



Review Article

Unraveling the Genetic and Geographic Diversity of *Puccinia striiformis* f. sp. *Tritici* (Pst) Populations for Effective Control of Stripe Rust in Global Wheat Production

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Abstract | Stripe rust, caused by *Puccinia striiformis* f.sp. *tritici* (Pst), results in reduced yield and grain quality substantially, and increases production expenses, leading to billions of dollars in economic damages globally every year. Understanding the lifecycle of pathogens is vital in formulating effective management strategies for plant diseases. Pst has a complex life cycle that entails both sexual and asexual reproduction, facilitating the rapid evolution of new strains. The evolution of new races is primarily driven by the selection pressure imposed by the deployment of resistance genes in wheat cultivars. Work documented by prominent researchers conducted in diverse regions of the planet has been reviewed in this article to understand how disease perpetuates from one year to next year. Recent studies have shown that Pst populations can undergo rapid adaptation to changing environmental conditions such as temperature and humidity, which can influence the timing and severity of stripe rust epidemics. The evolution and diversity of Pst pose significant challenges for the management and control of stripe rust in wheat crops. Effective strategies for disease control require a better understanding of the genetic and geographic diversity of Pst populations and the factors driving their evolution. Effective monitoring of Pst populations is critical for developing strategies to control stripe rust and ensure the long-term sustainability of wheat production. Pathogenicity surveys, which involve testing Pst samples against differential host plants, and molecular techniques such as PCR and DNA sequencing are discussed as effective tools for tracking Pst populations, identifying new introductions and monitoring their evolution over time. A combination of traditional and molecular techniques has generated valuable data for understanding populations virulence of Pst.

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Introduction

Wheat is a significant staple crop that provides a substantial amount of daily calorie intake for billions of people globally. The demand for wheat is projected to rise to 900 million tons by 2050 due to several factors such as population growth, increasing incomes, and evolving dietary preferences. There is a need to invest in research and development of new wheat varieties that can produce higher yields, have better nutritional quality, and resist pests and diseases. Furthermore, sustainable farming practices should be adopted to increase wheat production and minimize the environmental impact of agriculture (Alexandratos and Bruinsma, 2012). Wheat production is vulnerable to multiple challenges, including pests and diseases that can significantly reduce global harvests. According to estimates, as much as 16% of the global wheat harvest is lost each year due to these debilitating factors. This underscores the critical importance of sustained investment in developing advanced varieties of wheat that exhibit enhanced resistance to pests and diseases, while simultaneously integrating sustainable agricultural practices to counteract their negative impact (Oerke, 2006; Strange and Scott, 2005). The escalating domestication of ecosystems, the impact of climate change, and the expanding scope of global trade have collectively accelerated the rate at which pathogens emerge and spread throughout the world. The ongoing evolution of persistent pathogens continues to be a major cause for concern, as it entails the potential for re-emergence through spontaneous dissemination of novel, multi-virulent variants or highly aggressive strains. Precise comprehension of the source, dispersal of diversity reservoirs, and migration routes of these pathogens is of utmost importance for formulating effective risk-assessment models and mitigating the potential adverse consequences of disease emergence (Ali et al., 2014a).

Rust pathogens: A threat to wheat production

Rust pathogens are a significant concern for wheat production (Ijaz et al., 2023). These pathogens are known to cause severe damage to crops, posing a constant threat to the production of wheat (Afzal et al., 2021, 2022a). The rust pathogens of wheat are considered to be among the most important crop pathogens due to their ability to spread quickly and infect entire fields, leading to significant yield losses (Afzal et al., 2015, 2022b). The disease caused by

these pathogens is commonly referred to as rust, which appears as small, yellowish-orange pustules on the leaves, stems, and other parts of the plant. If left untreated, rust can cause threat to food security. Farmers often have to resort to costly and environmentally harmful chemical treatments to control the spread of rust, highlighting the urgency of finding more sustainable and effective solutions to combat these pathogens. In conclusion, the rust pathogens of wheat pose decreased crop production, and their effective management is critical to ensure food security and sustainable agriculture (Dean et al., 2012).

Crop suffers three different types of rusts: Stem rust, leaf rust, and stripe rust. The three rusts that affect wheat are characterized by different etiology (causal agents), symptomology (visible symptoms), and epidemiology (patterns of disease spread). Stem rust, caused by *Puccinia graminis* f.sp. *tritici*, produces elongated, reddish-brown pustules on stems and leaves. Leaf rust, caused by *Puccinia triticina*, produces circular or oval-shaped, orange-brown pustules on leaves. Stripe rust, caused by *Puccinia striiformis* f.sp. *tritici*, produces yellow-orange stripes of pustules on leaves and other above-ground plant parts. These rusts also differ in their patterns of disease spread, with stem rust being more prevalent in warmer regions, leaf rust in moderate regions, and stripe rust in temperate regions. Understanding these differences is indispensable for effective disease management and control. Among them, stripe rust, is a major concern for wheat growers worldwide due to its ability to rapidly evolve new races and cause epidemics that can result in severe yield losses. Therefore, it is vital to monitor and understand the genetic diversity and evolution of stripe rust populations to develop effective strategies for disease management and control.

