

REVIEW

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# Fighting wheat rusts in China: a look back and into the future

Jie Zhao\*  and Zhensheng Kang\*

## Abstract

Wheat rusts, including stripe, leaf, and stem rusts, are severe wheat diseases and cause huge yield loss in China annually. Benefiting from utilizing the genetic resistance wheat varieties, wheat stem rust has been effectively controlled since the 1970s; however, the wheat stripe and leaf rusts are still threatening the wheat production in China due to lack of effective agricultural regulations. This review summarizes the research advances on wheat rust physiology, epidemiology, and fungicide resistance in China. In addition, the corresponding field management strategies for the integrated control of rust diseases are also discussed.

**Keywords** Wheat stripe rust, Wheat leaf rust, Wheat stem rust, Epidemiology, Fungicide resistance, Integrated management

## Background

Wheat is one of the four staple crops in China. Stripe, leaf, and stem rusts are the three dominant rust diseases on wheat, which are caused by three *Puccinia* species in phylum Basidiomycota. Historically, the three wheat rust diseases caused severe epidemic incidents and significant wheat yield loss in China. Currently, stripe rust is the most devastating disease on wheat among the three in China. Several excellent reviews have summarized the occurrence and management of wheat stripe and leaf rusts in China (Shen and Wang 1962; Wang et al. 1988; Wu and Niu 2000; Li and Zeng 2002; Zeng and Luo 2006; Wan et al. 2007; Song et al. 2010; Wang et al. 2010; Chen et al. 2013; Kang et al. 2015; Ma 2018; Zhao et al. 2016a, 2018; Zeng et al. 2022), but the research advances of wheat stem rust in China have not been comprehensively reviewed yet. Recently, many exciting progresses

related to the wheat rust disease controls have been achieved in China. Here, we reviewed the history of the wheat rust in China and proposed the future perspective for the disease control from following aspects: the economic importance, epidemiology, fungicide resistance, and integrated managements.

## Historical and current status of wheat rusts

Common wheat (*Triticum aestivum* L.) is one of the most important staple cereal crops, the rice, corn, wheat, and potato. China is the largest wheat-producing and consuming country, which produces an annual yield of over 128 million metric tons, accounting for approximately 17.5% of the global wheat production based on the 10-year's data from 2011 to 2020 (FAOSTAT 2020). In 2021, the total planting area of wheat is 23.6 million hectares, which produces approximately 137 million tons of wheat (<http://www.stats.gov.cn/>). Therefore, wheat is of extremely and economically important crop in China. Currently, the major wheat-planting regions are distributed in five provinces, Shandong, Hebei, Henan, Jiangsu, and Anhui, which is also known as 'the Huang-Huai-Hai winter wheat areas' (Wan et al. 2007).

Wheat rusts, including stripe rust (or yellow rust) (Fig. 1), leaf rust (or brown rust) (Fig. 2), and stem rust

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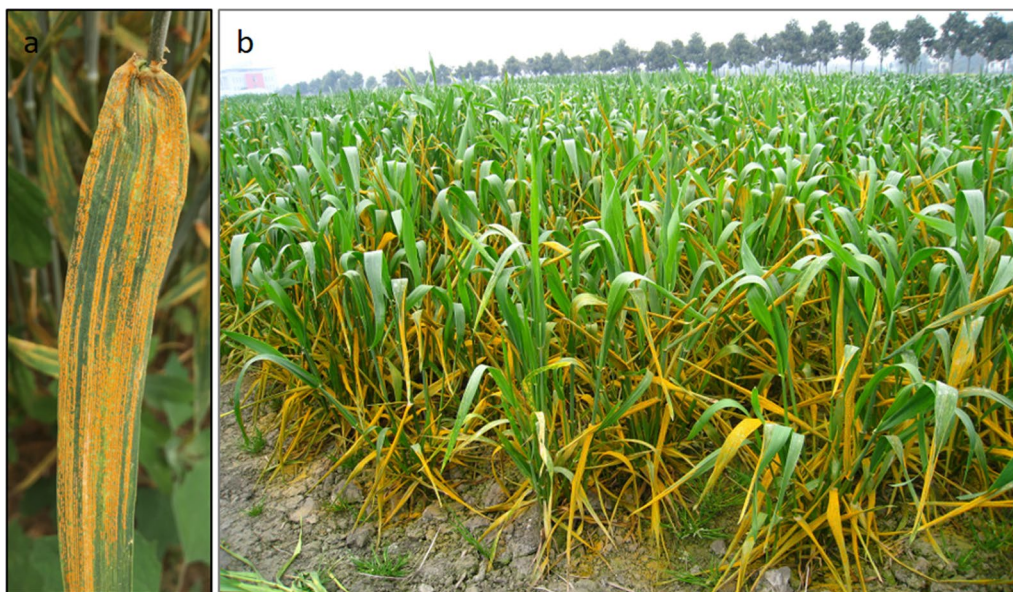
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**Fig. 1** Single stripe signs of uredia between leaf veins of wheat stripe rust (a) and a nursery field showing severe stripe rust infection on wheat plants at elongation stage in Mianyang, Sichuan on March 18, 2011 (b)



**Fig. 2** Symptoms of leaf rust on wheat leaves. a A few uredia at early stage of the development. b Numerous uredia produced on a leaf at late stage of the development

(or black rust) (Fig. 3), are the dominant wheat fungal diseases. These wheat diseases significantly limit the yield reduction. Wheat rust is an ancient disease. The recorded occurrence of wheat rusts in China can be tracked back to as early as 4000 years ago, the time of

the introduction of wheat into Hexi Corridor in Gansu during the Shang Dynasty (Li and Zeng 2002; Yang et al. 2016; Wei 2021). It was first documented in detail in a Chinese ancient agricultural book, *Qimingyao* 《齐民要术》 by the author Sixie Jia during AD 533 to 544



**Fig. 3** Symptoms of stem rust in wheat fields. **a** Uredia on a diseased stem. **b** Uredia on awns and glumes of a wheat head

in the Beiwei Dynasty. In this book, it was documented that wheat was vulnerable to ‘jaundice’ disease (actually stripe rust) and the disease was figuratively described as ‘jaundice’ because it resembled the color of newly born infants. Currently, wheat stripe rust is the most destructive disease among the three wheat rust diseases in China. It mainly prevails in the northwest and southwest China. Because of the severe epidemics, the stripe rust disease is listed in first class crop diseases management in the 333th bulletin by Ministry of Agriculture and Rural Affairs of the People’s Republic of China on September 15, 2020 ([http://www.moa.gov.cn/govpublic/ZZYGLS/202112/t20211224\\_6385489.htm](http://www.moa.gov.cn/govpublic/ZZYGLS/202112/t20211224_6385489.htm)).

Wheat leaf rust usually takes place in the North China Plain, the middle-lower reaches of the Yangtze River, southwestern and northeastern regions of China (Liu and Chen 2012). Wheat leaf rust has been well controlled in China in the last decades, but the epidemic of the disease has often occurred in many wheat-growing provinces, especially in ‘Huang-Huai-Hai regions’ recently (Zhao et al. 2008; Zhang et al. 2018, 2020b; Wang et al. 2022b). The increasing incident of wheat leaf rust has potentially threatened the wheat production in these regions, and is a major rust disease after stripe rust in China.

Wheat stem rust primarily occurred in the northeastern spring wheat-growing region of China (Zeng et al. 1963; Li and Zeng 2002). This disease has been problematic in China prior to the 1970s. However, the disease rarely occurs in China nowadays (Han et al. 2010; Li et al. 2017), which benefits from extensive application of wheat cultivars that carry the stem rust-resistant gene *Sr31* since the 1970s (Li and Zeng 2002). Although Ug99 (race TTKSK) and its variants that successfully overcome the resistance of *Sr31* and have widely spread from the origin of Uganda to many other African and Asian countries ([https://rusttracker.cimmyt.org/?page\\_id=260](https://rusttracker.cimmyt.org/?page_id=260)), Ug99 has not been detected in China yet (Cao et al. 2007). However, most of tested Chinese native wheat cultivars (98.3% out of 118 varieties) are highly susceptible to Ug99. Ug99 also overcomes *Sr21* and *Sr38* that are two key resistance genes to stem rust in China. Therefore, invasion of Ug99 lineage races to China is of significantly potential risk. Regulations to prevent the invasion of Ug99 races are necessary.

#### Severe impacts recorded in the last 70 years

Prior to 1949, several severe epidemic incidents of wheat stripe rust were reported in Sichuan and Fujian provinces in 1939–1940, which resulted in a yield reduction

up to 15% and 60%, respectively. In the 1940s, the disease severely occurred in the middle regions (Guanzhong plain) of Shaanxi Province, especially in the years of 1942, 1946, 1948, and 1949 (Li and Zeng 2002). Since 1950, China has encountered five nationwide severe wheat stripe rust epidemics, which took place in 1950, 1964, 1990, 2002, and 2017, respectively. These epidemics resulted in the wheat rust outbreak in a total of 550 million hectares, leading to the yield loss up to 13.8 million metric tons (Li and Zeng 2002; Ma 2018). The most severe epidemics occurred in 1950 and 1964, which affected the growing area over 13.33 million hectares, with a yield loss of 6 million and 3.2 million metric tons, respectively (Li and Zeng 2002). From 1972 to 1983, several severe stripe rust epidemic events occurred in the key over-summering (Qinghai, Gansu) and overwintering regions, which are distributed in Sichuan, Shaanxi, Henan, and Hubei provinces. Each incident resulted in the infection of wheat areas approximately 1.33 million to 2.0 million hectares (Li and Zeng 2002). In addition, large-scale epidemics caused by the disease occurred in 1975, 1983, and 1985, resulting in an estimated crop yield reduction up to 0.865 million, 1.074 million, and 0.85 million metric tons, respectively. In 1991, an extremely severe nationwide epidemic took place in Gansu, Ningxia, Shaanxi, Henan, Hubei, and Shandong provinces, which destroyed approximately 6.53 million hectares of wheat and caused a conspicuous crop yield loss of 0.434 million metric tons, although the fungicides were timely applied (Li and Zeng 2002). Based on the data acquired from 2006 to 2015, the average yield reduction caused by wheat stripe rust is approximately 0.159 million metric tons annually (Liu et al. 2016). The most recent large scale of stripe rust epidemic occurred in 2019, which is believed infecting two million hectares of wheat. Notably, no significant yield loss was observed due to the application of fungicides.

Serious epidemics caused by wheat leaf rust have been reported in winter wheat-growing areas of northern China and spring wheat-growing areas of northeastern China. This disease has led to a disastrous decrease in yield during the 1950s–1980s (Hu and Roelfs 1985; Li and Zeng 2002; Zhou et al. 2013; Peng et al. 2016). In this period, four moderate epidemics of leaf rust occurred in the north winter wheat-planting areas in 1969, 1973, 1975, and 1979, respectively, which also resulted in a huge yield reduction (Li and Zeng 2002). Since the late 1990s, five severe leaf rust epidemics in China have been documented in the year of 2008, 2009, 2012, 2012, and 2015 (Zhou et al. 2013; Zhang et al. 2015, 2020b, 2020c; Wu et al. 2019), and the most severe epidemic of leaf rust occurred in Anhui, Gansu, Henan, Sichuan, and Shanxi provinces in 2012. It damaged more than 15 million hectares of wheat growing area and caused a yield reduction

near 3 million metric tons (Zhou et al. 2013; Wu et al. 2019).

Wheat stem rust is known as a serious issue in wheat-growing regions before the 1970s, especially in spring wheat growing regions of northeastern China, where nine severe epidemics were reported from 1923 to 1964 (Li and Zeng 2002). Two most severe wheat stem rust epidemics occurred in 1923 and 1948, which caused a massive yield reduction of 7.4 million and 5.6 million metric tons, respectively (Wu et al. 2020b). In 1956, 1958, and 1964, the moderate and severe large-scale epidemics occurred in ‘Jiang-Huai region’ (also known as ‘Yangtz-Huaihe region’), from 1949 to 1966. Each epidemic caused a massive yield loss. For instance, in 1956, the epidemic in Jiangsu and Anhui provinces caused a noteworthy yield loss up to 1.0 million metric tons (Li and Zeng 2002). Since the 1970s, wheat stem rust has not been a notable issue and the pathogen is considered as opportunistic pathogen and cannot cause a serious threat to wheat production. Therefore, wheat stripe rust is the most destructive rust disease and more attentions should be paid to control this disease.

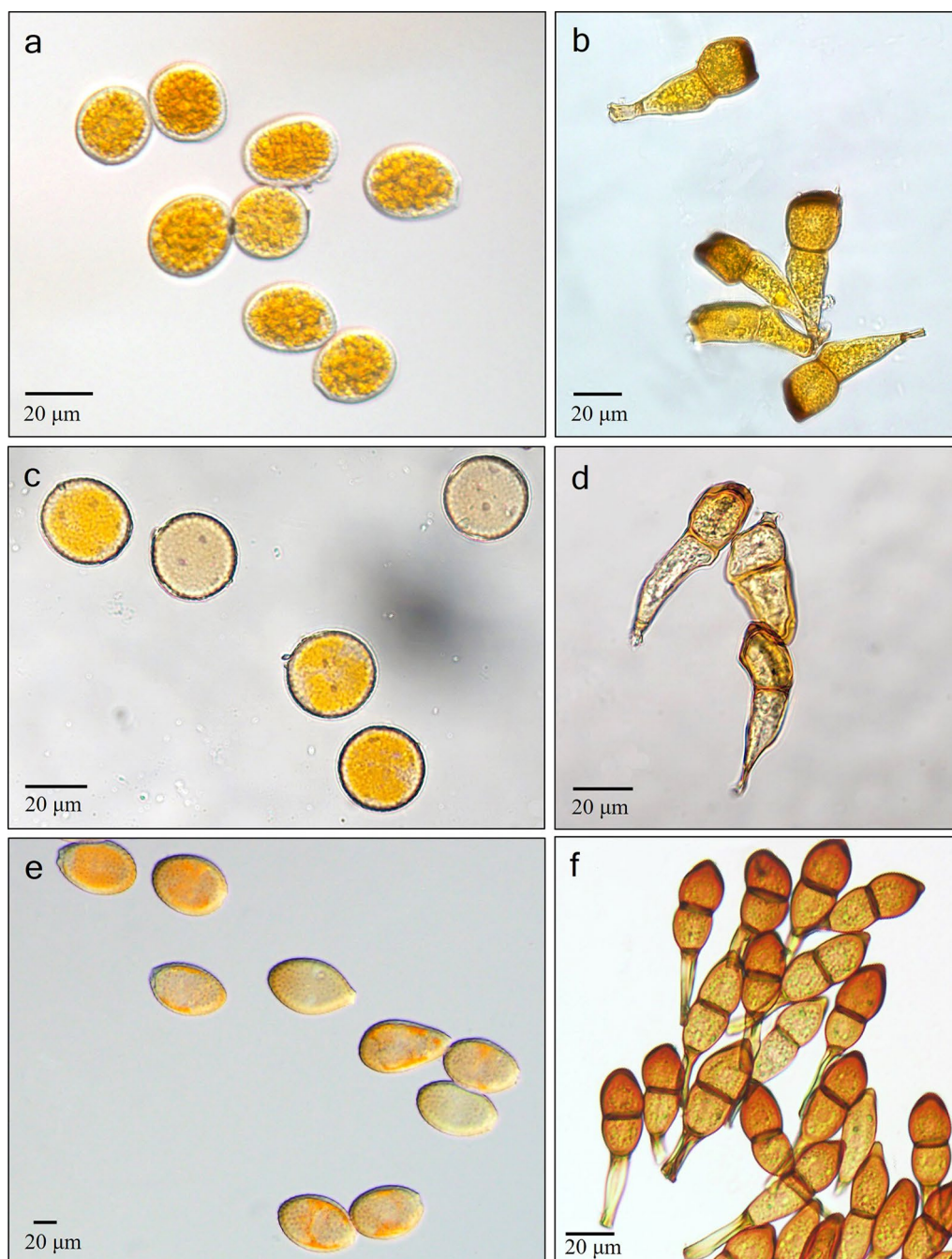
#### The causal agents

Stripe rust, leaf rust, and stem rust on wheat are caused by different *Puccinia* species in Pucciniaceae family of phylum Basidiomycota. Wheat stripe rust is caused by *Puccinia striiformis* Westendorp f. sp. *tritici* Eriksson (*Pst*) [syn. *P. glumarum* (Schumacher) Erichsen et Hennings] (Fig. 4a, b). Traditionally, *P. striiformis* f. sp. *tritici* is one of five different formae speciales (f. sp., pl.) of *P. striiformis* (Eriksson 1894; Stubbs 1985). Whereas, based on morphological and genomic data, *P. striiformis* (stripe rust agents of wheat, *Aegilops*, *Elymus*, and barley) were clustered into the same clade. Therefore, they were all re-designated as *P. striiformis* (Liu and Hambleton 2010). Wheat leaf rust is caused by *P. triticina* Eriksson (*Pt*) (syn. *P. recondite* Roberge ex Desmaz f. sp. *tritici* Eriksson et Hennings) (Mains 1932) (Fig. 4c, d); while wheat stem rust is caused by *P. graminis* f. sp. *tritici* Eriksson et Hennings (*Pgt*) (Fig. 4e, f). The differences are also reflected by the distinct uredia and urediospores of three rust species, where they exhibit differences in color, spore size and cause different symptoms on the hosts.

#### Primary hosts and alternate hosts

##### Primary hosts (uredial host)

The wheat rusts *Pst*, *Pt*, and *Pgt* are obligate parasites. These pathogens primarily infect wheat, other cereal crops, and grasses. By infecting these hosts, they go through the uredial or telial stages (Stubbs 1985). The monocot plants *Triticum*, *Aegilops*, *Agropyron*, *Bromus*, *Elymus*, *Hordeum*, and *Secale* are all vulnerable to



**Fig. 4** Urediospores and teliospores of the wheat stripe, leaf, and stem rust fungus. **a, b** Urediospores (**a**) and teliospores (**b**) of *Puccinia striiformis* f. sp. tritici. **c, d** Urediospores (**c**) and teliospores (**d**) of *Puccinia triticina*. **e, f** Urediospores (**e**) and teliospores (**f**) of *Puccinia graminis* f. sp. tritici

*Pst* (Stubbs 1985). In fact, many approaches have been made to determine the susceptibility of grass plants to *Pst*, *Pt*, and *Pgt* (Ling 1945; Lu et al. 1958; Peng and Chen 1987; Wang et al. 1987; Niu et al. 1991a, 1991b; Yuan et al. 1994; Wei et al. 2021; Qin et al. 2022; Li and Zeng 2002). Currently, 88 grass species (including varieties) from 16 genera in the family Poaceae could serve

as uredinial hosts or accessory hosts for *Pst* (Li and Zeng 2002). However, *Pt* isolated from leaf rust of six grass species, *Agrimonia Pilosa*, *Bromus inermis*, *Elymus dahuricus*, *E. sibiricus*, *Roegneria penduline*, and *R. ciliaris*, could infect wheat (Wang et al. 1987), suggesting that these plants assist the wheat leaf rust prevailing in field.

### Alternate host (aecial host)

The pathogens *Pgt*, *Pt*, and *Pst* are known to be heteroecious and macrocyclic. They have to infect alternate hosts to complete the sexual reproduction. For *Pgt* and *Pt*, their alternate hosts were discovered over a century ago (de Bary 1866; Jackson and Mains 1921); however, the alternate hosts for *Pst* remained to be mysterious till 2010 (Jin et al. 2010). Now it is known that *Berberis* and *Mahonia* are the alternate common hosts for *Pgt* and *Pst* (Roelfs 1985; Jin et al. 2010; Zhao et al. 2013; Cheng et al. 2022). Notably, there are some differences for *Berberis* and *Mahonia* species or subspecies when they serve as alternate hosts for *Pgt* and *Pst*. For example, *Berberis circumserrata* could be an alternate host for *Pst* but not for *Pgt* (Roelfs 1985; Zhao et al. 2013). There are 215 endemic *Berberis* and 36 endemic *Mahonia* species in China, while there are 500 *Berberis* and 60 *Mahonia* species around the world (Ying and Chen 2001). So far, more than forty Chinese *Berberis* species and four *Mahonia* species/subspecies have been reported to serve as alternate hosts for *Pst* (Zhao et al. 2013, 2016b, 2018; Du et al. 2019; Zhuang et al. 2019; Cheng et al. 2022). However, only one endemic *Berberis* species, the *B. amurensis* Rupr., was identified as an alternate host for *Pgt* in China (Zeng et al. 1963). Under field conditions, *Pgt* infects five *Berberis* species, *B. aggregata*, *B. brachypoda*, *B. potaninii*, *B. shensiana*, and *B. soulieana*, and sexual reproduction of this rust is completed during the infection of these hosts (Zhao et al. 2015). These observations clearly indicated that the above mentioned *Berberis* species are alternate hosts for *Pgt*.

Although many *Thalictrum*, *Isopyrum*, and *Clematis* species in *Ranunculaceae* family, and a few *Anchusa* and *Echium* species in the *Boraginaceae* family have been identified as alternate hosts for *Pt* (Chester 1946; Sibilja 1960; d'Oliveira and Samborski 1966), only four meadow rue (*Thalictrum*) species are the native alternate hosts in China. These species were identified as *T. minus* L., *T. petaloideum* L., *T. minus* var. *hypoleucum*, and *T. baicalense* recently (Zhao et al. 1994, 2021).

