Status of wheat rust research and control in China

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Abstract In China, wheat is grown on approximately 24 million hectares with an annual yield of 100 million tonnes. Stem rust, caused by *Puccinia graminis* f. sp. *tritici*, is a threat mainly to spring wheat in northeastern China. Leaf rust, caused by *P. triticina*, occurs on crops in the late growth stages in the Yellow-Huai-Hai River regions. Stripe rust, caused by *P. striiformis* f. sp. *tritici* (*Pst*), is destructive in all winter wheat regions and is considered the most important disease of wheat in China. During the last 20 years, widespread stripe rust epidemics occurred in 2002, 2003, and 2009, and localized epidemics occurred in many other years. In recent years, major yield losses were prevented by widespread and timely applications of fungicides based on accurate monitoring and prediction of disease epidemics. A total of 68 *Pst* races or pathotypes have been identified using a set of 19 differential wheat genotypes. At present, races CYR32 and CYR33 virulent to resistance genes *Yr9*, *Yr3b*, *Yr4b*, *YrSu* and some other resistance genes are predominant. Moreover, these races are virulent on many cultivars grown in recent years. Of 501 recent cultivars and breeding lines 71.9% were susceptible, 7.0% had effective all-stage resistance, mostly *Yr26* (= *Yr24*), and 21.2% had adult-plant resistance. Several resistance genes, including *Yr5*, *Yr10*, *Yr15*, *Yr24/Yr26*, *YrZH84* and some unnamed genes, are still effective against the current *Pst* population. All have been widely used in breeding programs. Lines with one or more of *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9* and other unnamed resistance genes are susceptible to currently predominant races. Durable adult plant resistance sources are being increasingly used as parents in breeding programs. Progress has been made in genomics and population genetics of *Pst*, molecular mapping of resistance genes, and cytological and molecular mechanisms of the host-pathogen interactions involved in stripe rust.

Keywords disease management, epidemiology, leaf rust, stem rust, stripe rust, wheat

Introduction

Wheat (*Triticum aestivum* L.), the second largest food crop in China, was grown on approximately 24 million hectares in 2009 producing more than 100 million tonnes of grain. Barley (*Hordeum vulgare* L.) is annually grown on about 1 million hectares in the Yangze River valley, Huanghe River valley and Qinghai-Tibet Plateau where leaf rust and stripe rust are now the most important diseases of barley. Stripe rust is especially destructive on barley in Tibet (Wang ZH et al. 1989; Niu et al. 1994). Oats (*Avena sativa* L.) are planted on roughly 1.2 million hectares in Inner Mongolia, Hebei, Shanxi, Gansu, Shaanxi, Yunnan, Sichuan, Ningxia, Guizhou and Qinghai. Stem rust and crown rust on oats occur in the oat-growing areas, and are the most important diseases in some regions. Oat stem rust in

particular, can cause severe epidemics in Inner Mongolia and northeastern China in some years (Yang 1984).

Leaf rust (brown rust), caused by *Puccinia triticina* Eriks., was earlier a serious disease of wheat in southwestern China and the Yangze River valley. In the last three decades, it has become more important in northern, northwestern and northeastern China. Significant yield losses were caused by leaf rust in northern China in the 1970s (Zhang and Liu 2001). Research on leaf rust of wheat is mainly conducted at Hebei Agricultural University, Baoding, Hebei.

Stem rust (black rust), caused by *P. graminis* Pers. f. sp. *tritici* Eriks. & Henn., causes severe yield reductions in some years in northeastern China and the Yellow-Huai-Hai River areas (He et al. 2008). Currently, investigations on wheat stem rust are mainly carried out at Shenyang Agricultural University, Shenyang, Liaoning. The spread of race Ug99 (TTKSK) with *Sr31* virulence from Africa to Asia is a potential threat to wheat production in China, but the current risk level is considered to be low. Of 700 Chinese major wheat cultivars and breeding lines tested in Kenya, only four were highly resistant, 10 were moderately resistant, and the remaining 686 genotypes were highly susceptible (He et al. 2008). Therefore, if race Ug99 were to appear in China severe stem rust epidemics could follow.

Stripe rust (yellow rust), caused by *P. striiformis* Westend. f. sp. *tritici* Eriks., is the most destructive disease in all winter wheat growing regions in northwestern, southwestern, and northern China, as well as in the spring wheat areas in the northwest (Li and Shang 1989; Wan et al. 2004; Chen WQ et al. 2009). Severe epidemics in 1950, 1964, 1990, and 2002 resulted in yield losses of up to 6.0, 3.2, 1.8, and 1.3 million tonnes, respectively (Wan et al. 2007; Chen WQ et al. 2009).

Stripe rust is much more important than leaf rust or stem rust based on historical data and current disease situations. Plant pathologists, breeders, farmers, and governmental organizations have given much attention to research on, and control of, stripe rust. Nationwide cooperation on various aspects of the disease has occurred since 1950, mainly focusing on epidemiology, race identification, breeding resistant cultivars, and integrated management. In this paper, we will summarize recent research on, and control of, wheat stripe rust in China, including occurrence and control, evolution of virulence, and molecular research. Also, challenges and strategies for controlling stripe rust in China will be discussed.