Wheat in peril: Tackling the growing threat of yellow rust and the urgency for effective management strategies

Yellow rust, commonly known as stripe rust, is a prominent disease that affects wheat crops (Chen, 2020; Welling, 2011). It is caused by a biotrophic fungal pathogen called *Puccinia striiformis* Westend f. sp. *tritici* (Pst). Yellow rust primarily targets the leaves of the wheat plant, resulting in the deterioration of photosynthetic tissues, decreased light interception, and lowered radiation use efficiency, ultimately culminating in reduced yields (as illustrated in Figure 1). Indeed, moderate to severe epidemics of yellow

rust can lead to the infection of other structures of the wheat ear, such as glumes, lemma, and palea, which intensifies the adverse impacts and jeopardizes both the quality and quantity of grain yield (Bouvet *et al.*, 2022; Cromey, 1989; Wellings *et al.*, 2003, 2009). The presence of incursions of economic importance caused by Pst (*Puccinia striiformis* f. sp. *tritici*), also known as wheat stripe rust, has been reported in various regions. Wheat stripe rust is one of the most economically important wheat diseases and poses a serious threat to food security, particularly in regions heavily reliant on wheat as a staple crop. These incursions refer to the occurrence of significant outbreaks or outbreaks with potential economic consequences for wheat production in affected areas. The origin of these incursions refers to identifying the source or location from where the specific pathogen strains responsible for the outbreaks originated. Determining the origin of the pathogen is crucial for understanding how it spreads, assessing its genetic diversity, and developing appropriate control and management strategies.



Figure 1: Comparison of shriveled grains and healthy grains infected by stripe rust.

Confirming the origin of Pst incursions typically involves conducting extensive research and analyses, including genetic studies, molecular markers, and pathogen surveillance. By comparing the genetic characteristics of the pathogen strains found in affected areas with known strains from different regions, researchers can trace the likely source of the incursion. It's important to note that confirming the origin of pathogen incursions can be challenging, especially if the pathogen has already spread over large distances. In some cases, incursions might be linked to the movement of infected plant material, contaminated machinery, or wind-dispersed spores over long distances. Recent advancements in genetic and genomic technologies have improved our ability to trace the origins of pathogens more accurately. By understanding the sources and pathways of pathogen

spread, authorities can implement targeted measures to prevent or limit further spread and manage the impacts on wheat production effectively. Tracking and confirming the origin of Pst incursions is an ongoing process as pathogens can continually evolve and adapt. Therefore, continuous monitoring and research efforts are necessary to stay ahead of potential threats to wheat crops and ensure global food security. Over the past six decades, numerous recurrent epidemics of *Puccinia striiformis* Westend f. sp. *tritici* (Pst) have affected a substantial portion of the regions where wheat is cultivated. If left to proliferate unchecked, these epidemics can engender substantial yield losses and impair the quality of grain harvested (Ali *et al.*, 2014a).

Combatting the threat of rapidly evolving populations of Pst: Challenges and strategies

The pathogen has a complicated life cycle that encompasses sexual in addition asexual reproduction, which enables it to quickly acclimatize to rehabilitated ecological circumstances and effectively overcome resistance genes deployed in wheat cultivars. Consequently, it is of utmost importance to implement effective management and control strategies to combat this disease and guarantee the production of premium quality wheat (Wellings, 2011).

It is noteworthy that highly virulent Pst strains emerged rapidly during 21st century that exhibited a remarkable acclimatization to intense heat (Hovmøller *et al.*, 2016; Hubbard *et al.*, 2015; Milus *et al.*, 2009) As a consequence, numerous wheat varieties against Yellow Rust (YR) which exhibited resistance against stripe rust have been affected adversely. Pst populations are highly diverse, with multiple races identified based on their ability to overcome specific resistance genes in wheat. In response to the continuously evolving threat posed by *Puccinia striiformis* Westend f. sp. *tritici* (Pst), the breeding targets for Yellow Rust (YR) resistance have undergone adaptation, prompting the ongoing exploration of genetic resistance sources to advance wheat variety development. This proactive approach aims to effectively counter the rapid changes in pathogen dynamics and maintain sustainable wheat production in the face of emerging challenges. Recent advancements in wheat genomics approaches, coupled with thorough characterization of *Puccinia striiformis* Westend f. sp. *tritici* (Pst) population pathotypes, genetic diversity, effector characterization, and field monitoring, have significantly facilitated

these efforts. Ultimately, effective management of wheat fungal diseases will necessitate the adoption of an integrated approach that combines agronomic practices, disease surveillance, and varietal genetic improvement (Downie *et al.*, 2020). McIntosh *et al.* (2021) documented eighty-four genes exhibiting resistance against stripe rust and many of them if not all are being used successfully in wheat improvement programs. This comprehensive strategy aims to enhance crop resilience, minimize disease incidence, and sustainably enhance wheat productivity in the face of evolving pathogen threats. This article aims to provide a clear and concise summary of what we currently know about the lifecycle of Pst, how the fungus spreads, the genetic diversity of the fungus, and the genetic resistance of wheat against it. Moreover, it sheds light on the challenges that arise in our efforts to protect wheat from YR infection and how we can overcome them.

