REVIEW

WHEAT STRIPE RUST AND INTEGRATION OF SUSTAINABLE CONTROL STRATEGIES IN CHINA

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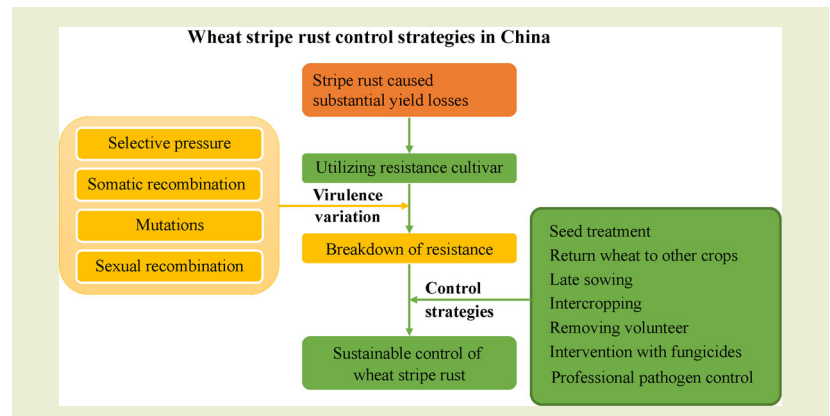
HIGHLIGHTS

- Stripe rust caused substantial yield losses in China.
- *P. striiformis* is highly variable and the change from avirulence to virulence.
- Different comprehensive control strategies were adopted in different epidemic region.

GRAPHICAL ABSTRACT

ABSTRACT

Stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici* occurs in almost all wheat-producing regions of the world. Severe countrywide epidemics in China have caused substantial yield losses. Growing resistant cultivars is the best strategy to control this disease but the pathogen can overcome resistance in wheat cultivars. The high variation in the virulence of the pathogen combined with the large areas of susceptible wheat cultivars enables the pathogen population to increase rapidly and disperse over long distances under favorable environmental conditions, resulting in severe pandemics within cropping seasons. Current stripe rust control measures are based on many years of research including the underlying epidemiology regarding year-to-year survival of the pathogen, pathways of pathogen dispersal within seasons and years, the role of *P. striiformis* sexual hybridization, the use of resistance sources in breeding programs, and year-round surveillance of national wheat crops that are present in different parts of the country throughout the year. All these strategies depend on accurate prediction of epidemics, more precise use of fungicides to meet national requirements and better deployment of resistance genes. New ideas with potential application in sustainable protection of stripe rust include negative regulatory gene editing, resistance gene overexpression and biological control based on microbiomes.

1   INTRODUCTION

Wheat (*Triticum aestivum*) production is challenged by a number of threats among which stripe or yellow rust caused by *Puccinia striiformis* f. sp. *tritici* is one of the most important[1]. Stubbs[2] considered China to be the largest epidemic region in the world[2] because China has the largest wheat acreage of annual harvest and favorable climate and ecosystem for stripe rust occurrence. Several severe countrywide stripe rust epidemics have occurred since 1950 and caused very large losses in wheat production[3]. Stripe rust continues to be a significant threat in most wheat growing areas despite much effort by pathologists, breeders, farmers, and government organizations to control this disease[4]. Current integrated management mainly depends on deployment of resistant cultivars and rational applications of fungicides[4]. However, the arms race in the rust and wheat system never ceases[5], i.e., introduction of resistant cultivars and subsequent occurrence of virulent races to overcome resistance[6,7]. In the last decade the discovery of a sexual cycle in *P. striiformis*[8], a more precise understanding of virulence variation[9] and increased epidemiological knowledge[4] have provided better guidance on comprehensive sustainable control of stripe rust of wheat.

The most important breakthrough in the last decade was the identification of *Berberis* spp. as an alternate host of *P. striiformis*, uncovering a century-old mystery regarding the life cycle of this pathogen[8]. Subsequent work demonstrated that *P. striiformis* could complete a sexual stage under natural conditions in China playing an import role in reproducing new pathogenic races[10–12]. This progress provided new perspectives for prevention of sexual reproduction to slow virulence variation[9]. Based on countrywide genotyping and phenotyping of stripe rust genotypes[13–16], a urediniospore movements law and accurate epidemic system were revealed and provided the basis for classified region management. Recently, control of stripe has faced new challenges including a national policy for zero-growth in the use of pesticides[17], the threat of pathogen resistance to fungicides[18,19] and adaptation of *P. striiformis* to higher temperatures[1].

Here we first summarize advances in understanding the biological characterization, stripe rust epidemiology in China, host resistance breakdown, and pathogenic variation in *P. striiformis*. This is followed by a description of integrated sustainable control of stripe rust across different epidemic regions. Finally, we discuss existing issues and potential new technologies that may help in providing better strategies for the sustainable control of stripe rust.

2   IMPACT OF WHEAT STRIPE RUST IN CHINA

Common bread wheat with the A, B and D subgenomes[20] is the most widely cultivated crop worldwide[21]. It is the second most important staple food in China. Over the past five years the average planting area has been ~ 24 Mha with average production of about 133 Mt[22]. The planting area decreased from 24.7 (2016) to 23.7 (2019) Mha while the yield increased from 5.4 (2015) to 5.6 t·ha−1 (2019). Although total wheat production increased slightly each year (except 2018) the country still imported ~ 3.5 Mt wheat per year[23]. Given that there is some export of wheat production from China there is an overall balance between supply and demand.

