 2000).

Although Sr31 alone is no longer fully effective against Ug99, it remains a valuable component in broader gene-stacking strategies. By combining Sr31 with other resistance genes, breeders can create multilayered defenses that make it more difficult for pathogens to overcome all resistance genes at once. This strategy reduces the likelihood of resistance breakdown by diversifying the plant's defense mechanisms, ensuring the longevity of the resistance (Afzal et al., 2018). In regions unaffected by Ug99, Sr31 continues to be effective against other rust strains, making it a valuable tool in regional breeding efforts. Integrating Sr31 with other genes in areas with Ug99 also helps manage selective pressure on the pathogen, discouraging the evolution of new, more virulent strains (Jin et al., 2007).

The Sr31 gene exemplifies the dynamic nature of plant-pathogen interactions, illustrating the importance of sustainable and adaptable resistance strategies in crop protection. The initial success of Sr31 followed by its partial vulnerability to Ug99 highlights how pathogen evolution can erode even the most effective resistance over time. This evolution underscores the need for an integrated approach to rust management: combining diverse resistance genes, closely monitoring pathogen evolution, and continuously developing new genetic defenses. Gene pyramiding extends the effectiveness of each resistance gene, reducing the risk of breakdown and ensuring that wheat crops remain protected against rust threats worldwide (Singh et al., 1998; Pretorius et al., 2000; Jin et al., 2007).

Genetic source of gene Sr31

The Sr31 gene is derived from the rye chromosome segment 1RS (Mago et al., 2005), which has been transferred into wheat through a specific genetic modification known as the 1RS. 1BL translocation (Sharma et al., 2018). This translocation involves the transfer of a segment of rye chromosome 1RS to wheat chromosome 1B. The integration of this rye segment into wheat has provided enhanced resistance to stem rust (*Puccinia graminis* f. sp. *tritici*): making it a valuable tool in wheat breeding programs (Singh et al., 2006). This genetic modification has been instrumental in offering broad-spectrum resistance to various strains of stem rust, contributing to wheat's resilience against this devastating pathogen.

Sr22

The Sr22 gene is an important resistance gene in wheat, providing protection against a range of stem rust strains, including certain races within the Ug99 lineage. Its introduction into modern wheat varieties has been instrumental in bolstering resistance to the evolving stem rust pathogen (*Puccinia graminis* f. sp. *tritici*). Sr22 is known for its broad effectiveness across various genetic backgrounds, making it a highly valuable asset in wheat breeding programs (Baranova et al., 2016). This gene enhances the crop's resilience against disease, especially in regions where Ug99 and other aggressive stem rust strains are a threat to wheat production. By integrating Sr22 into wheat cultivars, breeders are able to develop varieties with improved durability against rust, helping to safeguard yields and ensure food security. Additionally, Sr22’s utility in diverse genetic backgrounds underscores its potential for use in multi-gene strategies, helping to delay the breakdown of resistance by making it harder for pathogens to overcome multiple layers of defense (Gao et al., 2024).

Mechanism of gene action

The Sr22 gene provides resistance to stem rust (*Puccinia graminis* f. sp*. tritici*) by initiating a hypersensitive reaction (HR) in infected plant cells. Upon pathogen attack, Sr22 triggers programmed cell death, effectively isolating the infection and limiting the pathogen's ability to spread within the plant tissues. This localized response reduces damage and helps maintain the overall health of the wheat plant, thus contributing to yield protection (Pretorius et al., 2000).

One of the key advantages of Sr22 is its broad resistance spectrum. Unlike some resistance genes that may only function at specific growth stages or against certain pathogen strains, Sr22 is effective in both seedlings and adult plants, making it especially valuable in regions prone to stem rust epidemics. While Sr22 offers strong protection, it is often considered to provide partial resistance. This means it slows down the infection process rather than preventing it entirely. This type of resistance is beneficial as it reduces the selection pressure on the pathogen to evolve and

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overcome the resistance quickly. As a result, partial resistance like Sr22 can help prolong its effectiveness in the field, making it a key component in integrated resistance strategies (Singh et al., 2006).