Understanding the lifecycle of Pst and the crucial role of the erotic stage in wheat stripe rust outbreaks?

The lifecycle of Pst involves five distinct stages, and it entails two different species to complete cycle. The lifecycle of Pst can be broadly classified into two stages: The parthenogenetic stage that happens on wheat, which is the primary host, and the erotic stage that happens on Berberis species, which is the alternate host.

Symptoms of YR disease appear in wheat during the asexual stage of the Pst lifecycle. Wheat stripe rust is triggered by multiple cycles of dikaryotic *Puccinia striiformis* urediniospores, which have two nuclei in each cell, infecting the primary host repeatedly contributing significantly to its spread and impact on wheat crops. During the early stages of wheat infection by the pathogen, the process begins with urediniospores landing on the surface of the wheat leaf (Chen *et al.*, 2014). These spores are a type of asexual spore produced by the pathogen. Under favorable conditions, such as adequate moisture and temperature, the urediniospores germinate, extending germ tubes that eventually give rise to appressoria. Appressoria are specialized structures that form at the tips of germ tubes. They are responsible for facilitating the penetration of the pathogen into the host tissue. The appressorium generates turgor pressure, enabling it to exert mechanical force and penetrate the host surface, primarily through stomata, which are tiny openings on the leaf surface that allow gas exchange.

Once the appressorium successfully penetrates the wheat leaf, it develops hyphae (Mapuranga *et al.*, 2022). Hyphae are thin, thread-like structures that grow and form a dense network between and inside the host mesophyll cells. Mesophyll cells are the main photosynthetic cells of the plant, and the pathogen's hyphal network grows between these cells to access nutrients. Within this network of hyphae, the pathogen will form specialized infection structures called haustoria. Haustoria are structures that the pathogen develops specifically to invade and exploit the host cells. They penetrate the host cell walls and establish a close association with the host's vascular system, extracting nutrients from the plant cells to support their growth and reproduction. By forming haustoria, the pathogen establishes a parasitic relationship with the wheat plant, tapping into its resources and weakening its overall health. The nutrients extracted by the pathogen are then utilized to fuel the further growth and proliferation of the pathogen within the plant, perpetuating the infection cycle. Understanding the various stages of the pathogen's infection process is crucial for developing effective strategies to combat wheat diseases and mitigate their impact on crop yields and food security. By targeting specific stages of the pathogen's life cycle, researchers and farmers can work towards the development of resistant wheat varieties or other management approaches to control the spread and damage caused by these pathogens (Szabo and Bushnell, 2001). The pathogen produces yellow to orange urediniospores that appear on the mature leaves about 12-14 days after infection. These urediniospores are produced within pustules, which are small, raised structures on the leaf surface. The infection causes stripe-like patterns along the veins of the leaf blade, where the urediniospores are arranged. The appearance and severity of symptoms can vary depending on the susceptibility of the wheat variety and the specific rust pathogen involved.

Mildly susceptible to resistant wheat varieties may exhibit a range of symptoms that differ from those seen in highly susceptible varieties. Instead of the typical stripe-like patterns with abundant urediniospores, these varieties may show symptoms such as small, non-sporulating flecks on the leaves or chlorotic patches with limited sporulation. These symptoms are often less severe and may not lead to extensive damage or spread of the disease.

It's essential to understand the variability in symptom

expression and the life cycle of the rust pathogen to develop effective management strategies, including the use of resistant varieties and cultural practices, to minimize the impact of rust diseases on wheat crops. Regular monitoring and early detection can aid in implementing appropriate control measures to protect the crop and maximize yield potential. Subsequent meiosis leads to the formation of a basidiospore, capable of infecting the alternate host ([Chen et al., 2014](#)). The sexual stage of *Puccinia striiformis* f. sp. *tritici* (Pst) was not well understood, but it had been hypothesized that *Berberis* species may serve as alternate hosts for the pathogen's life cycle (e.g. [Straib, 1937](#); [Hart and Becker, 1939](#)). In addition, *Berberis* species have been implicated as alternate hosts for related rust species, such as *Puccinia graminis* f. sp. *tritici*, which is the causal agent of stem rust. As a result, there have been attempts to eliminate completely *Berberis* species in numerous countries in Europe and North America ([Barnes et al., 2020](#)). It was the team work of [Jin et al. \(2010\)](#) who legitimately established the role of *Berberis* species in supporting the evolution of pycnia and aecia in Pst. Interestingly, in the wild, *Berberis* species infected with Pst are observed rarely ([Zhao et al., 2011, 2013](#)). This situation could be rationalized as finding appropriate atmosphere that accommodates the germination of both teliospores (which belong to the asexual stage and are enclosed in telia formed on wheat leaves at the end of the infection season, producing basidiospores) and basidiospores (which belong to the sexual stage and form on barberry leaves, necessitating evening dew for sprouting). Moreover, the viability period for both types of spores is short, which further complicates their detection in natural settings ([Wang and Chen, 2015](#)). A research work conducted recently has provided evidence that *Berberis* species do not play substantial role in the incidence and spread of epidemics of Yellow Rust (YR) in the in Pacific Northwest region in the United States ([Wang and Chen, 2015](#)). The study's findings suggest that *Mahonia aquifolium* may serve as a reservoir for YR spores during the non-crop season, potentially enabling the pathogen to survive and persist until the next growing season. However, further research is needed to understand the specific mechanisms underlying the interaction between *Mahonia aquifolium* and YR, as well as the potential impact of this alternate host on YR epidemics in the Pacific Northwest ([Wang and Chen, 2013](#)). The sexual stage of *Puccinia striiformis* f. sp. *tritici* (Pst),