Epidemiology, occurrence and control of wheat stripe rust in recent years

China is considered the largest independent epidemic region in the world (Stubbs 1985). Based on historical epidemiological data for stripe rust, the wheat-growing regions can be divided into the western over-summering areas, the over-wintering areas, and the eastern epidemic areas (Li and Zeng 2002). The over-summering areas include the northwestern (Shaanxi, Gansu, Sichuan, Ningxia, and Qinghai), southwestern (Yunnan and Guizhou), and Xinjiang regions (Li and Shang 1989; Li and Zeng 2002). Stripe rust can complete its year-round cycle in Xinjiang, Yunnan, southern Gansu and northwestern Sichuan where wheat can be grown from lowland valleys at 1,000 m to highland terraces at 3,300 m which provide a “green bridge” for pathogen migration from late-maturing highland areas to early-sown wheat plants in the lowlands (Li and Zeng 2002; Zeng and Luo 2006; Chen WQ et al. 2009). The over-wintering regions are mainly in Sichuan, Hubei and Shaanxi. The eastern epidemic areas cover the largest wheat-producing areas, including Henan, Hubei, Shandong,

Shanxi, Hebei, Sichuan, Shaanxi and Anhui. In over-summering areas, the infected autumn-sown wheat and volunteer wheat in the lowlands, and late-maturing spring wheat in the highlands serve as inoculum sources for local recycling throughout the year (Li and Zeng 2000). Previous studies showed that urediniospores from the over-summering regions, particularly the northwestern and southwestern areas, spread eastward to eastern China. Fall-sown winter wheat in the over-wintering regions becomes infected during late autumn and early winter and the pathogen survives mainly as latent mycelial infections until temperatures increase in spring when inoculum then moves to the major winter wheat regions to the northeast (Li and Zeng 2002; Zeng and Luo 2006). Thus, interregional disease distribution in time and urediniospore spread are mainly from west to east in autumn and from south to north in spring (Li and Zeng 2002; Zeng and Luo 2006). The over-summering areas provide initial inoculum for the eastern plain regions of China (Li and Zeng 2002; Zeng and Luo 2006).

Over the last decade wheat stripe rust has remained at high levels posing a threat to wheat production across the entire country. This follows the development and spread of races CYR32 detected in 1994 and CYR33 found in 1997 which are now the predominant races (Chen WQ et al. 2009). The main reason is that winter wheat cultivars with *Yr9*, *Yr3b*, *Yr4b* and *YrSu*, now susceptible to both races, account for 90% of total area of winter in the entire country. Survey data from the last ten years show that the areas affected annually by stripe rust (Table 1) were on average about 4 million hectares. For example, stripe rust affected 6.6, 4.9, and 4.08 million hectares in 2002, 2003, and 2009, respectively (Table 1). It is considered that the stripe rust epidemic in 2002 was the most widespread in the past three decades (Li and Zeng 2002; Wan et al. 2004).

TABLE 1 HERE

In 2009, the early occurrence of stripe rust, 10-55 days in earlier than usual, posed the greatest threat for many years, following widespread over-wintering of urediniospores due to mild winter and favorable early spring conditions. It was estimated that the total area of wheat infected by stripe rust reached 4.08 million hectares (Table 1). Fortunately, intense disease monitoring and forecasting allowed timely application of fungicides which effectively prevented losses and further spread to the wheat production regions further east. Thus, a potentially huge yield loss nationwide was avoided through timely use of fungicides based on earlier accurate disease forecasts. Moreover, the surveys and forecasting of disease provided information to pathologists, growers, county agents, extension services, the fungicide trade, and government administrators from village level to the Ministry of Agriculture enabling them to make decisions on chemical intervention to minimize yield losses. Fungicides, spray equipment, and personnel training were well-organized in advance.

In the present situation where most currently grown cultivars are susceptible, fungicide use will continue to play a key role in control of wheat rusts until resistant varieties can be grown across large areas. Seed treatment and foliar sprays are the major means of application to decrease infection of seedlings of autumn-sown wheat in the over-summering and over-wintering areas. This can reduce the available inoculum for later windborne dispersal to more eastern regions (Chen YL et al. 1988). For other areas, generally a single foliar application is recommended in early spring when disease incidence reaches 2 to 4% or when disease severity reaches 1% at the jointing and stem elongation

stages. The areas of stripe rust occurrence and fungicide treatment during 1999-2009 are shown in Table 1. In 2008, about 80% of seed autumn-sown in southern Gansu, northwestern Sichuan, and southern Shaanxi was fungicide-treated and this delayed the occurrence stripe rust in these regions in the 2008-2009 crop seasons.

Effective control of stripe rust by the "family-unit" cultivation system is becoming increasingly difficult as many young villagers in the rural areas migrate to the cities for employment. Currently, government administrators from the townships and ministries guide growers in implementing disease control. This involves training, technical guidance, fungicide supply, seed treatment, and timing of fungicide application. Further measures are being taken to help growers understand the potential threat of stripe rust on grain yield and disease management generally, through television programs, internet websites, radio broadcasts, and cell phone messages.

Race identification and virulence evolution

Stripe rust race identification in China is conducted by the Chinese National Wheat Rust Collaborative Group (CNWRCG) comprising the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, Institute of Phytopathology, Northwest A&F University, Yangling, Shaanxi, and the Academies of Agricultural Sciences in the provinces of Gansu, Sichuan and Yunnan. Rust collections in the different provinces are sent to the corresponding branches of the CNWRCG. Methods described by Li and Zeng (2002) for collecting rust samples, testing on differentials, and data recording and analysis are used.

