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STEM RUST: AN EVOLVING THREAT TO WHEAT AND STRATEGIES FOR ITS MANAGEMENT

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ABSTRACT

Ug99, a menacing strain of stem rust, emerged as a specter haunting wheat fields worldwide. Its arrival in Uganda in 1999 sent shockwaves through the agricultural community, raising alarm bells for the vulnerability of vital wheat crops. This formidable adversary, armed with mutations that defy conventional resistance in wheat, poses a substantial threat to global food security. The super strain, the ability of Ug99 to swiftly overcome resistant varieties propelled an urgent quest for new, innovative defense strategies. Researchers and scientists mobilized in a race against time, collaborating across borders to develop resistant wheat varieties capable of withstanding Ug99's destructive might. The battle against this potent rust strain symbolizes a relentless pursuit to protect the world's wheat supply, ensuring sustenance for generations to come. This review delved into Stem Rust's past to present: history, life cycle, control measures especially marker assisted selection for controlling its pace.

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INTRODUCTION

Wheat stem rust caused by the basidiomycetes fungus *Puccinia graminis* f.sp. *tritici* Ericks & E. Henn, stands as one of the most destructive ailments affecting wheat crops (Alexopoulos et al., 1996). This disease has the capability to transform a seemingly healthy field on the verge of harvest into a mass of blackened stems and shrunken grains (Calpouzios et al., 1976). Stem rust manifests as a jagged texture on the plant surface caused by clusters of uredinospores formed within brick-red pustules. These spores can easily dislodge from the plant when disturbed (Katsuya and Green, 1967; Mont, 1970). The mobility of wheat stem rust is remarkable, easily spreading across vast distances either through wind dispersal (Rowell, 1984) or unintentional transfer by humans, such as via infected clothing or plant material

(Hogg et al., 1969). For over three decades, the use of resistant cultivars has largely kept wheat stem rust in check (Luig, 1985). However, in 1999, a highly virulent strain called Ug99, identified in Ugandan wheat fields, emerged as a significant threat (Pretorius et al., 2000). Known scientifically as race TTKSK, Ug99 exhibits distinct virulence patterns, unlike any other known strain (Singh et al., 2008). It has managed to overcome several wheat resistance genes, notably Sr31, raising significant concerns (Pretorius et al., 2000). By 2007, Ug99 (Race TTKSK) had swiftly spread from East Africa to regions like Yemen and Iran, carried by wind movements. Rust pathogens, prone to rapid mutation; have given rise to six additional variants within the Ug99 lineage (Singh et al., 2015). Despite sharing the same DNA fingerprint, these variants differ in their virulence

patterns. Moreover, key resistance genes such as Sr24 and Sr36 have succumbed to these Ug99 variants (Mago et al., 2005). This situation poses a considerable threat to global wheat production, as an estimated 80-90% of wheat cultivars worldwide are susceptible to Ug99 or its variants (Jin et al., 2007). Ug99, a lineage of wheat stem rust has established itself in wheat fields across various African and Middle Eastern countries (Patpour et al., 2014). There are concerns about its rapid spread within these regions and the potential for it to extend further, posing a severe threat to global food security by potentially triggering a significant decline in wheat production (Singh et al., 2011). The renowned figure in the green revolution, Norman Borlaug, drew considerable attention to this issue in 2005, sparking subsequent efforts largely driven by his advocacy. With the capacity to cause complete crop losses of up to 100%, Ug99 displays virulence against numerous resistance genes that were previously effective in protecting wheat from stem rust (Omara et al., 2017). The initial strain of Ug99, identified as "TTKSK" according to the North American naming system, was first found in Uganda in 1998 and officially characterized in 1999,

hence the name Ug99. Since then, it has been observed in various locations including Kenya, Ethiopia, Eritrea, Sudan, Yemen, Iran, Tanzania, Mozambique, Zimbabwe, South Africa, and Egypt (Nazari et al., 2009). Presently, there are 15 recognized strains of Ug99. Stem rust is present in many countries of the world (Schumann and Leonard, 2000) including, USA, Kenya, Iran, Yemen, India and Pakistan. In Pakistan, a study on stem rust was conducted by Mirza et al. (2010) in Sindh, who reported that Sindh was predominated by varieties TD-1, TJ-83, Kiran, Sarsabaz, and Bhakar. Local stem rust was present in many parts of Sindh, including Badin, Thatta, Jhuddo, Sajawal, Matli, and Talhar. Samples were collected for the identification of Ug99. Data have shown the absence of Ug99 in Sindh. However, the local race exhibits virulence for Sr38 and Sr37 of *Triticum tauschii*. While these strains share a common ancestor, they exhibit differences in their virulence/avirulence profiles and the countries where they have been identified. Despite these variations, they maintain a close genetic relationship (Pretorius et al., 2000), as depicted in Figure 1, which also illustrates the current status and geographical distribution of the Ug99 race group.