which is the pathogen responsible for wheat stripe rust, is of great importance in wheat infection. During this stage, new combinations of genetic variation might happen, leading to generating novel isolates of the pathogen. These newly formed isolates can have a significant impact on wheat resistance profiles resulting in epidemics, leading to swift fluctuations in the pathogen population. This process of genetic recombination during the sexual stage allows the pathogen to overcome resistance in wheat varieties that were previously effective against the pathogen. This is because the new genetic combinations that arise may result in the pathogen having a different set of virulence genes, which can then enable it to infect previously resistant wheat varieties. Understanding the importance of the sexual stage in the Pst life cycle is crucial for developing effective strategies for managing wheat stripe rust outbreaks. By monitoring the occurrence and spread of sexually recombined isolates of the pathogen, researchers can develop more targeted and effective approaches for controlling the disease and minimizing its impact on wheat production.

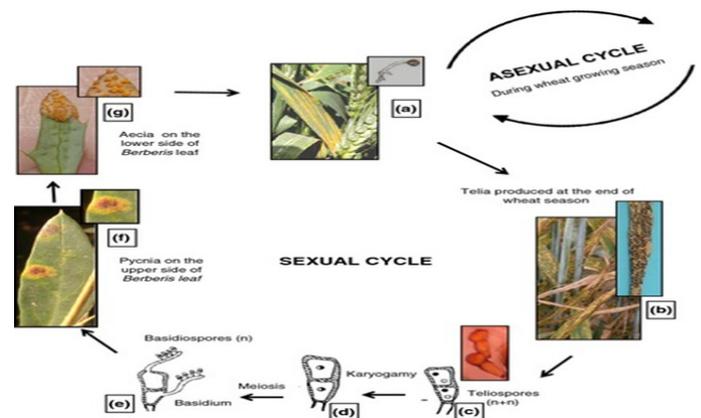


Figure 2: Disease cycles of *Puccinia striiformis* f. sp. *tritici*: (a) Insights into uredinial stage formation and epidemic progression; (b) Transition from Uredinial to Telial stage; (c) Teliospore production on wheat; (d) Karyogamy; (e) Formation on basidiospore production; (f) Basidiospore dispersal and disease initiation on *Berberis* spp. at the pycnial stages (g) and aecial stages on the upper and lower leaf surfaces of *Berberis* spp. ([Ali et al., 2014](#)).

The Pst lifecycle begins with the production of thick-walled resting spores called teliospores on infected wheat plants. These spores germinate to produce unicellular basidiospores, which can infect alternate host plants. These spores can cause secondary infections, leading to the formation of cup-shaped structures called aecia that produce aeciospores. The lifecycle also includes the production of small, dark, round-shaped structures called pycniospores, which

are involved in the sexual reproduction of the fungus. Overall, the Pst lifecycle involves multiple stages of spore production and infection, and the fungus can cause significant damage to wheat crops if left untreated (Figure 2). For more info, consult [Chen *et al.* \(2014\)](#), [Schwessinger \(2016\)](#) or [Mehmood *et al.* \(2020\)](#).

Monitoring virulence changes in Pst populations to protect wheat crops: The importance of pathogenicity surveys and other methods

Pathogenicity surveys are a commonly used method for monitoring changes in virulence in Pst populations. These surveys involve growing sets of differential wheat lines, which are either near-isogenic lines or cultivars carrying known resistance genes, and characterizing the pathotypes of Pst at the seedling stage. By observing which lines are susceptible to the Pst infection and which lines remain resistant, researchers can gain insight into the virulence changes of the Pst population over time. The use of differential wheat lines is important because different lines carry different resistance genes. By testing a range of differential lines, researchers can determine which resistance genes are effective against the Pst population in a given region. If previously resistant lines become susceptible, it suggests that the Pst population has adapted to overcome the resistance gene in question. These surveys are typically conducted over multiple years to track changes in Pst virulence over time. By monitoring changes in the Pst population, researchers can develop strategies to manage the disease and protect wheat crops from devastating losses. In addition to pathogenicity surveys, other methods such as DNA sequencing and genotyping can also be used to track changes in Pst populations. These methods can provide more detailed information about the genetic makeup of the pathogen and help researchers better understand how it is evolving and adapting over time ([Wellings *et al.*, 2009](#)).

