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Grasses are able to harbor the oversummering of urediospores and the overwintering of teliospores of *Puccinia striiformis* f. sp. *tritici* in China

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Abstract

Puccinia striiformis f. sp. *tritici* (*Pst*), the cause of wheat stripe rust, is a biotrophic and heteroecious rust fungus with five spore types. Cool and humid climatic conditions are conducive for the development of wheat stripe rust, and in turn, temperatures above 22 °C limit or even cease the disease. The survival of *Pst* during summer after wheat harvest is responsible for the infection on autumn-sown wheat to maintain disease cycle all the year round. Teliospores formed at late stage of wheat growth are essential for initiating sexual reproduction in spring. Although Chinese native grasses have been experimentally testified as susceptible hosts for *Pst* and teliospores produced on wheat have been shown to be potential inoculum sources causing infection on alternate hosts (mainly *Berberis*) in spring, the roles of grass hosts in harboring the survival of urediospores and teliospores of *Pst* and promoting the emergence of diverse races under field conditions in China have not been known. Herein, Gansu, as a hotspot and an important oversummering region for *Pst*, was exemplified to demonstrate these roles of grass hosts. As a result, 63 *Pst* isolates, derived from 2184 uredial samples collected from grass hosts during harvesting period (from mid-June to mid-to-late July) and seeding period (mid to late September) in 2012 and 2013, were identified as 52 diverse phenotypes (82.5%) on the Chinese differential hosts. Subsequently, after inoculation of barberry, 52 *Pst* isolates with high infection type, 20 known races and 32 new races, were recovered from 1,712 single aecium, which are derived from 35 telial samples of grass hosts. Our experiments showed that *Pst* urediospores can oversummer on grass species in Gansu or other oversummering regions with similar ecological and climatic conditions. *Pst* teliospores, which are produced on these grass hosts, are important inoculum source for barberry infection in spring. Therefore, treatment of grasses hosts should be taken into consideration in management of wheat stripe rust.

Keywords: Wheat stripe rust, Grass, Oversummering, Overwintering, Barberry, Disease management

Background

Wheat stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Eriks. (Basidiomycota), is one of the most devastating diseases threatening wheat production worldwide. The disease occurs in all wheat-producing regions, particularly in cool and humid areas, and results in a yield loss of 10–30% in epidemic years (Li and Zeng 2002; Wellings 2011), and even a complete

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harvest failure after severe early infections on highly susceptible wheat cultivars (Chen 2005).

Pst is an obligate, biotrophic and heteroecious cereal rust fungus with a complex life cycle consisting of five different spore stages on two taxonomically different plant species. The urediospore stage is on wheat and grasses (the primary hosts) where the pathogen completes serial asexual transmission; the teliospore stage required for the sexual cycle is on the alternate dicot hosts (Hovmøller et al. 2011). Production of teliospores can occur at all wheat growth stages especially when plants reach maturity (Chen et al. 2021). Basidiospores ejected from germinated teliospores infect *Berberis* and *Mahonia* species, the alternate (or aecial) hosts on which the pathogen has pycnial and aecial stages, to accomplish sexual reproduction. Aeciospores are spread by wind to the primary hosts where uredia are produced. Therefore, teliospore production is essential for *Pst* to complete sexual cycle.