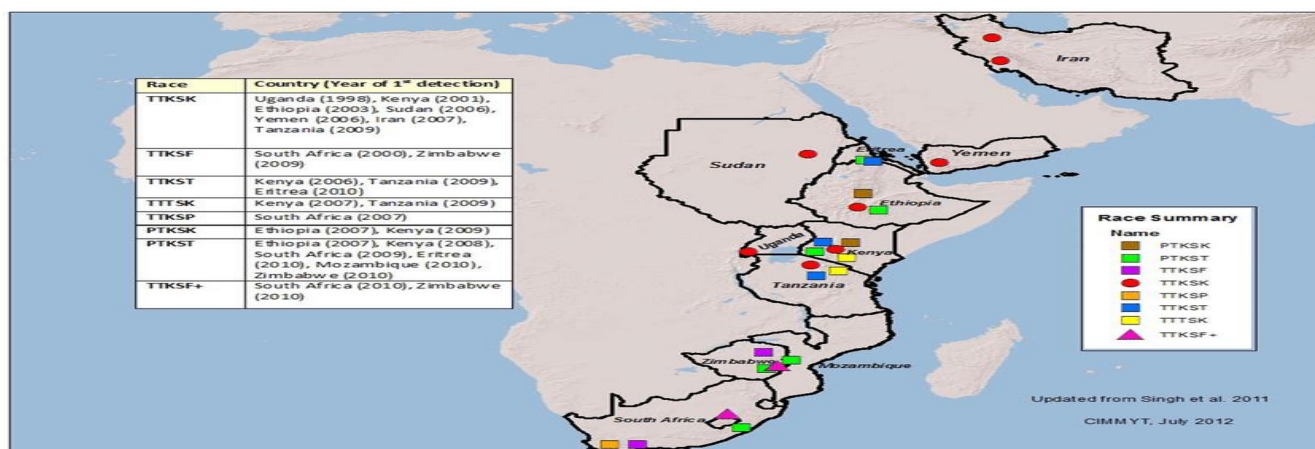


Figure 1. An overview of the current status and geographical distribution of the Ug99 race group (Singh et al., 2011).

Taxonomy

The system of classification of wheat stem rust places it in the basidiomycota subdivision, pucciniomycetes class and uredinales order, characterized by red-colored spores produced by members of this group (Choudhuri, 1958). The historical background reveals stem rust's long standing impact on grasses and wheat crops. Stem rust outbreaks, documented between 1917 and 1962, underscore the significance of this pathogen. The

discovery of Ug99 in 1999 heightened concerns, tracing back to ancient practices like sacrificing red animals to the rust god Robigo, reflecting efforts to safeguard wheat crops (Peterson and Ronald, 1974).

History of stem rust

The ancient roots of stem rust date back millennia, infecting both grasses and wheat crops (Fontana, 1932). Its havoc on U.S. wheat, with losses exceeding 20% in history, has been a recurring nightmare (Tozzetti, 1952;

Rowell, 1984). From the early 20th century till the 1960s, devastating outbreaks caused significant damage, even as far back as Aristotle's era. Romans, in a peculiar prehistoric ritual on 25th April each year, offered red animals to the rust god Robigo during the Robigalia festival, hoping to safeguard their wheat crops (Agrios, 2005). Climate tales suggest that rainy periods during the fall might have contributed to the decline of the Roman Empire, inviting harsher rust episodes, reducing wheat harvests the link between barberry and stem rust epidemics emerged in 1660, leading to the banishment of barberry plants near wheat fields, a groundbreaking step long before understanding stem rust's parasitic nature in the 1700s (Fontana, 1932).