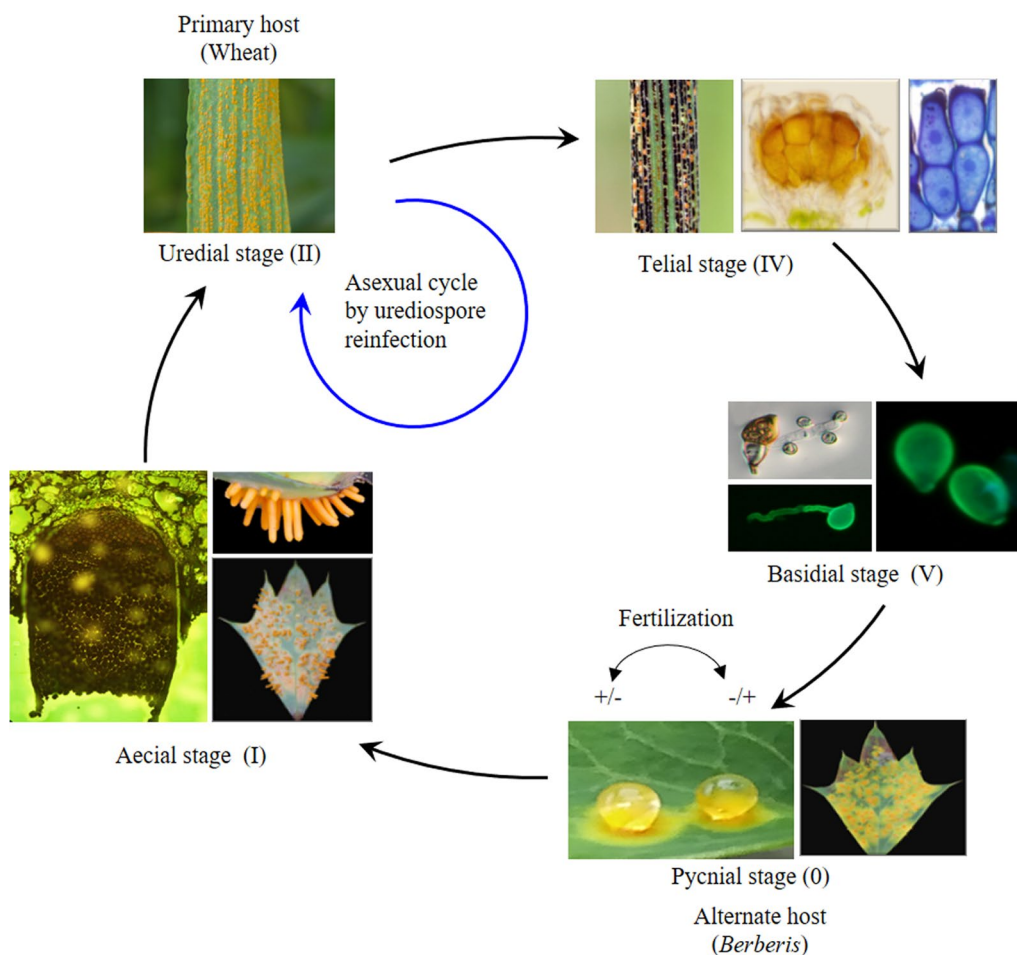
### Life cycle of the rusts

*Pst*, *Pgt*, and *Pt* are the heteroecious, macrocyclic rust fungi. They complete their life cycle with five different types of spores on two unrelated hosts (Fig. 5). Their full life cycle includes asexual and sexual stages. Under favorable conditions, basidiospores generate from teliospores. After germination, it can infect an alternate host to produce pycnia and pycniospores, as well as receptive hyphae (trichogyne) and paraphyses. With these mating type and receptive hyphae, they complete their sexual life cycle and consequently produce aecial clusters from abaxial leaves, where the aeciospores generate inside of

the aecial clusters. Once the aecial clusters broke, aeciospores are released from aecial clusters and spread by wind to infect primary hosts, wheat and grasses. Urediospores are produced after aeciospores infect the primary hosts. However, teliospores are primarily formed in wheat host tissues at a late wheat growth stage.

### Wheat rust epidemiology

The wheat stripe rust epidemic in China can be divided into different epidemiological regions. In fact, the epidemiological regions of the disease are consistent (Li and Zeng 2002) till 1995, when Zeng and the colleagues proposed that the Chinese epidemiological region of wheat stripe rust can be divided into three regions (Zeng and Sun 1995). Based on a combined method of large-scale and long-term field surveillances, geographic information system (GIS) system and molecular data, they divided the epidemiological regions into overwintering region (for the autumn spores), winter *Pst*-reproducing region that for the spring spores, and spring epidemic region (Chen et al. 2013). Later, Zeng and Luo (2006) proposed to subdivide China's main stripe rust epidemiological region into 15 epidemiological zones according to the geographic features, crop cultivation modes, the regularity for pathogen overwintering and overwintering, and the frequency of stripe rust epidemics. It is worth to mention that because of the unique geography, the Yunnan epidemiological region is relatively independent because the pathogen can complete the disease cycle and overwintering and overwintering without traveling to other regions (Li and Zeng 2002). As a result, this epidemiological region is almost isolated from other regions. However, recent studies revealed that the Yunnan epidemiological region and other southwestern epidemiological regions are also involved in wheat stripe rust epidemics in China (Awais et al. 2022; Huang et al. 2022; Ju et al. 2022; Zhan et al. 2022a). In addition to Yunnan region, Tibet and Xinjiang also developed to be the independent stripe rust epidemiological regions (Li and Zeng 2002; Hu et al. 2017; Awais et al. 2022). Importantly, Xinjiang and other Chinese provincial *Pst* populations are all isolated from that of Pakistan due to extremely high genetic divergence (Awais et al. 2023). Chen et al. (2013) considered that Chinese stripe rust epidemiological regions include overwintering regions, winter-*Pst* reproductive regions, and spring epidemic regions. The overwintering regions include Gansu (area of Longnan, Tianshui, Dingxi, Linxia, Pingliang, Qingyang, and Gannan), Ningxia (Guyuan), Qinghai (Haidong), Shaanxi (Baoji), and Sichuan (Ganzi, Aba, and Liangshan area). However, the winter-*Pst* reproductive regions include low mountain, valley, mountain dam, and plain areas in Sichuan, South Shaanxi, Northwest Hubei, Yunnan,



**Fig. 5** Life cycle of *Puccinia striiformis f. sp. tritici*

Guizhou, and Chongqing. While, the spring epidemic regions are the most of winter wheat-growing regions, including the ‘Huang-Huai-Hai Plain’, the regions of Beijing, Tianjin, Hebei, Henan, Shandong, Jiangsu, Anhui, the Guanzhong Plain of Shaanxi, and mid-lower reaches of Yangtz River.

For wheat stem rust, spring wheat-growing regions of Northeast China and Inner Mongolia, Northwest China, and wheat-growing regions of South Yunnan Province (Dehong, Honghe, Wenshan, and Simao regions) are important epidemiological areas. Weak winter wheat-growing regions of middle and lower reaches of Yangtz River and Sichuan (Ganzi) are regular epidemiological areas. Wheat-growing regions of Fujian Province and Southeastern coastal regions (Guangdong and Guangxi provinces) are also epidemiological areas (Wu and Huang 1987; Cao and Chen 2009).

Wheat leaf rust frequently occurs in wheat-growing regions of Southwest China and the mid-lower reaches of Yangtz River, but many of them appear in Yangtz

River reaches, ‘Huang-Huai-Hai Plain’, and southwestern China. Occasionally, severe epidemics can occur in wheat-planting regions of North and Northeast China, and even Northwest China (Jin et al. 2017; Zhou et al. 2013).

**The disease cycle of *Puccinia* species**

*Puccinia* species are obligate pathogens when they infect wheat, where they fully depend on this living host to complete disease cycle. Temperature is the key factor for their disease cycle, and the rust diseases require different temperature for their growth. Wheat stem rust prefers higher temperature (opt. 30°C) than wheat leaf rust (opt. 25°C) and wheat stripe rust (opt. 12–15°C) (Roelfs et al. 1992). Cool and humid weather favor the development of wheat stripe rust. By contrast, high temperature inhibits the disease development (Rapilly 1979). In China, wheat stripe rust complete disease cycle by windborne urediospore infection, including oversummering and overwintering spores and the spores of infected autumn-sown

wheat (Li and Zeng 2002). In susceptible hosts, the temperature for *Pst* overwintering period cannot exceed 23°C (max. aver. Temp. of a 10-day duration) in July and August, the two hottest months (Li and Zeng 2002; Zeng and Luo 2006). In general, the lowest altitude for *Pst* overwintering is over 1600 m above sea level, where the highest average temperature is typically below 23°C. Urediospores in overwintering areas are spread to autumn-sown wheat seedlings by wind in the local and overwintering areas, where the pathogen infects the plants and develops the stripe rust. In addition, the lowest temperature for *Pst* overwintering period is -6°C to -7°C from December to next January which are the coldest months. However, as long as the wheat seedlings are covered by snow, these pathogens can safely overwinter even if temperature drops to -10°C (Fig. 6) (Li and Zeng 2002). *Pst* usually overwinters in infected wheat tissues in the form of hyphae. In these regions, wheat grows slowly in autumn and winter, which is usually warmer than other regions. Under such circumstances, *Pst* continuously grow on infected wheat plants during winter and subsequently develop as the *Pst*-reproducing regions. South Henan, North Hubei, Longnan of South Gansu, South Shaanxi, and Sichuan Basin are the primary overwintering regions (Li and Zeng 2002; Chen et al. 2013). In spring, the pathogens in overwintering regions are transmitted to wide wheat-growing regions in East China and other regions to cause inter-regional epidemics.

Importantly, Chinese researchers found that in spring of the Northwest overwintering areas, such as Qinghai, Gansu, Western Shaanxi, and Tibet, *Pst* basidiospores can infect susceptible barberry to complete their sexual cycle (Zhao et al. 2013, 2022; Wang et al. 2016; Chen



**Fig. 6** Autumn-sown winter wheat seedling leaves showing developing stripe rust infection underneath snow patches in Baoji, western of Shaanxi Province in China, based on field observations on December 14, 2015

et al. 2021a; Liu et al. 2021; Du et al. 2022). In some regions, such as Qinghai, Shaanxi, and Gansu, susceptible barberry released basidiospores are the major source of infection, and often cause the epidemics of wheat stripe rust (Chen et al. 2021a; Liu et al. 2021; Zhao et al. 2022). Nevertheless, it was found recently that in Tibet, *Pst* can infect susceptible barberry to complete their sexual reproduction in autumn (Du et al. 2022), but whether susceptible barberry is related to stripe rust infection on wheat is unknown.

Unlike other rusts, wheat leaf rust has wider overwintering and overwintering areas in China. In particular, in some places, *Pt* urediospores can continuously infect the young wheat stumps after harvesting and are preserved in the local for overwintering. In autumn, the pathogens further infect the winter wheat seedlings that are sown in autumn season to cause leaf rust and overwinter in the infected wheat tissues in the form of hyphae. Generally, the frequency of overwintering in warmer regions is higher than that in cold regions, and the frequency of overwintering is positively correlated to the level of wheat leaf rust epidemic in the coming spring. The epidemic is mainly attributed to the continuous re-infection via the windborne urediospores.

In contrast, wheat stem rust has narrow overwintering areas due to the nature of urediospores that are sensitive to cold. As such, the pathogens overwinter in southeastern regions (i.e. Fujian, Guangdong) and South Yunnan rather than in north wheat-producing regions. The rust can parasitize wheat plants in overwintering areas in which the average minimum temperature in December to next January is above 10°C (Huang et al. 1993). *Pgt* can attack autumn-sown wheat seedlings in Shandong Peninsula and 'Xuhuai regions' of Jiangsu Province. However, they cannot survive the cold winter in most of these regions. Although few pathogens may successfully overwinter in these regions, they contribute inconsiderably to wheat stem rust epidemics (Huang et al. 1993). In spring and summer, spores in overwintering areas spread from south to north and west via the Yangtze River reaches, the North China Plain and reach spring wheat-producing regions in Northeastern and Northwestern China as well as Inner Mongolia. Thus, the dispersal of the pathogen causes vast wheat stem rust epidemics. *Pgt* urediospores mostly overwinter on late-maturing spring wheat and wheat stump in Northwestern and Southwestern China, and also on volunteer winter wheat in the plains of Jiaodong of Shandong Province and Huaibei of Jiangsu Province (Huang et al. 1993).

#### The race evolution of the pathogens

In nature, pathogens can rapidly evolve. The rule is also seen in the three wheat rust pathogens. Indeed, wheat



rust pathogens can evolve to new virulent races with a high frequency in the field. New races often overcome the resistance of wheat varieties and cause disease. Some of the races dominate epidemics in the field by overcoming a certain resistance gene and evolve as the emerging new races.

### The *Pst* races

Race identification of *Pst* in China was commenced in the 1940s by Fang (1944), who identified nine races from isolates in southwestern of China. These pathogen races are mostly from Yunnan Province (Fang 1944). Later, Lu et al. (1956) identified 10 isolates that were collected from seven provinces in 1951 as 5 races which were used by Gassner and Straib on wheat cultivars Carsten V, Michigan Amber, Spaldings Prolific, Blé rouge Décosse, and Heines Kolbens (Gassner and Straib 1930). Based on the maximum scores of reaction on the differentials including Early Premium, Nongda 3, Bima 1, Bima 4, Liying 3, and Yupi, fifty *Pst* isolates collected in 1953–1955 were determined as 16 races, and 8 of which were recovered from *Elymus sibiricus*, *E. chinense*, and *Agropyron* spp. (Lu et al. 1956). Since 1957, CY (CY=Chinese yellow) series were assigned to Chinese *Pst* races, and later CYR (CYR=Chinese yellow rust) series designation for races of this rust has been used till nowadays. In addition, pathotypes that are virulent to a certain genotype of Chinese differential sets, such as Hybrid 46 (Hy46) pathotype, Suwon 11 (Su11) pathotype, Lovrin 10/13 (Lv10/13) pathotype, Guinong 22 (G22) pathotype, and Jubilejina 2 (Ju2) pathotype, were also determined as *Pst* races that were not designated to CYR series. Since the designation of physiological CYR series races (CYR1 to CYR34) (Table 1), it has been designated according to the race with an outbreak frequency higher than 10% and a continuous prevalence in China (Lu et al. 1963; Liu et al. 2017). During 1957–1961, 10 CYR races (CYR1–CYR10) were identified from 325 *Pst* isolates. Among the races, three of which, the CYR1, CYR8, and CYR3 were widespread (Lu et al. 1963). During 1963–1966, CYR1 and CYR10 were the dominant races, while CYR10 displayed the highest outbreak frequency in 1964, but CYR8 decreased to rare race. CYR13 was firstly found in Lintao County of Gansu Province in 1962 and it exhibited an increasing frequency from 6.4% to 16.3% during 1964–1966. By contrast, during 1971–1979, CYR1, CYR8, CYR10, and CYR13 displayed a decreasing frequency and were not detected any more after 1975. Meanwhile, CYR17, CYR18 (virulent to *Abbondanza*), and CYR19 rapidly developed into major races. CYR17 caused an epidemic in Shaanxi Province in 1965. It gradually developed to be dominant race during 1974–1976 in North and East China; whereas, CYR18 that was founded for

the first time in Gangu County in Gansu Province exhibit an extremely low frequency of outbreak. At the same time, in Sichuan Province, CYR18 was prevalent, but CYR17 was not. In Gansu Province, however, CYR18 was conspicuous and CYR17 had a high frequency of epidemic. Both races showed high outbreak frequency in Shaanxi Province (Wang et al. 1986). Since 1975, the outbreak frequency of CYR17 and CYR18 remarkably decreased, but CYR19 rapidly increased as a major race, where the outbreak frequency reached the highest of 81.1% in all the countrywide races in 1977 after the first appearance in Qingsheng County of Sichuan Province in 1972 (Wang et al. 1986). During 1980–1985, the CYR19 was proved as a complex of races, which was further separately designated as CYR23 (previously 19-1); however, CYR24 (previously 19-3), CYR25 (previously 19-4), CYR26 (previously 19-2), CYR23, CYR25, and CYR26 were prevalent races, and CYR25 was predominant race (Wang et al. 1986). CYR20 was first found virulent to the wheat variety Fengchan 3 in Shaanxi Province in 1971 (SXIPP 1976). CYR21 was initially detected in the Pingliang of Gansu Province in 1975. However, both CYR20 and CYR21 were not developed to be the dominant races (Wang et al. 1986). In 1982, Su11 pathotypes that are virulent to wheat genotype Suwon 11 were first detected in an experimental field at Qinghai Academy of Agricultural Sciences (Li 1983; Wang et al. 1986). CYR22 was first detected in Tianshui of Gansu Province in 1975, which then developed to be the dominant race in Gansu and Shaanxi provinces with the outbreak frequency of 25.5% and 22.7% in 1983, respectively. Lv10 and Lv13 pathotypes that are virulent to wheat genotypes Lovrin 10/13 (*Yr9*) were initially detected in Longnan of Gansu Province in 1975 and 1979, respectively (Kang and Li 1984; Kang et al. 1987). CYR27, also known as pathotype 82-1, was first detected in Xihe County of Gansu Province in 1980. Later, it reached a high outbreak frequency in 1983. The trend was promptly decreased in 1984 in the provinces Gansu, Shaanxi, Sichuan, Yunnan as well as eastern regions of China, including Shanxi, Hebei, Shandong, Henan, Jiangsu, Anhui, Hebei, Hunan, and Inner Mongolia (CNWRCCG 1985; Wang et al. 1986). CYR28 is a Lv10 pathotype complex and CYR29 is also known as Lv13-1. Both races are the members of Lv10/13 pathotypes. They were first detected in 1983 and 1985, respectively (CNWRCCG 1987). During 1986–1990, CYR29 rapidly became the top outbreak frequency race over others in 1988, and reached the maximum frequency of 40.3% in 1989. The frequency remained the highest in the following 2 years (Wu et al. 1993). Meanwhile, Lv10/13 pathotypes rapidly developed into a prevalent pathotype. Due to rapid development of CYR29 and Lv10/13 pathotypes, the susceptible wheat which was planted about 8.8

**Table 1** Chinese historic and current predominant races of *Puccinia striiformis* f. sp. *tritici*

Race <sup>a</sup>	Differential host	Lutescens	Xibel 54	Bima 1	Xibeifengshou	Strubbes Dickkopf	Trigo-Eureka	Fulhard	Mentana	Virgilio	Abbondanza	Early Premium	Danish 1	Fengchan3	Year detected	References
CYR1	V	V	V	V	V	A	A	A							1958	Lu et al. (1963)
CYR2	A	A	A	A	V	V	V	V							1958	Lu et al. (1963)
CYR3	V	A	AV	A	A	A	A	A							1958	Lu et al. (1963)
CYR4	V	A	V	V	V	V	A	A							1958	Lu et al. (1963)
CYR5	V	A	V	V	V	A	-	-							1958	Lu et al. (1963)
CYR6	A	V	A	A	A	A	-	-							1958	Lu et al. (1963)
CYR7	A	A	A	A	A	A	A	A							1958	Lu et al. (1963)
CYR8	VA	A	A	A	A	A	A	A	A	A	A	A	A	A	1960	Lu et al. (1963)
CYR9	V	V	A	A	A	A	A	V							1960	Lu et al. (1963)
CYR10	A	V	V	V	V	A	A	V	A	A	A	A	A	A	1960	Lu et al. (1963)
CYR11	A	V	V	V	V	-	A	A	V	A	V	V	V	V		Yang and Sun (1983)
CYR12	V	V	V	V	V	-	A	A	A	A	A	V	V	V		Yang and Sun (1983)
CYR13	V	V	A	V	V	-	V	V	A	A	A	A	A	A	1962	Wang et al. (1986)
CYR14	-	-	-	-	-	-	-	-	-	-	-	-	-	-		Not available
CYR15	-	-	-	-	-	-	-	-	-	-	-	-	-	-		Not available
CYR16	-	-	-	-	-	-	-	-	-	-	-	-	-	-		Not available

**Table 1** (continued)

Race <sup>a</sup>	Differential host	Race <sup>a</sup>										Year detected	References					
		Fulhard 128	Lutescens 128	Mentana	Virgilio	Abbondanza Early Premium	Funo	Danish1 2	Jubilejina 2	Fengchan 3	Lovrin 10			Zhong 11	Suwon 11	Hybrid 46	Triticum spelta 22	Guinong 22
CYR17	VA	V	A	VA	A	VA	A	VA	A	AV	A	A	A	A	A	A	1965	Wang et al. (1986)
CYR18	A	A	V	AV	A	AV	AV	V	A	AV	A	A	A	A	A	A	1969	SXIPP (1976)
CYR19	A	V	V	V	A	V	V	V	A	V	A	A	A	A	A	A	1972	SXIPP (1976)
CYR20	A	V	A	V	A	V	A	V	A	V	A	A	A	A	-	A	1972	SXIPP (1976)
CYR21	VA	V	V	VA	A	VA	VA	VA	VA	V	A	A	A	A	A	A	1975	Wang et al. (1986)
CYR22	V	V	V	VA	A	V	V	VA	VA	V	A	A	A	A	A	A	1975	Wang et al. (1986)
CYR23	V	V	V	V	A	V	V	V	V	V	A	A	A	A	A	A	1978	Wang et al. (1986)
CYR24	VA	V	V	V	A	V	V	A	A	V	A	A	A	A	A	A	1978	Wang et al. (1986)
CYR25	VA	V	V	V	V	V	V	V	V	V	A	A	A	A	A	A	1978	CNWRCC (1985), Wang et al. (1986)
CYR26	VA	V	V	A	A	V	V	V	V	V	A	A	A	A	A	A	1978	CNWRCC (1985), Wang et al. (1986)
CYR27	V	V	V	V	V	V	V	V	V	V	A	A	A	A	A	A	1980	CNWRCC (1985), Wang et al. (1986)
CYR28	V	V	V	V	V	V	V	V	V	V	A	A	A	V	A	A	1983	Wang et al. (1986), Wu et al. (1993)
CYR29	V	V	V	V	V	V	V	V	V	V	V	A	A	V	A	A	1985	Wang et al. (1986), Wu et al. (1993)
CYR30	V	V	V	V	V	V	V	V	V	V	V	A	A	V	V	V	1991	Wan et al. (1999)

**Table 1** (continued)

Race <sup>a</sup>	Differential host	Fulhard 128	Lutescens 128	Virgilio	Abbondanza Premium	Early Premium	Funo	Danish1 2	Jubilejina 3	Fengchan 3	Lovrin 655	Kangyin 11	Suwon 10	Zhong 4	Lovrin 10	Hybrid 46	Triticum spelta 22	Guinong album	Year detected	References
CYR31	V	V	V	V	V	V	V	A	V	V	V	A	V	A	V	V	V	V	1993	Wan et al. (1999)
CYR32	V	V	V	V	V	V	V	V	V	V	V	V	V	A	V	V	V	V	1991	Wan et al. (2003)
CYR33																			1997	Chen et al. (2009)
CYR34	V	V	V	V	V	V	V	V	V	V	V	V	V	A	V	V	V	V	2009	Liu et al. (2010)
																				Liu et al. (2017)