It has been proven that grasses can be infected by *Pst*. Besides wheat, *Pst* potentially over-summer for surviving on 320 grass species of 50 genera (Hassebrauk 1965; Stubbs 1985). Grasses are demonstrated to have roles in the overwintering survival of *Pst* in temperate regions of the world, but their roles in initiating stripe rust on wheat varies from one region to another are not clearly known. In the United States, *Pst* overwintering on grass hosts is regarded as an important inoculum source for wheat stripe rust epidemics in the mountainous regions of the Pacific Northwest and California (Hendrix et al. 1965; Tollenaar and Houston 1967). Whereas, wild grasses were found to have only minor roles in wheat stripe rust epidemics compared with volunteer wheat in Oregon (Shaner and Powelson 1973) and Montana (Sharp and Hehn 1963), and have no role in the Sacramento Valley of California in 1975 (Line 1976). However, in Europe, the survival of the wheat stripe rust on wild grasses has been shown to provide inoculum sources for epidemics in the Harz regions of Germany (Becker and Hart 1939), but not in northwestern Europe (Zadoks 1961). In southeast Kazakhstan, *Pst* survival on wild grasses during the summer was demonstrated to be an important inoculum source for stripe rust infections of wheat (Abiev et al. 1982). In China, although 88 gramineous grass species from 16 genera have been experimentally confirmed as uredial hosts of *Pst* (Lin and Li 1990; Niu et al. 1991; Li and Zeng 2002), studies have suggested that *Pst* can not survive on grasses during the summer in Chengdu Plain, Sichuan (Chen et al. 1957). Moreover, it has not been known the role of grass hosts in the survival of *Pst* for overwintering, and the role of overwintering urediospores as potential inoculum source for infection on autumn-sown wheat (Li and Zeng 2002).

Tianshui in Gansu has been considered the most crucial overwintering region for *Pst* and is therefore an important inoculum source in China. In this region, winter wheat is sown in the autumn from mid-late September to late October and is harvested during the following summer from late June to mid-to-late July (Additional file 1: Figure S1). As an obligate, biotrophic pathogen, *Pst* depends on living hosts and requires relatively low temperatures (0–22 °C for germination, infection, growth and survival. Once the air temperature exceeds 23 °C *Pst* can not overwinter (Li and Zeng 2002). Hence, during the period from wheat harvest to the emergence of autumn-sown winter wheat, an average 10-day (called 'Xun' in Chinese) temperature below 22 °C is required for *Pst* survival (Li and Zeng 2002). Tianshui is located in the mountainous region with elevations ranging from 1000 to 3120 m. During the summer, the climate in this region is usually cool and humid, which is favorable for the overwintering survival of *Pst*. So far, it has been demonstrated that *Pst* can overwinter on late-maturing wheat or volunteer wheat in the highland areas (>1600 m) where the average 'Xun' temperature during the hottest days in July and August is below 22 °C and suitable for the development of the disease. After overwintering, viable urediospores in high-elevation regions are spread from grasses to seedlings of autumn-sown winter wheat grown in the low-elevation regions in September (Li and Zeng 2002). Based on previous studies in China, considerable attentions have been paid to the susceptibility of grasses to *Pst*. Although a few *Pst* isolates have been recovered from some grass species, most of those are known races with low virulence diversity (Ling 1945; Lu et al. 1956; Chen et al. 1957; Peng and Chen 1987; Niu et al. 1991; Yuan et al. 1994). However, it has not been determined whether *Pst* can overwinter on grass hosts in Tianshui, and thus the role of grass hosts that harbor *Pst* for overwintering has not been clearly defined in the Gansu region.

It has been suggested that *Pst* completes its sexual cycle on alternate hosts in the spring in Gansu and other regions of China (Zhao et al. 2013; Wang et al. 2016). This indicates that teliospores can maintain viability and are able to germinate in the spring to form basidiospores, which can infect newly emerging barberry leaves. A recent study in China has demonstrated that valid *Pst* teliospores potentially provided inoculum for barberry infection by stripe rust-infested wheat plants growing in fields adjacent to barberry bushes and a great deal of diseased wheat straws or debris inside wheat stacks around barberry bushes in Gansu and other wheat-growing regions. In those areas, *Pst* teliospores, which are produced at all growth stages of wheat and on diseased wheat straw or debris after wheat harvests,

can germinate to produce basidiospores to infect barberry shoots emerging in the next spring (Chen et al. 2021). But, in contrast, the sexual stage is not detected in the U. S. Pacific Northwest (Wang and Chen 2015) and other regions of the world. Asexual hosts of *Pst*, besides wheat, also include grasses (Stubbs 1985). However, little is known about the survival of *Pst* teliospores on grass hosts in spring.