Advances in understanding wheat stripe rust through molecular and genomics techniques

In recent times, there has been a notable rise in the application of advanced molecular and genomics techniques to elucidate the population structure and genetic diversity of *Puccinia striiformis* f. sp. *tritici* (Pst). These cutting-edge methodologies have provided invaluable insights into the intricacies of Pst's genetic makeup and its diverse population dynamics.

The use of molecular tools has facilitated the examination of genetic markers, such as microsatellites or single-nucleotide polymorphisms (SNPs), to explore the relatedness among Pst isolates collected from different geographical regions ([Yirgu *et al.*, 2023](#)). By analyzing these markers, researchers have been able to discern patterns of gene flow, identify distinct populations, and infer migration events. These findings offer valuable clues about how Pst spreads and evolves, helping us comprehend its global dissemination and adaptability to different environments.

Moreover, genomics approaches have ushered in a new era of investigation by enabling comprehensive whole-genome analyses of Pst. High-throughput sequencing technologies have facilitated the rapid decoding of Pst's entire genetic blueprint, allowing scientists to scrutinize its genes, regulatory elements, and potential virulence factors. The comparative genomic analyses of different Pst isolates have revealed genetic variations, including gene gain or loss, and identified candidate genes associated with pathogenicity and host adaptation. These discoveries hold immense promise for understanding the underlying mechanisms behind the evolution of virulent strains and their capacity to overcome host resistance ([He *et al.*, 2021](#)).

Furthermore, the integration of molecular and genomics data has unveiled the complex population structure of Pst. It has become evident that the pathogen exists as a diverse array of lineages, each with unique genetic characteristics. The knowledge of such diversity is essential in devising targeted disease management strategies, especially in regions where specific Pst variants predominate.

These new approaches have provided valuable insights into the evolution and adaptation of the pathogen, confirming some of the patterns previously hypothesized through pathotype-based studies. Over the past three decades, research on Pst has yielded a wealth of knowledge on the patterns of spore dispersal and pathogen evolution. For example, studies have shown that Pst spores can travel long distances and rapidly colonize new geographic regions, contributing to the emergence of new pathogen races and the rapid spread of epidemics. Additionally, genomic studies have revealed the genetic basis of pathogen adaptation, including the identification of virulence

genes that enable Pst to overcome wheat resistance genes. These findings have important implications for the development of new wheat varieties with durable resistance to Pst, as well as for the design of strategies for disease management and control. Overall, the past three decades of research on Pst have greatly advanced our understanding of the ecology and evolution of this important plant pathogen. The continued use of molecular and genomics techniques will undoubtedly contribute further to our knowledge of Pst and its interactions with wheat, with the potential to inform new approaches for disease management and crop protection (Bouvet *et al.*, 2022)

In summary, the adoption of molecular and genomics techniques has revolutionized our comprehension of Pst's population dynamics and genetic diversity. These advancements have paved the way for more informed approaches to combat Wheat Stripe Rust, promoting the development of resistant wheat varieties and fostering sustainable disease management practices. As our understanding of Pst's genetics continues to deepen, we are better equipped to safeguard global wheat production and ensure food security for future generations.

Understanding the dispersal patterns of Puccinia striiformis f. sp. tritici (Pst) urediniospores: Implications for disease management

The global spread of wheat stripe rust, is a significant concern for wheat production worldwide.

Several factors contribute to the dispersal of stripe rust (*Puccinia striiformis* f.sp. *tritici*) worldwide:

1. Long-range spore dispersal: Pst urediniospores are capable of being dispersed over long distances by wind. This allows the pathogen to cross continents and reach distant regions, leading to its global dissemination. Wind patterns, atmospheric stability, and geographic features all influence the extent and direction of spore movement.
2. International trade and travel: Wheat and other plant materials are commonly traded and transported between countries. Infected plant materials, including seeds and seedlings, can carry the pathogen to new locations, facilitating its introduction into previously uninfected regions.
3. Global climate change: Changes in climate, including temperature, humidity, and precipitation patterns, can influence the distribution and severity of wheat stripe rust. Shifts in environmental

conditions may create new favorable areas for the pathogen or alter the timing and intensity of disease outbreaks.

4. Pathogen genetic variability: Pst populations can exhibit genetic variability and evolve new races that overcome previously resistant wheat varieties. The emergence and spread of new virulent races can contribute to the disease's global spread by affecting susceptible wheat varieties in various regions.
5. Lack of resistant wheat varieties: In regions where wheat stripe rust is a recurring problem, the cultivation of susceptible wheat varieties increases the risk of disease spread. Planting resistant wheat varieties can help mitigate the spread of the pathogen.
6. Limited surveillance and monitoring: In some regions, limited resources and infrastructure for disease surveillance and monitoring may hinder the early detection and response to wheat stripe rust outbreaks. Timely identification and reporting of the disease are crucial for implementing effective control measures.