There are both biotic and abiotic stress threats to wheat production. Stripe rust infections can occur during all growth stages and can cause total grain yield losses in highly susceptible cultivars[1] especially following early infection. Although epidemics occurred in China before 1949[3] countrywide cooperation on stripe rust epidemiology, race identification, resistance breeding, and integrated management started after 1950[4]. In 1950, there was a major epidemic that caused losses estimated at 6 Mt at a time when overall production was 14.5 Mt. There were subsequent important epidemics during the 1950s and 1960s, viz., 1956, 1958, 1960, 1962 and 1964. The countrywide epidemic in 1964 caused losses of 3.2 Mt[3]. Moderate to severe epidemics were recorded in nine years during the 1970s and 1980s. The areas of incidence in 1975, 1983 and 1985 stretched from the north-west and south-west provinces to the major wheat production areas of the Yellow, Huai and Hai Rivers and caused yield loss of ~ 1 Mt per year[3]. In the 1990s, countrywide epidemics in 1991 and 1992 affected estimated areas of 6.5 and 4.3 Mha of wheat production and caused losses of 1.83 and 0.43 Mt, respectively[3]. Over the other eight years, areas of infection were < 1 Mha and no yield losses were documented[24]. In the 2000s, the areas affected by stripe rust were twice those in the 1990s. A countrywide epidemic in 2002 affected about 6 Mha of wheat and resulted in a loss of 1.3 Mt of grain[24]. A moderate epidemic in 2003 affected 5 Mha of wheat but widespread organized chemical intervention led to relatively small losses in production[7]. In the 2010s, the average area affected by stripe rust was about 2 Mha. A countrywide epidemic in 2017 affected about 5.5 Mha[24]. Another epidemic in 2020 affected > 4 Mha but with appropriate control strategies production was not affected[22,24].

Stripe rust has occurred each year over the past 30 years and has affected ~ 2.5 Mha per year. As a result of early stripe rust

outbreaks in oversummering regions and in warm autumn and winter in overwintering regions, a national epidemic is possible in 2021 that may affect ~ 4 Mha[24]. In this situation the relevant departments need to strengthen forecasting and implement timely comprehensive control strategies. Overall, since 2003, although several moderate and severe epidemics have occurred, the wheat yield losses were largely prevented. These benefit from widespread and timely applications of fungicides on the basis of accurate monitoring, prediction and forecasting of stripe rust outbreaks[4].

3   BIOLOGICAL CHARACTERIZATION

P. striiformis is an obligate fungal pathogen that grows only on living hosts. The primary hosts of this fungus are mainly wheat species and the alternate hosts are *Berberis* spp. and *Mahonia* spp. There are 88 species (or varieties) of 16 genera of grasses in China that serve as accessory hosts of the pathogen[3]. The pathogen infects the green tissues of the host plants. Symptoms emerge about one week post-infection and sporulation begins about one week later. Aeciospores produced on alternate hosts infect primary hosts that generate urediniospores. Urediniospores reinfect primary hosts to cause multiple reinfections within a cropping season (Fig. 1(a)). Attempts to cultivate this rust pathogen on artificial media have failed.

P. striiformis requires low temperatures for germination, penetration, growth and sporulation. Urediniospores germinate after at least 3 h of contact with free water or continuous moisture. Urediniospores germinate at 0–23 °C with an optimum range of 9–13 °C. Minimum and maximum temperatures for infection are 2 and 23 °C and the optimum temperature range for fungal growth and spore production is 12–15 °C. Sporulation can occur at 5–20 °C and is favored at 12–15 °C[25]. The latent period and amount of sporulation are determined by host response, light intensity and day length, and host nutrient conditions[26]. Lower temperatures extend the latent period, and during the winter the latent period can reach 118 days or > 188 days in the presence of snow cover[27]. However, a shorter latent period of 6–11 days is possible at 15–20 °C. Temperatures > 30 °C suppress sporulation and accordingly lead to a prolonged latent period[28].

Temperature is an important factor affecting both summer and winter survival of *P. striiformis*. The pathogen can survive over summer at 10-day average temperatures < 22 °C in the hottest months, and over winter at average temperatures from –7 to –5 °C in the coldest months and even below –10 °C with snow cover[3,28]. However, exceptionally, high temperature-adapted

genotypes can oversummer and/or overwinter in Australia after *P. striiformis* was first introduced in 1979[29] and has become an endemic disease of wheat, and in some states of the United States since 2000[30].

P. striiformis is a heteroecious, macrocyclic rust fungus with uredinia and telia on primary hosts and pycnia and aecia on alternate hosts. The first description of *P. striiformis* can be traced to 1777[31]. All searches for alternate hosts of *P. striiformis* failed[31–33]. Common barberry (*Berberis vulgaris*) was discovered as the alternate host for *P. striiformis* by Jin et al.[8]. To date, many *Berberis* spp. from China, Germany and Pakistan, and *Mahonia* spp. from the USA and China, have now been identified as alternate hosts[10,34–38]. Studies in China demonstrate that *P. striiformis* can complete the sexual stage on susceptible barberry under natural conditions in both spring and autumn[10–12] and that susceptible barberry provides aeciospores as (primary) inocula to cause stripe rust of wheat[12] (Fig. 1(b)). This is important in the management of wheat stripe rust in spring and autumn in these regions. Some methods have been implemented to control sexual reproduction such as removing the source from infection from barberry and chemical control to prevent sexual reproduction[9]. So far, the usual method to monitor variation in virulence has been to collect infected samples from the field, recovering and reproduction on a universal susceptible cultivar, at last testing on the differentials host to identify the pathogen genotypes[1]. This process is time- and energy-consuming and inefficient. Some new methods based on resequencing and the transcriptome may be developed with the rapid development of high-throughput sequencing technology.