In recent years, in our field investigations of the *Pst* overwintering regions in Gansu, we routinely observed stripe rust infections on *Agropyron* and *Elymus* plants, and we also found the production of teliospores in these grass species in autumn. However, we did not directly determine whether the teliospores could overwinter on the grasses and germinate to provide inoculum for barberry infections. Therefore, the objectives of the current study were: (1) to determine whether grasses could harbor *Pst* teliospores for overwintering, and (2) to investigate the potential of teliospores originating from grasses to germinate in the next spring and infect barberry plants under natural conditions.

Results

Characterization of *Pst* isolates from uredial samples of grasses

In Gansu, during two successive years (2012 and 2013), 2184 uredia from three stripe rust-infected grass species (*Agropyron cristatum*, *Elymus cylindricus* and *E. excelsus*) were collected at 21 sampling sites (Fig. 1a–f; Table 1). Among the samples, 1,905 uredial infections elicited immune or necrotic reactions on seedlings of the susceptible wheat cultivar Mingxian 169 (Fig. 2a) according to the 0-to-4 scale (Hungerford and Owens 1923), and 279 produced uredia derived from 12.8% of the total samples, with different infection types (ITs) ranging from 1 to 4 on the Mingxian 169 seedlings (Fig. 2b–e; Table 2). Among the 279 samples, 63 (22.6%) developed highly pathogenic infection types of 3 or 4, and 216 (77.4%) had relatively low pathogenicity with infection type of 1 and 2 on the cultivar (Table 2).

Infection type classification of *Pst* isolates from telial samples of grasses

Teliospores from leaves of two grass species, *A. cristatum* and *E. cylindricus*, were tested for germination in March, 2014 (Fig. 3a–d). Teliospore germination was initiated at 6 h post incubation, increased with prolonged incubation and peaked at 72 h (Fig. 4). The capacity of teliospore germination for *E. cylindricus* was higher than that for *A. cristatum* with a germination ratio of 31.4% and 26.4%, respectively.

Both 26 telial samples of *A. cristatum* and 9 ones of *E. cylindricus* produced aecia on barberry leaves after

inoculation (Fig. 5a, b; Table 3). In total, four ITs 3–4 isolates and four ITs 1–2 ones were recovered from 227 single aecial cups of 60 aecia derived from teliospores on 26 *A. cristatum* leaf segment samples (Table 3). Likewise, forty-eight ITs 3–4 isolates, and twenty-two ITs 1–2 ones were obtained from 1,485 single aecial cups of 339 aecia derived from teliospores of 9 *E. cylindricus* leaf segment samples (Table 3). Thus, 78 (4.6%) isolates were pathogenic to the wheat cultivar Mingxian 169. Among these isolates, 52 (66.7%) were highly pathogenic (ITs 3-4) and 26 (33.3%) showed low pathogenicity (ITs 1-2). Most of aecial cups, accounting for 95.4% (1634/1712) of the total, only elicited necrotic flecks that failed to produce uredia on Mingxian 169 (Fig. 5c–g; Table 3).

Characterization of nonpathogenic and pathogenic *Pst* isolates recovered from grass plants

A total of 63 *Pst* isolates, with infection types of 3 and 4, were recovered from uredial samples of grass. Phenotyping of the isolates on a set of 19 Chinese differential hosts (genotypes) indicated that the 63 isolates elicited 52 different phenotypes, Ph1–Ph52, which exhibited variation as high as 82.5% in virulence (Table 4). Among the 63 isolates, many had mixed AV or VA phenotypes to some wheat genotypes. These included isolate 3-28-5, which had an AV reaction to the Lutescenes 128 wheat genotype with an unknown resistance gene, and isolate 2-56-1, which had a VA response against the *Yr6* locus in the Trigo Eureka wheat genotype. Results as above indicated that these isolates were heterozygous in their abilities to infect plants with both known and unknown resistance loci. The results also demonstrated that grass species could harbor *Pst* for overwintering survival during the non-wheat growing season and could provide potential inoculum sources for *Pst* epidemics on autumn-sown winter wheat.