Significance of gene Sr22

The importance of the Sr22 gene has grown significantly with the rise of Ug99 and its derivatives, which pose a major threat to wheat production globally. Ug99 has overcome several previously reliable resistance genes, highlighting the urgent need for more robust and durable resistance strategies. In this context, Sr22 has become a critical defense mechanism, particularly in regions where stem rust remains a persistent challenge.

To extend the durability of Sr22, breeders often combine it with other resistance genes such as Sr24 and Sr36 through gene stacking. This strategy results in multilayered resistance profiles, which are more difficult for pathogens to overcome. By using multiple resistance genes, wheat cultivars become less susceptible to pathogen adaptation, ensuring that rust resistance remains effective over time (Jin et al., 2007).

In conclusion, Sr22 plays a pivotal role in enhancing wheat's resilience to stem rust. Its incorporation into breeding programs not only reduces reliance on chemical fungicides, promoting more sustainable crop protection practices, but also strengthens global food security by protecting wheat yields from devastating rust outbreaks (Pretorius et al., 2000; Jin et al., 2007; Singh et al., 2006).

Genetic source of resistance gene Sr22

The Sr22 gene is sourced from *Triticum boeoticum*, a diploid relative of domesticated wheat (Paull et al., 1994). This wild ancestor of modern wheat has provided valuable genetic resources for wheat improvement, particularly in terms of disease resistance (Savadi et al., 2018). The Sr22 gene from *T. boeoticum* contributes to wheat's defense against stem rust (*Puccinia graminis* f. sp. *tritici*) including some races within the Ug99 lineage, which poses a significant threat to wheat production worldwide (Olson et al., 2010). This source of resistance enhances wheat's resilience to evolving stem rust pathogens, helping to ensure food security in regions vulnerable to rust epidemics (Aljadi, 2020).

Sr24

The Sr24 gene is a key resistance gene in wheat, providing defense against multiple races of *Puccinia graminis* f. sp. *tritici*, including certain strains of the highly virulent Ug99 lineage. This gene functions through a gene-for-gene resistance mechanism, where it detects specific avirulence (Avr) factors produced by the pathogen. Upon recognition of these factors, Sr24 triggers a rapid immune response, leading to restricted fungal growth and limiting the spread of stem rust within the plant tissues (McIntosh et al., 1995).

One of the significant advantages of Sr24 is its effectiveness against Ug99, a stem rust race that has caused widespread damage to wheat crops in Africa and the Middle East. While Ug99 has overcome many other resistance genes, Sr24 has remained largely effective, making it crucial in breeding programs focused on regions at high risk from this pathogen. However, some variants of Ug99 have shown partial virulence against Sr24. Despite this, the gene remains valuable, especially when used in combination with other resistance genes in a strategy known as gene pyramiding. This approach creates multilayered resistance that enhances protection and reduces the likelihood of pathogen adaptation (Jin et al., 2007). Sr24's ability to perform well across various wheat backgrounds also contributes to reducing stem rust severity and decreasing the reliance on fungicides in affected areas.

Mechanism of gene action

The Sr24 gene is commonly stacked with other resistance genes, such as Sr36 and Sr57, to create a robust, multilayered defense system against stem rust (*Puccinia graminis* f. sp. *tritici*). This strategy, known as gene pyramiding (Li et al., 2016), combines multiple resistance genes into a single wheat variety, thereby enhancing the plant's ability to withstand a range of pathogen races, including the highly virulent Ug99 strain (Sivasamy et al., 2017). The layered defense mechanism significantly impedes the pathogen's ability to adapt, making it more difficult for the pathogen to overcome the collective resistance of the stacked genes (Guest and Brown, 1997).