Teliospores are essential in sexual reproduction. In general, teliospores are produced at the later growth stages of wheat in the field and also at all growth stages of wheat in winter wheat-growing Chinese regions before either winter or spring in the field[39]. Teliospores can also be induced to form in laboratory conditions. *P. striiformis* teliospores do not have dormancy, or only a short dormancy, and germinate directly to produce basidiospores as soon as they mature[39–41]. Telia can survive in the field for a long time in dry and cool conditions until the following spring[41]. Telia can persist in stacks of wheat straw (common in China) following harvest and hence overwinter until the next spring[39]. Production of telia varies between different races or race groups and is affected by environmental conditions[42]. Teliospores form precociously under unfavorable conditions and can germinate at 5–22 °C (optimum 10–15 °C)[41]. They require at least 32 h of continual saturation to infect barberry and infection reaches a peak after 3–4 days[41]. In contrast to China, studies in the Pacific North-west of the United
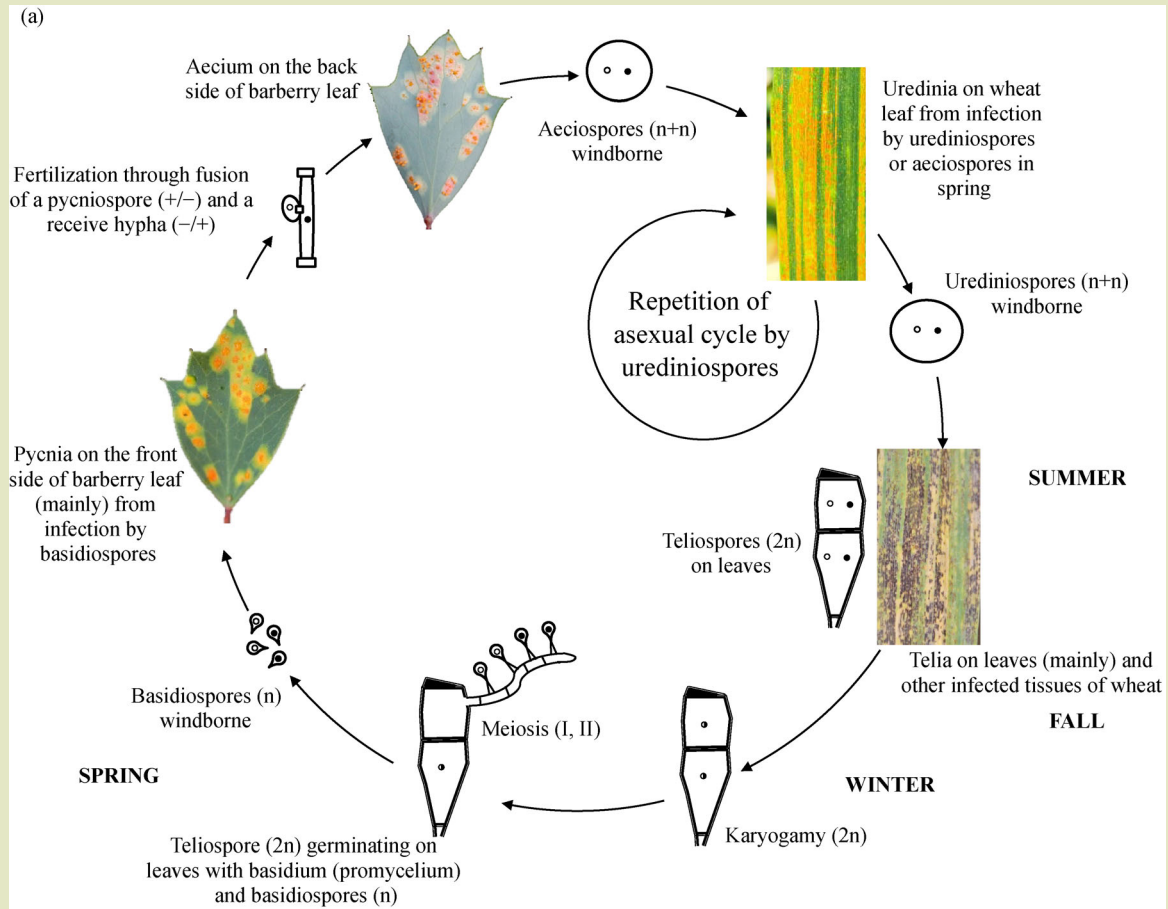
Fig. 1 (a) Simplified life cycle of *Puccinia striiformis* f. sp. *tritici*. n (haploid), n+n (dikaryotic), and 2n (diploid). Spores are drawn to approximately the same scale. (b) The phenomenon of wheat and barberry growing adjacent to one another under natural conditions.

States reveal that basidiospores did not infect barberry under natural condition since the wheat straws were degraded in the wet winter climate resulting in a lack of telia the following spring when the barberry shoots appeared[41].

P. striiformis is heterothallic. The pathogen is assumed to have a haploid chromosome number of six like other forms of *P. striiformis*[40] but this has not yet been determined. Each of the two cells of a teliospore can produce four basidiospores after independent meiosis, these consist of two positive and two negative mating types. The basidiospores are aerially spread and infect barberry to generate the pycnial stage. Fertilization to restore the dikaryon condition occurs by transfer of nectar (or honeydew) from one pycnium to another one with opposite mating type in the laboratory, or by insects or rain under natural conditions. Aeciospores are generated in chains inside the aecium (aecial cup). The mature aeciospores released are aerially dispersed to primary hosts (wheat and grasses) to cause stripe rust after infection. Reinfections then occur by airborne urediniospores which can spread over hundreds (or even thousands) of kilometers from the original disease foci[27,43,44]. Transmission distance of spores is dependent on direction and strength of the wind. Urediniospores can be elevated to high altitudes ranging from 5 to 10 km. Higher relative humidity limits the spread of heavier urediniospore clumps[28].