After barberry seedlings were inoculated with basidiospores from germinating telia that had overwintered on grasses, 52 *Pst* isolates with high infection types of 3 and 4, were obtained. Of these 52 isolates, 48 were recovered from *E. cylindricus* with 17 being previously reported races and 31 belonging to undescribed races. The remaining 4 *A. cristatum* samples consisted of 3 known races and 1 unknown race (Table 5). The 20 isolates of known races corresponded to 9 races, including 5 CYR33, 3 CYR32, 1 G22-9, 6 Su11-126, 1 Fo-2, 1 Hy8-1, 1 Hy-92, 1 Ky-3, and 1 ZS-6 types (Fig. 6; Table 5). In addition, the 32 isolates of unknown races were classified as virulent on the wheat genotypes Hybrid 46 (HyG) and Suwon 11 (SuG), and represented previously undescribed races (Fig. 6; Table 5). These results indicate that *Pst* teliospores formed on grasses in the autumn can successfully survive throughout the winter to germinate the next

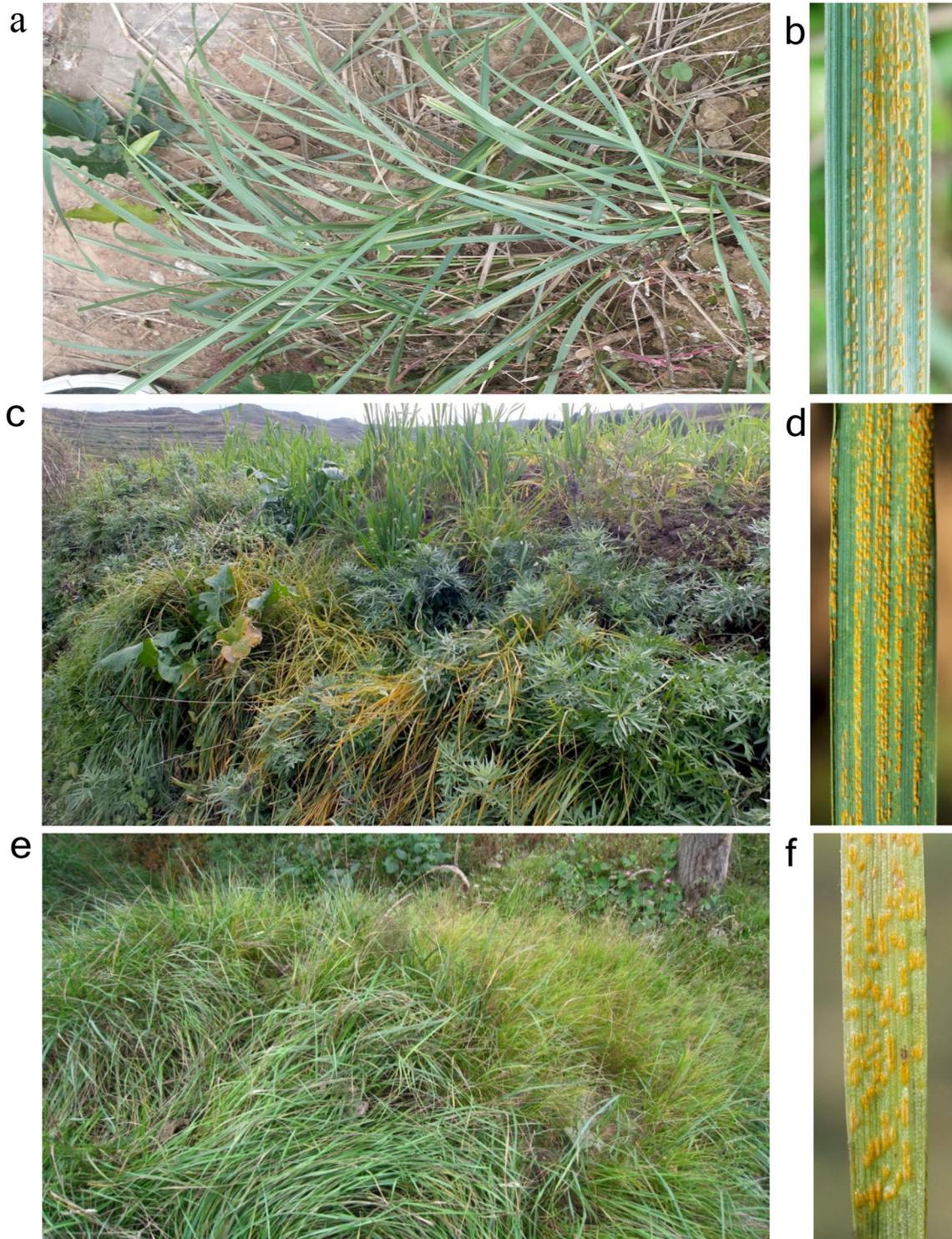


Fig. 1 Grass plants with stripe rust symptoms near crop fields in Tianshui, Gansu Province, China. **a** *A. cristatum* plants close to a rapeseed field in Pingnan, Tianshui (12 October, 2012). **c** *E. cylindricus* adjacent to a wheat field in Pingnan, Tianshui (2 October 2012). **e** *E. excelsus* near a corn field in Daimen, Tianshui (2 October 2012). **b, d, f** Close up images showing uredia on the grass leaves correspond to **a, c** and **e**, respectively