Efforts to combat the global spread of wheat stripe rust include:

- Developing and deploying resistant wheat varieties: Breeding for resistance to specific races of Pst is an essential strategy for reducing the impact of wheat stripe rust in various regions.
- International collaboration and information sharing: Cooperation between countries and research institutions allows for the exchange of knowledge, resources, and data on disease outbreaks, enabling a more coordinated response to wheat stripe rust on a global scale.
- Disease surveillance and monitoring: Improving surveillance systems to detect the presence and spread of wheat stripe rust in different regions helps facilitate early warning and rapid response measures.
- Integrated disease management: Implementing a combination of cultural practices, chemical control, and resistant varieties can provide effective control of wheat stripe rust.

The global nature of wheat stripe rust highlights the importance of collaborative efforts among researchers, policymakers, and farmers to tackle this significant threat to wheat production and food security worldwide.

Understanding the dynamics of Pst dispersal is crucial for effective disease management and control. By studying the mechanisms and patterns of spore dispersal, researchers can develop strategies to predict and mitigate the spread of the pathogen, such as through targeted monitoring and early warning systems. Additionally, research on the factors influencing the survival and transmission of Pst spores can inform the development of new approaches to disease management, including the use of fungicides and the breeding of resistant wheat varieties (Zeng and Luo, 2006; Brown and Hovmöller, 2002).

Understanding Pst population movement and adaptation: Implications for disease management and crop protection

Pst populations rely on the presence of living host plants to survive and reproduce. In regions where wheat is grown, Pst survives between cropping seasons as dormant mycelium on infected crop residue, or in the form of spores on volunteer wheat plants or other grasses. However, in regions where wheat is not grown year-round, *Puccinia striiformis* f. sp. *tritici* (Pst) is unable to over-winter in the absence of living host tissue, and its survival during the off-season solely relies on spore dispersal to establish new populations in cropping season each year. Spore movement follows prevailing winds and the seasonality of cropping seasons because these factors determine the availability of suitable hosts for Pst. Prevailing winds carry Pst spores from regions where wheat is grown to regions where wheat is not currently being grown, but where it will be grown in the upcoming cropping season. The seasonality of cropping seasons also plays a role, as Pst spores are more likely to establish new populations in regions where the timing of wheat planting and growth coincides with the availability of spores from nearby regions. Overall, the movement and adaptation of Pst populations is a complex process that is influenced by a range of environmental factors, including host availability, prevailing winds, and seasonality. By monitoring these factors and tracking changes in Pst populations over time, researchers can develop effective strategies to manage the disease and protect wheat crops from losses (Chen, 2005). In Northwestern Europe, the spore dispersion of *Puccinia striiformis* f. sp. *tritici* (Pst) appears to be consistent with the continental-island model, which was first described by Hedrick (1985). This model proposes that pathogen populations in island-like regions, such as the British Isles, are influenced by long-distance dispersal events from larger continental

populations, resulting in a mosaic-like distribution of pathogen diversity. In this scenario, Pst populations in the British Isles are thought to be maintained by frequent introductions of new pathogen races from the European mainland. The prevalence of particular pathogen races in the British Isles can thus be seen as a result of the balance between the introduction of new races and the extinction of established ones, as well as local adaptation to environmental conditions. Understanding the underlying mechanisms of Pst spore dispersal in different regions is important for predicting disease outbreaks and designing effective management strategies. By characterizing the spatial and temporal patterns of Pst spore dispersal, researchers can gain insight into the sources of inoculum, the likelihood of disease spread, and the potential for evolution and adaptation of the pathogen.

Mosaic-like distribution of wheat stripe rust in northwestern Europe: Causes and consequences

The continental-island model, proposed by Hedrick in 1985, is identified as the primary model of *Puccinia striiformis* f. sp. *tritici* (Pst) spore dispersion in Northwestern Europe. The spores of this fungal pathogen are able to travel up to 1700 km with prevailing winds, leading to their migration between countries such as the United Kingdom, Germany, France, and Denmark (Hovmöller *et al.*, 2002). The spatiotemporal patterns of Pst spore dispersion in Northwestern Europe can be attributed to the combination of long-distance spore dispersal events and the existence of isolated populations on geographic islands, such as the British Isles. This results in a mosaic-like distribution of pathogen diversity, with different pathogen races being prevalent in different regions. Understanding the mechanisms and patterns of Pst spore dispersal in Northwestern Europe is essential for developing effective strategies for disease management and control. By characterizing the sources of inoculum and the likelihood of disease spread, researchers can develop targeted monitoring and early warning systems to predict and mitigate the spread of the pathogen. Additionally, studying the genetic diversity and adaptation of Pst populations can inform the development of new approaches to disease management, such as the breeding of resistant wheat varieties.

Emergence of stripe rust through foreign incursion: Implications for global agriculture

The phenomenon observed in investigations of yellow

rust (YR) emergence events in countries where it was previously absent can be described as inter-continental foreign incursion. This term refers to the introduction and establishment of the disease in new regions through the inadvertent movement of rust spores from one continent to another.