Italian scientists in the 18th century were pioneers in understanding the stem rust fungus and identifying its stages and connections (Babajants, 1972). Further experiments established the spore stages' reliance on barberry as a host (Chester, 1946). The discovery led to concerted efforts to eliminate barberry plants near wheat fields (Beeson, 1923). With programs initiated in 1918 and later reintroduced in the 1970s, involving federal and state-level cooperation and even federal quarantine against susceptible barberry sales (Azbukina, 1972). Despite attempts to eradicate barberry, stem rust pressure persisted, shifting alongside farmers' westward movements (Basile, 1964). The historical journey

against stem rust remains a testament to humanity's quest to safeguard its wheat crops against this relentless foe (Beeson, 1923). The North American epidemic of stem rust in the early 20th century was a significant event that profoundly affected wheat crops across the continent (Roelfs, 1978). Stem rust caused widespread devastation to wheat fields during this period (Saari et al., 1968). Around the early 1900s, wheat varieties commonly grown in North America were highly susceptible to this fungal disease (Borlaug, 1954). The pathogen spread rapidly, facilitated by the prevalence of susceptible crops and conducive environmental conditions (Brondy et al., 1986).

Symptoms of stem rust and its life cycle

Stem rust predominantly impacts cereal crops such as wheat, barley, and rye. Signs consist of reddish-brown pustules seen on stems, leaves, and grains, resulting in stunted growth, weaker stems, and decreased grain yield (Roelfs, 1985). Its significance in agriculture lies in the threat it poses to crop productivity. Detecting and managing it early is vital to mitigate its harmful effects (Luig, 1985). The life cycle of stem rust fungus is fascinating (Craigie, 1927). It undergoes a complex series of stages involving both sexual and asexual reproduction (Figure 2) impacting various plant hosts, especially cereal crops like wheat, barley, and rye (Chester, 1946).

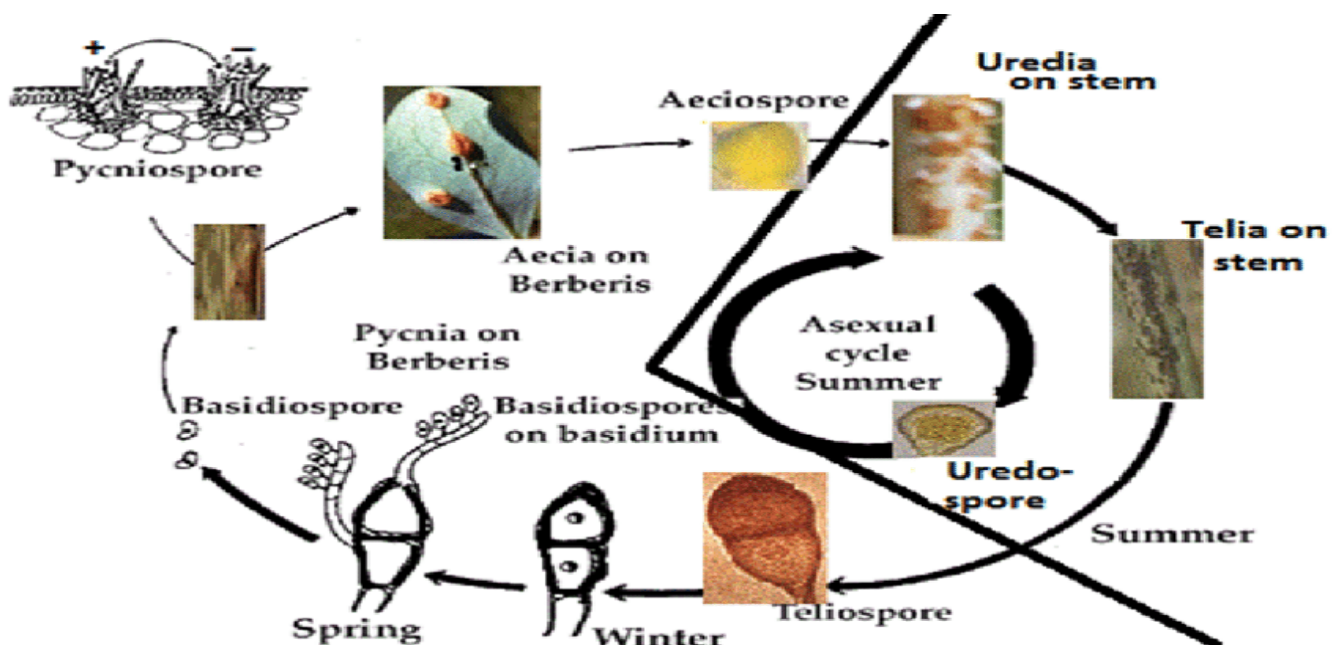


Figure 2. Life cycle of *Puccinia graminis* f.sp. *tritici* (Gupta et al., 2017).