<sup>a</sup> CYR22 was designated from Kangyin 655 pathotype. CYR23, CYR24, CYR25, and CYR26 were designated from the isolates 19-1, 19-3, 19-4, and 19-2, respectively. CYR27 was designated from the isolate 82-1. CYR28 and CYR29 were designated from the isolates LV10-1 and LV13-1, respectively. CYR32 and CYR34 were designated from the isolates HY-3 and G22-9, respectively  
A, Avirulent; V, Virulent; AV or VA mixed reaction in which the avirulent is predominant as AV and the virulent is predominant as VA. '-'; data not available

million hectares in 1990 and accounted for 62.7% of the total planted areas in that year, was suffered with severe wheat stripe rust epidemic (CNWRRCG 1991). In contrast, CYR28 remained low outbreak frequencies consistently. During the same period, the outbreak frequency of CYR23, CYR25, and CYR26 races were rapidly decreased (CNWRRCG 1991). In 1991–1996, CYR29 kept prevailing and emerged as the most dominant race till 1995, but it became inconsiderable to the rust epidemic since 1996. Although CYR25 ever developed as a second dominant race during 1991–1992, its outbreak frequency was low. CYR30, previously names as race 91-1, is virulent to the genotypes Hybrid 46 (*Yr3b*, *Yr4b*, and *YrH46*). Similarly, CYR31 previously named as race 93-1, is virulent to genotypes Hybrid 46 and Suwon 11 (*YrSu*). CYR30 and CYR31 were first detected in Sichuan in 1991 and in Gansu in 1993, respectively; both pathogens have a broad virulence spectrum than CYR28 and CYR29. As a result, CYR 30 and CYR31 rapidly became third and second prevalent races during 1993–1995. In particular, CYR31 ever emerged as the top prominent race in 1996 (Wang et al. 1996; Wan et al. 1999). Notably, Hy46 and Su11 became the major pathotypes during 1994–1996, and they were further classified to 9 and 12 sub-pathotypes, respectively, based on their virulence differentiation (Wan et al. 1999). CYR32, a previous name Hy-3, is designated in 2002 and is more virulent than CYR30 and CYR31. This race was first detected in the wheat cultivar Red Abbondanza in Huangzhong of Qinghai Province in 1994 (Wan et al. 2003). The outbreak frequency of this race is comparable to that of CYR31, which are about 11.7% in 2000. However, in 2001, the outbreak frequency reached incredibly to 28.8% (Wan et al. 2003). CYR33 (also known as Su11-14 previously) is virulent on Suwon 11, which was designated in 2008. This race was detected in 1997 with an outbreak frequency less than 1%, but the frequency unbelievably jumped to 26.72% in 2007 (Chen et al. 2009). Since 2000, CYR32 and CYR33 become the dominant races (Wan et al. 2003; Liu and Chen 2012; Wang et al. 2014; Li et al. 2016b; Wang et al. 2017; Jia et al. 2018a, 2021); with an exception of CYR33 that exhibited a remarkably low frequency (<5%) in Gansu in 2018 (Jia et al. 2021). Based on the annual reports from 2010 to 2011, CYR32 and CYR33 were mostly detected in Gansu, Shaanxi, and Sichuan provinces (Liu et al. 2012). There are 133 races and pathotypes were identified from 1014 isolates that are collected from 14 provinces. Thirteen of which are CYR races, including CYR17, CYR20, CYR21, CYR23, CYR25, CYR26, CYR27, CYR28, CYR29, CYR30, CYR31, CYR32, and CYR33. The remaining 115 isolates were known pathogens (Liu et al. 2012), which increases 35 pathotypes than that of identified before 2004 (Wan et al. 2004). Su11 pathotypes include 586

isolates (57.8% of the total) and is followed by Hy46 pathotypes that consist 273 isolates (26.9% of the total). G22 pathotypes, known to be virulent on genotype Guinong 22 which harbors resistance gene *Yr26*, *Yr24*, and *Yr10*, are spreading since the first detection of the sub-pathotype 9 (G22-9) in Pi County of Sichuan Province in 2009 (Liu et al. 2010). Due to rapid spreading, the outbreak frequency of G22-9 increased from 0.11% in 2009 to 10.56% in 2015. As the result, the sub-pathotype G22-9 promptly developed to be the dominant pathotype and therefore was designated as CYR34 in 2016 (Liu et al. 2017). Currently, CYR34, CYR33, CYR32, and G22 pathotypes are dominate races/pathotypes (Han et al. 2016; Li et al. 2016b; Jia et al. 2018a, 2021). Meanwhile, more attention should be paid on monitoring the emerging pathotypes. For instance, the ZS pathotype, which is virulent to wheat genotype Zhong 4 (ZS). This pathotype was first detected from wheat cultivar Baomai in Taibai County of Shaanxi Province in 2003. It exhibits a similar virulence spectrum on 19 Chinese wheat varieties in addition to Zhong 4. (Li et al. 2016b). However, a pathotype ZS-1 suddenly caused epidemics in Gansu Province during 2017–2018 (Jia et al. 2021). A rising concern is the high virulence pathotypes that have broken the fence of the resistance gene *Yr-5* that exists in the genotype *Triticum aestivum* subsp. *spelta* var. *album*. This pathotype displays similar virulence to the widely distributed CYR32 and CYR34 races and currently has evolved to generate the same lineage pathotypes (Zhang et al. 2020a, 2022). Recently, more *Pst* races have been sporadically identified in a few provinces since 2012. Race identification of *Pst* is very important to understand temporal dynamics, and can guide *Yr* gene deployment in the epidemiological regions. It is equally important for managing wheat stripe rust and race-targeted wheat breeding program.

### The *Pt* races

*Pt* race identification in China started from 1940 by professor Huanru Wang who temporarily worked at the Institute of Agricultural Research, Tsinghua University in Kunming, Yunnan Province (Wang 1947). He identified three races, the race 1, 63, and 123 from Yunnan isolates that were collected in 1940–1942 using the same international differential hosts applied by Mains and Jackson (1926). Later, Kening Wang identified 417 *Pt* isolates collected from 1949 to 1951 using the international differential hosts set; however, the differentials was not suitable for identifying *Pt* races of China (Wang 1961). Until the early 1970s, the uniform differential hosts set, including eight wheat cultivars, viz. Lovrin 10, 6068, INR66-331, Redman, Dongfanghong3, Fengchan 3, Baiyoubao, and Taishan 4, were used as Chinese differentials

to differentiate *Pt* races. Meanwhile, local wheat cultivars were added to the differential hosts. Therefore, the non-uniform names of *Pt* races, such as Zhi, Chun, Yu, and Lu series, were used in designating isolates in different regions of China (Wang et al. 1982). By 1977, a uniform nomenclature was determined to designate Chinese *Pt* races with CL (CL=China leaf rust) plus a hyphen and a number (also Chinese Yezhong) series. Using this nomenclature rule, 1237 *Pt* isolates were identified annually from 18 provinces during 1974–1979, and finally were identified as 11 races by the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, the College of Plant Protection, Hebei Agricultural University, and the Institute of Plant Protection, Heilongjiang Provincial Institute of Agricultural Sciences. Three out of 11 prevalent races were renamed as CL-1 (Yezhong 1), CL-2 (Yezhong 2), and CL-3 (Yezhong 3). The remaining 8 races, including Zhi 2 to Zhi 7, Zhi 13, and Shandong A, were not uniformly determined (Wang et al. 1982). In 1981, a combination of original standard differentials and additional eight wheat cultivars (Taishan 1, Zhong 5, Rulofen, Lovrin 12, Predgorina 2, Avrora, Kavkez, and Kangyin 655) was used to differentiate *Pt* races. In 1986, 16 races, CL-4, CL-38, CL-34, CL-7, CL-2, CL-44, CL-3, CL-19, CL-29, CL-12, and CL-17, and 5 unnamed races with additional virulence patterns were identified from 113 isolates using eight Chinese differentials. Among them, CL-4 was the most prevalent race in China, with a highest 29% outbreak frequency (Hu and Roelfs 1989). It is worth to mention that Hu and Roelfs (1989) used 16 Thatcher near-isogenic lines to identify *Pt* races in China. They detected a virulence frequency of 84% to 95% on *Lr2c*, *Lr14a*, *Lr14b*, *Lr21*, *Lr17*, and *Lr3*. Unified designated race 13, with virulence on *Lr1*, *Lr2a*, *Lr2c*, and *Lr3*, was prevalent across China. From 1996, 48 races, viz. CL-1 to CL-48 (also Yezhong 1 to 48), were identified in China. During 1976–1996, the dominant races, CL-1, CL-2, CL-3, CL-29, CL-38 (Yezhong series), and Lovrin 10 pathotypes (virulent to wheat cv. Lovrin 10, including CL-4, 34, 46, 19, and 45) have been detected annually (Yuan et al. 1983, 1991; Yuan 1984; Chen et al. 1994; Yuan and Zhu 1995). In 1997, PHT (virulent to *Lr1*, *Lr2c*, *Lr3*, *Lr3ka*, *Lr11*, *Lr16*, *Lr17*, *Lr26*, and *Lr30*), PCR (virulent to *Lr1*, *Lr2c*, *Lr3*, *Lr3ka*, *Lr11*, *Lr26*, and *Lr30*), and THT (virulent to *Lr1*, *Lr2a*, *Lr2c*, *Lr3*, *Lr3ka*, *Lr11*, *Lr16*, *Lr17*, *Lr26*, and *Lr30*) were dominant races among 41 races identified from 110 isolates collected from nine provinces (Qin et al. 1998). During 1998–2000, four out of 162 races, the FHB, PHT, FHG, and THT, were identified from 479 *Pt* isolates and exhibit an outbreak frequency much higher than other races. Races TTJ, TRT, THD, FCJ, FCD, FHD, KHD, THB, and PHB in Shanghai, FHB in Hebei, PHT in Shandong, FHJ, FHG, FRG, and KRB in

Shaanxi, and FHT, NHJ, PHJ, and THT in Yunnan were dominant races in the corresponding regions. In contrast, although the outbreak frequency of races FHB, PRF, and TMG were higher than 36 other races identified from 43 isolates in Jiangsu Province, only three isolates were detected among all isolates, and there were no dominant races in this region (Yang et al. 2002). Isolates with virulence to *Lr2c*, *Lr3*, *Lr2b*, *Lr16*, *Lr26*, *Lr10*, *Lr37*, and *Lr14b* exhibited an outbreak frequency over 80%, and isolates displaying virulent to *Lr1*, *Lr2a*, *Lr9*, *Lr11*, *Lr14a*, *Lr29*, *Lr18*, *Lr14ab*, *Lr17*, and *Lr28* showed a frequency around 50%. Notably, increasing number of isolates show virulence to *Lr2a*, *Lr2b*, *Lr3*, *Lr9*, *Lr19*, *Lr24*, *Lr28*, and *Lr29*, but there are also decreasing numbers with virulence to *Lr1*, *Lr3ka*, *Lr15*, *Lr14B*, *Lr6*, *Lr7*, and *Lr30* in the 3 years (Yang et al. 2002). In addition, 79 races were identified from 613 *Pt* isolates during 2000–2006. The races PHT, THT, PHJ, and THJ were prominent in the field and were virulent to *Lr1*, *Lr2c*, *Lr3*, *Lr11*, *Lr16*, *Lr17*, and *Lr26*. An increasing virulence diversity has been seen in those years, although no pathotypes showed virulence to *Lr9* and *Lr24* (Liu and Chen 2012). In 2007, 96 isolates from Shaanxi, Hebei, and Sichuan provinces were discovered that, PHST and FHST in Shaanxi, THQT, THQS, THQR, THQN, and PHSP in Hubei, and THTT in Sichuan were dominant races, respectively. The outbreak frequency of isolates with virulence to *Lr2c*, *Lr3*, *Lr3bg*, *LrB*, *Lr11*, *Lr14a*, *Lr14b*, *Lr16*, *Lr25*, *Lr26*, and *Lr33* accounted for over 70% in the three provinces, and those isolates displayed avirulence to *Lr9*, *Lr24*, and *Lr38* were null (Wu et al. 2009). To make a conveniently comparison for *Pt* races between countries, a set of wheat Thatcher genetic background-based near-isogenic lines with *Lr1*, *Lr2a*, *Lr2c*, *Lr3*, *Lr9*, *Lr16*, *Lr24*, *Lr26*, *Lr3ka*, *Lr11*, *Lr17*, and *Lr30* was suggested to use (Jin et al. 2008). During 2009–2010, three races, the FCBQQ, PCGLN, and PCGLL, which are the three out of 48 races identified from 155 *Pt* isolates collected from seven provinces were determined to be prevalent races. Almost all isolates, except for four isolates, showed virulence to *Lr26*, and none of them was virulent to *Lr18* and *Lr24* (Kolmer 2015). During 2011–2015, 158 *Pt* races were identified from isolates collected from 18 provinces. Six races, the THTT, THTS, PHTT, THJS, and THJT are the most prominent. In particular, THTT and THTS were widely spread (Zhang et al. 2020b, 2020c). Over 90% of the isolates (2296) collected from 18 provinces in 2011–2013 were virulent to *Lr1*, *Lr2c*, *Lr3*, *Lr3bg*, *Lr10*, *Lr14a*, *Lr14b*, *Lr16*, *Lr17*, *Lr26*, *Lr33*, *Lr37*, *Lr50*, and *LrB* (Zhang et al. 2020c). More than 80% of the isolates (1143) from 15 provinces in 2014–2015 showed virulence to *Lr1*, *Lr2a*, *Lr2b*, *Lr2c*, *Lr3*, *Lr3bg*, *Lr10*, *Lr11*, *Lr14a*, *Lr14b*, *Lr16*, *Lr17*, *Lr26*, *Lr32*, *Lr33*, *Lr50*, and *LrB* (Zhang et al. 2020b). In 2017, 52 races were identified

from 1407 *Pt* isolates collected from nine provinces using 16 Thatcher near-isogenic lines (*Lr1*, *Lr2a*, *Lr2c*, *Lr3*, *Lr9*, *Lr16*, *Lr24*, *Lr26*, *Lr3ka*, *Lr11*, *Lr17*, *Lr30*, *LrB*, *Lr10*, *Lr14a*, and *Lr18*), where THTT, THTS, PHTT, THKT, PHTS, THKS, and THJT were the dominant races. THTT, PHTT, and THTS in Sichuan, THTT, THKT, and THJT in Shandong, THTT and PHTT in Hebei, THTT and THTS in Hubei, Henan, and Gansu, and THTS and THTT in Anhui and Jiangsu provinces were the prevalent races, respectively (Jia et al. 2018b).

### The *Pgt* races

In China, Tu (1934) first identified six *Pgt* races in Guangdong Province in 1934, and subsequently, Yin (1947) identified fifteen races from *Pgt* isolates collected from twelve provinces in 1947. Later, the race 1 was detected in 15 sampling sites in Northeast China and race 2 was identified in Jiangsu, Hebei, and Shandong provinces (Wang et al. 1950). Wu and Huang (1987) summarized that, during 1959–1965 and 1973–1985, sixteen races, including 17, 19, 21, 21C1, 21C2, 21C3, 34, 34C1, 34C2, 34C3, 34C4, 40, 116, 194, 207, and Ketai 1 were detected from 10068 *Pgt* isolates in China. Of these races, race 21 and 34, and their race group (C series) were dominant. These races were virulent to *Sr* resistance genes *Sr7a*, *Sr7b*, *Sr8*, *Sr9a*, *Sr12*, *Sr14*, *Sr17*, *Sr23*, and *Sr29*, but avirulent to *Sr11*, *Sr15*, *Sr21*, *Sr22*, *Sr24*, *Sr26*, *Sr27*, *SrTmp*, and *SrTt-2* (Wu and Huang 1987). During 1956–1961, six races, the race 1 to race 6, were identified on a set of differential hosts that consisted of 12 wheat cultivars, viz. Hezuo 6, Songhuajiang 1, Songhuajiang 2, Gansu 96, Mailiduo, Tubuqi, Manggou 335A-531, Khapli, Fule, Einkorn, Reliance, and Kehua (Zeng et al. 1963). Three of which, race 1, 2 and 3, were identified from 1700 *Pgt* isolates. However, race 1 was dominant race, and race 3 was rarely discovered (Zeng et al. 1963). In addition, race 4 and 5 were recovered from aecia produced on *B. amurensis* via artificial inoculation (Zeng et al. 1963). Based on rust tests using standard (international) differentials that are comprised of the wheat varieties Little Club, Marguis, Reliance, Kota, Arnautka, Mindum, Spelmar, Kubanka, Acme, Einkorn, Uernal, and Khapli, with additional wheat cultivars (Mianzi 52/Mianzi49) as accessory differential hosts. As a result, 26 and 334 isolates, collected in Liaoning Province in 1960 and 1961 respectively, were determined as six races including 17, 21, 34, 40, 21C1 (C = Chinese), and 34C1 (Wu et al. 1964). The race 116 was first detected during 1952–1957 by the team of Institute of Northeast Agricultural Sciences and Institute of Applied Fungi, Chinese Academy of Sciences, but not recorded pathogenicity on wheat genotypes. This race was detected and identified

from samples collected on wheat cultivar Mentana in Huaihua County in Hunan Province in 1982. This race was detected late than the race 40. However, both races were highly virulent to the wheat cultivar Vernal (Huang et al. 1984b). Race 34C3, detected on the wheat cultivar Orofen that was introduced into China in 1970s and used as resistance germplasm against wheat stem rust, was avirulent to the wheat cultivar Rulofen that was introduced as a resistance germplasm to wheat leaf rust (Huang et al. 1984a). By 1977, race 34C4 (provisionally 34CR), virulent to Orofen and Rulofen, was detected based on reactions on a set of differential hosts including Reliance, Mianzi 52, M2761, Huadong 6, Rulofen and Orofen (Huang et al. 1984a). During 1990 to 1994, 19 races (pathotypes) that are 21C3CKH, 21C3CKR, 21C3CTR, 21C3CTH, 21C3CPH, 21C3CPR, 21C3CFH, 21C3CFR, 34C2MKH, 34C2MKR, 34C2MKK, 34C2MFK, 34C2MFR, 34MKG, 34MFG, 34MFK, 34C1MKH, 34C1MKR, and 34C1MFH were identified among 1224 *Pgt* isolates from 18 provinces (Yunnan, Fujian, Sichuan, Guizhou, Hunan, Hubei, Zhejiang, Shanghai, Jiangsu, Shaanxi, Henan, Hebei, Gansu, Inner Mongolia, Jilin, Liaoning, Heilongjiang, and Qinghai) of China (Yao et al. 1997). Among those races, race 21C3 and race 34C2 were dominant ones (Yao et al. 1997). The new race (or pathotype) 21C3CTR that is virulent to *Sr11* was first detected in Emeishan of Sichuan Province in 1993, and later it reached an outbreak frequency as high as 31.0% by widely spreading in Sichuan, Yunnan, Hubei, Henan, Hebei, and Gansu provinces (Yao et al. 1996). During 2007–2008, four races 21C3CTH, 21C3CFH, 21C3CPH, and 34MKG were identified from 59 *Pgt* isolates in Heilongjiang, Sichuan, and Yunnan provinces. Of which, 21C3CTH was prevalent with high outbreak frequency of 72.9% (Han et al. 2010). During 2012–2013, 13 races (pathotypes), 21C3CTHTM, 21C3CTQSM, 21C3CTTSC, 21C3HTTTM, 34MKGQM, 34MRGQM, 34MRGSM, 34MTGSM, 34Oroll-MTGSM, 34Oroll-MRGQM, 34C3RTGQM, 34C3RKGQM, and 34C3RKGSM, were identified from 23 *Pgt* isolates collected from wheat plants and 30 from *Berberis* species. Two of which, 34C3RTGQM and 34Oroll-MRGQM, were prominent races. Six of these races, 34MRGQM, 34MRGSM, 34MTGSM, 34Oroll-MTGSM, 34Oroll-MRGQM, and 34C3RTGQM, emerged recently and were first detected with a combined virulence to *Sr5* + *Sr11* (Cao et al. 2016). Over the past decade, many dominant races have decreased in the field. However, there is an exception that 21C3 and 34C2 have remained prominent with a consistently high outbreak frequency so far (Wu et al. 1964; Yao et al. 1993; Han et al. 2010; Cao et al. 2016).

### Variable oversummering and overwintering regions for the pathogens

#### *Variable oversummering regions of Pst*

Intriguingly, many studies showed that most of the new *Pst* races in China were originally uncovered in north-western regions and some of southern regions, especially in Longnan of Gansu Province and northwestern of Sichuan Province, such as CYR13, CYR17, CYR18, CYR19, CYR21, CYR22, CYR27, CYR28, CYR29, CYR30, CYR31, CYR32, and CYR34 (Wang et al. 1986, 1996; Wan et al. 2003; Liu and Hambleton 2010; Liu et al. 2017). Due to the emergence of new *Pst* races, the resistance of wheat cultivars was often overcome in these regions. Molecular studies revealed that the *Pst* population in Gansu, especially in the Longnan region, had a high level of genetic diversity (Shan et al. 1998; Zheng et al. 2005; Duan et al. 2010; Lu et al. 2012). Therefore, the regions mentioned above are considered as the most important *Pst* genetic variation regions, and are also the origins of new *Pst* races. These races in turn provide vast *Pst* inoculum to the wheat plants grown in eastern regions. The formation of *Pst* genetically variable region is not known until recently. So far, more than 40 barberries (*Berberis* spp.) and four *Mahonia* spp. that are native in China have been identified as alternate hosts for *Pst* and more than 10 *Berberis* species and at least two *Mahonia* spp. are widely distributed in *Pst* oversummering regions (Zhao et al. 2013, 2016b; Zhuang et al. 2019; Du et al. 2019; Li et al. 2021; Cheng et al. 2022) (Fig. 7). Importantly, it has been demonstrated that under natural conditions, sexual cycle of *Pst* in China occurs more frequently based on known and new races of *Pst* isolates that were recovered from naturally-rusted barberry (Zhao et al. 2013; Li et al. 2016a; Wang et al. 2016), and *Mahonia* (Cheng et al. 2022). Accordingly, wide distributed *Berberis* spp. and frequent occurrence of sexual cycle of *Pst* resulted in the latently genetic recombination and the continual generation of new races, which represents the formation of oversummering *Pst* genetically variable regions in China.