Table 1 *Puccinia striiformis* f. sp. *tritici* (*Pst*) isolates from grass leaf samples (with uredia) collected in Tianshui, Gansu Province, China

Sampling sites	Grass species	No. of samples inoculated	No. of samples producing necrotic or immune reaction on wheat cv. Mingxian 169	No. of samples recovering <i>Pst</i> isolates ^a	Percentage ^b (%)	Year ^c
Chenjiazhuang, Qishou	<i>Agropyron cristatum</i>	174	155	19	10.9	2012
Pingnan, Qinzhou	<i>A. cristatum</i>	56	51	5	8.9	2013
Pingnan, Qinzhou	<i>A. cristatum</i>	70	68	2	2.9	2013
Pingnan, Qinzhou	<i>A. cristatum</i>	24	23	1	4.2	2013
Pingnan, Qinzhou	<i>A. cristatum</i>	190	182	8	4.2	2012
Shuidonggou, Wushan	<i>A. cristatum</i>	66	65	1	1.5	2012
Shuidonggou, Wushan	<i>A. cristatum</i>	20	16	4	20.0	2013
Pingnan, Qingzhou	<i>Elymus cylindricus</i>	204	185	19	9.3	2013
Pingnan, Qingzhou	<i>E. cylindricus</i>	320	302	18	5.6	2013
Pingnan, Qingzhou	<i>E. cylindricus</i>	53	29	24	45.3	2013
Pingnan, Qingzhou	<i>E. cylindricus</i>	266	150	116	43.6	2013
Pingnan, Qingzhou	<i>E. cylindricus</i>	109	107	2	1.8	2013
Tongjiamo, Taijing, Qingzhou	<i>E. cylindricus</i>	66	65	1	1.5	2013
Baizhai, Daimen	<i>E. excelsus</i>	242	198	44	18.2	2012
Laojunshan, Wushan	<i>E. excelsus</i>	35	33	2	5.7	2012
Lvjiapo, Daimen	<i>E. excelsus</i>	17	13	4	23.5	2013
Lvjiapo, Daimen	<i>E. excelsus</i>	54	53	1	1.9	2013
Lvjiapo, Daimen	<i>E. excelsus</i>	33	31	2	6.1	2013
Nanyu, Tianshui	<i>E. excelsus</i>	74	70	4	5.4	2012
Xujiadian, Zaojiao, Qingzhou	<i>E. excelsus</i>	83	82	1	1.2	2012
Baizhai, Daimen	<i>E. excelsus</i>	28	27	1	3.6	2013
Total		2184	1905	279	12.8	