Initial infection

The cycle typically begins when fungal spores, known as urediniospores, land on a susceptible plant's leaf surface (Roelfs, 1972).

Adhesion and germination

Once on the plant, the spores germinate, producing specialized structures called germ tubes, which penetrate the plant's outer layer, the epidermis (Hogg et al., 1969).

Infection and colonization

The fungus then spreads within the plant, forming structures called haustoria. These haustoria tap into the plant's vascular system, extracting nutrients for the fungus's growth and reproduction. This stage can cause visible symptoms such as reddish-brown pustules or lesions on the plant's surface (Zadock and Bouwman, 1965).

Asexual reproduction

Stem rust primarily reproduces asexually through urediniospores, which are produced abundantly on the plant surface within these pustules. These spores are easily dispersed by wind, water, or human activity, contributing to the spread of the disease.

Sexual reproduction

Under specific conditions, the fungus can also undergo sexual reproduction. It produces specialized spores called teliospores, which form on the plant in response to environmental cues. Teliospores are produced in structures called telia and are relatively resistant to adverse conditions. They serve as a survival mechanism for the fungus during unfavorable periods, such as winter or drought (Melching et al., 1974).

Alternate hosts

Stem rust has an intricate life cycle involving alternate hosts, such as barberry plants (Hermansen, 1968). This is where sexual reproduction occurs, completing the cycle. Teliospores formed on cereal crops infect barberry plants, leading to the formation of different spores (basidiospores) that, in turn, reinfect cereal crops, restarting the cycle (Roelfs, 1982). This cycle perpetuates the spread and persistence of stem rust, posing a significant threat to global cereal production. Crop management practices, resistant crop varieties, and fungicides are used to mitigate the impact of stem rust and prevent severe crop losses (Roelfs, 1978).

Control strategies

Control measures for stem rust involve genetic resistance, with over 50 stem rust resistance genes

cataloged. Notably, the Sr31 gene, present in 1BL/1RS translocations from rye, has played a pivotal role in preventing stem rust epidemics worldwide. However, the emergence of virulence in Ug99 poses a new challenge, prompting ongoing efforts to identify genes capable of countering this threat (Peterson and Ronald, 1974). Chemical control, through fungicides targeting sterol biosynthesis, is employed in high-disease-pressure wheat-growing areas. The distribution of stem rust is global, affecting countries like the USA, Kenya, Iran, Yemen, India, and Pakistan (Schumann and Leonard, 2000). In Pakistan, stem rust prevalence has been studied, revealing the presence of local races with virulence for specific resistance genes. Molecular markers, such as those linked to stem rust resistance genes like Sr2, Sr22, Sr24, Sr25, Sr28, Sr36, Sr39, and SrCad, play a crucial role in marker-assisted selection for breeding (Singh et al., 2006).

Genetic control

Genetic resistance, a paramount strategy for stem rust control, has demonstrated remarkable efficacy, particularly in North America post-barberry eradication (McVey and Roelfs, 1975). The decline in funding for this program raises concerns about the potential resurgence of barberry bushes, serving as both inoculum sources and facilitators for the fungus's sexual cycle. Despite the absence of barberry, the ongoing effectiveness of current resistance genes is uncertain due to the emergence of new fungal races through mutation (Mcintosh and Gyrfas, 1971). Over 50 distinct race-specific (vertical) resistance genes against stem rust have been identified or transferred to wheat through wide crosses with its wild relatives (Mcintosh and Luig, 1973). However, not all these genes prove equally valuable, with some succumbing to prevalent virulent races (Mcintosh et al., 1983). Notably, Sr31, originating from rye and integrated into wheat through interspecific hybridization, enjoyed global success since the 1980s, providing resistance against stem rust and enhancing grain yield (Mcintosh and Luig, 1973). However, Sr31 faced its match with the discovery of Ug99, a highly virulent wheat stem rust fungus race in Uganda in 1999. Despite Sr31's historical effectiveness, Ug99 swiftly overcame its resistance, spreading across Africa, Yemen, and as far as Iran (Pretorius, 2000). This poses a substantial threat to wheat production, especially in regions like the Punjab of India. In response to this looming global threat, the Borlaug Global Rust Initiative

was established in 2008, uniting international efforts to bolster wheat crop resilience against rust diseases. Focused on developing and deploying new global resistance strategies, the initiative emphasizes combining multiple vertical resistance genes for short-term effectiveness (Singh and McIntosh, 1984). In the long term, reliance on minor genes expressing horizontal resistance in adult plants becomes crucial. The International Center for Wheat and Maize Research has already produced high-yielding wheat lines with moderate horizontal resistance, which are being intercrossed to create varieties with multiple horizontal resistance genes (Simmonds and Rajaram, 1988). Genetic markers will play a pivotal role in preserving these combinations even after the Ug99 epidemics subside, enabling breeders to select for resistance in the absence of disease pressure (Singh, 1983).