Many factors such as temperature, humidity, light, and air pollution affect the survival of *P. striiformis* urediniospores. Air pollution and long exposure to strong light and ultraviolet light significantly reduce urediniospore survival. These factors may affect the survival of the pathogen during long-distance dispersal[28,45,46].

4　WHEAT STRIPE RUST EPIDEMIOLOGY SYSTEM

Numerous Chinese studies suggest that long-distance dispersal of *P. striiformis* urediniospores occurs annually across hundreds or even thousands of kilometers[47,48]. Many Chinese plant pathologists support the concept of regional epidemic units according to cropping times and designate different epidemic regions in China based on unique features[2,3,48–53]. These features include (1) geographic factors such as elevation, isotherm and isohyet zones and montane environments; (2) meteorological factors such as maximum temperature in summer, minimum temperature in winter and monthly precipitation; and (3) agronomic factors such as sowing and harvest dates, wheat growing period with seedling growth in the

autumn and early or late return green stage in the spring. These features determine the development, frequency, and intensity of stripe rust and the specific infection situation of the regions. Based on all these factors and historical epidemiological data for stripe rust, the wheat-growing regions have been divided into the north-west oversummering areas, the south-western overwintering areas and the eastern epidemic areas[3].

According to the biology of *P. striiformis* the oversummering regions are defined by average maximum temperature < 22 °C in the hottest months (generally July and August), wheat crops with different maturity times being grown at different elevations enabling an overlap between epidemics on late crops and infected volunteer seedlings from earlier crops. Stripe rust can complete a year-round cycle of this type in Xinjiang, Yunnan, southern Gansu and north-western Sichuan where wheat is grown in lowland valleys at 1000 m up to highland terraces at 3300 m providing a green bridge for pathogen migration from late-maturing highland areas to early-sown wheat plants in the lowlands[3,4,48,54]. Most oversummering areas are in high-elevation mountains growing late mature or volunteer wheat in the cool summer. Five oversummering areas have been identified, namely (1) north-western region comprising eastern Qinghai, eastern Gansu, southern Gansu, western Shaanxi, and Ningxia; (2) north-western Sichuan region comprising Aba, Ganzi, and Xichang; (3) southern region comprising south-eastern Tibet, northern Yunnan and south-western Guizhou; (4) northern China region comprising northern Shanxi, northern Hebei, and southern Inner Mongolia; and (5) western region, mostly western Xinjiang.

P. striiformis cannot overwinter in the northern wheat growing zone stretching from Shijiazhuang and Dezhou in Hebei Province to Jiexiu in Shanxi Province and Huangling in Shaanxi Province (latitude N 37°–38°) due to low temperature limitation of *P. striiformis* survival. South of this zone it can overwinter if susceptible host plants are available, and sometimes the pathogen can slowly multiply in the winter[48]. The conditions conducive to *P. striiformis* overwintering in these regions are (1) average minimum temperature < −7 °C (< −10 °C under snow cover) in the coldest month (usually January), and (2) wheat cultivars susceptible to stripe rust but with cold resistance. Wheat can still grow after winter in the region without returning to the green stage, termed the overwintering reproduction region. These regions are located at the south of the Qinling Mountain-Huai River line.

Some studies report that in addition to urediniospore movement from the oversummering regions to the overwintering regions, spore movements can occur at relatively low frequencies

between the different oversummering regions on the basis of *P. striiformis* races and molecular genotypes[13–16]. However, all wheat-growing areas in China within the geographic ranges 22°–53° N and 97°–135° E consist of a single large epidemic area, whereas Xinjiang and Xizang (Tibet) can be considered as two separate disease epidemic sub-areas where wheat acreages are small and the disease is mainly restricted to the local crops. In terms of disease severity and yield loss, the important epidemic region is located in north-central China and along the upper and middle reaches of the Yangtze River.

It seems reasonable to combine the north-western Sichuan oversummering area with the north-western area covering parts of eastern and southern Gansu based on proximity, similar climatic conditions, and new race dispersal patterns[15,55]. Thus, the largest epidemic area contains all the autumn-sowing regions and some parts of the spring sowing regions. Eastern and southern Gansu is the core oversummering region and the main overwintering regions are the Sichuan basin, north-western Hubei, southern Shaanxi and southern Henan.

The eastern epidemic area covers the largest wheat-producing region, comprising Henan, Hubei, Shandong, Shanxi, Hebei, Sichuan, Shaanxi and Anhui. In oversummering areas, infected autumn-sown wheat and volunteer wheat in the lowlands and late-maturing spring wheat in the highlands serve as inoculum sources for local disease recycling throughout the year[3]. Urediniospores from the oversummering regions, particularly the north-western and south-western areas, spread eastward to eastern China. Autumn-sown wheat in the overwintering regions becomes infected during late autumn and early winter and the pathogen survives mainly as latent mycelial infections until temperatures increase in the spring when inoculum then moves to the major winter wheat regions to the north-east[3,48]. Thus, temporal interregional disease distribution and urediniospore spread occur mainly from west to east in autumn and south to north in spring. The oversummering areas provide initial inoculum for the eastern plains.

In summary, the epidemic system of wheat stripe rust in China comprises oversummering, overwintering and spring sowing epidemic regions. In the oversummering region, stripe rust can both oversummer and overwinter and is the inoculum source for autumn-sown wheat in eastern China. Stripe rust cannot oversummer in the overwintering region but can increase in winter and represents the spring inoculum source for local and northern areas. Stripe rust cannot oversummer in the spring epidemic region and rarely overwinters. Disease epidemics depend on the time and amount of inoculum during the spring.