#### *Pgt genetically variable regions*

Based on the studies of *Pgt* isolates in 1963–1967 and 1973–1992, Yunnan, Sichuan, and, Guizhou provinces are known as *Pgt* genetically variable regions. In these regions, new virulent races emerge and accumulate more rapidly than other regions. One of the reasons is that the pathogens can oversummer and overwinter to complete their disease cycle locally (Huang et al. 1993).

#### *Pt genetically variable regions*

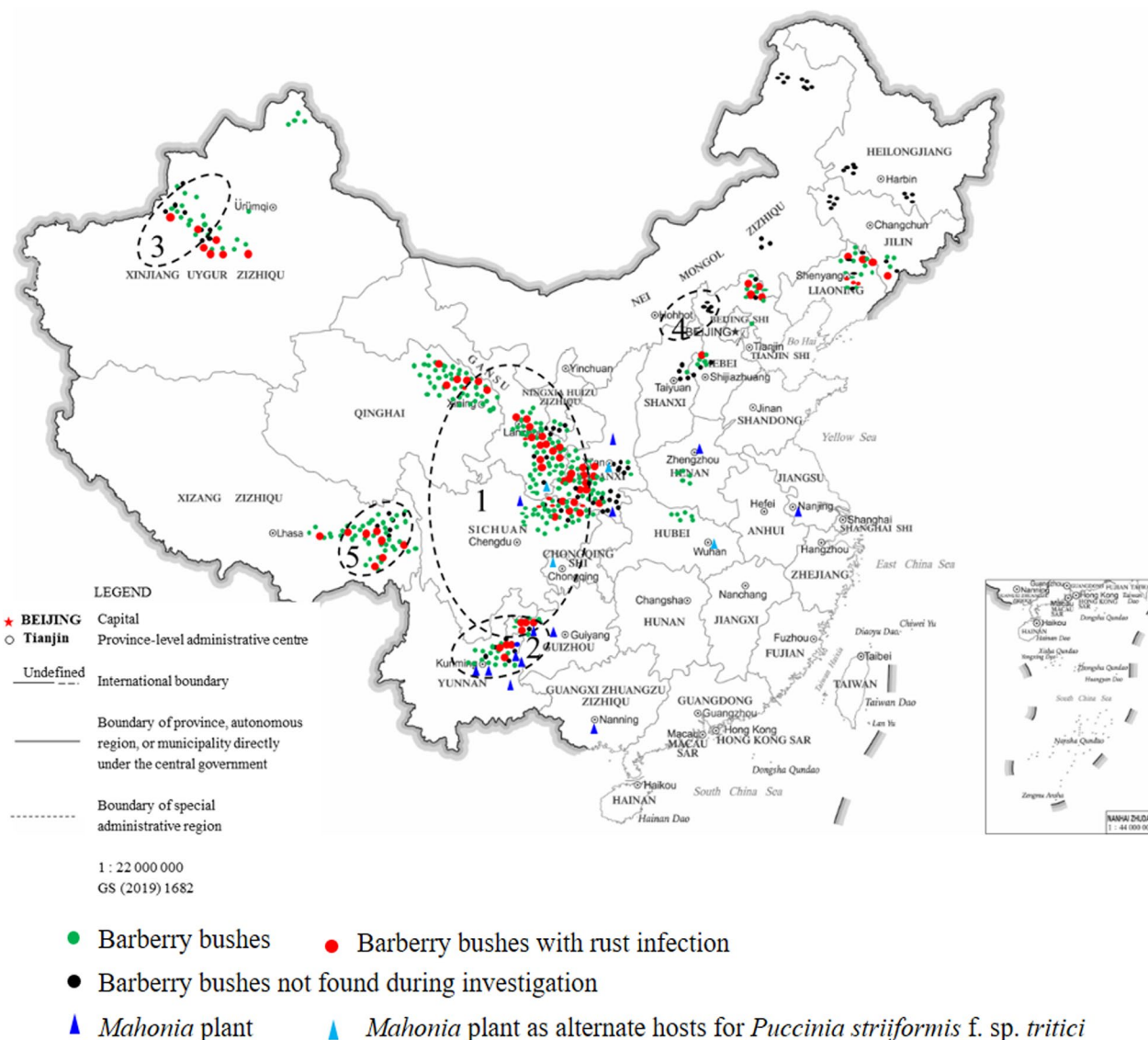
Although many *Pt* genetically variable regions in China have not been designated due to the lack of evidence, an increasing number of high genetic and virulence diversity

have been found in the pathogen population habitats distributed in Hebei, Henan, Shandong, Sichuan, Yunnan, Gansu, and Shaanxi provinces (Xu et al. 2013; Ge et al. 2015; Kolmer 2015; Ma et al. 2020). However, these regions are considered unlikely the potentially variable regions for *Pt* in China due to low clonal population (Kolmer 2015).

#### High temperature-tolerant isolates

Temperature is a key factor that affects wheat rust fungi growth and development. Relatively, *Pst* requires the lowest high temperatures, which is lower than *Pt* and *Pgt* (Roelfs et al. 1992), as high temperature restricts the development of *Pst*. When the average 10-day temperatures are above 23°C in July and August, which is the two hottest months, can halt the development of the disease (Roelfs et al. 1992; Li and Zeng 2002). The data of global land–ocean temperature index indicate that the annual average temperature has arisen 0.85°C in 2021 (<https://climate.nasa.gov/vital-signs/global-temperature/>). In China, especially the Central and East regions, it has increased 0.97°C (CMA 2021). Recently, studies on high-temperature tolerance have been investigated using a Chinese *Pst* population consisting of 126 isolates from 12 provinces. Results showed that the Chinese *Pst* population had a remarkable adaptation to high temperature and the average ET<sub>50</sub> values, a temperature that is required to obtain 50% of the maximum effect, were 24.1°C with a range of 18.46–27.01°C, which has passed the highest temperature limitation of 23°C (Zhang et al. 2013). Moreover, genetic diversity of *Pst* population had a nicely negative correlation with average ET<sub>50</sub> values as well as a significantly positive correlation with the coefficient of ET<sub>50</sub> variation, but there was no correlation with genetic diversity (Lian et al. 2016). Field investigations revealed that *Pst* can oversummer during 23–25°C in Pingliang of Gansu Province (Wang 2009), and that *Pst* can overwinter in high altitude with higher temperature and oversummer in lower altitude with lower temperature. The overwintering altitudes can be seen in Tianshui of Gansu Province from 1800 m up to 2080 m, and oversummering altitude can be the place of 1650 m down to 1450 m. While, in Yunnan Province which is at a higher altitude, the oversummering altitude for *Pst* ranges from 2300 to 1950 m (Pan et al. 2011). Therefore, under high temperature conditions (> 23°C), high temperature-tolerant *Pst* isolates have greater potential to complete the disease cycle than high temperature-sensitive ones. The potential influence of high temperature-tolerant *Pst* isolates on wheat stripe rust occurrence should be under consideration. Recently, in the eastern coastal epidemiological regions of Zhejiang and Jiangsu provinces,





**Fig. 7** The map showing extensive distribution of most of Chinese *Berberis* spp. and *Mahonia* spp. serving as alternate hosts for *Puccinia striiformis* f. sp. tritici in North-western area of overwintering areas, and a few *Berberis* spp. for *P. graminis* f. sp. tritici in Gansu, Shaanxi and Tibet in China based on data collections of field investigations during 2010–2020 (Zhao et al. 2013, 2015, 2016b; Wang et al. 2016; Du et al. 2019; Li et al. 2021; Zhuang et al. 2019; Cheng et al. 2022). Geographic outline of overwintering areas were redraw according to a review by Wan et al. (2007) and Tibet of overwintering area was added. 1 North-western area. 2 South-western area. 3 Xinjiang area. 4 Northern area. 5 Tibet area. Map resource: <http://bzdt.ch.mnr.gov.cn/>. Data resource: Information on barberry data in Northeast China from Yuanxin Cao’s laboratory at Shenyang Agricultural University, Shenyang, Liaoning Province

wheat stripe rust is usually an ignorable issue because it normally develops slowly and sometimes stops infection in early April; however, it is not a severe issue until early May in 2019 (Ju et al. 2022). The outbreak is possibly due to the warmer weather where the high temperature-tolerant isolates prevailed. Following the global warming, the race dynamics of high temperature-tolerant *Pst* isolates should be paid more attention and taken necessary measures to manage wheat stripe rust in China.

**Fungicide resistance of *Puccinia* species**

There are a variety of fungicides used to control *Puccinia* species pathogen infection. One of the key fungicides triazole plays an important role in preventing wheat from rust disease infection. In China, fungicide application for wheat rust control can be tracked back to the 1950s (Ou and Meng 1958; Lu et al. 1962). Now, more than ten chemicals are used as fungicides to control this disease, such as sodium sulfanilate and fluo-rides; however, wheat often suffers from yield lose when

severe epidemic hits (Wang et al. 1988). Nevertheless, those chemicals had been extensively applied to control wheat rust diseases in the 1960s–1970s, and made a considerable success (Wang et al. 1988). Notably, the fungicide triadimefon was introduced into China in 1976 and was locally synthesized by Institute of Elemental Organic Chemistry of Nankai University (Wang et al. 1988). This fungicide effectively controlled wheat rust infection by seed treatment and foliar spray inoculation (Wang et al. 1988). Additionally, other triazole fungicides, such as tebuconazole and hexaconazole, have been developed to control wheat rusts. Triazole type of fungicides has maintained high efficiency in controlling the wheat rusts for 5 decades. A worrisome situation is that following the long duration use of triazole type of fungicides, especially triadimefon, the insensitive and anti-fungicide isolates have been found in Chinese wheat rust populations (Cook et al. 2021; Zhan et al. 2022b). A recent study by Zhan et al. (2022b) showed that there are about 7% of *Pst* isolates in total of 446 isolates collected from winter-producing regions and northwest overwintering regions exhibiting triadimefon resistance and cross-resistance to triadimefon, tebuconazole, and hexaconazole. However, the majority of the resistance isolates are from southwestern of China. The isolates in Xinjiang and Tibet epidemic regions are still high sensitive to triadimefon. Compared with the *Pst* isolates from Europe, United States, Ethiopia, and Chile, Chinese *Pst* isolates have a high percentage of fungicide-resistant mutants (Cook et al. 2021). Genetic analyses revealed that single-site mutation by Y134F substitution in the target gene of demethylase inhibitor (DMI; *Cyp51*) resulted in fungicide resistance in Chinese *Pst* population (Cook et al. 2021; Zhan et al. 2022b).

Notably, fungicide-resistance has also been detected in Chinese *Pgt* population recently. A study by Wu et al. (2020a) reported that low to moderate triadimefon-resistance had been detected in 29 *Pgt* isolates accounting for ~32.6% in the tested 89 *Pgt* isolates that were sampled from wheat and barberry in Heilongjiang, Liaoning, Sichuan, and Shaanxi provinces during 2013–2015. Chinese *Pgt* population had a positive correlation between resistance to triadimefon and carbendazim, and no cross-resistance to triadimefon, thiophanate-methyl, and kresoxim-methyl. In addition, triazole type of fungicides have been consistently used to control wheat leaf rust in China since the late 1970s. While, isolates of *Pst* and *Pgt* with the resistance to triazole fungicides have emerged in China. Although no evidence to demonstrate *Pt* isolates are resistant to fungicides, it is plausible to propose that the risk of anti-fungicide of *Pt* against triazole type of fungicide may need to be investigated.

### Emergence of new rust races

Although wheat cultivars carrying resistance genes have been effectively used to control the three rusts, new races often overcome the resistance of these wheat cultivars and cause disease. As a result, many of which developed to be the prevalent races and cause huge yield reduction annually. The emergence and rapid accumulation of new pathogenic rust races are usually accompanied with the high level of threatening to wheat production. Due to the emergence of new pathogenic races, the resistance of many cultivated varieties are facing danger than ever before, where they turn to be vulnerable to the new emerged races. It has been observed that a few new strip rust races quickly diffused to other wheat-growing regions that are far away from their origin sites. These new races caused a severe interregional wheat stripe rust epidemic. So far, eight main cultivated wheat cultivars across China have been displaced (Li and Zeng 2002; Wan et al. 2007; Han et al. 2016). Recently, a newly-emergence race, named TSA-6 which is virulence to *Yr5*, has been identified in Shaanxi Province (Zhang et al. 2020a). Later, it was detected in Qinghai Province (unpublished data). The *Yr5*-virulent race and its mutant TSA-9 possess similar pathogenicity with dominant *Pst* races CYR34 and CYR 32, which are pathogenic to most of the 165 tested Chinese wheat cultivars (Zhang et al. 2022). Historically, in China, a new race could develop into a prevalent race within 6–9 years, and sometimes within the frame of 3–5 years after initial emergence (Lu et al. 1963; Wang et al. 1986; Wu et al. 1993; Jiang et al. 1996; Wan et al. 2003, 2004; Li et al. 2016b; Liu et al. 2017). Thus, the enhanced surveillance on the dynamics of new emerging *Pst* isolates should be taken in consideration.

New races of Chinese *Pgt* population have been intensively reported for nearly 5 decades since the 1970s. Dominant 21C3 and 34C0 race families have been existed for many years. However, during 2009–2015, three new races, 21C3CTTTM and 34C0MRGSM identified from wheat, and 34C3MTGQM identified from *Berberis* species become the dominant races in China (Zhao et al. 2013, 2015; Li et al. 2018; Cao et al. 2019).

Recent studies have reported that although new races of China *Pt* population emerged over the past years, occurrence frequencies of new races were extremely low and new races were somewhat different from surveillance years (Zhang et al. 2020b, 2020c). Generally, leaf rust epidemics are thought to be closely related to the appearance of new races, but the outbreaks of wheat leaf rust in China during 2011–2015 were considered as a result of climatic and host conditions instead of new races (Zhang et al. 2020b, 2020c). Since 2011, no case with regard to new races developing to be prevalent races to cause

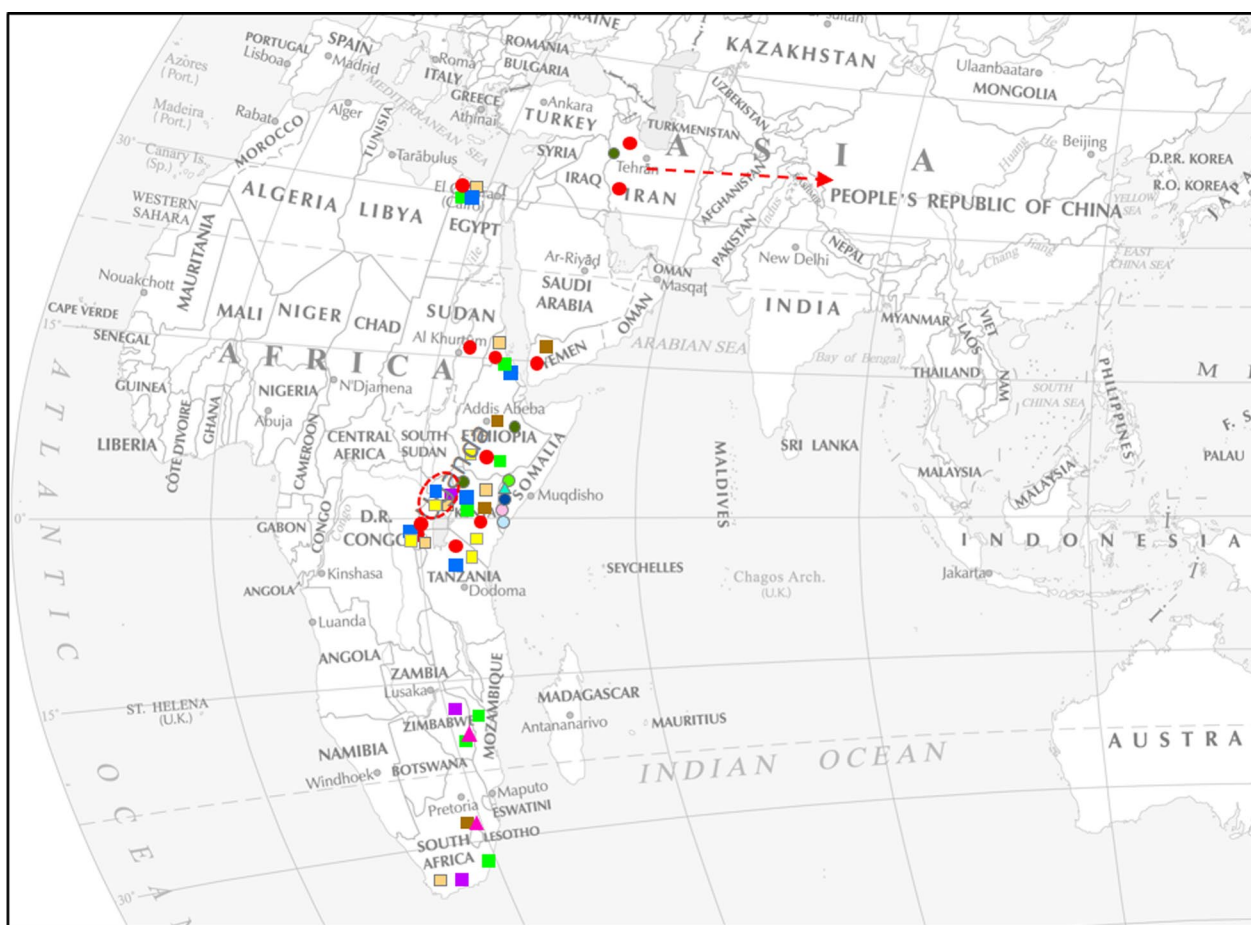
wheat leaf rust epidemics in China during these years have been reported.

**Invasion risk of alien races**

Wheat rusts are air borne diseases where the fungal spores can spread with a long distance. Theoretically, the wind can help the spores travel across regions and even continents. In particular, human activities accelerate the spread by the travel between continents. In fact, the inter-continental spread of wheat rusts have become a major disease propagation means. Over the past 30 years, stripe rust has spread to Australia in 1979 (O'Brien et al. 1980; Wellings et al. 2003; Wellings 2007), New Zealand in 1980 (Beresford 1982), and South Africa in 1996

(Pretorius et al. 1997). A recent well known case is the spread of the *Pgt* race Ug99 (TTKSK) lineage that traveled from Uganda in 1999, and finally landed in Iran in 2019, demonstrating the incredible long-distance travel of wheat rusts (Fig. 8; relabeled based on data information from [https://rusttracker.cimmyt.org/?page\\_id=22](https://rusttracker.cimmyt.org/?page_id=22)).

In China, since 1970s, wheat stem rust has been effectively controlled for 5 decades because of the cultivation of stem rust-resistant wheat cultivars. Notably, *Pgt* races have been found to mutate at a low frequency in the field, and two race groups, 21C3 and 34C, finally become dominant for nearly 5 decades since the 1970s (Wu and Huang 1987; Yao et al. 1998; Cao et al. 2016). However, the new *Pgt* race TTKSK (previously TTKS, also known



**Race** ■ PTKSK ■ PTKST ■ TTKSF ● TTKSK ■ TTKSP ■ TTKST ■ TTTSK ▲ TTKSF+  
 ● TTKTT ■ TTKTK ▲ TTHSK ○ PTKTK ○ TTHST ● TTKTT+ ● THTTT

**Fig. 8** The re-labelled map sketch illustrating origin (Uganda indicated by red-dotted circle), evolution and dispersal of the *Puccinia graminis* f. sp. *tritici* race TTKSK (Ug99) lineage and potential invasion risk to China. Data resource: CIMMYT, September 2021 at [https://rusttracker.cimmyt.org/?page\\_id=22](https://rusttracker.cimmyt.org/?page_id=22)

as Ug99) breaks the resistance of *Sr31*, a resistance gene that maintains a long-lasting protection from wheat stem rust infection for over a half century and introduced to most of the wheat variety worldwide. This race was first detected in Uganda in 1998 (Pretorius et al. 2000). Currently, Ug99 has developed to 15 Ug99 lineage variants through somatic recombination (Li et al. 2019b), and each has a combined virulence not only to *Sr31* but also to some of the eight important *Sr* genes, which are *Sr21*, *Sr24*, *Sr30*, *Sr36*, *Sr38*, *Sr9h*, *SrTmp*, and *Sr8155B1*. Since Ug99 race group has invaded Iran, much attention should be paid as they are geographically not far from China, although Ug99 and its variants have not been detected in China yet. In fact, only two (~1.7%) wheat varieties out of 118 in the tested Chinese wheat varieties are moderately resistant or fully resistant to the Ug99 race (Singh et al. 2006). Therefore, wind-borne spores of Ug99 lineage have a strong potential to be spread to China.

#### Discovery of the sexual cycle of the rusts

The sexual stage of *Pgt* has been known for a long time. The finding of susceptible barberry serving as alternate host has greatly pushed our understanding of *Pst* sexual cycle forward. It was recognized that susceptible barberry plays an important role in providing rust spores that cause primary stem rust infection of wheat in United States (Roelfs 1982). In China, although attempts were made to verify the role of barberry relating to occurrence of wheat stem rust under field conditions over the past decades (Wang 1955; Zhang et al. 1957; Wang et al. 1958; Zeng and Xue 1963), they all failed. Until recently, the existence of sexual cycle of *Pgt* in the fields has been discovered in China (Zhao et al. 2015). However, the role of susceptible barberry in a wheat stem rust epidemic is still not fully understood. Further work should be focused on this issue in China.

Since many Chinese barberry (*Berberis* spp.) and *Mahonia* spp. were identified as alternate hosts for *Pst*, the occurrence of *Pst* sexual cycle has been intensively investigated under field conditions. Chinese researchers demonstrated that *Pst* could infect susceptible *Berberis* and *Mahonia* spp. which are native in China to complete the sexual cycle in spring (Zhao et al. 2013, 2022; Wang et al. 2016; Liu et al. 2021; Chen et al. 2021a; Cheng et al. 2022), and that *Pst* could infect endemic *Berberis* to achieve sexual reproduction in autumn in Tibet (Du et al. 2022). In regions such as Qinghai and Shaanxi provinces, where susceptible *Berberis* spp. and wheat grow adjacently, under this situation, barberry provides aeciospores as inoculum to cause stripe rust infection on wheat (Chen et al. 2021a; Zhao et al. 2022). In addition, whether susceptible *Mahonia* spp. is

involved in providing aeciospores as inoculum to trigger stripe rust outbreak on wheat also needs further investigation.