To date, a total of 68 *Pst* races have been identified (Wan et al. 2007; Chen et al. 2009) based on avirulence/virulence patterns using a set of 19 differential wheat genotypes consisting of Trigo Eureka (*Yr6*), Fulhard, Lutescens 128, Mentana, Virgilio (*YrVir1*, *YrVir2*), Abbondanza, Early Premium, Funo (*YrA*, + (+ = additional resistance genes)), Danish 1 (*Yr3*), Jubilejina 2 (*YrJu1*, *YrJu2*, *YrJu3*, *YrJu4*), Fengchan 3 (*Yr1*), Lovrin 13 (*Yr9*, +), Kangyin 655 (*Yr1*, *YrKy1*, *YrKy2*), Suwon 11 (*YrSu*), Zhong 4, Lovrin 10 (*Yr9*), Hybrid 46 (*Yr3b*, *Yr4b*), *Triticum spelta album* (*Yr5*) and Guinong 22 (Li and Zeng, 2002; Wan et al. 2004, 2007; Chen WQ et al. 2009). Of the 68 races, 33 are designated as "races" CYR1 (Chinese Yellow Rust) to CYR33 in chronological sequence and 35 are described as "pathotypes". A "race" is named based on the avirulence/virulence pattern on major differentials and a significant frequency (>3%), whereas a "pathotype" is named based on a virulence variation on a minor differential or an additional differential wheat genotype and a low frequency (<3%) (Wang KN et al. 1986). Changes in races and frequencies occur with changes in wheat cultivars (Wan 2001). Since most of the differentials are used only in China, and since the genetic bases of their resistances are not fully established on an international basis, it is difficult to compare Chinese *Pst* races with those in other countries. Near-isogenic lines (NILs) developed by Australian and Chinese scientists, along with Chinese local supplementary cultivars, may resolve some of these difficulties in the near future.

None of the current races is virulent on *Triticum spelta album* (*Yr5*) or Guinong 22 (*Yr*+) (Chen WQ et al. 2009). Virulence to Zhong 4 (*Yr*+) occurs in a pathotype identified 2009 (Wang BT et al. 2009). All races are virulent to Fulhard and Early Premium, except pathotype CYR18, and to Abbondanza, except Su11-1. CYR32 possesses the widest virulence spectrum, comprising a

combination of virulence to the differential genotypes Lovrin 10 and Lovrin 13 (both *Yr9*), Hybrid 46 (*Yr3b,Yr4b*) and Suwon 11 (*YrSu*). In contrast, CYR18 has the narrowest virulence spectrum, being virulent only to Lutescens (*Yr*+), Abbondanza (*Yr*+), and Danshi 1 (*Yr3*). Races CYR17 to CYR27 were first detected before 1980. The 31 races identified after 1980 were divided into three groups, viz. the Lovrin group (LvG), the Suwon 11 group (SuG), and the Hybrid 46 group (HyG) (Chen WQ et al. 2009). Nine races (CYR32, CYR33, Su11-4, Su11-7, Su11-5, CYR31, Hy46-8, Su11-11 and Hy46-7) were detected with frequencies of 29.6, 17.4, 6.2, 5.5, 4.2, 3.6, 2.9, 2.3, and 2.2%, respectively, during 2003-2007 (Chen WQ et al. 2009). The remaining races had low frequencies of less than 2%. Races CYR18, CYR19, CYR27, CYR30, Lv10-3, Lv13-2, and Hy46-4 were occasionally detected in some years or in some regions, and occurred with frequencies less than 1% during 2003-2007 (Chen WQ et al. 2009). The most frequently identified race from 2003 to 2009 was CYR32 accounting for a frequency of 29.6% throughout the country. CYR33 (previously called pathotype 'Su11-14') with a frequency of 17.4% was detected in all 15 wheat-growing provinces except Shandong (Chen WQ et al. 2009). Importantly, CYR32 and CYR33 have broad virulence and high fitness which makes them widely distributed and adapted to popular cultivars, and therefore, will likely continue to be the major races to cause widespread epidemics of stripe rust in the near future.

From 2001 to 2007, the frequencies of CYR33 and Su11-7 increased from 4.21% and 1.5% in 2001 to 26.72% and 9.46% in 2007, respectively. However, frequencies of CYR30, CYR31, and Su11-4 decreased from 7.33%, 9.51%, and 9.51% in 2001 to 0.51%, 2.26%, and 4.93% in 2007, respectively. CYR32 was first found in 1994, and then became a predominant race at a frequency of 11% in 2000, and remarkably increased to 28.79% in 2001 and 34.60% in 2002 (Wan et al. 2002). Later, the frequency of CYR32 slightly declined but was still at 29.23% in 2003 and 29.97% in 2007. Pathotype CYR33 (named Su11-14 before 2008) was first detected at a frequency of less than 1% in 1997, and subsequently increased from 4.21% in 2001 to 26.72% in 2007. Pathotype Su11-7, first identified in 1995, gradually increased to 10% in 2007. Pathotypes Su11-5, Hy46-7, and Hy46-8 occurred at average frequencies of 4.20, 2.86, and 2.23%, respectively, ranging between 0.11 and 6.28% from 2003 to 2007 (Chen WQ et al. 2009).