5   CULTIVAR RESISTANCE BREAKDOWN AND VARIATION IN *P. STRIIFORMIS* VIRULENCE

5.1   Breakdown of resistance

Host resistance is a highly effective approach to manage wheat stripe rust due to the advantages of low cost and environmental friendliness. The problem is that many highly effective sources of resistance controlled by single genes become ineffective at various times after deployment. For example, during the 12-year period 1965–1976, high yielding cultivars maintained resistance across the epidemic region of the middle and downstream areas of the Yellow River[6]. While some resistance sources such as this might remain effective for 5–10 years, other sources can become ineffective after as little as one season (five years on average). This loss of effective resistance is due to new races that arise mainly from mutation or sexual hybridization on barberry[6,7] not somatic hybridization. Introduction of urediniospores from outside the region and selective increase in races previously present at undetectable levels are other possibilities. The sequence of major historic introductions of new resistance sources (genes) and consequent breakdowns in China since 1950 led to a series of 'boom and bust' cycles that are summarized in Section 5.2. Prevention of these cycles or at least prolongation of these cycles include a focused control of stripe rust in the key oversummering and overwintering regions, deployment of different sources of resistance in the main wheat production regions further east, resistance gene combinations throughout to reduce the survival of single-gene pathogen mutants, and the use of nonspecific slow rusting sources that reduce the amount of disease thereby contributing to reduced grain loss in the host cultivars and contributing less inoculum for disease spread and perhaps lower mutation rates in the pathogen. These consequences can be achieved to some extent by avoiding highly susceptible cultivars that undergo the highest losses in an epidemic and contribute the most inoculum for disease spread.

From wheat stripe rust epidemics over more than seven decades from 1950 to 2020 in China[3,6,56–58], we conclude that the overuse of an easy-to-use *Yr* gene and stable selection of *P. striiformis* based on extensive growing of wheat cultivars and derivatives with the same *Yr* gene, accelerated directed adaptive evolution of *P. striiformis* to generate a new race corresponding to a *Yr* gene, contribute to the breakdown of cultivar resistance to stripe rust. Continuous growing of the susceptible wheat cultivars results in quick accumulation of the new race. Thus, the race promptly develops to become predominant and causes continuing epidemics until the next resistance cycle comes into effect.

Although > 80 *Yr* genes and > 200 QTLs (quantitative trait loci) resistant to wheat stripe rust have been identified, most resistant germplasm or wheat cultivars with *Yr* genes (such as *Yr5*, *Yr15* and *Yr61*) or QTLs cannot be used in wheat breeding due to associations with undesirable agronomic traits. Consequently, relatively few of these resistance sources have been successfully exploited in widely-grown cultivars[59]. Rational gene steward-ship and regional gene deployment across epidemiological regions should therefore be practiced to reduce the likelihood of widespread epidemics due to large scale use of individual wheat cultivars or overuse of the single *Yr* gene.

5.2 Race evolution and replacement of wheat resistance cultivars

To date there have been eight major resistance source replacement events in the wheat programs in China since 1950[3,60,61] as follows.

(1) 1950–1960, in cv. Bima 1 and derivatives followed by emergence of race CYR1 with virulence to *Yr1* in 1957.

(2) 1960–1962, resistance in wheat cvs Quality, CII2203, Xibei 134 and Shaannong 9 (unknown resistance gene) were overcome by races CYR8 and CYR10 in 1960.

(3) 1962–1970, the resistance of the introduced wheat resistant cv. Mentana (possibly *Yr2*) and its derivatives was overcome by races CYR13 and CYR16. Mentana also has slow rusting *Yr18* and it is assumed that the change in race did not involve this adult plant resistance factor.

(4) 1970–1976, resistance in cvs Beijing 8 (*Yr1*), Shijiazhuang 54 and Abbondanza lost effectiveness due to races CYR17 and CYR18. Assuming the effective gene(s) in the cultivars was not *Yr1* then Beijing 8 has a second unknown gene for resistance in common with the other two genotypes.

(5) 1976–1985, cvs Fengchan 3, Tianxuan 15, Zhongliang 5 and others (unknown resistance gene) no longer expressed resistance to races CYR19, CYR23 and CYR25.

(6) 1985–1994, extensively planted cultivars with *Yr9*, namely cvs Lovrin 10, Lovrin 13, Fengkang 8, Lumai series, Jimai series, and Yangmai series were overcome by races CYR28, CYR29 in 1986, and race groups of L10 (pathotypes virulent on Lovrin 10), and L13 (pathotypes virulent on Lovrin 13), that caused the 1990 stripe rust epidemic.

(7) 1994–2000, Fan 6 and its derivatives (unknown gene) were overcome by races Suwon 11, Mianyang 11, Mianyang 15, Mianyang 19, Mianyang 20, Chuanmai 22 and Chuanmai 23, successively lost their stripe rust resistance by CYR30, CYR31, CYR32, Hy46 (pathotypes virulent on Hybrid 46; *Yr4*) and Su11 (pathotypes virulent on Suwon 11; resistance gene unknown) in 1994.

(8) Post 2000, cultivars with *Yr26*, including *Yr10* and many others, were overcome by race CYR34 (formerly G22-9) in 2008[62]. The source of this gene was first believed to be *Dasypyrum villosum* but later concluded to be durum (*Triticum durum*). An added problem was other cultivars such as Chuanmai 42 obtained the same gene from CIMMYT-sourced synthetic wheats that also involve durum as a parent. More than half the cultivated wheat cultivars had this gene, suggesting the potential to replace cultivars with *Yr26* nationwide. A new race virulent to *Yr5* has been detected most recently and this gene should not be used in wheat resistance breeding programs[58].