Attempts have also been made to demonstrate the relationship between *Thalictrum* spp. as alternate hosts of *Pt* and leaf rust on wheat and grasses, but the relationship remains obscure. In 1960s, Guichao Huang at Institute of Agricultural Sciences in Jiamusi, testified that rusts on *Thalictrum* spp. were related to leaf rust on *Agropyron* instead of leaf rust on wheat (Wang et al. 1987). In 1980s, Wang et al. (1987) reported that, in the Baishitougou village of Inner Mongolia, leaf rust on *Agrostis* spp. can complete sexual cycle on *T. petaloideum*; however the aeciospores from *T. minus*, *T. minus* var. *stipellatum*, *T. minus* var. *hypoleucum*, and/or *T. petaloideum* failed to cause wheat leaf rust by artificial inoculation. Although a few Chinese *Thalictrum* spp. have been identified as alternate hosts for *Pt*, the role of *Thalictrum* spp. in the occurrence of leaf rust on wheat under natural conditions remains unknown. Sequence alignment of internal transcribed space (ITS) indicated that more than 20 aeciospores from susceptible *T. baicalense* plants had 95–96% of sequence similarity with *P. triticina* (Zhao et al. 2021). However, inoculation experiment of aeciospores on susceptible wheat cultivars were not conducted to justify the potential infection by *Pt* urediospores in fields.

#### Sources of *Pst* teliospores for alternate host infection

Teliospores are essential for infecting alternate hosts (*Berberis* and *Mahonia*) to invoke sexual cycle. Under favorable conditions, basidiospores, which germinate from teliospores, infect alternate hosts to initiate sexual reproduction in the three wheat rusts. Therefore, vigorous teliospore sources are associated with sexual stage of the three rust pathogens. Field investigations and laboratory experiments demonstrate that *Pst* teliospores can be produced at all growth stages and possess germination capacity in field. However, the teliospore production and germination rate are dependent of the fungi growth stage, weather condition, and locations (Chen et al. 2021b). In addition, wheat straw stacks of diseased tissues are the harbor of *Pst* teliospores in overwintering regions, such as Gansu and Qinghai provinces (Chen et al. 2021b). A study by Qin et al. (2022) reported that grass residues can harbor the overwintering *Pst* for the primary infection in the coming spring. Survival of *Pst* teliospores on grasses after overwintering can also serve as the potential source to infect alternate hosts of *Pst*.

### Wheat stripe rust management

Planting rust-resistant wheat cultivars has been considered as an effective, economical, and green strategy to control wheat rust diseases. In China, comprehensive application of wheat cultivars carrying *Sr* resistance genes has been successful for long-term disease control. By deploying an integrated management strategy for wheat stripe rust, the disease has been effectively controlled in most wheat-producing areas since 2004 in China (Chen et al. 2013). After the year 2010, wheat stripe rust has led to the infection around 2.67 million hectares perennially, and caused annual yield loss around 0.17 million metric tons (Huang et al. 2018). One of the key reasons is that the resistance genes in wheat cultivars were frequently overcome by the emerging new races, resulting in the wheat cultivars to be vulnerable within a short period after released in the fields. Therefore, an integrated strategy should be considered to slow down the new rust race emergence.

### Mining novel resistance genes for durable control

At present, 83 wheat stripe rust (yellow rust) resistance genes (*Yr*), viz. *Yr81-Yr83*, have been designated (McIntosh et al. 2017; Li et al. 2020). Of the 83 *Yr* genes, only *Yr15*, *Yr45*, and *Yr61* possess effective resistance to prevalent Chinese *Pst* races (Zhang et al. 2020a; Feng et al. 2022). Moreover, unnamed new *Yr* genes from current wheat varieties or other *Triticum* species, such as *YrElm*, *YrElm1-4*, *YrElm4*, *YrLm2*, *YrM97*, and *YrM852* from *Elymus mollis* (Yang et al. 2009b, 2010; He et al. 2010; Xu et al. 2012; Bai et al. 2013; Zhang et al. 2014), *YrHua*, *YrHy*, *YrH122*, *YrH9014*, *YrH9020a*, *YrHua9020*, and *YrHu* from *Psathyrostachys huashanica* (Cao et al. 2005; Liu et al. 2008; Yao et al. 2010; Tian et al. 2011; Ma et al. 2013, 2015a, b, 2016; Liu et al. 2014), *YrVI*, *YrHV*, *YrWV*, and *YrV3* from *Haynaldia villosa* (Zhou et al. 2008; Hou et al. 2009, 2013; Wang et al. 2011a), *YrCH5383*, *YrL693*, and *YrCH5026* from *Thinopyrum intermedium* (Hou et al. 2015; Huang et al. 2014; Zhan et al. 2014b), and *YrM8003* from rye (Xu et al. 2010), have been identified. In addition, 12 meta-quantitative trait loci (MQTL), including both quantitative resistance loci (QRL) and major resistance genes, were discovered from 194 QRL that have been identified previously (Cheng et al. 2019), which can be used for breeding stripe rust-resistant wheat cultivars by marker-assisted selection (MAS).

So far, 63 wheat stem rust resistance genes (*Sr*) have been identified worldwide (Mago et al. 2022). In China, eight *Sr* genes, including *Sr9e*, *Sr26*, *Sr31*, *Sr33*, *Sr37*, *Sr38*, *Sr47*, and *SrTt3*, are still resistant to local *Pgt* races. Nevertheless, much attention should be paid to those races with combined virulence to the resistances *Sr5* and

*Sr11* (Cao et al. 2016). The stem rust resistance genes have been confirmed to be effective against the dominant races 34MKGQM, such as *Sr9e*, *Sr10*, *Sr11*, *Sr13*, *Sr14*, *Sr17*, *Sr18*, *Sr19*, *Sr20*, *Sr21*, *Sr23*, *Sr25*, *Sr26*, *Sr30*, *Sr31*, *Sr32*, *Sr33*, *Sr34*, *Sr35*, *Sr36*, *Sr37*, *Sr38*, *Sr47*, *Srdp-2*, *SrTmp*, *SrTt3*, and *SrWld-1*. The resistant genes against the dominant race 21C3CTHSM include *Sr5*, *Sr9e*, *Sr19*, *Sr20*, *Sr21*, *Sr22*, *Sr23*, *Sr25*, *Sr26*, *Sr27*, *Sr30*, *Sr31*, *Sr32*, *Sr33*, *Sr36*, *Sr37*, *Sr38*, *Sr47*, and *SrTmp* (Han et al. 2018). Fifteen *Sr* genes, viz. *Sr9e*, *Sr19*, *Sr20*, *Sr21*, *Sr23*, *Sr25*, *Sr26*, *Sr30*, *Sr31*, *Sr32*, *Sr36*, *Sr37*, *Sr38*, *Sr47* and *SrTmp* exhibited resistance to both predominant races. Li et al. (2019a) reported that 83 Heilongjiang wheat cultivars, carrying *Sr2*, *Sr24*, *Sr25*, *Sr26*, *Sr31*, and *Sr38* based on molecular detection, were resistance to three prevalent races 21C3CTHQM, 34MKGQM, and 34C3RTGQM, respectively. Field adult-plant resistance to all three prevalent *Pgt* races 21C3CTH, 21C3CFH, and 34MKG were identified in 56 out of 78 (71.79%) alien Ug99-resistance wheat varieties (lines) that were introduced from International Maize and Wheat Improvement Center (CIMMYT), and 72 out of 142 (50.7%) domestic wheat varieties from 15 provinces of China (Han et al. 2013). Wu et al. (2020b) identified the wheat lines from CIMMYT carrying *Sr9e*, *Sr21*, *Sr26*, *Sr33*, *Sr35*, *Sr37*, *Sr38*, *Sr47*, and *SrTt3* resistance genes against Ug99, and the lines possessing resistance genes against the prevalent *Pgt* races 21C3CTTMM, 34C0MRGSM, and 34C3MTGQM in China. Those *Sr* genes are important resistance germplasm resources for wheat breeding.

Currently, over 100 wheat leaf rust resistance genes (*Lr*) have been identified worldwide, and 80 of which have been officially named (McIntosh et al. 2017; Kumar et al. 2021). Wu et al. (2020a) reported that, based on resistance of 100 Chinese cultivars that challenged with 20 prevailing *Pt* isolates, nine *Lr* genes, viz. *Lr9*, *Lr18*, *Lr19*, *Lr24*, *Lr28*, *Lr29*, *Lr47*, *Lr51*, and *Lr53*, exhibited a broad resistance spectrum to all tested isolates. It is worth to mention that the *Lr* genes can be utilized for leaf rust-resistant wheat breeding, but *Lr* genes, including *Lr2c*, *Lr3*, *Lr16*, *Lr17*, *LrB*, *Lr3bg*, *Lr14b*, *Lr23*, and *Lr39*, should be avoided since they are high susceptible to the 20 prevailing *Pt* isolates in the fields (Wu et al. 2020a). In addition, six *Lr* genes, *Lr1*, *Lr33*, *Lr34*, *Lr45*, and *Lr46*, were identified in 37 Chinese wheat cultivars. Of which, 29 cultivars carrying *Lr34* and *Lr46*, and exhibit adult-plant resistance to leaf rust (Wu et al. 2020a). Chinese cultivar Shanghai 7 displays high resistance to Ug99, but it is difficult to identify the Ug99-resistance gene in this cultivar due to the unknown genetic background of this wheat variety (Singh et al. 2006). Currently, over 70 quantitative trait loci (QTL) against wheat leaf rust have been identified, and 11 of which possess pleiotropic resistance to

the disease (Zhang et al. 2016; Liu and Li 2019; Yan et al. 2022).

#### Pyramiding multi-gene resistance to wheat rusts

Pyramiding rust-resistant genes is an important strategy to breed wheat resistance cultivars. Previously, 1BL/IRS translocation lines that carry the stem rust gene *Sr31*, and the stripe rust gene *Yr9* were widely used in stem rust-, and stripe rust-resistant wheat breeding. Chinese wheat cultivars carrying both genes play an important role in controlling stripe and stem rust. Wheat cultivars with multi-resistance genes exhibit a broader resistance spectrum. Multi-gene pyramiding strategy therefore has been verified to be practicable for durable control of wheat rusts. By pyramiding *Yr15* and *Yr64* to the resistance wheat line RIL-*Yr64/Yr15*, a wider spectrum and durable resistance wheat variety was obtained (Qie et al. 2019). Zhang and Zhang (2016) introduced both *YrSM139-1B* and *YrSM139-2D* into the wheat cultivar Shaanmai 139, which increased the reception wheat with a broad resistance to wheat rusts remarkably. Zeng et al. (2015) reported that wheat cultivars carrying multi-*Yr* genes displayed stripe rust resistance in adult plant. However, pyramiding multi-*Lr* or *Sr* genes to a wheat cultivar has not been reported in China yet. Notably, the wheat variety carrying tandem resistance genes, such as *Sr24-Lr24* and *Lr37-Yr17-Sr38*, can simultaneously resist the three wheat rusts, which is a good donor germplasm for wheat breeding.

#### Deployment of wheat cultivars carrying rust resistance genes

The deployment of wheat varieties carrying resistance genes in epidemiological regions can theoretically control disease outbreak. Wheat varieties with whole growth stage resistance have been grown in epidemiological regions now. In 1965, wheat varieties Abbondanza and Fengchan 3 were widely grown in South Shaanxi and central Shaanxi Province to control wheat stripe rust for 9 years (SXIPP 1976). In the 1970s, breeding and application of stem rust-resistant wheat cultivars, especially those carrying *Sr31*, play a significant role in controlling the rust disease outbreak in China. Since then, wheat stem rust has been a sporadic-occurring disease in China (Cao et al. 1994; Wang et al. 2010). One of the suggestions regarding the deployment of resistance genes is to cultivate the wheat varieties carrying multi-resistance genes but not a single resistance gene at a large scale or in epidemiological region.

#### Regulation of alternate hosts

Alternate hosts and vigorous teliospores are required for wheat rusts to complete the sexual stage. Sexual genetic

recombination of wheat rusts can conceive high virulence progenies of the pathogen. Some techniques have been employed to reduce possibility of the new race generation by controlling the pathogen's sexual reproduction on alternate hosts, which largely reduced the potential emergence of new races generated in the habitat of barley species. Some useful tips are recommended: (1) triazole fungicides (i.e. triadimefon) should be frequently used on alternate host plants; (2) eradicating alternate host plants close to wheat fields; (3) reducing overwintering teliospore levels by removing wheat straw.

#### Use of fungicides

Chemical fungicides, such as Flutriafol, hexaconazole, diniconazole, propiconazole, tebuconazole, and triadimefon, have been registered and applied in China. However, long-term and intensive application of triazole fungicides has led to the emergence of anti-fungicide *Pst* and *Pgt* races in China (Wu et al. 2020a; Zhan et al. 2022b). The trouble is that the fungicide-resistant isolates are continuously emerging. Therefore, exploring new fungicides or alternative utilization of fungicides is an issue on table.

#### Biocontrol of the rust disease

Mycoparasitism mechanism is common in rust fungi, especially in the genus of *Puccinia*, which can be a useful and environmental-friendly method to control the rust diseases in addition to the fungicides. To date, approximately 30 genera of fungi are able to hyper-parasitize rust fungi. However, only five fungal species, *Lecanicillium lecanii*, *Typhula idahoensis*, *Microdochium nivale* (Littlefield 1981), *Cladosporium cladosporioides* (Zhan et al. 2014a), and *Alternaria alternata* (Zheng et al. 2017), have been reported to infect and kill *Pst* urediospores. Likewise, hyper-parasitism of two *Verticillium* spp., *V. psalliotae* and *V. tenuipes*, on *P. triticina* (syn. *P. recondita*), and *Aphanocladium album* on *P. graminis* have been reported (Koc et al. 1981; Leinhos and Buchenauer 1992). In addition, the biocontrol agent *Pseudomonas aurantiaca* was reported to have a potential control effect on wheat leaf rust (Wang et al. 2011b). However, effects of hyper-parasitic mycoparasites and biocontrol agents on three wheat rusts were observed under laboratory conditions. Application of hyper-parasites and biocontrol agents in fields to control wheat rusts is on the way.

#### Monitoring and forecasting wheat rust epidemics

Monitoring and forecasting dynamics of crop disease can help to manage crop diseases. These field managements include pathogen spore volume, the planting area of susceptible host plants, and environmental conditions. By monitoring race dynamics, virulence variation, and pathogen population structure, we can obtain valuable

information of the pathogen dynamics which will determine how and why to deploy the agricultural regulations. A classical case is that in 1958, a monitoring and forecasting method was employed to control wheat stripe rust. Based on the pathogen volume in winter and the coming early spring, the susceptible wheat cultivars planted, and the climatic factors, it predicted the epidemics of wheat stripe rust in 1964, 1973, and 1977. By 1977, more than 30 monitoring and forecasting stations were established national wide. This prediction method was proved to be reliable and it still is adopted nowadays. For instance, monitoring and forecasting wheat stripe rust was carried out in 14 individual years during 1960–1979, 8 epidemics were successfully predicted (Wang et al. 1988). Later, the computer-based models to predict the mid/long term epidemics of wheat stripe and leaf rusts were established and successfully applied (Yucheng Plant Protection Station 1979; Zeng et al. 1981; Xiao et al. 1983; Dong et al. 1987; Wu et al. 1991; Cao et al. 1995; Jiang et al. 1996; Pu et al. 2012). For the short-term prediction, overwintering inoculum and weather conditions during/after overwintering are predicted to be associated with the occurrence of wheat rust epidemics. In addition, high virulence frequency of a single dominant race and a few other races, the virulence spectrum, parasite fitness, and susceptible wheat cultivars planted can be used to predict epidemics of wheat rusts. For instance, the 1990s severe nationwide epidemic of wheat stripe rust was predicted in advance based on the high virulence frequency of the race CYR29 (up to 40.3%) and 6.7 million planting areas of susceptible wheat cultivars in 1989 (Wu et al. 1991). Currently, a series of internet-based devices or technologies, such as inoculum trapping, remote sensing, geographic information system (GIS), Global positioning system (GPS), atmospheric circulation modelling, and Internet of Things (IoT), have been developed and applied to manage crop diseases including wheat rusts (Hu et al. 2022). The modern agricultural technologies will undoubtedly enable us to precisely monitor and predict the development of wheat rusts and other crop diseases, and as a result to control the wheat rusts.

#### **Planting wheat variety mixtures**

Monoculture often fosters compatible pathogen accumulation. Growing a mixture of different wheat varieties can effectively control epidemics in fields. Many studies indicated that planting multi-wheat variety mixtures is an effective approach to reduce wheat stripe and leaf rusts outbreak in field. The low density susceptible wheat plants, such as 3:1 (resistant: susceptible) ratio, will decline disease development in wheat variety mixtures (Cao and Zeng 1994; Shen et al. 2008; Lü et al. 2014; Wang et al. 2022a). However, it is not determined if

increasing of wheat variety can further reduce the occurrence of wheat rusts. Nevertheless, the mixing planting of distinct wheat varieties to reduce rust infection is worth of further filed practicing.

#### **Intercropping**

Intercropping of wheat and other crops can also decrease wheat rust occurrence. For example, intercropping of rust-resistant wheat cultivars with faba bean can reduce wheat stripe rust infection by 22–100% according to 1-year field trial (Xiao et al. 2005). Likewise, Yang et al. (2009a) reported that, based on 6 years trials, intercropping of wheat and faba bean can decrease 30.4–63.55% wheat stripe rust occurrences with an increase of 0.28–0.63 metric tons per hectare of crop yields. In addition, intercropping of wheat and faba bean, namely the Yumai 1(wheat)/Yuxi (local bean variety) and Qiekuina (wheat)/Yuxi (local bean variety), achieve 38.7–39.6% of control to wheat leaf rust (Yang et al. 2003).

#### **The outlook to the future**

Due to the emerging new rust pathogens, there is a potential risk that the new rust pathogens would overcome the resistance of currently-growing wheat cultivars and cause a large scale of epidemics. Therefore, the work that monitoring and analyzing the emerging rust races in field should be strengthened to avoid wheat rust outbreaks. On the other hand, monitoring the effectiveness of wheat rust resistance genes will help to guide the rust managements, such as the deployment and introducing of new resistance genes. Mining of new wheat rust resistance genes would always promote our capability to fight against these devastating pathogens.

New technologies, especially the novel biotechnology, will assist to defend wheat rusts. The techniques, such as the molecular-assisted selection, and gene-editing technology have been applied to help breed disease resistant wheat cultivars, including wheat stripe rust (Li et al. 2022; Wang et al. 2022b). MAS breeding is not only shortening the breeding procedure but also can rapidly locate the resistance genes for further pyramiding multi-resistance genes in a given variety. Multi-resistance gene wheat cultivars possess the merit of broad disease resistance spectrum, which can be generated by introducing the all-stage resistance genes.

In addition, management of alternate hosts is important for reducing the generation of new wheat rust races. Eradication of barberry bushes has been confirmed as an effective long-term control of wheat stem rust in the United States (Roelfs 1982). In China, the barberry species are abundant and widespread and are often observed in spring, even autumn-wheat planting regions (Du et al. 2022). Therefore, controlling the

barberry rust infection by applying fungicides timely prior to the early stage of pycnial development has been successful in interrupting sexual cycle of rust pathogens.

Investigation of the avirulence genes in rust pathogens is essential for understanding the pathogenesis variation of the wheat rusts and for the targeted wheat breeding. Although some avirulence genes have been cloned in *Pgt*, such as *AvrSr27*, *AvrSr35*, and *AvrSr50* (Chen et al. 2017; Salcedo et al. 2017; Upadhyaya et al. 2021), none of the avirulence genes in *Pst* and *Pt* has been cloned so far. Therefore, identification of avirulence genes of *Pst* and *Pt* and more avirulence genes of *Pgt* should be taken into consideration.

## Conclusions

Wheat stripe, leaf, and stem rusts are destructive fungal diseases on wheat in China. Their spores can travel a long distance by wind. Severe epidemics of the three wheat rust diseases frequently occurred and have resulted in huge yield and economic losses. Strategies for the management of the wheat rusts have been made, which has achieved the effective control on wheat rusts in China, especially the wheat stem rust. Recently, new research progresses have been achieved on the control of wheat rusts. Herein, we summarized the rust epidemics, fungicide-resistance and the agricultural managements in China. With the aids of new bio-technologies, we are confident to fully control the wheat rust epidemics in China in the near future.

## Abbreviations

<i>Pgt</i>	<i>Puccinia graminis</i> f. sp. <i>tritici</i>
<i>Pst</i>	<i>Puccinia striiformis</i> f. sp. <i>tritici</i>
<i>Pt</i>	<i>Puccinia triticina</i>
CYR	Chinese yellow rust
f. sp.	Formae specialis
<i>Yr</i>	Yellow rust
<i>Lr</i>	Leaf rust
<i>Sr</i>	Stem rust
<i>Avr</i>	Avirulence

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## Authors' contributions

JZ and ZK wrote and modified the manuscript. Both authors read and approved the final manuscript.

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## Availability of data and materials

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## Declarations

### Ethics approval and consent to participate

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### Consent for publication

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### Competing interests

The authors declare that they have no competing interests.