This multi-gene approach has become a cornerstone of modern wheat breeding, as it promotes the development of durable and resilient wheat varieties that can maintain high yields even in the face of disease pressure. By diversifying the genetic resistance, breeders can ensure that wheat crops remain protected from evolving stem rust pathogens, supporting long-term food security and sustainable wheat production (Singh et al., 2011).

Genetic source of gene

The Sr24 gene, originally derived from *Agropyron elongatum* (tall wheat grass) was successfully transferred to common wheat (Mago et al., 2005), where it significantly enhanced resistance to stem rust caused by *Puccinia graminis* f. sp. *tritici* (Plotnikova and Knaub, 2024). This gene has proven effective against several races of stem rust, including those within the Ug99 lineage, which poses a major threat to global wheat production (Prasad et al., 2017).

By incorporating Sr24 into wheat cultivars, breeders have been able to improve disease resistance and reduce the vulnerability of wheat crops to stem rust (Elkot et al., 2020). The transfer of Sr24 has played a key role in boosting the resilience of wheat, particularly in regions where stem rust is a persistent problem (McIntosh et al., 1995; Jin et al., 2007; Singh et al., 2011).

Sr36

The Sr36 gene plays a pivotal role in managing stem rust (*Puccinia graminis* f. sp. *tritici*) in wheat, particularly against virulent races within the Ug99 lineage. It provides broad-spectrum resistance, safeguarding wheat crops from multiple races of the stem rust pathogen that threaten global food production (Tsilo et al., 2007). Sr36 has shown strong effectiveness against Ug99, a strain that has overcome many other resistance genes. However, as some variants of Ug99 have developed partial virulence against Sr36, the gene is often integrated into breeding programs in combination with other resistance genes, such as Sr24 or Sr57. This stacking approach creates a multi-gene resistance profile, enhancing the durability and stability of wheat's defense against evolving stem rust strains (Jin et al., 2007).

Sr36's adaptability across diverse wheat varieties has made it a cornerstone of wheat breeding programs. By combining it with other complementary genes, breeders can create wheat cultivars that are more resilient to stem rust, ensuring sustained protection against the disease (Savin et al., 2024). This integrated strategy helps reduce the risk of resistance breakdown, supports sustainable wheat production, and minimizes the need for fungicides. Consequently, Sr36 significantly contributes to global food security, particularly in regions prone to stem rust epidemics, by providing long-term, effective disease management (Singh et al., 2011). Because *Sr36*-virulent strains prevail, breeding for durable resistance would entail pyramiding *Sr36* with other genes, a procedure that can be facilitated by DNA markers (Tsilo et al., 2007).

Mode of action of gene

The Sr36 gene functions through a gene-for-gene resistance mechanism, where it recognizes specific avirulence factors produced by the stem rust pathogen (*Puccinia graminis* f. sp*. tritici*) (McIntosh, 1988). Upon detection of these factors, Sr36 activates a robust immune response in the wheat plant. This response involves a hypersensitive reaction, where infected cells undergo programmed cell death to limit the spread of the pathogen. By isolating the infection to a small, localized area, Sr36 helps reduce the severity of stem rust and prevents it from spreading throughout the wheat tissue, thereby minimizing the overall damage to the plant (McIntosh et al., 1995).

Genetic source of gene Sr36

Originally sourced from *Triticum timopheevii* (a tetraploid wild wheat species) (Martynov et al., 2018).