Marker-assisted selection

Marker-assisted selection (MAS) is a vital technique used in safeguarding vulnerable crops like wheat from various environmental factors, particularly harmful pathogens such as rusts, bunt, and mildew (Quarrie et al., 2005). Scientists employ molecular techniques to trace the susceptibility of crops to these attacks, utilizing genetic markers or 'signboards' within the crop's genome (Kuchel et al., 2005). These markers act as constant landmarks on chromosomes, allowing the identification of genes that confer resistance or susceptibility to specific pathogens (Mohan et al., 1997). Unlike traditional methods focused on morphological traits linked to diseases, MAS directly targets genes associated with pathogen presence (Kamusa et al., 2015). By selecting crops based on these markers, MAS not only shields them from pathogens but also enhances crop yield significantly (Anderson, 2003).

Selection of important genes linked to markers

Choosing essential genes associated with markers is a common practice in the realm of plants. These significant genes regulate disease resistance, susceptibility, and male sterility, often displaying mono- or digenic characteristics, alongside traits like color, shape, and overall plant structure. Molecular markers closely tied to these key genes serve as loci for selection, proving at times to be more effective than directly targeting the specific gene of interest (Gupta et al., 2017). In both breeding and pathology, molecular markers play a crucial role in identifying genetic traits (Bariana et al., 2013). This is especially useful in

scenarios where the chosen characteristic might only manifest later in the plant's growth, such as flower and fruit features, or when dealing with adult traits that stem from a juvenile period. To achieve multiple desirable traits, selecting genes providing disease resistance can be coupled with phenotypic features or even genes unrelated to the primary characteristic. This approach, known as gene pyramiding, allows for the simultaneous selection of multiple traits.

Molecular markers for stem rust resistance genes

The Sr2 gene, utilized in breeding for over six decades, serves as a resilient source of adult plant resistance (APR) against stem rust. Notably, it offers protection against Ug99 and its related strains and is situated on chromosome 3B's short arm (Jin et al., 2008). Initially introduced from Yaroslav emmer wheat to hexaploid wheat, (Spielmeyer et al. 2003) found a strong correlation between Sr2 and a 120-bp allele at the Xgwm533 microsatellite locus in multiple lines. Hayden developed sequence-tagged microsatellite (STM) markers capable of distinguishing between various Xgwm533 variants. Sr22 gene was first identified in diploid wheat before being introduced into tetraploid and hexaploid wheat through interspecific hybridizations (Bashir et al., 2019). This gene provides effective resistance against Ug99. Haplotyping of this locus was accomplished using three linked markers (CFA2019, CFA2123, and BARC121) as described by Yu (2010). Sr24 gene first determined Sr24 to reside on the chromosome 3DL a spontaneous translocation from the 3Ag chromosome of *Agropyron elongatum*. Sr25 originating from *Thinopyrum ponticum* by Barkworth and Dewey was introduced into wheat and is effective against Ug99 (Liu et al., 2010). Additionally, the leaf rust gene Lr19 is connected to Sr25, having been relocated onto wheat chromosomes 7D (1) and 7A. Subsequently, this gene was incorporated into Australian wheat varieties through backcrossing and has been actively involved in the CIMMYT wheat breeding program (Omara et al., 2017). The gene's haplotyping utilized the co-dominant marker BF145935 and the dominant marker Gb, as reported for Sr25. Sr28 experienced a minor infection during the seedling stage and displayed an infection response in the field, classified as MS-S (moderately susceptible - susceptible) in 2005 and MS-MR (moderately susceptible-moderately resistant) in 2006. The Sr28 gene's location was identified on chromosome arm 2BL using a PCR marker, derived from