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## References

- Awais M, Ali S, Ju M, Liu W, Zhang GS, Zhang ZD, et al. Countrywide inter-epidemic region migration pattern suggests the role off-season population to wheat stripe rust epidemics in China. *Environ Microbiol.* 2022;24:4684–701. <https://doi.org/10.1111/1462-2920.16096>.
- Awais M, Zhao J, Cheng XR, Khoso AG, Ju M, Rehman ZU, et al. Himalayan mountains imposing a barrier on gene flow of wheat yellow rust pathogen in the bordering regions of Pakistan and China. *Fungal Genet Biol.* 2023;164:103753. <https://doi.org/10.1016/j.fgb.2022.103753>.
- Bai YB, Zhang Y, Yao WY, Li Q, Jing JX, Wang BT. Genetic analysis and molecular mapping of stripe rust resistance gene in wheat *Leymus mollis* translocation line M852-1. *Acta Phytopathol Sin.* 2013;43(2):166–72. <https://doi.org/10.13926/j.cnki.apps.2013.02.017>. (in Chinese).
- Beresford RM. Stripe rust (*Puccinia striiformis*), a new disease of wheat in New Zealand. *Cereal Rusts Bull.* 1982;10(2):35–41.
- Cao YY, Chen WQ. Stepwise shift of differential hosts and racial designation of *Puccinia graminis* f. sp. *tritici*. *J Triticeae Crops.* 2009;30(1):167–72 (in Chinese).
- Cao KQ, Zeng SM. The population resistance of wheat variety mixture to *Puccinia striiformis*, *P. recondita* and *Erysiphe graminis*. *Acta Phytopathol Sin.* 1994;24(1):21–5. <https://doi.org/10.13926/j.cnki.apps.1994.01.005>. (in Chinese).
- Cao YY, Yao P, Zhu GQ, Wu YS. A preliminary analysis of probable genes for stem rust resistance and resistance stability of 41 wheat cultivars in China. *J Shenyang Agric Univ.* 1994;25(4):392–7 (in Chinese).
- Cao KQ, Zhu ZY, Wang SM. The establishment of a mid-term forecast model for leaf rust of wheat. *J Plant Prot.* 1995;22(1):57–61. <https://doi.org/10.13802/j.cnki.zwbhxb.1995.01.001>. (in Chinese).
- Cao ZJ, Wang XP, Wang MN, Cao SH, Zhang XQ. Genetic analysis and molecular markers of a novel stripe rust resistance gene *YrHua* in wheat originated from *Psathyrostachys huashanica* Keng. *Acta Genet Sin.* 2005;32(7):738–43 (in Chinese).
- Cao YY, Han JD, Zhu GQ, Zhang L. Ug99, a new virulent race of *Puccinia graminis* f. sp. *tritici*, and its effect on China. *Plant Prot.* 2007;33(6):86–9 (in Chinese).
- Cao YY, Wang H, Li TY, Wu XX, Xu XF, Wang WL. Race dynamics and new virulence spectra of *Puccinia graminis* f. sp. *tritici* during 2012–2013 in China. *Mycosystema.* 2016;35:684–93. <https://doi.org/10.13346/j.mycosystema.150011>. (in Chinese).
- Cao YY, Si BB, Zhu GQ, Xu XF, Li WH, Chen S, et al. Races and virulence of asexual and sexual populations of *Puccinia graminis* f. sp. *tritici* in China from 2009 to 2015. *Eur J Plant Pathol.* 2019;153:545–55. <https://doi.org/10.1007/s10658-018-1581-x>.
- Chen WQ, Yan SB, Hu CC, Xie SX. Physiologic race and pathogenicity of *Puccinia recondita* f. sp. *tritici* in China during 1990–1993. *Acta Phytopathol Sin.* 1994;21(4):289–95 (in Chinese).
- Chen WQ, Wu LR, Liu TG, Xu SC, Jin SL, Peng YL, et al. Race dynamics, diversity, and virulence evolution in *Puccinia striiformis* f. sp. *tritici*, the causal agent of wheat stripe rust in China from 2003 to 2007. *Plant Dis.* 2009;93(11):1093–101. <https://doi.org/10.1094/PDIS-93-11-1093>.
- Chen WQ, Kang ZS, Ma ZH, Xu SC, Jin SL, Jiang YY. Integrated management of wheat stripe rust caused by *Puccinia striiformis* f. sp. *tritici* in China. *J*



- Integr Agric. 2013;46(20):4254–62. <https://doi.org/10.3864/j.issn.0578-1752.2013.20.008>. (in Chinese).
- Chen JP, Upadhyaya NM, Ortiz D, Sperschneider J, Li F, Bouton C, et al. Loss of *AvrSr50* by somatic exchange in stem rust leads to virulence for *Sr50* resistance in wheat. *Science*. 2017;358(6370):1607–10. <https://doi.org/10.1126/science.aao481>.
- Chen W, Zhang ZD, Ma XY, Zhang GS, Yao Q, Kang ZS, et al. Phenotyping and genotyping analyses reveal the spread of *Puccinia striiformis* f. sp. *tritici* aeciospores from susceptible barberry to wheat in Qinghai of China. *Front Plant Sci*. 2021a;12:764304. <https://doi.org/10.3389/fpls.2021.764304>.
- Chen W, Zhang ZD, Chen XM, Meng Y, Huang LL, Kang ZS, et al. Field production, germinability, and survival of *Puccinia striiformis* f. sp. *tritici* teliospores in China. *Plant Dis*. 2021b;105(8):2122–8. <https://doi.org/10.1094/PDIS-09-20-2018-RE>.
- Cheng YK, Yao FJ, Ye XL, Jiang QT, Li W, Deng M, et al. Construction of linkage map of the meta quantitative trait loci (MQTL) on stripe rust resistance in wheat (*Triticum aestivum* L.). *Acta Phytopathol Sin*. 2019;49(5):632–49. <https://doi.org/10.13926/j.cnki.apps.000292>. (in Chinese).
- Cheng XR, Zhuang H, Zhao J, Zhan GM, Kang ZS, Zhao J. Identification of *Mahonia* species as alternate hosts for *Puccinia striiformis* f. sp. *tritici* and determination of existence of sexual propagation of the rust pathogen on *Mahonia* under natural conditions in China. *Phytopathology*. 2022;112(7):1422–30. <https://doi.org/10.1094/PHYTO-12-21-0502-R>.
- Chester KS. The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. Waltham, MA; New York: Chronica Botanica Co.; Stechert-Hafner Inc.; 1946.
- CMA (China Meteorological Administration). Blue book on climate change in China in 2021. Beijing: Science Press; 2021. (in Chinese).
- CNWRG (Chinese National Wheat Rust Collaborative Group). Brief summary on identification of physiologic races of *Puccinia striiformis* f. sp. *tritici* in China in 1984. *Plant Prot*. 1985;11(2):16–8 (in Chinese).
- CNWRG (Chinese National Wheat Rust Collaborative Group). Brief summary on identification of physiologic races of *Puccinia striiformis* f. sp. *tritici* in China in 1989 and 1990. *Plant Prot*. 1991;17(3):22–3 (in Chinese).
- CNWRG (Chinese National Wheat Rust Collaborative Group). Brief summary on identification of physiologic races of *Puccinia striiformis* f. sp. *tritici* in China in 1985 and 1986. *Plant Prot*. 1987;13(3):25–6 (in Chinese).
- Cook NM, Chng S, Woodman TL, Warren R, Oliver RP, Saunders DG. High frequency of fungicide resistance-associated mutations in the wheat yellow rust pathogen *Puccinia striiformis* f. sp. *tritici*. *Pest Manage Sci*. 2021;77(7):3358–71. <https://doi.org/10.1002/ps.6380>.
- d'Oliveira BD, Samborski DJ. Aecial stage of *Puccinia recondita* on *Ranunculaceae* and *Boraginaceae* in Portugal. In: Macer RC, Wolfe MS, editors. Proceedings of the First European Brown Rust Conference. Cambridge; 1966. p. 133–50.
- de Bary A. Neue Untersuchungen über die Uredineen insbesondere die Entwicklung der *Puccinia graminis* und den Zusammenhang derselben mit *Aecidium berberidis*. *Akad Wiss: Monatsber K Preuss*; 1866. p. 15–50
- Dong YX, Guo YX, Li YH. Prediction of wheat stripe rust in irrigation regions of Ningxia using stepwise discriminant analysis. *Plant Prot*. 1987;13(6):12–5 (in Chinese).
- Du ZM, Yao Q, Huang SJ, Yan JH, Hou L, Guo QY, et al. Investigation and identification of barberry as alternate hosts for *Puccinia striiformis* f. sp. *tritici* in eastern Qinghai. *Acta Phytopathol Sin*. 2019;49(3):370–8. <https://doi.org/10.13926/j.cnki.apps.000290>. (in Chinese).
- Du ZM, Peng YL, Zhang GS, Chen L, Jiang SC, Kang ZS, et al. Direct evidence demonstrates the fact that *Puccinia striiformis* f. sp. *tritici* infects susceptible barberry to complete sexual cycle in autumn. *Plant Dis*. 2022. <https://doi.org/10.1094/PDIS-08-22-1750-RE>.
- Duan XY, Tellier A, Wan AM, Leconte M, de Vallavieille-Pope C, Enjalbert J. *Puccinia striiformis* f. sp. *tritici* presents high diversity and recombination in the over-summering zone of Gansu, China. *Mycologia*. 2010;102(1):44–53. <https://doi.org/10.3852/08-098>.
- Eriksson J. Über die Spezialisierung des Parasitismus bei den Getreiderostpilzen. *Ber Dtsch Bot Ges*. 1894;1:292–331.
- Fang CT. Physiologic specialization of *Puccinia glumarum* Erikss. and Henn. in China. *Phytopathology*. 1944;34:2010–4.
- FAO/STAT (Food and Agriculture Organization of the United Nations). Crops and livestock products. 2020. <https://www.fao.org/faostat/en/#data/QCL>. Accessed 23 April 2022.
- Feng J, Wang FT, Lin RM, Xu SC, Chen WQ. Research progress on genetics of wheat stripe rust resistance and distribution of resistant genes in inoculum source areas. *J Plant Prot*. 2022;49(1):263–75. <https://doi.org/10.13802/j.cnki.zwbhxb.2022.022834>. (in Chinese).
- Gassner G, Straib W. über das Auftreten einer neuen Gelbrostform auf Weizen. *Züchter*. 1930;2:313–7. <https://doi.org/10.1007/BF01811545>.
- Ge RJ, Liu TG, Gao L, Liu B, Chen WQ. Virulence of *Puccinia triticina* from 6 provinces in China in 2011–2012. *Acta Phytopathol Sin*. 2015;45(2):175–80. <https://doi.org/10.13926/j.cnki.apps.2015.02.008>. (in Chinese).
- Han JD, Cao YY, Sun ZG. Race dynamics of *Puccinia graminis* f. sp. *tritici* in China and the virulence of CIMMYT wheat germplasm resistant to Ug99. *J Triticeae Crops*. 2010;30(1):163–6. <https://doi.org/10.2334/josnuds.52.439>. (in Chinese).
- Han JD, Cao YY, Wan C, Yao Q, Li WH. Identification and evaluation of resistance to stem rust in exotic Ug99-resistant wheat germplasm and domestic varieties. *J Plant Prot*. 2013;40(4):289–95. <https://doi.org/10.13802/j.cnki.zwbhxb.2013.04.017>. (in Chinese).
- Han DJ, Wang XM, Chen XM, Zeng QD, Wu JH, Xue WB, et al. Emerging Yr26-virulent races of *Puccinia striiformis* f. sp. *tritici* are threatening wheat production in the Sichuan Basin. *China Plant Dis*. 2016;99(6):754–60. <https://doi.org/10.1094/PDIS-08-14-0865-RE>.
- Han R, Li TY, Gong WP, Li HS, Song JM, Liu AM, et al. New resistance sources of wheat stem rust and molecular markers specific for relative chromosomes that the resistance genes are located on. *Sci Agric Sin*. 2018;51(7):1223–32. <https://doi.org/10.3864/j.issn.0578-1752.2018.07.001>. (in Chinese).
- He MM, Song XH, Wang Y, Yao Q, Li Y, Jing JX. Molecular mapping of stripe rust resistance gene in wheat translocation line M853-4 derived from *Leymus mollis* (Trin.) Hara. *J Plant Prot*. 2010;37(2):118–22. <https://doi.org/10.13802/j.cnki.zwbhxb.2010.02.011>. (in Chinese).
- Hou L, Ding PH, Hu ML, He MM, Zhou XL, Jing JX. Genetic analysis and SSR molecular mapping of translocation line V9128-3 derived from *Triticum aestivum*-*Hayaldia villosa* resistance to stripe rust. *Acta Phytopathol Sin*. 2009;39(1):67–75. <https://doi.org/10.13926/j.cnki.apps.2009.01.013>. (in Chinese).
- Hou L, Ma DF, Hu ML, He MM, Lu Y, Jing JX. Genetic analysis and molecular mapping of an all-stage stripe rust resistance gene in *Triticum aestivum*-*Hayaldia villosa* translocation line V3. *J Integr Agric*. 2013;12(12):2197–208. [https://doi.org/10.1016/S2095-3119\(13\)60293-2](https://doi.org/10.1016/S2095-3119(13)60293-2).
- Hou LY, Qiao LY, Zhang XJ, Li X, Zhan HX, Chang ZJ. Genetic analysis and molecular mapping of a stripe rust resistance gene *YrCH5026*. *Acta Agric Boreal-Sin*. 2015;30(5):7–15 (in Chinese).
- Hu CC, Roelfs AP. The wheat rust in the People's Republic of China. *Cereal Rusts Bull*. 1985;13:11–28.
- Hu CC, Roelfs AP. Races and virulence of *Puccinia recondita* f. sp. *tritici* in China in 1986. *Plant Dis*. 1989;73:499–501. <https://doi.org/10.1094/PD-73-0499>.
- Hu XP, Ma LJ, Liu TG, Wang CH, Peng YL, Pu X, et al. Population genetic analysis of *Puccinia striiformis* f. sp. *tritici* suggests two distinct populations in Tibet and the other regions of China. *Plant Dis*. 2017;101(2):288–96. <https://doi.org/10.1094/PDIS-02-16-0190-RE>.
- Hu XP, Hu XM, Ma LJ, Huang C, Zhou YL, Xu XM. Research progresses in monitoring and prediction of crop diseases. *J Plant Prot*. 2022;49(1):298–315. <https://doi.org/10.13802/j.cnki.zwbhxb.2021.2021134>. (in Chinese).
- Huang ZT, Liu WZ, Li SF, Wu YS. Discovery of *Puccinia graminis* var. *tritici* race 34C4 and its pathogenicity. *Sci Agric Sin*. 1984a;1:79–80 (in Chinese).
- Huang ZT, Wu YS, Yao P. Discovery of *Puccinia graminis* var. *tritici* race 116. *Sci Agric Sin*. 1984b;1:79–89 (in Chinese).
- Huang ZT, Wu YS, Wei SX. Studies on overwintering, overwintering and disease cycle of wheat stem rust in China. *Liaoning Agric Sci*. 1993;3:1–6 (in Chinese).
- Huang Q, Li X, Chen WQ, Xiang ZP, Zhong SF, Chang ZJ, et al. Genetic mapping of a putative *Thinopyrum intermedium*-derived stripe rust resistance gene on wheat chromosome 1B. *Theor Appl Genet*. 2014;127(4):843–53. <https://doi.org/10.1007/s00122-014-2261-7>.
- Huang C, Jiang YY, Li PL, Peng H, Cui Y, Yang JJ, et al. Epidemics analysis of wheat stripe rust in China in 2017. *Plant Prot*. 2018;44(2):162–6. <https://doi.org/10.16688/j.zwbh.2017268>. (in Chinese).
- Huang L, Yang H, Xia CJ, Li HF, Wang JF, Wang AL, et al. Long-distance transport of *Puccinia striiformis* f. sp. *tritici* by upper airflow on the Yunnan-Guizhou Plateau disrupts the balance of agricultural ecology

- in central China. *Plant Dis.* 2022;106:2940–7. <https://doi.org/10.1094/PDIS-01-22-0038-RE>.
- Jackson HS, Mains EB. Aecial stage of the orange leaf rust of wheat, *Puccinia triticina* Eriks. *J Agric Res.* 1921;22(3):151–72.
- Jia QZ, Cao SQ, Huang J, Zhang B, Sun ZY, Luo HS, et al. Monitoring the variation of physiological races of *Puccinia striiformis* f. sp. *tritici* in Gansu Province, China during 2013–2016. *Plant Prot.* 2018a;44(6):162–7. <https://doi.org/10.16688/j.zwbh.2020147>. (in Chinese).
- Jia QZ, Cao SQ, Wang XM, Huang J, Sun ZY, Zhang B, et al. Monitoring the variation of physiological races of *Puccinia striiformis* f. sp. *tritici* in Gansu Province during 2017–2018. *Plant Prot.* 2021;47(2):214–8. <https://doi.org/10.16688/j.zwbh.2020147>. (in Chinese).
- Jia SY, Hui HJ, Guo P, Yan HF, Meng QF, Liu DQ. Identification of physiological races of *Puccinia triticina* in China in 2017. *Agric Sci-Technol.* 2018b;49.
- Jiang RZ, Liu WC, Xiao YY. Research on long term prediction of wheat stripe rust disease. In: Proceedings on integrated management of pests in China. Kunming: China Agricultural Press; 1996. p. 397–407 (in Chinese).
- Jin W, Liu TG, He YQ, Chen WQ. Differential hosts and nomenclature of races and virulence of *Puccinia triticina* in the world. *Plant Prot.* 2008;34(4):138–42 (in Chinese).
- Jin Y, Szabo LJ, Carson M. Century-old mystery of *Puccinia striiformis* life history solved with the identification of *Berberis* as an alternate host. *Phytopathology.* 2010;100(5):432–5. <https://doi.org/10.1094/PHYTO-100-5-0432>.
- Jin XH, Feng GH, Liu DT, Ma HB, Zhang HY. Review on genetic research on leaf rust in wheat. *J Triticeae Crops.* 2017;37(4):504–12. <https://doi.org/10.7606/j.issn.1009-1041.2017.04.11>. (in Chinese).
- Ju M, Liu W, Wang L, Sun MD, Kang ZS, Zhao J. Two different main routes of spore migration contributing for occurrence of wheat stripe rust in Jiangsu and Zhejiang coastal sporadic epidemiological region in 2019 based on phenotyping and genotyping analyses. *Plant Dis.* 2022;106:2948–57. <https://doi.org/10.1094/PDIS-11-21-2581-RE>.
- Kang ZS, Li ZQ. Discovery of a normal T. type new pathogenic strain to Lovrin 10. *J Northwest a&f Univ (nat Sci Ed).* 1984;4:18–28 (in Chinese).
- Kang ZS, Li ZQ, Zhang SC. A preliminary studies of pathogenic strain to Lovrin 13 of yellow rust of wheat. *J Northwest a&f Univ (nat Sci Ed).* 1987;15(2):105–6 (in Chinese).
- Kang ZS, Wang XJ, Zhao J, Tang CT, Huang LL. Advances in research of pathogenicity and virulence variation of the wheat striper rust fungus *Puccinia striiformis* f. sp. *tritici*. *Sci Agric Sin.* 2015;48(17):3439–53. <https://doi.org/10.3864/j.issn.0578-1752.2015.17.011>. (in Chinese).
- Koc NK, Forrer HR, Kern H. Studies on the relationship between *Puccinia graminis* and the hyperparasite *Aphanocladium album*. *J Phytopathol.* 1981;101(2):131–5. <https://doi.org/10.1111/J.1439-0434.1981.TB03330.X>.
- Kolmer JA. Collections of *Puccinia triticina* in different provinces of China are highly related for virulence and molecular genotypes. *Phytopathology.* 2015;105:700–6. <https://doi.org/10.1094/PHYTO-11-14-0293-R>.
- Kumar S, Bhardwaj SC, Gangwar OP, Sharma A, Quresh N, Kumaran VV, et al. *Lr80*: a new and widely effective source of leaf rust resistance of wheat for enhancing diversity of resistance among modern cultivars. *Theor Appl Genet.* 2021;134:849–58. <https://doi.org/10.1007/s00122-020-03735-5>.
- Leinhos GME, Buchenauer H. Hyperparasitism of selected fungi on rust fungi of cereals. *J Plant Dis Prot.* 1992;99(5):482–98.
- Li JY. Preliminary study on new isolate virulent to wheat variety Suwon 11, a germplasm against wheat stripe rust. *Shaanxi J Agric Sci.* 1983;6:37–8 (in Chinese).
- Li ZQ, Zeng SM. Wheat rusts in China. Beijing: China Agriculture Press; 2002.
- Li Q, Qin JF, Zhao YY, Zhao J, Huang LL, Kang ZS. Virulence analysis of sexual progeny of the wheat stripe rust pathogen recovered from wild barberry in Shaanxi and Gansu. *Acta Phytopathol Sin.* 2016a;46(6):809–20. <https://doi.org/10.1926/cnki.apps.2016.06.011>. (in Chinese).
- Li Q, Li GB, Yue WY, Du JY, Yang LJ, Kang ZS, et al. Pathogenicity changes of wheat stripe rust fungus and disease resistance of wheat cultivars (lines) in Shaanxi Province during 2002–2014. *Acta Phytopathol Sin.* 2016b;46(3):374–83. <https://doi.org/10.13926/j.cnki.apps.2016.03.011>. (in Chinese).
- Li TY, Liu MJ, Wu HD, Li DD, Xu XF, Cao YY. Seedling resistance appraisal and detection of three important genes conferring resistance to stem rust in wheat cultivars or lines from Yunnan Province. *Acta Phytopathol Sin.* 2017;47(1):128–32. <https://doi.org/10.13926/j.cnki.apps.000004>. (in Chinese).
- Li TY, Ma YC, Wu XX, Chen S, Xu XF, Wang H, et al. Race and virulence characterization of *Puccinia graminis* f. sp. *tritici* in China. *PLoS ONE.* 2018;13(5):e0197579. <https://doi.org/10.1371/journal.pone.0197579>. eCollection.
- Li DD, Gao Y, Xu XF, Xuan YH, Cao YY, Li TY, et al. Molecular identification of wheat stem rust resistance genes in 83 wheat cultivars from Heilongjiang Province. *Acta Phytopathol Sin.* 2019a;49:235–45. <https://doi.org/10.13926/j.cnki.apps.000142>. (in Chinese).
- Li F, Upadhyaya NM, Sperschneider J, Matny O, Nguyen-Phuc H, Mago R, et al. Emergence of the Ug99 lineage of the wheat stem rust pathogen through somatic hybridization. *Nat Commun.* 2019b;10:5068. <https://doi.org/10.1038/s41467-019-12927-7>.
- Li JB, Dundas I, Dong CM, Li GR, Trethowan R, Yang ZJ, et al. Identification and characterization of a new stripe rust resistance gene *Yr83* on rye chromosome 6R in wheat. *Theor Appl Genet.* 2020;133(4):1095–107. <https://doi.org/10.1007/s00122-020-03534-y>.
- Li SN, Chen W, Ma XY, Tian XX, Liu Y, Huang LL, et al. Identification of eight *Berberis* species from the Yunnan-Guizhou plateau as aecial hosts for *Puccinia striiformis* f. sp. *tritici*, the wheat stripe rust pathogen. *J Integr Agric.* 2021;20(6):1563–9. [https://doi.org/10.1016/S2095-3119\(20\)63327-5](https://doi.org/10.1016/S2095-3119(20)63327-5).
- Li SN, Lin DX, Zhang YW, Deng M, Chen YX, Lv B, et al. Genome-edited powdery mildew resistance in wheat without growth penalties. *Nature.* 2022;602:455–60. <https://doi.org/10.1038/s41586-022-04395-9>.
- Lian ZC, Liu B, Liu TG, Gao L, Chen WQ. Associations among temperature sensitivity, virulence and genetic diversity of *Puccinia striiformis* f. sp. *tritici* during 2010–2011. *Plant Prot.* 2016;42(6):67–71. <https://doi.org/10.3969/j.issn.0529-1542.2016.06.010>. (in Chinese).
- Ling L. Epidemiology studies on stripe rust of wheat in Chengtu Plain, China. *Phytopathology.* 1945;35:885–94.
- Littlefield LJ. *Biology of the plant rust: an introduction.* Ames: Iowa State University Press; 1981.
- Liu TG, Chen WQ. Race and virulence dynamics of *Puccinia triticina* in China during 2000–2006. *Plant Dis.* 2012;96(11):1601–7. <https://doi.org/10.1094/PDIS-06-10-0460-RE>.
- Liu M, Hambleton S. Taxonomic study of stripe rust, *Puccinia striiformis* sensu lato, based on molecular and morphological evidence. *Fungal Biol.* 2010;114(10):881–99. <https://doi.org/10.1016/j.funbio.2010.08.005>.
- Liu Y, Li ZF. QTL mapping for adult-plant resistance gene to leaf rust in RIL population of Chinese wheat Zhou8425B/Chinese spring. *J Hebei Normal Univ Sci Technol.* 2019;33(2):12–8. <https://doi.org/10.3969/J.ISSN.1672-7983.2019.02.002>. (in Chinese).
- Liu P, Yang MN, Zhou XL, Wu HJ, Jing JX. Genetic analysis and molecular mapping of stripe rust of wheat translocation line H9020-1-6-8-3 derived from *Psathyrostachys huashanica* Keng. *Acta Phytopathol Sin.* 2008;38(1):104–7. <https://doi.org/10.13926/j.cnki.apps.2008.01.011>. (in Chinese).
- Liu TG, Peng YL, Chen WQ, Zhang ZY. First detection of virulence in *Puccinia striiformis* f. sp. *tritici* in China to resistance genes *Yr24* (= *Yr26*) present in wheat cultivar Chuanmai 42. *Plant Dis.* 2010;94(9):1163. <https://doi.org/10.1094/PDIS-94-9-1163C>.
- Liu TG, Wang BT, Jia QZ, Zhang ZY, Li Q, Cao SQ, et al. Physiological specialization of *Puccinia striiformis* f. sp. *tritici* in China during 2010–2011. *J Triticeae Crops.* 2012;32(3):574–8 (in Chinese).
- Liu ZG, Yao WY, Shen XX, Chao KX, Fan Y, Li MZ, et al. Molecular mapping of a stripe rust resistance gene *YrH9020a* transferred from *Psathyrostachys huashanica* Keng on wheat chromosome 6D. *J Integr Agric.* 2014;13(12):2577–83. [https://doi.org/10.1016/S2095-3119\(14\)60755-3](https://doi.org/10.1016/S2095-3119(14)60755-3).
- Liu WC, Liu ZD, Huang C, Lu MH, Liu J, Yang QB. Statistics and analysis of crop yield losses caused by main diseases and insect pests in recent years. *Plant Prot.* 2016;42(5):1–9. <https://doi.org/10.3969/j.issn.0529-1542.2016.05.001>. (in Chinese).
- Liu B, Liu TG, Zhang ZY, Jia QZ, Wang BT, Gao L, et al. Discovery and pathogenicity of CYR34, a new race of *Puccinia striiformis* f. sp. *tritici* in China. *Acta Phytopathol Sin.* 2017;47(5):681–7. <https://doi.org/10.13926/j.cnki.apps.000071>. (in Chinese).
- Liu Y, Chen XY, Ma Y, Meng ZY, Wang FL, Yang XJ, et al. Evidence of roles of susceptible barberry in providing (primary) inocula to trigger stripe rust infection on wheat in Longnan, Gansu. *Acta Phytopathol Sin.*