5.3 Approaches and mechanisms of variation in *P. striiformis* virulence

Selective increase of new races, or previously races present at extremely low frequencies, are the cause of resistance breakdown of previously resistant cultivars. Many studies on the develop-ment of new races in *P. striiformis* and other cereal rust pathogens have historically demonstrated that the causative factors are spontaneous mutation of avirulence genes by point mutation or loss of chromosome segments[63,64], asexual genetic recombination known as somatic recombination that likely involves greater complexity than simple nuclear exchange. The discovery of the sexual cycle of *P. striiformis* added a very significant dimension and is functional in China and Pakistan. High frequencies of heterozygosity of predominantly dominant avirulence genes enables allele reassortment to homozygous virulence. Moreover, sexual recombination leads to a multitude of races and reassortment of multiple genes such that wheat cultivars with effective combinations of resistance genes may be overcome.

Production of new pathogen genotypes is mainly attributable to mutations. The spontaneous mutation rate of *P. striiformis* is estimated at 0.8×10^{-5} to 1.6×10^{-5}. Studies on induced mutation of *P. striiformis* report that mutations can be induced by mutagens such as EMS, UV radiation and γ-rays under

controlled conditions[65–68], producing a mutation rate of 10^{-6} to 10^{-4} caused by UV[67] or 2×10^{-6} to 4×10^{-5} by EMS[68].

Heterokaryotization (also somatic recombination) is a process of fusion and reassignment of nuclei of heterokaryotic binuclear urediospores. Studies demonstrate that under laboratory conditions new pathogen genotypes can be produced after inoculation with mixtures of two genotypes[69–71], showing a higher percentage of tri-nuclei or tetra-nuclei in a germ tube than those of parent genotypes with fusion of germ tubes from two binucleate urediniospores[69,71]. Also, the state of tri-nuclei or tetra-nuclei of urediospores has been commonly found in natural populations of *P. striiformis* in China[69]. Two different nuclei may be reassorted into a urediniospore to produce new genotypes.

Sexual genetic recombination is a major approach for producing new races. Studies demonstrate that sexual genetic recombination of *P. striiformis* can be conducted by selfing, race-race hybridization, forma speciales hybridization, and interspecies hybridization. Inheritance of *P. striiformis* sexual reproduction is complicated, showing that each of different avr loci is controlled by unequal numbers of avirulence genes. Under natural conditions sexual reproduction of *P. striiformis* is important in providing aeciospores as (primary) inocula to infect wheat to initiate local stripe rust infection in China (Fig. 1(b)). Moreover, aeciospores are the result of sexual recombination and populations of aeciospore-generated infections are in reality a mixture of races, some of which might be selected for on a resistant cultivar. However, it was demonstrated[8] for the *P. striiformis* life cycle on common barberry that there is a multitude of barberry species throughout China and the Himalayan Mountains that extend into southern China and elsewhere, and each (possibly including specific genotypes within each) required investigation of a potential role as an alternate host of *P. striiformis*. *P. striiformis* infections of several barberry species, including six of the most commonly infected, were confirmed to coexist with wheat in various locations and shown to support the sexual cycle in the laboratory[10,35,37,38]. Aecial collections from barberry species infected wheat in the laboratory[12,36] and urediniospore isolations from infected wheat crops in the vicinity of barberry plants consisted of a multitude of races as expected for a population derived from aeciospore infections[12,36]. This research has uncovered an extensive geographic distribution of susceptible barberry and the frequent occurrence of sexual reproduction of *P. striiformis* on susceptible barberry under natural conditions contributes to high genetic diversity of *P. striiformis* populations and formation of regional diversity of the pathogen in China.

6　STRATEGIES FOR CONTROL OF WHEAT STRIPE RUST IN CHINA

Under the guidance of a national plant protection policy ("early intervention represents comprehensive protection"), we present an overview of an of ecological strategy to manage and constrain the threat of wheat stripe rust based on current knowledge of the occurrence, spread and prevalence of the disease in China. This strategy focuses on control in the oversummering region where pathogens vary frequently, continuous control in the over-wintering region where the pathogen proliferates rapidly in early spring to provide inoculum for the major cropping regions and comprehensively prevents the spring epidemic region. Multiple key technologies for rust control have been successfully developed such as gene layout, availability of seed of elite rust resistant cultivars for farmers, seed treatment to prevent early infection, return of wheat land to other crops, late sowing, intercropping, removing volunteer wheat seedlings (green-bridging), intervention with fungicides, real-time crop surveillance and professional pathogen control systems for large-scale prevention. According to the different epidemic regions all of these technologies are used for integration, assembly and matching. Finally, based on the use of biodiversity, a technology system for wheat stripe rust zonal control has established target containment of stripe rust when it occurs and biological control and reduced use of pesticides for both environmental and human safety[59,72,73]. Clearly, components of these strategies will vary across different regions.