Evaluation of stripe rust resistance in wheat cultivars

Growing resistant cultivars is considered the most effective, low-cost, and environmentally safe approach to control stripe rust (Röbbelen and Sharp 1978; Line and Chen 1995). To better understand resistance characteristics of wheat cultivars, and the distribution and utilization of resistance genes in major wheat-growing regions, we evaluated 501 wheat cultivars and advanced breeding lines from 13 provinces in the northwest, north, and Yangze River Valley from 2006 to 2009. Testing was performed on seedlings in the greenhouse and on adult-plants in fields at Yangling, Shaanxi, and Tianshui, Gansu. The recorded data showed that 35 lines (7%) had all-stage resistance, 110 (22.0%) had adult plant resistance, and 356 (71.0%) were highly susceptible. Pedigree analyses indicated that most of the resistant cultivars had *Yr26*/*Yr24*. Also, Guinong 22 and wheat-*Thinopyrum intermedium* derivatives, as well as some genotypes from CIMMYT (e.g. synthetic hexaploid wheat (*Triticum turgidum* × *Aegilops tauschii*)) had high resistance levels (Han DJ et al. unpublished data). There were distinct differences in the frequencies of resistant cultivars tested in several regions as shown in Table

2. The results revealed a low number of all-stage resistant cultivars and a low diversity of resistance genes in Chinese cultivars. Currently, *Yr26* is the most frequent effective resistance gene both in wheat breeding programs and among currently resistant cultivars. Once resistance of *Yr26* is overcome by a new race, there will be severe epidemics and consequent yield losses. Therefore, the continuing widespread use of *Yr26* is a major concern. Earlier, from a study of 98 Chinese cultivars with 26 CYR races, Li GQ et al. (2006) reported that 42.9% had *Yr9*, and 19.3% had *Yr24*/*Yr26*. Wan et al. (2004) evaluated approximately 200 cultivars or breeding lines each year at 20 different field sites located in many provinces. The successive field and greenhouse tests indicated the presence of high-temperature adult-plant (HTAP) resistance and slow-rusting in Chinese cultivars (Wan et al. 2000a, 2000b; Guo et al. 2008). Many studies in China and elsewhere (e.g. Line and Chen 1995; Singh et al. 2000; Chen XM 2005; Li ZF et al. 2006; Lin and Chen 2007, 2009) characterized durable non-race specific HTAP and slow-rusting resistances under field conditions. The advantages of utilizing HTAP and slow-rusting resistances must be considered for sustainable control of stripe rust in the major wheat-growing areas in China. Dr R. P. Singh, CIMMYT, Mexico, is working with breeders in Sichuan and Yunnan to introduce *Yr18* and other APR genes into local varieties.

TABLE 2 HERE

Developing resistance sources to stripe rust

To date, more than 70 stripe rust resistance genes have been reported (McIntosh et al. 2008 http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbolClassList.jsp); most confer race-specific all-stage resistance, and some confer adult-plant or HTAP resistance (Chen XM 2005; Lin and Chen 2007, 2009). Based on recent evaluations in China, genes *Yr5*, *Yr10*, *Yr15*, *Yr18*, *Yr24*/*Yr26, Yr36, Yr39* and *Yr41*, as well as the source lines possessing *Yr12*, *Yr13*, *Yr14* and *Yr16*, and some temporarily designated genes are still effective and could be used in breeding programs (Wan et al. 2004, 2007). Resistance genes *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr17*, *Yr20*, *Yr21*, *Yr22*, *Yr25*, *Yr27* and *Yr29* are ineffective to the currently prevalent races (Han DJ, unpublished data). Thus, identification and development of new resistance sources are needed. Chinese scientists have made contributions to this research area. Ma JX et al. (2001) documented *Yr26* conferring all-stage resistance on chromosome 1BS. *Yr41* on chromosome 2BS, and conferring resistance to most prevalent races, was identified in cultivar Chuannong 19 by Luo et al. (2005, 2008). Zeng et al. (2007) identified a resistance gene on chromosome 1B in line 101-3. *YrY201* on chromosome 7DL derived from *Aegilops tauschii* was identified in accession Y201 (Zhang YH et al. 2008). Zhou et al. (2008) identified a *Haynaldia villosa*-derived resistance gene *YrV1* on chromosome 3B, and Feng et al. (2008) found that wheat cultivars Aquileja and Xian Nong 4 had quantitative resistance. Cultivars of the Chuanmai series with good stripe rust resistance (*Yr24/Yr26*) were developed by the Sichuan Academy of Agricultural Sciences through crossing synthetic hexaploid wheat (*Triticum turgidum* × *Aegilops tauschii*) lines from CIMMYT with locally adapted cultivars (mainly wheat cultivar Fan 6 derivatives). Lin RM et al. (2007) characterized the genetics of resistance to stripe rust in Zhong 4 (partial amphiploid, 2n=56), which was resistant to all races, except the recent T4, and widely used in wheat resistance breeding programs. Several derivatives of this cultivar have been released in Gansu

province, e.g. Zhongliang and Lantian cultivars or lines.

Additionally, resistance from related species, including *Haynaldia villosa*, *Secale cereale*, *Thinopyrum intermedium* and *Th. bessarabicum* and *Aegilops tauschii* were transferred into wheat backgrounds to further develop wheat germplasm (Yang et al. 1999; Chen YF et al. 2003; Li GR et al. 2006; Chen QZ et al. 2008;).