^a This indicates stripe rust-infected grass samples that produce uredia on leaves of highly susceptible wheat cultivar Mingxian 169 seedlings with infection types from 1 to 4 after inoculation

^b Percentage (%) = (the number of samples recovering *Pst* isolates/the number of samples inoculated) × 100

^c Sampling was carried out from September to October in 2012, and August to October in 2013

spring during low temperature and dry weather conditions. Thus, the conclusion is that surviving teliospores can germinate to produce basidiospores that can infect newly emerging barberry leaves and provide new sources for virulence in the spring. Therefore, *Pst* teliospores on grasses represent important inoculum source of barberry infections that function in the sexual cycle of the wheat stripe rust pathogen.

Discussion

Grass hosts harbor the survival of *Pst* for overwintering and *Pst* isolates from grass hosts exhibit high-level phenotypic variation

Over the past decades, a few studies of *Pst* infection on grasses in China have been carried out, which have mainly concentrated on grass species susceptible to *Pst* to serve as uredial hosts (Ling 1945; Lu et al. 1956; Chen et al. 1957; Peng and Chen 1987; Lin and Li 1990; Niu et al. 1991; Yuan et al. 1994). Previous studies in China described recovery of 20 *Pst* isolates from 17 grass species, including *Aegilops binucialis*, *A. columnaris*, *A.*

crassa, *A. cylindrica*, *A. squarrosa*, *A. tauschii*, *Agropyron* spp. (two), *Elymus chinense*, *E. sibiricus*, *Elytrigia dasystachys*, *El. spicata*, *Glyceria* sp., *Psathyrostachys haushanica*, *Puccinellia distans*, *Roegneria ciliaris* and *Thinopyrum podperae*. Most of these 20 *Pst* isolates belonged to 7 races (CYR17, CYR18, CYR22, CYR24, CYR25, CYR26 and CYR29), the prevalent races at that time (Lu et al. 1956; Peng and Chen 1987; Lin and Li 1990; Yuan et al. 1994). In comparison, there was a low frequency of new races. Totally, only five isolates, Y1 from *E. chinense* (Lu et al. 1956), Y9 and Y10 from two *Agropyron* spp. (Lu et al. 1956), one unnamed isolate from *E. sibiricus* (Lu et al. 1956) as well as W8403 from a *Glyceria* sp. (Peng and Chen 1987), were classified as new races. However, those previous studies as above have not determined the roles of grass hosts in harboring the survival of *Pst* for overwintering and in generating diverse pathogenic races in China. Our study extends these results because uredia derived from several *Pst* grass isolates failed to correspond to any known races. Furthermore, we found that telia-derived *Pst* isolates from grass hosts