- 2021;51(3):366–80. <https://doi.org/10.13926/j.cnki.apps.000704>. (in Chinese).
- Lu SY, Fan GF, Xie SM, Wu WZ, Kong XL, Yang ZM, et al. Studies on stripe rust of wheat I. Physiologic specialization of *Puccinia glumarum* (Schmidt) Erikss. & Henn. *Acta Phytopathol Sin.* 1956;2(2):153–66. <https://doi.org/10.13926/j.cnki.apps.1956.02.006>. (in Chinese).
- Lu SY, Yang ZM, Wu WZ, Fan GF, Li WN, Li GX. A study on stripe rust of wheat and grasses. *Acta Phytopathol Sin.* 1958;4(2):137–44. <https://doi.org/10.13926/j.cnki.apps.1958.02.006>. (in Chinese).
- Lu SY, Fan GF, Pan RR, Cai MY, Yao HQ. Chemical control for plant diseases. *J Plant Prot.* 1962;4(1):417–26 (in Chinese).
- Lu SY, Hong XW, Si QM, Wang JX, Shen JP. Studies on the physiologic specialization of stripe rust of wheat in China. *J Plant Prot.* 1963;2(1):23–36 (in Chinese).
- Lu NH, Wu LM, Wang JF, Zhan GM, Huang LL, Kang ZS. Population genetic diversity of *Puccinia striiformis* f. sp. *tritici* in Longnan of Gansu Province. *J Triticeae Crops.* 2012;32(2):366–9 (in Chinese).
- Lü XJ, Kang XH, Chen WQ, Liu TG, Liu B, Gao L. Controlling efficiency against wheat stripe rust by near-isogenic lines cultivars at mix-planting condition. *China Plant Prot.* 2014;34(4):5–9 (in Chinese).
- Ma ZH. Researches and control of wheat stripe rust in China. *J Plant Prot.* 2018;45(1):1–6. <https://doi.org/10.13802/j.cnki.zwbhxb.2018.2018900>. (in Chinese).
- Ma DF, Hou L, Tang MS, Wang HG, Li Q, Jing JX. Genetic analysis and molecular mapping of a stripe rust resistance gene *YrH9014* in wheat line H9014-14-4-6-1. *J Integr Agric.* 2013;12(4):638–45. [https://doi.org/10.1016/S2095-3119\(13\)60271-3](https://doi.org/10.1016/S2095-3119(13)60271-3).
- Ma DF, Fang ZW, Li Q, Yin JL, Wang WK, Wang BT. Molecular mapping of a stripe rust resistance gene of wheat translocation line H9015-17 derived from *Psathyrostachys huashanica* Keng. *Acta Phytopathol Sin.* 2015a;45(5):501–8. <https://doi.org/10.13926/j.cnki.apps.2015.05.008>. (in Chinese).
- Ma DF, Yin JL, Liu SY, Wang WK, Fang ZW, Jing JX. Genetic and molecular mapping of stripe rust resistance gene in wheat-*Psathyrostachys huashanica* translocation line 9020-17-25-6. *J Plant Prot.* 2015b;42(3):327–33. <https://doi.org/10.13802/j.cnki.zwbhxb.2015.03.007>. (in Chinese).
- Ma DF, Fang ZW, Yin JL, Chao KX, Jing JX, Li Q, et al. Molecular mapping of stripe rust resistance gene *YrHu* derived from *Psathyrostachys huashanica*. *Mol Breed.* 2016;36(6):64. <https://doi.org/10.1007/s11032-016-0487-6>.
- Ma YT, Liu TG, Liu B, Gao L, Chen WQ. Population genetic structures of *Puccinia triticina* in five provinces of China. *Eur J Plant Pathol.* 2020;156:1135–45. <https://doi.org/10.1007/s10658-020-01956-4>.
- Mago R, Chen CH, Xia XD, Whan A, Forrest K, Basnet BR, et al. Adult plant stem rust resistance in durum wheat Glossy Huguénot: mapping, marker development and validation. *Theor Appl Genet.* 2022;135:1541–50. <https://doi.org/10.1007/s00122-022-04052-9>.
- Mains EB. Host specialization in the leaf rust of grasses, *Puccinia rubigo-vera*. *Pap Mich Acad Sci.* 1932;17:289–394.
- Mains EB, Jackson HS. Physiologic specialization in the leaf rust of wheat, *Puccinia triticina* Erikss. *Phytopathology.* 1926;16:89–119.
- McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Xia XC. Catalogue of gene symbols for wheat: 2017 supplement. 2017. <https://shigen.nig.ac.jp/wheat/komugi/genes/macgene/supplement2017.pdf>. Accessed 20 July 2022.
- Niu YC, Li ZQ, Shang HS. *Puccinia striiformis* West. f. sp. *leymi* and f. sp. *elymi*, two new formae speciales. *Acta Univ Agric Boreal-Occident.* 1991a;19:58–62 (in Chinese).
- Niu YC, Li ZQ, Shang HS. Evaluation of 50 grass species for resistance to stripe rust. *Pratac Sci.* 1991b;8(3):46–8 (in Chinese).
- O'Brien L, Brown JS, Young RM, Pascoe T. Occurrence and distribution of wheat stripe rust in Victoria and susceptibility of commercial wheat cultivars. *Australas Plant Pathol.* 1980;9:14. <https://doi.org/10.1071/AP9800014>.
- Ou YY, Meng QY. Effect of fluorides on controlling wheat stripe rust. *Agric Sci Bull.* 1958;1:38–9 (in Chinese).
- Pan G, Chen WQ, Liu TG, Gao L, Cao SQ, Wang XM. Survey of overwintering of *Puccinia striiformis* f. sp. *tritici* at different altitudes in the areas of Tianshui, Gansu Province. *Plant Prot.* 2011;37(2):103–6 (in Chinese).
- Peng YF, Chen SM. Comparative study on pathogenicity of *Puccinia striiformis* on wheat and grasses in China. *Plant Prot.* 1987;13(6):19–20 (in Chinese).
- Peng H, Lv GQ, Wang JR. Analysis on the characteristics and causes of main diseases of wheat in Henan Province in 2015. *China Plant Prot.* 2016;36(4):29–33 (in Chinese).
- Pretorius ZA, Boshoff WHP, Kema GHJ. First report of *Puccinia striiformis* f. sp. *tritici* on wheat in South Africa. *Plant Dis.* 1997;81(4):424. <https://doi.org/10.1094/PDIS.1997.81.4.424D>.
- Pretorius ZA, Singh RP, Wagoire WW, Payne TS. Detection of virulence to wheat stem rust resistance gene *Sr31* in *Puccinia graminis* f. sp. *tritici* in Uganda. *Plant Dis.* 2000;84(2):203. <https://doi.org/10.1094/PDIS.2000.84.2.203B>.
- Pu CJ, Liu WH, Chen Z. Discussion on the forecasting method of mid-long term epidemic trend of wheat stripe rust. *Acta Phytopathol Sin.* 2012;42(5):556–60. <https://doi.org/10.13926/j.cnki.apps.2012.05.016>. (in Chinese).
- Qie YM, Liu Y, Wang MN, Li X, See DR, An DG, et al. Development, validation, and re-selection of wheat lines with pyramided genes *Yr64* and *Yr15* linked on the short arm of chromosome 1B for resistance to stripe rust. *Plant Dis.* 2019;103(1):51–8. <https://doi.org/10.1094/PDIS-03-18-0470-RE>.
- Qin JF, Wang ZY, Lv YJ, Kang ZS, Zhao J. Grasses are able to harbor the overwintering of urediniospores and the overwintering of teliospores of *Puccinia striiformis* f. sp. *tritici* in China. *Phytopathol Res.* 2022;4:24. <https://doi.org/10.1186/s42483-022-00129-x>.
- Qin QM, Chen WQ, Chen YL. Analysis on virulence of *Puccinia triticina* population in China in 1997. In: Symposium on outlook of plant protection in 21st century and the 3rd youth science technology researchers in China. Chongqing, China. 1998.
- Rapilly F. Yellow rust epidemiology. *Annu Rev Phytopathol.* 1979;17:59–73. <https://doi.org/10.1146/annurev.py.17.090179.000423>.
- Roelfs AP. Effects of barberry eradication on stem rust in the United States. *Plant Dis.* 1982;66(2):177–81. <https://doi.org/10.1094/PD-66-177>.
- Roelfs AP. Wheat and rye stem rust. In: Roelfs AP, Bushnell WR, editors. The cereal rusts. Orlando, FL: Academic Press; 1985.
- Roelfs AP, Singh RP, Saari EE. Rust diseases of wheat: concepts and methods of disease management. *Texcoco de Mora: CIMMYT*; 1992. p. 81.
- Salcedo A, Rutter W, Wang SC, Akhunova A, Bolus S, Chao SM, et al. Variation in the *AvrSr35* gene determines *Sr35* resistance against wheat stem rust race Ug99. *Science.* 2017;358(6370):1604–6. <https://doi.org/10.1126/science.aao7294>.
- Shan WX, Chen SY, Kang ZS, Wu LR, Li ZQ. Genetic diversity in *Puccinia striiformis* Westend. f. sp. *tritici* revealed by pathogen genome-specific repetitive sequence. *Can J Bot.* 1998;76(4):587–95. <https://doi.org/10.1139/B98-035>.
- Shen QY, Wang KN. Current research status of wheat stripe rust epidemic regularity and symposium on future research. *J Plant Prot.* 1962;4(1):393–402. <https://doi.org/10.13802/j.cnki.zwbhxb.1962.04.007>. (in Chinese).
- Shen L, Ye XP, Liao HM, He HJ, Wang S, Liu RD, et al. Control of wheat stripe rust and ensuring high level of crops under planting of wheat variety mixtures. *Southwest Agric Sci Technol.* 2008;9(1):134–8. <https://doi.org/10.16175/j.cnki.1009-4229.2008.01.008>.
- Sibilia C. La forma ecidica della ruggine bruna delle foglie di grano *Puccinia recondita* Rob. ex. Desm. in Italia. *Boll Stn Patol Veg, Rome* [3]. 1960;18:1–8.
- Singh R, Hodson DP, Jin Y, Huerta-Espino J. Current status, likely migration and strategies to mitigate the threat to wheat production from race Ug99 (TTKS) of stem rust pathogen. *CABI Int.* 2006;1(54):1–13. <https://doi.org/10.1079/PAVSNNR20061054>.
- Song WF, Xin WL, Li JL, Cao YY, Zhang CL. Research progress on stem rust of wheat in China. *Heilongjiang Agric Sci.* 2010;3:112–5 (in Chinese).
- Stubbs RW. The Cereal Rusts. In: Roelfs AP, Bushnell WR, editors. disease, distribution, epidemiology, and control, vol. II. Orlando, FL: Academic Press; 1985.
- SXIPP (Shaanxi Provincial Institute of Plant Protection). Preliminary report on breakdown of resistance of wheat varieties Abbondanze and Fengchan 3. *Shaanxi J Agric Sci.* 1976;6:38–9 (in Chinese).
- Tian YE, Huang J, Li Q, Hou L, Li GB, Wang BT. Inheritance and SSR mapping of a stripe-rust resistance gene *YrH122* derived from *Psathyrostachys huashanica* Keng. *Acta Phytopathol Sin.* 2011;41(1):64–71. <https://doi.org/10.13926/j.cnki.apps.2011.01.007>. (in Chinese).
- Tu C. Physiologic forms of *Puccinia graminis tritici* in Kwangtung Southern China. *Phytopathology.* 1934;24:423.

- Upadhyaya NM, Mago R, Panwar V, Hewitt T, Luo M, Chen J, et al. Genomics accelerated isolation of a new stem rust avirulence gene-wheat resistance gene pair. *Nat Plants*. 2021;7:1220–8. <https://doi.org/10.1038/s41477-021-00971-5>.
- Wan AM, Niu YC, Wu LR, Yuan WH, Li GB, Jia QZ, et al. Physiologic specialization of stripe rust of wheat in China during 1991–1996. *Acta Phytopathol Sin*. 1999;29(1):15–21. <https://doi.org/10.13926/j.cnki.apps.1999.01.003>. (in Chinese).
- Wan AM, Wu LR, Jin SL, Yao G, Wang BT. Discovery and studies on CY32, a new race of *Puccinia striiformis* f. sp. *tritici* in China. *Acta Phytopathol Sin*. 2003;30(4):347–52. <https://doi.org/10.13802/j.cnki.zwbhxb.2003.04.003>. (in Chinese).
- Wan AM, Zhao ZH, Chen XM, He ZH, Jin SL, Jia QZ, et al. Wheat stripe rust epidemic and virulence of *Puccinia striiformis* f. sp. *tritici* in China in 2002. *Plant Dis*. 2004;88(8):896–904. <https://doi.org/10.1094/PDIS.2004.88.8.896>.
- Wan AM, Chen XM, He ZH. Wheat stripe rust in China. *Aust J Agric Res*. 2007;58(6):605–19. <https://doi.org/10.1071/AR06142>.
- Wang HR. Notes on physiological specialization in leaf rust of wheat in China. *Phytopathology*. 1947;37(9):680–1.
- Wang JS. Experimental results of inoculation on spring wheat with aeciospores from *Berberis amurensis* Rupr. *Agric Sci Bull*. 1955;1:54 (in Chinese).
- Wang XJ. Distribution of the wheat stripe rust and the main influencing factors. *Plant Prot*. 2009;35(6):130–4 (in Chinese).
- Wang HR, Chen SM, Liang XS. Preliminary studies on stem rust on spring wheat in Northeast China. *Chin J Agric Res*. 1950;1:37–48 (in Chinese).
- Wang YZ, Wang HR, Zeng GR, Zhang GC, Xue LX. Primary study on association of *Berberis amurensis* Rupr. with wheat stem rust in the middle part of Northeastern China. *Northeast Agric Sci Bull*. 1958;3:77–88 (in Chinese).
- Wang KN, Liu MY, Xie SX, Li FC. On the physiologic specialization of leaf rust of wheat in China. *Acta Phytopathol Sin*. 1982;12(3):13–20. <https://doi.org/10.13926/j.cnki.apps.1982.03.002>. (in Chinese).
- Wang KN, Wu LR, Meng QY, Xie SX, Lu DY, Yuan WH, et al. On the physiologic specialization of stripe rust of wheat in China during the years 1975–1984. *Acta Phytopathol Sin*. 1986;16(2):79–85. <https://doi.org/10.13926/j.cnki.apps.1986.02.003>. (in Chinese).
- Wang HR, Zhao LB, Yuan JS, Chi GT, Zhang Z. Relationship between alternate hosts of *Puccinia triticina*, leaf rust on wheat and grasses (1985–1986). *Inner Mongol Agric Sci Technol*. 1987;3:27–31 (in Chinese).
- Wang KN, Xie SX, Liu XK, Wu LR, Wang JX, Chen YL. Progress in studies on control of wheat stripe rust in China. *Sci Agric Sin*. 1988;21(2):1–8 (in Chinese).
- Wang FL, Wu LR, Xu SC, Jin SL, Jia QZ, Yuan WH, et al. The discovery and studies on new races CYR30 and CYR31 of wheat stripe rust in China. *Acta Phytopathol Sin*. 1996;23(1):39–44. <https://doi.org/10.13802/j.cnki.zwbhxb.1996.01.009>. (in Chinese).
- Wang GJ, Zhao YL, Wang YB. Reviews on harm and prevention of stem rust in wheat. *Heilongjiang Agric Sci*. 2010;12:169–71 (in Chinese).
- Wang R, Zhang SY, Xu ZQ, Chen J, Li Q, Hou L, et al. Genetic analysis and SSR molecular mapping of new stripe-rust resistance gene *Yr17W* derived from *Triticum aestivum*-*Haynaldia villosa* translocation line V9125-2. *Sci Agric Sin*. 2011a;44(1):9–19. <https://doi.org/10.3864/j.issn.0578-1752.2011.01.002>. (in Chinese).
- Wang YF, Song YX, Zhang D, Liu DQ, Ran LX. Screening of biocontrol agents for suppression of wheat leaf rust caused by *Puccinia triticina*. *J Agric Univ Hebei*. 2011b;34(3):12–7 (in Chinese).
- Wang FP, Zhan GM, Wei GR, Huang LL, Kang ZS, Han QM. Population virulence analysis of *Puccinia striiformis* f. sp. *tritici* on tow wheat cultivars in different zones in Longnan. *J Triticeae Crops*. 2014;34(8):1146–52 (in Chinese).
- Wang ZY, Zhao J, Chen XM, Peng YL, Ji JJ, Zhao SL, et al. Virulence variation of *Puccinia striiformis* f. sp. *tritici* collected from *Berberis* spp. *China Plant Dis*. 2016;100(1):131–8. <https://doi.org/10.1094/PDIS-12-14-1296-RE>.
- Wang Q, Ma JJ, Yang LJ, Li Q, Wang BT. Population structure and diversity analysis of *Puccinia striiformis* f. sp. *tritici* in Hubei Province in 2015. *J Triticeae Crops*. 2017;37(2):275–80. <https://doi.org/10.7606/j.issn.1009-1041.2017.02.17>. (in Chinese).
- Wang HL, Jiang Q, Cao SQ, Sun ZY, Wang HG. Effects of cultivar mixture on wheat stripe rust caused by *Puccinia striiformis* f. sp. *tritici* and wheat yield. *J China Agric Univ*. 2022a;27(4):1–21. <https://doi.org/10.11841/j.issn.1007-4333.2022.04.01>. (in Chinese).
- Wang N, Tang CL, Fan X, He MY, Gan PF, Zhang S, et al. Inactivation of a wheat protein kinase gene confers broad-spectrum resistance to rust fungi. *Cell*. 2022b;185:2961–74. <https://doi.org/10.1016/j.cell.2022.06.027>.
- Wang KN. Investigation on physiological races of three rusts on wheat in China. In: China Society of Plant Protection, editors. *Plant Protection Science in China*. Beijing: China Science Publishing & Media Ltd; 1961. p. 307–18 (in Chinese).
- Wei YM. Origin, spread and evolution of wheat in China. *J Triticeae Crops*. 2021;41(3):305–9. <https://doi.org/10.7606/j.issn.1009-2041.2021.03.06>. (in Chinese).
- Wei GR, Liu W, Wang L, Kang ZS, Zhao J. Population structure and virulence of *Puccinia striiformis* f. sp. *tritici* infecting *Aegilops tauschii* in Guanzhong area of Shaanxi. *Acta Agric Boreali-Occident Sin*. 2021;30(8):1232–42. <https://doi.org/10.7606/j.issn.1004-1389.2021.08.014>. (in Chinese).
- Wellings CR. *Puccinia striiformis* in Australia: a review of the incursion, evolution, and adaptation of stripe rust in the period 1979–2006. *Aust J Agric Res*. 2007;58(6):567–75. <https://doi.org/10.1071/AR07130>.
- Wellings CR, Wright DG, Keiper F, Loughman R. First detection of wheat stripe rust in Western Australia: evidence for a foreign incursion. *Australas Plant Pathol*. 2003;32:321–2. <https://doi.org/10.1071/AP03023>.
- Wu YS, Huang ZT. Twenty year's racial identification and fluctuation analysis of *Puccinia graminis* var. *tritici* in China. *J Shenyang Agric Univ*. 1987;18(3):105–38 (in Chinese).
- Wu LR, Niu YC. Strategies of sustainable control of wheat stripe rust in China. *Sci Agric Sin*. 2000;33(5):1–7 (in Chinese).
- Wu YS, Liu W, Huang ZT, Han YY. Race dynamics of *Puccinia graminis* var. *tritici* in 1960–1961. *Liaoning Agric Sci*. 1964;2:50–1 (in Chinese).
- Wu LR, Yang HA, Tao BH, Meng QY, Xie SX, Song WZ, et al. Studies on the epidemic forecast of new race of wheat stripe rust in China. *Sci Agric Sin*. 1991;24(5):59–63 (in Chinese).
- Wu LR, Yang HA, Yuan WH, Song WZ, Yang JX, Li YF, et al. On the physiologic specialization of stripe rust of wheat in China during 1985–1990. *Acta Phytopathol Sin*. 1993;23(3):269–74. <https://doi.org/10.13926/j.cnki.apps.1993.03.023>. (in Chinese).
- Wu YC, Meng QF, Yang WX, Wen XL, Liu DQ. Virulence of *Puccinia triticina* on wheat at seedling stage in Shaanxi, Hubei and Sichuan provinces of China in 2007. *Chin Agric Sci Bull*. 2009;25(17):195–8 (in Chinese).
- Wu JJ, Gao J, Bi WS, Zhao JJ, Yu XM, Li ZF, et al. Genome-wide expression profiling of genes associated with the *Lr47*-mediated wheat resistance to leaf rust (*Puccinia triticina*). *Int J Mol Sci*. 2019;20(18):4498. <https://doi.org/10.3390/ijms20184498>.
- Wu XX, Bian Q, Lin QJ, Sun Q, Ni XY, Xu XF, et al. Sensitivity of *Puccinia graminis* f. sp. *tritici* isolates from China to triadimefon and cross-resistance against diverse fungicides. *Plant Dis*. 2020a;104(8):2082–5. <https://doi.org/10.1094/PDIS-01-20-0009-RE>.
- Wu XX, Lin QJ, Ni XY, Sun Q, Chen RZ, Xu XF, et al. Characterization of wheat monogenic lines with known *Sr* genes and wheat lines with resistance to the Ug99 race group for resistance to prevalent races of *Puccinia graminis* f. sp. *tritici* in China. *Plant Dis*. 2020b;104(7):1939–43. <https://doi.org/10.1094/PDIS-12-19-2736-RE>.
- Xiao YY, Zeng SM, Zhang WY, Wang PY. SIMYR—a simple simulation model for epidemic of wheat stripe rust, *Puccinia striiformis* West. *Acta Phytopathol Sin*. 1983;13(1):1–13. <https://doi.org/10.13926/j.cnki.apps.1983.01.001>. (in Chinese).
- Xiao JX, Zheng Y, Tang L, Li L, Zhu YY, Yang JC. Effects of potassium and nitrogen supply on the occurrence of wheat rusts in wheat and faba bean intercropping system. *J Yunnan Agric Univ*. 2005;20(5):640–5. [https://doi.org/10.16211/j.issn.1004-390x\(n\).2005.05.009](https://doi.org/10.16211/j.issn.1004-390x(n).2005.05.009). (in Chinese).
- Xu ZQ, Zhang SY, Wang R, Wang WL, Zhou XL, Yin JL, et al. Genetic analysis and molecular mapping of stripe rust resistance gene in wheat line M8003-5. *Acta Agron Sin*. 2010;36(12):2116–23. <https://doi.org/10.3724/SP.J.1006.2010.02116>. (in Chinese).
- Xu WB, Yin JL, Ma DF, Tang MS, Yang Y, Jing JX. Genetic analysis and molecular mapping of stripe rust resistance gene in wheat *Leymus mollis* translocation line M97. *J Plant Prot*. 2012;39(1):24–30. <https://doi.org/10.13802/j.cnki.zwbhxb.2012.01.017>. (in Chinese).
- Xu MQ, Wang K, Meng QF, Liu DQ. Genetic diversity of *Puccinia triticina* by SSR in some regions of China. *J Agric Biotechnol*. 2013;21(1):89–96. <https://doi.org/10.3969/j.issn.1674-7968.2013.01.011>. (in Chinese).