Genetics and molecular markers for resistance genes

Molecular markers linked to resistance genes can improve selection efficiency in breeding programs. Although different kinds of molecular markers have been developed by gene mapping research, not all are applicable to breeding platforms where resistance to stripe rust is only one of many trait objectives. Thus, except in exceptional circumstances breeders will demand markers that are accurate (preferably perfect or functional markers), low cost, and built upon a single screening platform. Markers for various stripe rust resistance genes developed in China include amplified fragment length polymorphyism (AFLP) and random amplified polymorphic DNA (RAPD) markers for *Yr15* (Peng 2000), expressed sequence tag–simple sequence repeat (EST-SSR) and sequence tagged site (STS) markers for *Yr26* (Ma JX et al. 2001; Wang CM et al. 2008; Wen et al. 2008). AFLP and STS markers for *Yr10* (Shao et al. 2001; Wang LF et al. 2002), RAPD and SSR markers for *Yr5* (Zhong et al. 2002; Sun et al. 2002), SSR markers for *YrCH42* (identical to *Yr24/26*) and *YrZH84* (Li GQ et al. 2006), and SSR and AFLP markers for *YrC591* (Li et al. 2009) have been reported. The use of markers in pre-breeding and breeding programs not only circumvents the need for disease testing during the breeding process, but also allows the combining of genes including those for all-stage and HTAP or AP resistances. Many of the individual genes (or QTL) for APR do not confer sufficient protection when present alone, but often act additively permitting high levels of resistance to be achieved (Singh 1992). The use of this type of durable resistance in the US Pacific Northwest since the 1960s provides good evidence for its usefulness in sustainable control of stripe rust (Line and Chen 1995; Chen XM 2005). Molecular mapping of HTAP resistance and slow-rusting in Chinese wheat cultivars Xiaoyan 6 and Pingyuan 50 were studied byJin JX et al. (2007) and Yuan et al. (1995). We are using molecular markers to detect the presence or absence of the resistance genes (e.g. *Yr9* and *Yr18*) in current wheat cultivars in order to identify potentially new resistance genes or to help in deploying cultivars with different resistance genes in oversummering, overwintering and spring epidemic regions.

Mechanisms of *Pst* virulence variation

Growing resistant cultivars is the major component of integrated control of stripe rust. However, “breakdown” of resistance following the introduction of new genes for resistance is a major problem. According to Gassner and Straib (1932), Little and Manners (1967) and Godard (1976), virulence in *P. striiformis* can result from mutation or heterokaryosis.

Research on mechanisms of virulence variation in *Pst* has been conducted in China since the 1980s. Results from a series of studies suggested that asexual recombination acts as a possible mechanism of virulence variation for *Pst* (Kang et al. 1993a, 1994a, 1994b; Ma Q et al. 1993). Four new isolates of *Pst* were obtained from inoculating susceptible wheat genotypes with urediniospore mixtures of 120 combinations of 38 single-spore isolates. The virulence patterns of the new isolates were different

from those of the original isolates and the frequencies of urediniospores with three or more nuclei in the new isolates were much higher than those in the original isolates. Ma Q et al. (1993) observed germ tube fusions with one to four nuclei on the surface of wheat leaves. Kang et al. (1993b) observed that fusion also occurred between intercellular hyphae within the wheat leaf tissue. Fusions between germ tubes and intercellular hyphae provide the essential conditions for exchanging nuclei. Further studies by Kang et al. (1994b) showed that most urediniospores and germ tubes had two nuclei, but intercellular hyphae had various numbers of nuclei. About 20% of hyphal cells had two nuclei and 80% of the hyphal cells had three or more. They also found that haustorial mother cells and haustoria commonly had three or more nuclei. When *Pst* formed uredinia, all hyphal cells and urediniospores had just two nuclei (Kang et al. 1994b). Nuclear re-assortment could occur at the stage of differentiation from multinuclear cells to two-nuclear cells. Under natural infection conditions, the same leaves can be infected by more than one race allowing such events to occur. In contrast to Kang et al. (1994b), urediniospores with tri- and tetra-nuclei were found at rates of 0.42 and 0.55%, respectively, among field collections from Tianshui in Gansu from May 1997 to November 1998 (Wang Y et al. 2004). There is now increasing molecular evidence for somatic recombination as a likely mechanism of variation in Chinese *Pst* populations in the highland areas of Gansu (Lu et al. 2009; Duan X et al. 2010), and Mboup et al. (2009) suggested that the genetic recombination of *Pst* in the Tianshui area could be from either sexual or parasexual cycles.

Virulence in *Pst* can be produced by UV-irradiation of urediniospores and seven mutants were obtained in a screening experiment on wheat cultivars after UV treatment of urediniospores (Jin et al. 1992; Shang et al. 1994; Huang et al. 2005; Wang XL et al. 2009). The detectable mutation rate was estimated to be 10^{-4}~10^{-7}. The virulence patterns of the mutants were different from those of the wild-type isolates, suggesting that mutation may be one of the mechanisms of virulence variation for the asexual population of *Pst*.

However, it remains an open question as to whether virulence in *Pst* in China is from mutation, somatic recombination, or a sexual cycle.

Histology and cytology of wheat-*Pst* interactions

Pst development and host responses were examined by light and transmission electron microscopy in compatible and incompatible interactions in wheat cultivars Xinong 85 and Huxianhong and *Pst* race CYR25 (Kang et al. 1993b, 2002). The wheat cultivar Xinong 85 is highly resistant to CYR25, showing reaction type 1 according to the Stakman et al. (1962) scale, whereas cultivar Huxianhong is highly susceptible with reaction type 4. The infection process for *Pst* was similar to those of other cereal rust pathogens except for lack of an appressorium or development of an occasional small appressorium-like strucure over the stomata. However, *Pst* differs from the other cereal rust pathogens by the frequent occurrence of more than two nuclei in the intercellular hyphal cells, haustorial mother cells and haustoria (Kang et al. 1994b). The haustorial mother cells of *Pst* often invaginate their own intercellular hyphae in infected host tissues (Kang et al. 1993b). There is a striking difference in the fungal development and host responses between susceptible and resistant wheat cultivars following infection with *Pst*. The pronounced higher number of hyphae observed in the infected wheat leaves of susceptible cultivar Huxianhong compared to the corresponding tissues in resistant cultivar Xinong 85