The recorded instances of stripe rust incursion in Australia, starting from its initial detection in 1979, exemplify the trend of increased frequency of exotic incursions over the last century (Ding *et al.*, 2021; Liu *et al.*, 2021). This trend is attributed to various factors, including the heightened global travel by individuals and the unintentional transport of rust spores via contaminated clothing or other means (Welling, 2007). Rust fungi, including the wheat yellow rust fungus *Puccinia striiformis* f. sp. *tritici*, have the remarkable ability to rapidly overcome the effects of host resistance genes. Moreover, the spores of these fungi can disperse over long distances through wind, allowing them to be carried across continents. This wind-mediated dispersal, combined with their adaptability to evade host resistance, enables swift and simultaneous invasions in multiple regions. The study conducted by Hovmøller *et al.* (2008) demonstrated this phenomenon when strains of *Puccinia striiformis* f. sp. *tritici* invaded North America, Australia, and Europe within a remarkably short period of fewer than three years. Notably, the invading strains were found to be genetically similar to each other, indicating a high degree of relatedness among the different populations that spread across continents. Overall, this phenomenon of inter-continental foreign incursion highlights the need for heightened biosecurity measures and vigilance in monitoring and preventing the inadvertent movement of rust spores. Understanding the dynamics of exotic incursions and the rapid adaptability of rust fungi is essential in developing effective strategies to safeguard global wheat production and mitigate the impact of wheat stripe rust on agricultural systems

These incursions underscore the utmost importance of diligently monitoring and effectively controlling the propagation of yellow rust (YR) and other plant diseases across international borders. Implementing robust quarantine measures, involving meticulous inspection and rigorous testing of imported plant materials, can serve as a crucial line of defense to preclude the introduction of novel plant pathogens into a country's delicate ecosystem. Moreover, early

detection and swift response mechanisms for emerging disease outbreaks are indispensable in curtailing their diffusion and mitigating potential economic ramifications on the agricultural sector. Remarkably, genetic investigations have revealed a significant linkage between the Pst isolates that infiltrated South Africa in 1996 and populations originating from the Mediterranean and Central Asia. These findings underscore the relatively recent arrival of the pathogen to these regions (Boshoff *et al.*, 2002; Ali *et al.*, 2014a). Human activities, likely associated with unintentional transportation on garments, have been explicitly demonstrated or strongly implicated in all three instances, signaling the escalating significance of global trade and travel as instrumental conduits for the dispersal of Pst urediniospores (Bouvet *et al.*, 2022). In essence, these developments underscore the pressing need for heightened international cooperation in closely monitoring and controlling the cross-border movement of plant diseases. Concerted efforts aimed at implementing stringent quarantine protocols, timely disease surveillance, and prompt response strategies can effectively safeguard agricultural productivity and safeguard global food security.

The evolution and diversity of Puccinia striiformis f. sp. tritici pathogen

Research conducted before the year 2000 on the wheat rust pathogen, *Puccinia striiformis* f. sp. *tritici* (Pst), elucidated its primarily clonal propagation with limited genetic variability arising from single-step mutations (Hovmøller *et al.*, 2002, 2016; Enjalbert *et al.*, 2005; Chen, 2005; Steele *et al.*, 2001; Chen *et al.*, 2010; Ali *et al.*, 2014a; Hubbard *et al.*, 2015). The prevalence of clonally derived mutations in Pst resulted in devastating epidemics of yellow rust (YR) when wheat varieties possessing specific resistance genes failed to protect against these genetically homogenous strains. Although Pst isolates from regions outside the Himalayas exhibited low genetic variation, exceptions were noticed in isolates from the Himalayan and nearby areas, signifying higher levels of genetic recombination, sexual reproduction, and overall diversity (Duan *et al.*, 2010; Mboup *et al.*, 2009; Ali *et al.*, 2014b). These regions were identified as potential centers of Pst origin, indicating their pivotal role in shaping the genetic landscape of the pathogen. In more recent times, highly aggressive strains of Pst, exemplified by PstS1 and PstS2, have emerged on a global scale, attesting to the ongoing evolution and