6.1　Oversummering region

The oversummering region is the inoculum source of autumn-sown wheat seedlings in eastern China and is the first priority target for comprehensive control of wheat stripe rust nationally. Several strategies are followed, namely assured availability of seed elite rust- resistant cultivars for farmers, seed treatment to prevent early infection, and conversion of wheat growing to other crops, and late sowing and reduction of green-bridging by removal of volunteer wheat. First, different cultivars with different rust resistance genes such as those produced by local breeders and prefixed with Zhongliang, Tianxuan, Lantian, Zhongzhi are preferentially recommended in the highland (oversummering region) and lowland (overwintering region) survival areas. The strategy of deployment of different resistance genes at different altitudes constructed to inhibit the colonization of pathogen is practiced as far as possible. For recommended wheat cultivars with adult plant resistance but susceptible at the seedling stage (e.g., Lantian 15, Lantian 26, Lantian 31, Lanhangxuan 121 and Lanhangxuan 122)[74], seeds

should be treated using 0.03% triadimefon before sowing in autumn to lower the incidence of *P. striiformis*. Second, the wheat crop acreage should be reduce and replaced with other crops such as maize, potato, oil sunflower, vegetables, and forage grass in the key oversummering areas (1500–1800 m in altitude). Also, wheat should be sown late as far as possible in the suitable period of wheat sowing. Numerous practices demonstrate that this comprehensive management technology system enables the control of the inoculum sources of wheat autumn seedling effectively and has an important role in preventing pathogen transmission from north-western to eastern China.

6.2 Overwintering region

The overwintering region, also the spring inoculum source for local and northern areas, is key to the comprehensive control of wheat stripe rust regions in China. There are three main strategies. First, rust resistant cultivars with names prefixed with Chuanmai, Mianmai, Chuannong, and Xikemai from breeding groups in Sichuan Province are bred and planted. Second, seed of wheat cultivars without seedling resistance is treated and sown in autumn using 15%–25% triadimefon wettable powders, or 2% tebuconazole or 3% difenoconazole flowable concentrate. Third, systematic crop surveillance is conducted in late autumn and early spring by those engaged in plant protection work and fungicide treatment of crops is practiced when stripe rust is first detected. This comprehensive management system effectively prevents stripe rust spread and disrupts urediniospore dissemination to wheat production regions from southern to northern China and also further east.

6.3 Spring epidemic region

The spring epidemic region is the target of wheat stripe rust prevention and control in spring and summer. Two major technology strategies are applied, namely (1) the use of adapted wheat cultivars with adult plant resistance or slow-rusting such as those prefixed with Xinong, Xiaoyan, Yumai, Zhoumai, Zhongmai and Lumai produced by breeders located in Shaanxi, Shanxi, Henan, Hebei and Beijing, and (2) implementation of timely surveillance in spring based on early forecasting from the source regions. A single foliar application when disease incidence reaches 5% or when disease severity reaches 1% at the jointing and stem elongation stages is usually adequate to prevent yield loss.

6.4 Achievement of control strategies

Intense disease monitoring and forecasting in the source areas allows timely local application of fungicides to prevent losses and to minimize spore dispersal to the more easterly wheat production regions. Potentially very large yield losses nationally have been avoided through the timely use of fungicides based on early forecasts. Surveys and forecasts of disease provide information to pathologists, county agents, extension services, growers, the fungicide supplier and government administrators from village level to the Ministry of Agriculture enabling decisions on chemical supply and intervention to minimize yield losses. Fungicides, spray equipment and personnel training can be well-organized in advance. However, with the rapid decline in farming by family units and the migration of younger people to the cities and an increase in part-time farming by city-dwellers with alternative employment, effective control of stripe rust is becoming increasingly difficult. A consequence is that government administrators from the townships and ministries must guide growers in implementing disease control. This involves training, technical guidance, fungicide supplies, seed treatment and timing of fungicide applications. Further measures are being taken to help growers to understand the potential threat of stripe rust to grain yield and disease management generally, through television programs, internet websites, radio broadcasts and cell phone messages.

The application of ecological management of wheat stripe rust in the inoculum source areas has been widely disseminated and applied. This has significantly reduced losses caused by stripe rust allowing added production of an estimated 2 Mt per year, and fulfils the visions of "disease occurrence but no disaster" and "long-lasting control of disease"[7].

7 CHALLENGES AND COUNTERMEASURES IN FUTURE STRIPE RUST CONTROL

Norman Borlaug, Nobel Prize winner and the father of the Green Revolution in wheat, said "Rust never sleeps," and this reminds us to maintain vigilance against cereal rusts, a threat to global human food security. *P. striiformis* is an obligate biotrophic fungal pathogen that, except for teliospores, relies on living host plants for growth and survival. Within-season infection and epidemic development involves the asexual cycle (Fig. 1). The outcome of initial infection on a host plant depends upon the interaction between host genotype (resistance or susceptibility) and pathogen genotype (avirulence or virulence) and may be affected by environment (unfavorable or favorable)[1]. Following initial infection the extent of epidemic development depends upon a continuing favorable environment and the genetic

makeup of the host population. As favorable environments for disease development usually equate with favorable environments for yield generation there are limited opportunities for environmental modification without affecting yield potential. The industry in China is therefore limited to curtailing the flow of urediniospores from survival areas to the main production region, making better use of the limited available sources of genetic resistance through better genetics and wiser resistance gene deployment. The relatively recent discovery of a sexual cycle in *P. striiformis* and continuing demonstration of its effects in the survival regions adds a degree of difficulty in regard to reducing year-to-year survival and development of new races by sexual recombination. Many new technologies such as next-generation sequencing provide new opportunities to uncover pathogen variability and population structure for rust disease management[75].

7.1   Better prediction of stripe rust epidemics

Accurate prediction of epidemics is a prerequisite of effective disease control with limited use of fungicides. The first predictive work was "trial method for prediction of wheat rust" by the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, in 1958[3]. Many epidemic prediction models published subsequently from single factor to multifactors, from qualitative to quantitative have resulted in more exact predictions[53,61,76,77]. All models require field surveys of stripe rust in late autumn and early spring[1]. Standard surveys are time consuming, laborious and inefficient[78]. Advances in imaging and machine learning provide potential solutions based on automated and fast phenotyping such as chlorosis severity and stress severity[79]. Satellites provide high spatial resolution that can be investigated in greater detail by aerial devices such as small aeroplanes and drones[80]. A number of studies report estimating the severity of stripe rust and have attempted to develop automated machine-based and effective methods for disease assessment[78,80–83]. This work has just begun in China. Nevertheless, stripe rust epidemics are affected by wheat cultivars and environmental factors such as susceptible cultivar area, moisture, wind and temperature[1].