indicated that the fungal development in wheat leaves was restricted in the resistant cultivar. Structural defense reactions such as formation of cell wall appositions, collars or papillae, and encasements were essentially more markedly expressed in the infected leaves of the resistant cultivar than in the susceptible genotype. Immunogold labelling of lignin showed markedly higher labelling densities in host cell walls of infected resistant leaves than in susceptible leaves (Kang et al. 2002). Immuno-labelling studies demonstrated higher accumulations of chitinase and ß-1,3-glucanase in host cell walls, cell wall appositions, intercellular hyphal cell walls and extrahaustorial matrices in the incompatible interaction than in the compatible interaction (Kang et al. 2003). The two hydrolases may contribute to defense reactions against stripe rust along with other defense responses such as depositions of lignin and callose, formations of cell wall appositions, collars or papillae and encasements.

Generation and accumulation of reactive oxygen species (ROS), superoxide anion (O_2^-), and hydrogen peroxide (H_2O_2) were studied in leaves of wheat cultivar 'Suwon 11' infected with avirulent pathotype CYR23 and a virulent pathotype CYR31 (Wang CF et al. 2007, 2010). Generation of O_2^- and H_2O_2 was measured histochemically using nitro-blue tetrazolium (NBT) and 3,3-diamino-benzidine (DAB), respectively. At the pre-penetration stage, both avirulent and virulent races induced H_2O_2 accumulation in guard cells. In the incompatible interaction, rapid increases of O_2^- and H_2O_2 generation at infection sites were detected. The percentage of infection sites showing NBT- and DAB-staining was 36.1% and 40.0%, respectively, 12 h post inoculation (hpi). During the next 12 h H_2O_2 levels further increased, whereas O_2^- accumulation declined. The stage from 12 hpi to 24 hpi coincides with primary haustorial formation in mesophyll cells. In contrast, in the compatible interaction, O_2^- and H_2O_2 could not be detected at most infection sites. In the incompatible interaction, intensive DAB staining was also observed in mesophyll cells, especially in cell walls, surrounding the infected cells 16-24 hpi; thereafter, these cells contained fluorescing compounds and underwent the typical hypersensitive response (HR). The number of necrotic host cells surrounding the infection sites increased continuously from 20 hpi until 96 hpi. Thus, H_2O_2 accumulation during the early infection stage should be associated with the occurrence of hypersensitive cell death and the resistance response should result in stopping the growth of the avirulent race. In the compatible interaction at 96 hpi, H_2O_2 accumulation was observed in mesophyll cells surrounding infection sites.

Genomics of wheat-*Pst* interactions

To acquire further insights into wheat-*Pst* interactions, transcription profiles of genes involved in wheat-*Pst* interactions were generated. From a compatible interaction between wheat cultivar 'Suwon 11' and pathotype CYR31, 2,743 unisequences were obtained from a cDNA library consisting of 5,793 ESTs (Ma JB et al. 2009). Among the unisequences, 52.8% were highly homologous to plant genes, 16.3% to fungal genes, and 30% were non-hit. Nineteen genes had significant homologies to fungal pathogenicity/virulence factors. Thus, a new database was constructed for identifying functional genes involved in the wheat-*Pst* compatible interaction. To isolate differentially expressed genes during a compatible interaction, a suppressive subtractive hybridization (SSH)-cDNA library was constructed from the wheat variety 'Suwon 11' and race CYR31. A total of 787 unisequences were obtained from 1,707 ESTs, of which 397 unisequences (50.4%) were of unknown function. The

potential functions of these genes may have unique roles in the compatible interaction between wheat and *Pst*. Some host defense-related genes were also isolated from the compatible interaction. To determine the expression patterns of a wheat-*Pst* compatible interaction, cDNA-AFLP profiles were generated with 64 primer pairs at different time points after inoculation with a virulent race (Wang XJ et al. 2009b). In this study, 2,306 of 54,912 transcript-derived fragments (TDFs) displayed altered expression patterns after inoculation, of which 966 were up-regulated and 1,340 down-regulated. Interestingly, 48% and 35% of the differentially expressed genes showed different degrees of change during the periods 6-24 and 120-168 hpi, respectively. In contrast, only 17% of genes were differentially expressed at 48-96 hpi. The expression changes of these genes corresponded quite well to the different infection stages and were also supported by the histological study of compatible interaction between wheat and *Pst*. One hundred and eighty six TDFs were isolated, of which 9 were of pathogen origin as validated by PCR-based assays followed by sequencing. Moreover, low expressions of several host defense-related genes were also detected in the compatible wheat-*Pst* interaction in this study.

To study genes involved in an incompatible interaction, a SSH library was generated from Suwon 11 inoculated with avirulent race CYR23. A total of 652 unisequences were obtained, of which 31 were determined as genes involved in signal transduction and 77 were predicted to encode defense-related proteins (Yu et al. 2010). The expression of wheat signal transduction genes increased soon after inoculation. Various defense-related genes, including reactive oxygen species, ATP-binding cassette (ABC) transporters, pathogenesis-related proteins, and genes involved in the phenylpropanoid pathway were induced. These defense genes are known to work in a sequential and concerted manner resulting in HR. Wang XJ et al. (2010) identified transcriptionally regulated genes during an incompatible interaction between wheat and *Pst* using the cDNA-AFLP technique. A total of 52,992 (TDFs) were generated with 64 primer pairs, and 2,437 (4.6%) of them displayed altered expression patterns after inoculation, from which 1,787 were up-regulated and 650 down-regulated. A fascinating discovery in this study was the quenching of divergent expression of *Pst*-regulated genes in both incompatible and compatible interactions in the middle stages of *Pst* infection. By comparing TDFs identified for the incompatible interaction and those identified in the previous study for the compatible interaction (Wang XJ et al. 2009b), 161 TDFs were shared by both interactions and 94 were expressed specifically in the incompatible interaction. The specificities of 43 selected TDFs determined using quantitative real-time PCR (qRT-PCR) indicated that 11 expressed only in the incompatible interaction. The involvement of shared genes, but with different expression levels, indicated that plant responses in compatible and incompatible interactions are qualitatively similar, but become quantitatively different soon after *Pst* infection.