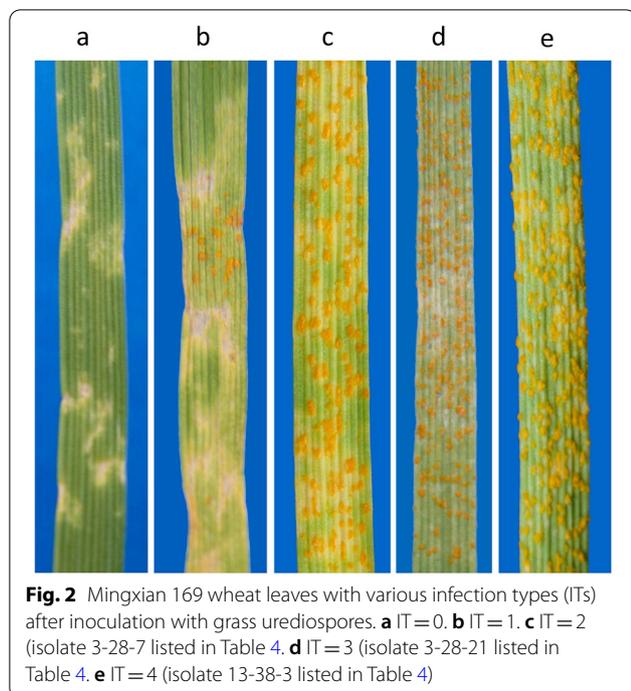


Table 2 Infection types (ITs) of *Puccinia striiformis* f. sp. *tritici* isolates (from grass plants with uredia) on highly susceptible wheat cultivar Mingxian 169

Samples	Low infection types ^a		High infection types		Total
	IT 1	IT 2	IT 3	IT 4	
Number	192	24	21	42	279
Percentage (%)	68.8	8.6	7.5	15.1	100

^a Infection type was determined based on a 0-to-4 scale described by Hungerford and Owens (1923)

included not only known races but also new races. Each of the *Pst* populations from either uredial or telial samples had high levels of phenotypic variation, and mixed reactions of races (with avirulent and virulent reactions) on wheat differential hosts were detected in both populations. Similar mixtures of newly emerged phenotypic races in wheat have subsequently developed into prevalent races due to widespread cultivation of susceptible wheat cultivars (Wan et al. 2002). In the present study, we determined that grass hosts are important for the over-summering survival of *Pst* in Gansu and other over-summering regions with similar environmental conditions in China. Moreover, *Pst* isolates derived from these grasses exhibited highly diversified phenotypes. Likewise, in the United States Cheng et al. (2016) found that grasses harbor more diverse phenotypic and genotypic stripe rust isolates than those on cereal plants. Additionally, the

results of annual race surveillances conducted during 2013–2018 in Gansu (Jia et al. 2018, 2021) showed that, besides a large number of known races, there was a proportion (an average of approximately 10%) of new races among *Pst* isolates, which were unclassified into any known races. It is speculated that grasses probably play a role in generating new races through somatic recombination between formae speciales of *P. striiformis* (Little and Manners 1969). On the other hand, it has been demonstrated that in recent years sexual reproduction of *Pst* on its susceptible alternate host, barberry plants, promotes the emergence of new races distinguished from the parent isolates. However, the main wheat cultivars grown in this region carry resistance genes against wheat stripe rust, which may reduce the occurrence of new races from grasses or barberry. Therefore, based on the identification of new races and known races recovered from uredial and telial samples of grass hosts, we suggest that grass hosts not only harbor *Pst* for over-summering to potentially provide inoculum sources to autumn-sown winter wheat in Gansu and other wheat-growing regions to cause stripe rust infection, but also play an important role in developing race diversity of *Pst* in China.

Grass hosts harbor viable *Pst* teliospores as potential inoculum sources for barberry infection and can be managed for the control of wheat stripe rust

Pst teliospores have very short or no dormancy. Eriksson and Henning (1896) first reported that *Pst* teliospores can germinate and generate basidiospores in both the fall and spring seasons. Raeder and Bever (1931) also found that some *Pst* teliospores can germinate immediately after maturation without a dormant period, and that the remainder could not germinate until the next spring. Both studies hinted that a part of *Pst* teliospores can maintain the germination capacity for a long time till next spring. Therefore, teliospore germination may have two phases, each of which can be affected by environmental conditions (Wellings 2011; Wang and Chen 2015; Chen et al. 2021).