7.2   Pesticide application faces two challenges

The high variability in stripe rust results from high reproductivity, long-distance spread, and adaption to host and environment[1,48]. Once the disease epidemic is predicted to be moderate or above, fungicides should be applied in a timely fashion and cover potential impacted areas[4]. However, we are facing two challenges in fungicide use. First, in 2015 China proposed a zero-growth policy for reducing and restraining pesticide usage by

2020[17]. The amount of chemical pesticides has been declining each year since 2015[84]. In response, advanced technology and machines (such as unmanned aerial vehicles, UAV) based on accurately predicted disease epidemics in advance has reduced fungicide applications. These new devices have been widely used in China because of their low cost and high efficiency[85]. In China, UAV spraying provided by professional plant protection companies costs 150–225 RMB·ha^{-1} (~ 30 USA·ha^{-1}, excluding the pesticides) and takes just 15 min. Secondly, we must be vigilant regarding resistance to fungicides by *P. striiformis*. Cook[19] presents evidence showing that some *P. striiformis* genotypes collected from China had elevated levels of resistance to the widely-used fungicides (demethylation inhibitors)[18,19]. Measures to address these issues include development of new fungicides, modification of existing fungicide mixtures and alternating application of different fungicide groups in time and space[18].

7.3   The mechanisms of variation in stripe rust remain unclear

Global warming has two important implications for stripe rust in China. The first is the compelling evidence from a range of countries for incursions of higher temperature-tolerant races that have become established in locations where stripe rust was previously not a problem. Stripe rust seems able to adapt to higher temperatures and numerous studies report this phenomenon worldwide[1]. Based on temperature sensitivity analysis of 126 genotypes from different provinces and periods, a moderate effect of temperature in Gansu, Sichuan and Yunnan was observed with sensitivity rising by 1.22, 1.32 and 2.63 °C between the 1980s and 2010s[86]. The result is that the potential oversummering area has extended and field surveillance must be adjusted accordingly.

P. striiformis is highly variable and the change from avirulence to virulence with selection on widely deployed cultivars with a common gene will result in epidemics proportional in size to the area of those genotypes along with past and continuing susceptibility[60]. In China, both mutation and recombination (both asexual and sexual), are causes[9]. The likelihood of mutation might be reduced only if pathogen populations can be brought to very low levels. Sexual recombination is a factor in the development of new races that will be reduced by separation of the cereal and alternative hosts by wheat field adjacent barberry eradication as has been practiced in parts of Europe and North America in past centuries. Europe has reduced barberry-initiated stem rust outbreaks in the past or has discouraged the cultivation of wheat in areas where susceptible barberry species are present.

7.4 Area of susceptible cultivars must be reduced

Growing resistant cultivars has reduced the infrequency of rust epidemics and reduced consequent yield losses in North America[87]. Until recently in China the emphasis was on very high resistance levels (immunity) that could be achieved only by host genotypes with (usually one) effective resistance gene and provided those genes remained effective their use was expanded until the inevitable loss of resistance ('boom and bust' cycle). Based on long-term evaluation, ~ 80% of cultivars released in China from 2003 to 2017 (> 2000) were susceptible at the time of release[59]. Although the percentage in the Yellow and Huai Valley region was lower at ~ 48%[88], this region is very large and remains vulnerable to epidemics. A major factor in the progression of an epidemic (and therefore its consequences in terms of grain loss) is the number of spores being generated. However, although highly and less susceptible genotypes are officially rated as equally susceptible, spores produced on the former greatly exceed those on the latter. Breeders and pathologists often rate host genotypes on a 0–9 scale representing the disease response from minimum to maximum level (or vice versa). They then refer to responses of 1–6 as resistant and 7–9 as susceptible. Clearly, if such classification is meaningful and repeatable across environments a host genotype with a rating of 7 will generate many fewer urediniospores than a genotype rated at 9. If genotypes rated 7 (or even 8) are favored and encouraged over those rated 9 there will be a great effect on rates of epidemic development. This aspect of disease management continues to be widely neglected in many counties despite the fact that we often advocate slow-rusting (ratings 4–6) as resistant. More attention should be given to the rational use of resistance to solve this problem. First, more effective resistance sources can be transferred to susceptible wheat. Landraces and wild relatives of wheat can provide sources of resistance to stripe rust[1]. Secondly, full utilization of existing limited resistance resources. (1) In the field, implementing rational resistance gene deployment, i.e., to deploy different resistance genes in over-summering, overwintering and eastern spring epidemic regions, has had a profound effect on stripe rust control[3,4,60,89]. (2) In breeding, pyramiding available genes by crossbreeding assisted by molecular markers. Pyramiding race-specific or non-race-specific genes into one cultivar might achieve higher-level and longer-lasting resistance and combine both effectiveness and durability[90–92]. Finally, new techniques such as positive regulatory gene knocking/overexpression of $Lr34$[93,94], $Lr67$[95] and negative regulatory genes knockout/downregulation by genome modification of $TaMLO$[96], $SlMlo$[97], $TaEDR1$[98], and $PsFUZ7$[99] have clear advantages (timesaving and expanded gene pool) over existing methods[100].

Compliance with ethics guidelines

Qingdong Zeng, Jie Zhao, Jianhui Wu, Gangming Zhan, Dejun Han, and Zhensheng Kang declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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