In addition, a number of candidate genes from wheat challenged by the stripe rust fungus, such as hypersensitivity induced reaction genes (*Ta-hir1*, *Ta-hir2*, *Ta-hir3*, *Ta-hir4*) (Yu et al. 2008; Zhang Y et al. 2009), a transcription factor gene *TabZIP1* (Zhang Y et al. 2009), a novel wheat NAC gene *TaNAC4* (Xia et al. 2010), a wheat HSP70 gene *TaHSC70* (Duan YH et al. 2010), a wheat ß-1,3-glucanase gene *TaGlu* (Liu et al. 2010), and a pathogenesis-related thaumatin-like protein gene *TaPR5* (Wang XJ et al. 2009a), were characterized in wheat-*Pst* interactions. The expressions of these genes in Suwon 11 wheat leaves infected with CYR23 (avirulent) and CYR31 (virulent) of *Pst* were also assessed following exogenous treatments with hormones, such as methyl jasmonate (MeJA),

salicylic acid (SA), ABA, and ethylene (ET). The expression levels of the above genes were significantly higher in the incompatible relative to compatible interaction again indicating that they may function in wheat defense response to *Pst*.

Genomics and population structures of *Pst* in China

Although *Pst* is economically important, little is known about its genome and gene functions. Zhang YH et al. (2008) constructed a cDNA library with RNA isolated from *Pst* urediniospores. A total of 4,798 ESTs were sequenced from a germinated urediniospore library and assembled into 315 contigs and 803 singletons. About 23.9% and 13.3% of the resulting 1,118 unisequences were homologous to functionally characterized proteins and hypothetical proteins, respectively, and 62.8% had no significant homolog in GenBank. Several ESTs shared significant homology with known fungal pathogenicity or virulence factors, such as HESP767 of the flax rust pathogen and PMK1, GAS1, and GAS2 of the rice blast fungus. They selected six ESTs (Ps28, Ps85, Ps87, Ps259, Ps261, and Ps159) and observed their expression patterns during urediniospore germination and infection of wheat seedlings using qRT-PCR. All showed the highest transcript levels in germinated urediniospores and much lower levels in ungerminated urediniospores and infected wheat leaves. The transcript level of Ps159 also increased at later infection stages. The data suggested that these genes that are highly expressed in germinated urediniospores, may have important roles in fungal-plant interaction during the early infection stages. In collaboration with Washington State University, USA, a cDNA library of *Pst* haustoria was generated (Yin et al. 2009); 5,126 EST sequences were also generated from *Pst* haustoria, and 287 contigs and 847 singletons were obtained from them. Approximately 10% and 26% of the 1,134 unique sequences were homologous to proteins with known functions and hypothetical proteins, respectively. The remaining 64% of unique sequences had no significant similarities in GenBank. Fifteen genes were predicted to be proteins secreted from *Pst* haustoria. Analysis of ten genes, including six secreted protein genes, using quantitative RT-PCR revealed changes in transcript levels in different developmental and infection stages. Although studies on *Pst* were focused on analyzing *Pst* transcripts, this work detected a number of candidate host genes possibly involved in fungal-plant interactions during the early infection stages.

Recently, some species of *Berberis* spp. were shown to be infected by *Pst* (Jin et al. 2010). Although barberry plants are widely distributed in different regions of China, including the provinces of Gansu, Sichuan and Shaanxi, an association of barberry plants and *Pst* has not been reported. The current view is that the fungus reproduces mostly if not always asexually by dikaryotic urediniospores. Despite asexual (clonal) reproduction new pathotypes are often found, especially when they are able to overcome resistance genes in previously resistant cultivars. Development of durable and effective control methods against stripe rust is largely based on the knowledge of the pathogen population structure and its potential for adaptation to new cultivars (Boshoff et al. 2002). To study the population genetic structures of *Pst* in China, DNA fingerprinting probes (moderately repetitive DNA sequences-PSR sequences) specific to the *Pst* genome and a group of SSR markers derived from expressed sequence tags of *Pst* were developed by Shan et al. (1997) and Chen CQ et al. (2009). Using these markers, high genetic diversity was reported in Chinese *Pst* populations from different regions (Shan et al. 1998; Zheng et al. 2000). Lu et al. (2009) showed that populations of *Pst* in Gansu

possessed a high level of genetic diversity, but there was a lower genetic differentiation using SSR markers. Duan X et al. (2010) also found that *Pst* possessed high diversity in Gansu, compared with European and Australian populations based on data reported in Hovmøller et al. (2002) and Steele et al. (2001). Although the over-summering areas in Gansu have attracted much attention concerning *Pst* virulence variation and population diversity in the past, we now have new knowledge and superior molecular tools for further study in the future.