- Yan XC, Duan ZY, Yang HL, Yao ZJ, Li ZF. QTLs mapping of leaf rust resistance in wheat variety Zhoumai 22. *Crops*. 2022;2:69–74. <https://doi.org/10.16035/j.issn.1001-7283.2022.02.010>. (in Chinese).
- Yang SC, Sun ML. Identification and dynamics of *Puccinia striiformis* f. sp. *tritici* physiological races in Yunnan Province. *Yunnan Agric Sci Technol*. 1983;3:4–11 (in Chinese).
- Yang JC, Yang QH, Wang SM, Zhu YY, Li HF, He XH, et al. Study on the pest and disease control of vernal crop diversity. *J Yunnan Agric Univ*. 2003;18(2):120–4. [https://doi.org/10.16211/j.issn.1004-390x\(n\).2003.02.003](https://doi.org/10.16211/j.issn.1004-390x(n).2003.02.003). (in Chinese).
- Yang JC, Liu JJ, An ZY, Zhu YY, Li CY, Chen XD, et al. Analyses on effect of interplanting on diseases and pest control and yield increase of wheat and faba bean. *J Yunnan Agric Univ*. 2009a;24(3):342–8. [https://doi.org/10.16211/j.issn.1004-390x\(n\).2009.03.020](https://doi.org/10.16211/j.issn.1004-390x(n).2009.03.020). (in Chinese).
- Yang MN, Yao Q, He MM, Hou L, Jing JX. Genetic analysis and SSR location of stripe rust resistance of wheat translocation line M853-4 derived from *Elymus mollis* (Trin.) Hara. *J Agric Biotechnol*. 2009b;17(4):695–700 (in Chinese).
- Yang MN, Peng YL, Yao Q, He MM, Jing JX. Genetic analysis and SSR location of stripe rust resistance of wheat translocation line M8657-1 derived from *Triticum aestivum-Leymus mollis* (Trin.) Hara. *J Agric Biotechnol*. 2010;18(5):861–6 (in Chinese).
- Yang YS, Shi NY, Shi ZL. Archeological findings on dual transition of agriculture during prehistoric times in the Hexi Corridor. *J Dunhuang Stud*. 2016;1:82–91 (in Chinese).
- Yang WX, Meng QF, Feng SD, Liu DQ. Monitoring of virulence of *Puccinia triticina* in China in 1998–2000. In: The 7th congress of Chinese Phytopathology Society membership and academic symposium. Beijing, China. 2002. (in Chinese).
- Yao P, Cao YY, Jia XL, Zhou ZJ, Wu YS. Race dynamics of *Puccinia graminis* f. sp. *tritici* in China in 1992. *Plant pro*. 1993;19(5):6–8 (in Chinese).
- Yao P, Cao YY, Liu WZ, Wu YS. Race dynamics analysis of *Puccinia graminis* f. sp. *tritici* in China. *J Shenyang Agric Univ*. 1996;27:263–8 (in Chinese).
- Yao P, Cao YY, Liu WZ, Wu YS. Race population trend of *Puccinia graminis* f. sp. *tritici* in 1990–1994 in China. *Acta Phytopathol Sin*. 1997;24(4):297–302. <https://doi.org/10.13802/j.cnki.zwbhxb.1997.04.003>. (in Chinese).
- Yao P, Cao YY, Zhang SS. Race dynamics analysis of *Puccinia graminis* f. sp. *tritici* in China. *Plant Prot*. 1998;24(1):3–6 (in Chinese).
- Yao Q, Wang Y, He MM, Li Y, Zhou XL, Wang BT, et al. SSR molecular mapping of stripe rust resistance gene of wheat translocation line H9020-20-12-1-8 derived from *Psathyrostachys huashanica* Keng. *J Agric Biotechnol*. 2010;18(4):676–81 (in Chinese).
- Yin SY. Studies on physiologic specialization in *Puccinia graminis tritici* Erikss. et Henn. in China and varietal resistance of wheat. *Acta Agric*. 1947;1:10–21.
- Ying JS, Chen DZ. *Berberidaceae*. Flora of China. Editorial Committee of Flora of China, editor. Beijing: Science Press; 2001. p. 76–211 (in Chinese).
- Yuan JS. Study on the physiologic specialization of *Puccinia recondita* f. sp. *tritici*-IX (1982–1983). *J Hebei Agric Univ*. 1984;7(4):73–87 (in Chinese).
- Yuan JS, Zhu ZY. The study on growth and decline of physiological race of *Puccinia recondita* f. sp. *tritici* from 1993 to 1995. *J Hebei Agric Univ*. 1995;17(3):85–8 (in Chinese).
- Yuan JS, Wang HR, Qi JL, Wang YM. Study of the physiologic specialization of *Puccinia recondita* f. sp. *tritici*-VIII (1981–1982). *J Hebei Agric Univ*. 1983;6(4):9–26 (in Chinese).
- Yuan JS, Yuan HR, Zhu ZY. Monitoring of physiologic races of *Puccinia recondita* f. sp. *tritici* and improving of viewpoint and method of research. *Acta Agric Boreali-Sin*. 1991;6:115–20 (in Chinese).
- Yuan WH, Li GB, Wang BT. *Aegilops squarrosa* L.—a host of *Puccinia striiformis* West. *J Hebei Agric Univ*. 1994;17(3):75–7 (in Chinese).
- Yucheng Plant Protection Station. Yucheng Agriculture and Forestry Bureau. *J Mar Meteorol*. 1979;3:18–27. <https://doi.org/10.19513/j.cnki.issn1005-0582.1979.03.007>. (in Chinese).
- Zeng SM, Luo Y. Long-distance spread and interregional epidemics of wheat stripe rust in China. *Plant Dis*. 2006;90(8):980–8. <https://doi.org/10.1094/PD-90-0980>.
- Zeng GR, Xue LX. Study on relation of *Berberis amurensis* Rup. to occurrence of wheat stem rust in the middle of North China. *J Plant Prot*. 1963;2:47–55 (in Chinese).
- Zeng GR, Zhang GC, Xue LX, Huang ZT. Investigations on races of *Puccinia graminis* Pers. var. *tritici* Erikss. & Henn. in Northeast China. *Acta Phytopathol Sin*. 1963;6(2):131–40. <https://doi.org/10.13926/j.cnki.apps.1963.02.005>. (in Chinese).
- Zeng SM, Zhang WY, Xiao YY. A simulation model for wheat stripe rust, *Puccinia striiformis* West. *J China Agric Univ*. 1981;7(3):1–12 (in Chinese).
- Zeng QD, Shen C, Yuan FP, Wang QL, Wu JH, Xue WB, et al. The resistance evaluation of the Yr genes to the main prevalent pathotypes of *Puccinia striiformis* f. sp. *tritici* in China. *Acta Phytopathol Sin*. 2015;45(6):641–50. <https://doi.org/10.13926/j.cnki.apps.2015.06.011>. (in Chinese).
- Zeng QD, Zhao J, Wu JH, Zhan GM, Han DJ, Kang ZS. Wheat stripe rust and integration of sustainable control strategies in China. *Front Agr Sci Eng*. 2022;9(1):37–51. <https://doi.org/10.15302/J-FASE-2021405>.
- Zeng SM, Sun P. Simulation study on inter-regional epidemics of wheat stripe rust—the role of inoculum sources in Northwestern Sichuan, Longnan and Longdong in Gansu in inter-regional epidemics of wheat stripe rust. In: Study on the implementation of plant-protection-system-engineering in the wheat pest management. Beijing: Beijing Agricultural University Press; 1995. p. 125–33.
- Zhan GM, Tian Y, Wang FP, Chen XM, Guo J, Jiao M, et al. A novel fungal hyperparasite of *Puccinia striiformis* f. sp. *tritici*, the causal agent of wheat stripe rust. *PLoS ONE*. 2014a;9(11):e111484. <https://doi.org/10.1371/journal.pone.0111484>.
- Zhan HX, Chang ZJ, Li GR, Jia JQ, Guo HJ, Zhang XJ, et al. Genetic analysis and molecular mapping of stripe rust resistance gene in wheat line CH5383. *Biotechnol Bull*. 2014b;6:96–100. <https://doi.org/10.13560/j.cnki.biotech.bull.1985.2014.06.030>. (in Chinese).
- Zhan GM, Ji F, Chen XM, Wang JX, Zhang DL, Zhao J, et al. Populations of *Puccinia striiformis* f. sp. *tritici* in winter spore production regions were spread from southwestern overwintering areas in China. *Plant Dis*. 2022a;106:2856–65. <https://doi.org/10.1094/PDIS-09-21-2070-RE>.
- Zhan GM, Ji F, Zhao J, Liu Y, Zhou AH, Xia MH, et al. Sensitivity and resistance risk assessment of *Puccinia striiformis* f. sp. *tritici* to triadimefon in China. *Plant Dis*. 2022b;106(6):1690–9. <https://doi.org/10.1094/PDIS-10-21-2168-RE>.
- Zhang H, Zhang L. Molecular mapping and marker development for the *Triticum dicoccoides*-derived stripe rust resistance gene YrSM139-1B in bread wheat cv. Shaanmai 139. *Theor Appl Genet*. 2016;129(2):369–76. <https://doi.org/10.1007/s00122-015-2633-7>.
- Zhang GC, Zeng GR, Xue LX. Report on association of *Berberis poiratii* Sch. with wheat stem rust. *Northeast Agric Sci Bull*. 1957;4:102–7 (in Chinese).
- Zhang JQ, Liu B, Chen WQ, Liu TG, Gao L. Temperature-sensitivity of population of *Puccinia striiformis* Westend. *Acta Phytopathol Sin*. 2013;43(1):88–90. <https://doi.org/10.13926/j.cnki.apps.2013.01.016>.
- Zhang Y, Chao KX, Gao X, Liu ZG, Yao WY, Li Q, et al. Genetic analysis and SSR markers of wheat stripe rust resistance gene YrElm derived from *Elymus mollis* (Trin.) Hara. *Acta Phytopathol Sin*. 2014;44(6):641–50. <https://doi.org/10.13926/j.cnki.apps.2014.06.011>. (in Chinese).
- Zhang LY, Meng QF, Kang J, Yang WX, Yan HF, Liu DQ. Genetic diversity analysis of *Puccinia recondita* by UP-PCR. *Mycosystema*. 2015;34(2):215–26. <https://doi.org/10.13346/j.mycosystema.130283>. (in Chinese).
- Zhang XH, Chang ZJ, Qiao LY, Guo HJ, Zhan HX, Li X, et al. Research progress and prospects of wheat leaf rust adult-plant resistance. *J Shanxi Agric Sci*. 2016;44(4):552–6. <https://doi.org/10.3969/j.issn.1002-2481.2016.04.33>. (in Chinese).
- Zhang MY, Meng QF, Zhang L, Gao Y, Yan HF, Liu DQ. Analysis of genetic diversity of *Puccinia triticina* isolated from different wheat cultivars. *J Henan Agric Sci*. 2018;47(9):77–81. <https://doi.org/10.15933/j.cnki.1004-3268.2018.09.013>. (in Chinese).
- Zhang GS, Zhao YY, Kang ZS, Zhao J. First report of a *Puccinia striiformis* f. sp. *tritici* race virulent to what stripe rust resistance gene Yr5 in China. *Plant Dis*. 2020a;104(1):284. <https://doi.org/10.1094/PDIS-05-19-0901-PDN>.
- Zhang L, Shi CC, Li LR, Li M, Meng QF, Yan HF, et al. Race and virulence analysis of *Puccinia triticina* in China in 2014 and 2015. *Plant Dis*. 2020b;104(2):455–64. <https://doi.org/10.1094/PDIS-05-19-1051-RE>.
- Zhang L, Xiao Y, Gao Y, Zhao N, An YJ, Yang WX, et al. Race and virulence analysis of *Puccinia triticina* in China during 2011 to 2013. *Plant Dis*. 2020c;104(8):2095–101. <https://doi.org/10.1094/PDIS-01-20-0047-RE>.
- Zhang GS, Liu W, Wang L, Cheng XR, Tian XX, Du ZM, et al. Evaluation on potential risk of the emerging Yr5-virulent races of *Puccinia striiformis* f.

- sp. *tritici* to 165 Chinese wheat cultivars. *Plant Dis.* 2022;106(7):1867–74. <https://doi.org/10.1094/PDIS-11-21-2622-RE>.
- Zhao LB, Yuan JS, Cao KQ, Wang HR, Zhang Z. On the problem of *Thalictrum* acting as alternating host of *Puccinia recondita* f. sp. *tritici*. *Acta Phytopathol Sin.* 1994;24(3):219–22. <https://doi.org/10.13926/j.cnki.apps.1994.03.009>. (in Chinese).
- Zhao X, Zheng TC, Xia XC, He ZH, Liu DQ, Yang WX, et al. Molecular mapping of leaf rust resistance gene *LrZH84* in Chinese wheat line Zhou 8425B. *Theor Appl Genet.* 2008;117:1069–75. <https://doi.org/10.1007/s00122-008-0845-9>.
- Zhao J, Wang L, Wang ZY, Chen XM, Zhang HC, Yao JN, et al. Identification of eighteen *Berberis* species as alternate hosts of *Puccinia striiformis* f. sp. *tritici* and virulence variation in the pathogen isolates from natural infection of barberry plants in China. *Phytopathology.* 2013;103(9):927–34. <https://doi.org/10.1094/PHYTO-09-12-0249-R>.
- Zhao J, Zhao SL, Chen XM, Wang ZY, Wang L, Yao JN, et al. Determination of the role of *Berberis* spp. in wheat stem rust in China. *Plant Dis.* 2015;99(8):1113–7. <https://doi.org/10.1094/PDIS-09-14-0928-RE>.
- Zhao J, Wang MN, Chen XM, Kang ZS. Role of alternate hosts in epidemiology and pathogen variation of cereal rusts. *Annu Rev Phytopathol.* 2016a;54:207–28. <https://doi.org/10.1146/annurev-phyto-080615-095851>.
- Zhao J, Zhao SL, Peng YL, Qin JF, Huang LL, Kang ZS. Investigation on geographic distribution and identification of six *Berberis* spp. serving as alternate host for *Puccinia striiformis* f. sp. *tritici* in Linzhi, Tibet. *Acta Phytopathol Sin.* 2016b;46:103–11. <https://doi.org/10.13962/j.cnki.apps.2016.01.012>. (in Chinese).
- Zhao J, Zheng D, Zuo SX, Wang L, Huang LL, Kang ZS. Research advances in alternate host and sexual reproduction on wheat stripe rust pathogen *Puccinia striiformis* f. sp. *tritici* Erikss. et Henn. *J Plant Prot.* 2018;45(1):7–19. <https://doi.org/10.13802/j.cnkizwbhxb.2018.2018901>. (in Chinese).
- Zhao J, Du ZM, Liu Y, Liang XF, Chen L, Kang ZS. Identification of two *Thalictrum* species as alternate hosts for *Puccinia triticina*, the wheat leaf rust pathogen. *Acta Phytopathol Sin.* 2021;51(1):70–84. <https://doi.org/10.13926/j.cnki.apps.000349>.
- Zhao YY, Li Q, Huang LL, Kang ZS, Zhao J. Virulence phenotyping and molecular genotyping reveal high diversity within and strong gene flow between the *Puccinia striiformis* f. sp. *tritici* populations collected from barberry and wheat in Shaanxi Province of China. *Plant Dis.* 2022. <https://doi.org/10.1094/PDIS-12-21-2713-RE>.
- Zheng WM, Chen SY, Kang ZS, Wang Y, Wu LR, Li ZQ. DNA fingerprinting of natural population of *Puccinia striiformis* f. sp. *tritici* in Tianshui area. *Mycosystema.* 2005;24(2):199–206. <https://doi.org/10.3346/j.mycosystema.2005.02.009>. (in Chinese).
- Zheng L, Zhao J, Liang XF, Zhan GM, Jiang SC, Kang ZS. Identification of a novel *Alternaria alternate* strain able to hyperparasitize *Puccinia striiformis* f. sp. *tritici*, the causal agent of wheat stripe rust. *Front Microbiol.* 2017;8:71. <https://doi.org/10.3389/fmicb.2017.00071>.
- Zhou XL, Wu HJ, Zhang RJ, Liu P, Jing JX. Microsatellite tagging of stripe-rust resistance gene *YrV1* derived from *Haynaldia villosa*. *Acta Phytopathol Sin.* 2008;38(1):69–74. <https://doi.org/10.13926/j.cnki.apps.2008.01.010>. (in Chinese).
- Zhou HX, Xia XC, He ZH, Li X, Wang CF, Li ZF, et al. Molecular mapping of leaf rust resistance gene *LrNJ97* in Chinese wheat line Neijiang 977671. *Theor Appl Genet.* 2013;126:2141–7. <https://doi.org/10.1007/s00122-013-2124-7>.
- Zhuang H, Zhao J, Huang LL, Kang ZS, Zhao J. Identification of three *Berberis* species as potential alternate hosts for *Puccinia striiformis* f. sp. *tritici* in wheat-growing regions of Xinjiang, China. *J Integr Agric.* 2019;18(12):2786–92. [https://doi.org/10.1016/S2095-3119\(19\)62709-7](https://doi.org/10.1016/S2095-3119(19)62709-7).

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