a DaRT locus closely associated with Sr28, and designated as wPt-7004-PCR (Rouse et al., 2012). GeneSr31, a significant gene in wheat genetics, confers resistance against various races of the stem rust pathogen (Visser et al., 2010). This gene, extensively studied and documented by provides robust resistance to *Puccinia graminis* f. sp. *tritici*, including the prevalent Ug99 race. Highlighted the marker Xgwm111 as tightly linked to the GeneSr31 locus, offering a reliable tool for molecular breeding programs aimed at incorporating this valuable resistance trait into wheat cultivars. The identification and utilization of this marker have paved the way for more precise selection and breeding strategies to enhance wheat's resilience against destructive stem rust diseases (Singh et al., 2006). Sr36 gene, a stem rust resistance trait, originates from *Triticum timopheevi* and confers resistance specifically to the Ug99 race of the stem rust fungus. However, it has been observed that this gene is susceptible to other races of the fungus, rendering it ineffective against them (Jin et al., 2009). Three co-dominant markers-Xstm773-2 (a derivative of Xstm773), Xwmc477, and Xgwm319- have been identified as closely linked to Sr36 according to Tsilo et al. (2008). Sr39 gene provides resistance against all known pathotypes of *Puccinia graminis* f. sp. *tritici* (Pgt), including Ug99. Through a combination of dominant PCR markers in the opposite phase, an analytical co-dominant marker for Sr39 has been developed: Sr39#22r, closely associated with the Sr39 gene (3), and an EST-derived marker, Sr39#50s, which indicates the presence of Sr39. Markers BE500705 or Sr39#50s are linked to the sr#39 gene (Mago et al., 2009). In a study, it was observed that the Canadian red hard wheat varieties "Peace" and "AC Cadillac" showed resistance to Ug99 and its variants both during the seedling stage and in field conditions (Hiebert et al., 2010). The researchers identified a potentially new gene, tentatively named SrCad, which is located on chromosome arm 6DS (Olson et al., 2010). They highlighted RSA-FSD as a linked marker associated with the bunt resistance gene, suggesting its use in molecular breeding.

CONCLUSION AND FUTURE PERSPECTIVES

Future perspectives for managing Ug99, a virulent strain of wheat stem rust, involve a comprehensive and collaborative approach. One key aspect is the continued development and deployment of resistant wheat

varieties. Research in plant breeding, including the integration of advanced technologies like gene editing, holds promise for creating crops that can withstand Ug99. These efforts aim to establish durable resistance; ensuring long-term protection against evolving rust strains. International collaboration is paramount in the battle against Ug99. Cooperation among countries, research institutions, and agricultural organizations facilitates the sharing of knowledge, resources, and surveillance data. A global network can enhance the early detection of new rust races and support timely responses to potential outbreaks. Establishing monitoring systems and adopting standardized protocols for information exchange are essential components of this strategy. Genomic studies for Ug99 involve analyzing the genetic material of both the wheat host and stem rust pathogen. Scientists study the pathogen's genome, identifying genes and variations associated with its virulence. Simultaneously, researchers investigate the genome of resistant wheat plants to pinpoint genes and markers linked to resistance. Comparative genomics helps identify key genetic differences between resistant and susceptible wheat varieties. This approach aids in developing molecular markers for marker-assisted breeding, allowing targeted selection of wheat varieties with higher resistance. Genomic studies also contribute to understanding how the Ug99 pathogen evolves; enabling researchers to anticipate new rust races and adjust breeding strategies. In summary, these studies provide a molecular understanding crucial for sustainable strategies, guiding breeding programs, and staying ahead of stem rust pathogen dynamics.

The relentless evolution of wheat stem rust, particularly the emergence of Ug99, has disrupted global wheat production, raising serious concerns about food security. Ug99's swift spread across African and Middle Eastern countries, accompanied by its ability to overpower previously resistant wheat strains, underscores the urgency of finding innovative defense strategies. The battle against this formidable rust strain represents a collaborative effort across borders, emphasizing the need for new resistant wheat varieties capable of withstanding Ug99's destructive force. Moving forward, concerted efforts are required to develop resilient wheat varieties equipped to counter the evolving threat of Ug99 and its variants. This involves leveraging genetic resistance, exploring marker-assisted selection (MAS)

techniques, and strategically deploying multiple resistance genes. Research initiatives, such as the Borlaug Global Rust Initiative, are pivotal in driving global collaborations aimed at enhancing wheat crop resilience. Molecular markers play a crucial role in MAS, enabling precise selection of genes conferring resistance against stem rust. Continued exploration of genetic control methods, alongside advancements in breeding strategies, will be instrumental in safeguarding wheat crops and ensuring food security in the face of the ever-evolving menace of stem rust.

AUTHORS' CONTRIBUTIONS

MSS collected, arranged and wrote the manuscript; AR proofread the paper; SS and ARJ provided technical assistance.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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