Monitoring stripe rust plays an important role in its control. A rapid and reliable detection of the pathogen in latent infections of wheat leaves during overwintering of the fungus should contribute to the early determination of the initial inoculum potential for improving effective management of the disease. To achieve this goal, molecular markers were identified and specific PCR primers were developed to differentiate predominant races (Zhao et al. 2007; Wang XJ et al. 2008; Wang BT et al. 2010). Detection of *Pst* in the infected wheat leaves from greenhouse and field demonstrated that these primers were highly specific and sensitive for *Pst* detection and the predominant races. However, an appropriate sampling strategy will be needed for *Pst* detection in wheat leaves lacking visible symptoms under field conditions using these molecular methods.

Strategies for sustainable control of wheat stripe rust

Based on epidemiological considerations, it has been suggested that different resistance genes for controlling wheat stripe rust should be deployed in the defined over-summering, over-wintering, and eastern spring epidemic regions (Li and Zeng 2002; Wan et al. 2007). This would be best achieved by the use of different all-stage resistance genes in the oversummering and overwintering areas and of APR and HTAP resistances in the eastern areas. Historically, virtual monocultures of single resistance genes were deployed throughout the country leading to widespread 'boom and bust' cycles as exemplified by Bima 1, Lovrin varieties and derivatives (Wan et al. 2004), Fan 6 and derivatives especially in Sichuan, and predictably varieties with *Yr24/Yr26* in the near future. Furthermore, previous research indicated that southern Gansu, northwestern Sichuan, southern Shaanxi, and Yunnan are favorable for *Pst* over-summering due to their unique geographic features, climatic conditions and farming systems (Li and Zeng 2002). *Pst* can complete its asexual cycle in these areas where cropping at altitudes ranging from hundreds meters to over 2,000 m, creates a huge variation in seeding and harvesting times, as well as favorable climatic conditions (Li and Shang 1989; Li and Zeng 2002). Undoubtedly, these areas are hotspots for stripe rust and its survival in China (Li and Zeng 2002). Moreover, they are reserviors of pathogenic variability since new races are usually detected there (Li and Zeng 2002). Therefore control of stripe rust to reduce inoculum levels in these regions will have a profound effect on inoculum levels throughout the country. The following strategies have been suggested to control stripe rust in the over-summering areas:

(1) Use of resistant cultivars with multiple or different resistance genes, or effective multilines capable of reducing the build-up of inoculum. If varieties become susceptible they should be withdrawn from use.

(2) Reduction of the wheat area, particularly in highland regions. Farmers are being encouraged to grow alternative crops such as rapeseed, potato, beans, Chinese medicinal herbs and vegetables (Li and Zeng 2002). Thus, the pathogen population and disease severity are decreased, and pathogen

mutation and survival rates are also expected to decline.

(3) Use of seed treatments to reduce autumn-sown wheat infection (Chen et al. 1988).

(4) Removal of self-sown wheat in lowland areas where it acts as a host for over-summering *Pst*, by physical removal, plowing, spraying or grazing.

(5) Adjustment of seeding time to reduce or avoid early infections.

Actually, these strategies are already being put into practice and areas of wheat being grown in the over-summering regions, especially in southern Gansu and northwestern Sichuan, have significantly declined. For example, the area of wheat in southern Gansu declined by nearly 30,000 ha during 2003-2006, being replaced by potato, vegetables, fruit trees, corn, rapeseed, walnut, tea and Chinese medicinal herbs (http://www.gs.gov.cn). This accounts for 16.8% of the planned reduction in wheat grown above 1,600 m. However, the issue remains as to how much the area has to fall in order to protect the country's eastern wheat-growing areas. Farmers in the over-summering regions must keep some land for wheat in order to produce their own food.

Thus effective control of stripe rust in China remains a huge challenge as in many other parts of the world. A national project for the integrated control of stripe rust in the over-summering areas was initiated in 2009. Breeding wheat cultivars with effective and durable resistance has received much attention and is supported nationwide. The current situation of high dependence on fungicides to reduce yield losses has to be addressed by the development and greater use cultivars with adequate and durable resistance particularly in the over-summering and over-wintering regions of the country. Varieties in the more eastern high production areas should have at least some resistance for protection in years of high disease risk.

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Table 1 Areas of stripe rust occurrence, and control using fungicides, 1999-2009

Year	Area of occurrence (m ha)	Area of fungicide treatment (m ha)	Amount of fungicide used (tonnes)
1999	1.34	1.43	1502
2000	0.73	0.77	806
2001	3.13	2.77	2910
2002	6.60	5.65	5928
2003	4.95	4.59	4817
2004	3.56	4.66	4900
2005	3.19	4.53	4760
2006	3.43	4.76	5003
2007	2.89	4.31	4533
2008	1.81	2.71	2842
2009	4.08	5.94	6225

Table 2 Status of resistance to stripe rust in wheat cultivars tested in the epidemic regions in 2009

		Number and frequency		
Epidemic region	Total number	ASR[a]	of APR [b]	Susceptibie
South Gansu	80	12 (13.8%)	20 (26.2%)	48 (60.0%)
Sichuan basin	86	15 (17.5%)	45 (52.3%)	26 (29.2%)
Central Shaanxi & east Gansu and south Shanxi	106	4 (5.6%)	29 (26.8%)	73 (67.6%)
South Shaanxi-northwest Hubei-south Henan	72	3 (4.2%)	9 (12.5%)	60 (83.3%)
Yellow-Huai-River valley and Middle-lower reaches of Yangze River valley	172	0	20 (11.6%)	152 (88.4%)

[a]ASR, all-stage resistance

[b]APR, adult plant resistance