Sr57

The Sr57 gene, also known as Lr34/Yr18/Pm38/Bdv1, is gene investigated the most, provides wheat with partial but durable resistance to multiple fungal diseases, including stem rust (*Puccinia graminis* f. sp. *tritici*), leaf rust (*Puccinia triticina*), stripe rust (*Puccinia striiformis*) and powdery mildew (*Blumeria graminis* f. sp. *tritici*) and Barley yellow dwarf virus (Li et al., 2023; Keller et al., 2012). This gene confers a unique form of resistance that limits disease severity rather than completely preventing infection, allowing it to maintain effectiveness over time. Its partial resistance helps slow the progress of the disease, which reduces the need for frequent control measures like fungicide applications (Radchenko et al., 2022). This makes Sr57 an important gene in breeding programs, as it provides broad-spectrum resistance that can be durable across various environmental conditions and resistances of pathogens. Additionally, Sr57's ability to slow disease development, rather than blocking it entirely, makes it less likely to be overcome by pathogen evolution compared to other resistance genes, which are often susceptible to rapid pathogen adaptation. This property is particularly beneficial for long-term disease management in wheat cultivation.

Mode of action of gene

The Sr57 gene encodes an ATP-binding cassette (ABC) transporter protein, which is involved in moving compounds across cell membranes, playing a critical role in the distribution of defense-related molecules (Peng and Yang, 2017). These compounds either signal plant defense mechanisms or directly interact with pathogens, helping to control disease levels without exerting excessive selective pressure on pathogens. This mechanism contributes to the gene’s long-term effectiveness and its ability to provide durable resistance across multiple environments (Kratinger et al., 2009).

Status of stem rust resistance in Sub-Continent

Wheat fields were surveyed from 2016 to 2022 on the prevalence of wheat stem rust branded 14 *Puccinia graminis* tritici (Pgt) pathotypes. Pathotypes 11 and 40A remained the most ubiquitous, consistent with former reports, while pathotypes 42, 117, and 117-6 recurred after an absence of more than nine years. Noteworthy stem rust resistance, attributed to numerous famous effective all-stage resistance (ASR) genes (Sr24, Sr31, and Sr38) and adult plant resistance (APR) genes (Sr2, Sr57, and Sr58), was detected among most wheat varieties. This resistance was confirmed through gene postulation and genetic analysis using markers closely linked to these genes. Furthermore, adult plant slow rusting parameters revealed highly promising values, highlighting their potential for managing stem rust through deployment or as durable resistance sources in future breeding programs. These findings provide valuable insights for deploying resistant varieties and refining wheat breeding strategies to combat stem rust effectively (Prasad et al., 2023).

CONCLUSION

The significance of wheat rust research extends beyond yield and economic benefits, addressing critical agronomic and environmental sustainability concerns. Extensive fungicide application, though effective in disease control, poses risks to environmental health, potentially disrupting ecosystems and impacting biodiversity. Evaluating these ecological effects is essential for promoting integrated pest management (IPM) approaches, which emphasize balanced, eco-friendly methods, including genetic resistance and minimal chemical intervention. Such strategies aim to create resilient agricultural systems that support both crop productivity and environmental integrity. The rapid mutation and genetic variability of rust pathogens necessitate the use of polygenic resistance strategies, such as gene pyramiding. This approach involves stacking multiple effective resistance genes to create cultivars with enduring resistance mechanisms. The emergence of highly virulent strains, like Ug99, highlights the importance of ongoing pathogen surveillance and the strategic incorporation of complementary resistance alleles from diverse germplasm sources. Global collaboration in pre-breeding and germplasm exchange is also critical. Global collaboration in pre-breeding and germplasm exchange provides access to a diverse array of genetic resources, thereby strengthening collective expertise and advancing efforts to combat transboundary pathogens. By integrating durable, race-nonspecific adult plant resistance (APR) genes with race-specific resistance genes, plant breeders can develop wheat varieties with robust genetic resistance, making it harder for rust pathogens to overcome plant defenses. This multi-layered, genetically diverse approach is vital for reducing yield losses, enhancing ecological resilience, and securing food systems in the long term. Ultimately, fostering a diverse gene pool through international cooperation will ensure resilient wheat production across various agro-ecological zones, thereby safeguarding food security amid evolving environmental and biotic challenges.

AUTHOR CONTRIBUTIONS

All authors contributed equally to this research.

COMPETING OF INTEREST

The authors declare no competing interests.

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