adaptation of the pathogen. Their rapid dissemination has been attributed to augmented spore production and superior tolerance to high-temperature conditions (Chen *et al.*, 2002; Hovmöller and Justesen, 2007; Markell and Milus, 2008). Moreover, various instances of genetic divergence have been observed in Pst populations across different regions, leading to the emergence of new races such as PstS7, PstS8, PstS10, and PstS4, which have displaced previously dominant races (Ali *et al.*, 2017; Hovmöller *et al.*, 2016; Hubbard *et al.*, 2015). The findings highlighted in this research emphasize the intricate and dynamic nature of *Puccinia striiformis* f. sp. *tritici* (Pst) evolution, necessitating vigilant and continual surveillance and assessment to comprehend its shifting genetic landscape. Such insights are of paramount importance for formulating and deploying effective disease management strategies to safeguard global wheat production. Furthermore, certain unconventional observations have given rise to speculations regarding the possibility of aerial-induced foreign incursions into Europe. The introduction of novel Pst strains from outside Europe has resulted in rapid invasions and substantial changes in Pst populations, leading to severe yellow rust (YR) epidemics in regions such as Central Asia, North Africa, and East Africa. Given the relentless evolution and dissemination of these aggressive Pst strains, it is imperative to prioritize ongoing research and monitoring efforts. These initiatives are critical in devising and implementing comprehensive strategies to control Pst and minimize its deleterious impact on global wheat production. In conclusion, a comprehensive understanding of Pst's evolutionary dynamics is essential in developing adaptive and robust approaches to combat this pathogen effectively and sustain wheat productivity on a global scale. Continuous vigilance and cutting-edge research are vital components of a proactive and pre-emptive response to the challenges posed by Pst and its potential to cause significant agricultural losses worldwide.

Conclusions and Recommendations

Investing in research and sustainable farming practices is crucial to meet the growing demand for wheat and combat the threat of rust pathogens like Pst. Pst is a fungal pathogen that causes stripe rust in wheat crops and can quickly adapt and evolve to overcome resistance genes, making it difficult to manage. The threat of *Puccinia striiformis* f. sp. *tritici*

(Pst) to global wheat production is a serious concern that needs immediate attention. The sexual stage, plays a critical role in the genetic diversity of Pst and its ability to overcome wheat resistance, highlighting the importance of controlling barberry bushes in areas where wheat is cultivated. In addition to genetic diversity, Pst populations also show geographic diversity, with different races and strains present in different regions of the world. This geographic diversity is thought to be driven by the movement of Pst spores through long-distance wind dispersal and the movement of infected plant materials. Genetic and geographic diversity of Pst populations are significant factors in its ability to overcome wheat resistance, and controlling barberry bushes in wheat-growing areas is essential. Monitoring changes in Pst populations' virulence is crucial for protecting wheat crops, and a combination of traditional and molecular techniques can provide a comprehensive picture of Pst populations' virulence and inform management decisions. This can be achieved through pathogenicity surveys that involve collecting samples and testing them against differential host plants. Molecular techniques like PCR and DNA sequencing can also be used to track the movement and spread of Pst populations and identify specific genetic markers associated with virulence. A combination of traditional and molecular techniques can provide a comprehensive picture of Pst populations' virulence and inform efforts to manage this pathogen effectively. To combat this disease, a thorough understanding of the genetic and geographic diversity of Pst populations is necessary. Investing in research and sustainable farming practices, such as genetic resistance breeding, pathogenicity surveys, and molecular monitoring techniques, is essential for ensuring the long-term sustainability and productivity of global wheat production. Continued commitment to innovative and sustainable approaches to disease management and control is crucial to secure a stable and reliable global food supply. The article emphasizes the need for a better understanding of Pst populations' genetics and evolution to develop effective strategies for disease control, including pathogenicity surveys and molecular monitoring techniques.

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Novelty Statement

Stripe rust, caused by *Puccinia striiformis* f.sp. *tritici* (Pst), results in reduced yield and grain quality substantially. Recent studies have shown that Pst populations can undergo rapid adaptation to changing environmental conditions such as temperature and humidity, which can influence the timing and severity of stripe rust epidemics. The evolution and diversity of Pst pose significant challenges for the management and control of stripe rust in wheat crops. Pathogenicity surveys, which involve testing Pst samples against differential host plants, and molecular techniques such as PCR and DNA sequencing are discussed as effective tools for tracking Pst populations, identifying new introductions and monitoring their evolution over time. A combination of traditional and molecular techniques has generated valuable data for understanding populations virulence of Pst.

Author's Contribution

Amir Afzal initiated the project, formulated the main conceptual ideas and proof outline, and played a leading role in the drafting and revision of the manuscript.

Sairah Syed was instrumental in acquiring funding, provided resources, and supervised the project.

Hafiz Hussnain Nawaz contributed to the design and implementation of the research, performed the data analysis, and assisted in writing the manuscript.

Ruqeah Mustafa led the data collection efforts, contributed to the data analysis, and participated in writing the relevant sections.

Marjan Aziz contributed to the critical review, commentary, and revision of the manuscript, enhancing its intellectual content.

Madeeha Khan offered technical expertise and advice on the methodology, significantly improving the research's design and execution.

Azra Khan played a key role in interpreting the results and contributed to the writing and editing of the discussion and conclusion sections.

Uzma Javed was responsible for the visualization and presentation of the data, including creating figures.

Attiq Ur Rehman contributed to the literature review, ensuring a comprehensive understanding of the topic and its current research landscape.

Rubab Altaf provided substantial contributions to the manuscript's introduction and theoretical framework, grounding the study in relevant academic discourse.

Qamar Shakil oversaw the project's compliance with ethical standards, managed the manuscript's submission process, and coordinated communication among co-authors.

Conflict of interest

The authors have declared no conflict of interest.

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