The duration of teliospore viability is affected by various environmental conditions, including sunlight, humidity and temperature. Anikster (1986) found that *Pst* teliospores failed to germinate when kept outdoors for a year and then exposed to sunlight or shade. Wang and Chen (2015) also determined that teliospores preserved their viability for less than one year (from July until May in the following year) under uncontrolled outdoor conditions in the US Pacific Northwest. On the other hand, teliospores could keep the ability to germinate for up to 3 years under low temperature and dry conditions, or for as long as 14 years in airtight, partial vacuum and dry conditions (Anikster 1986).

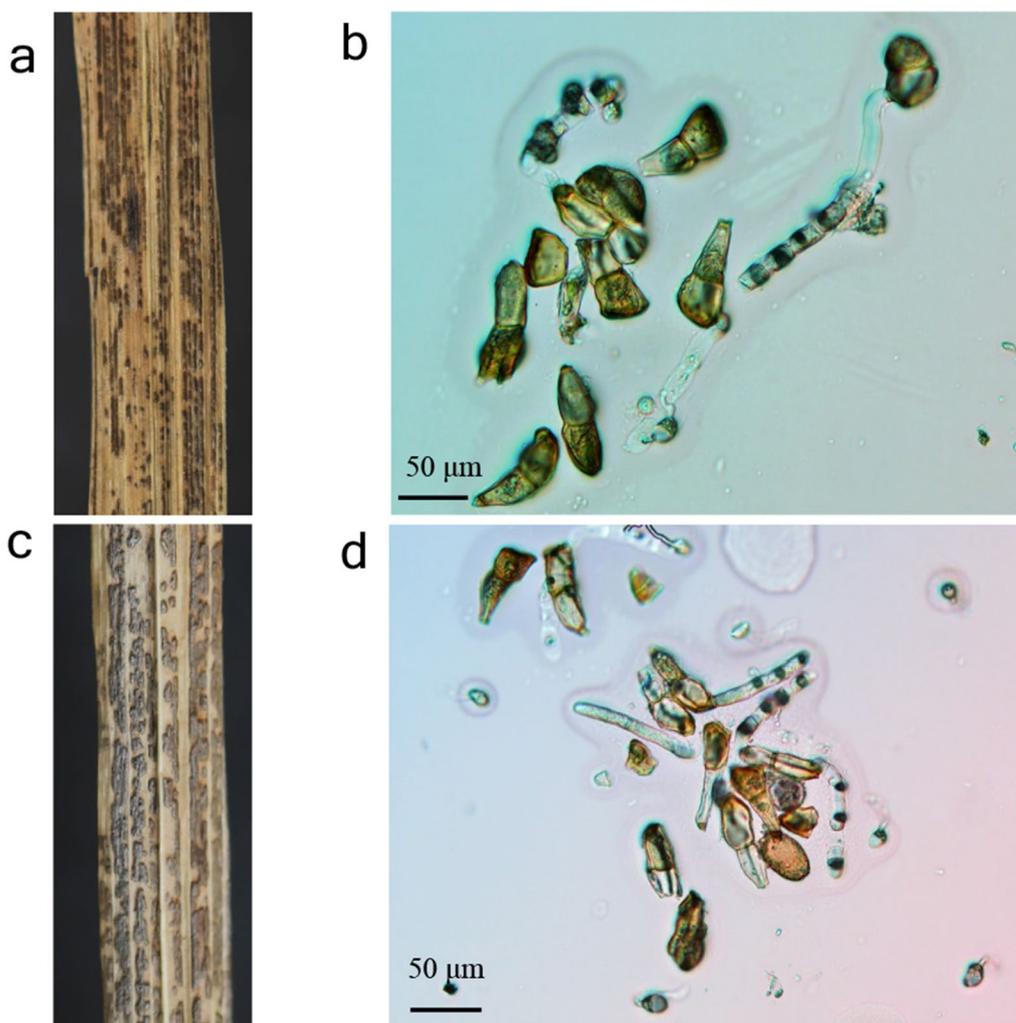
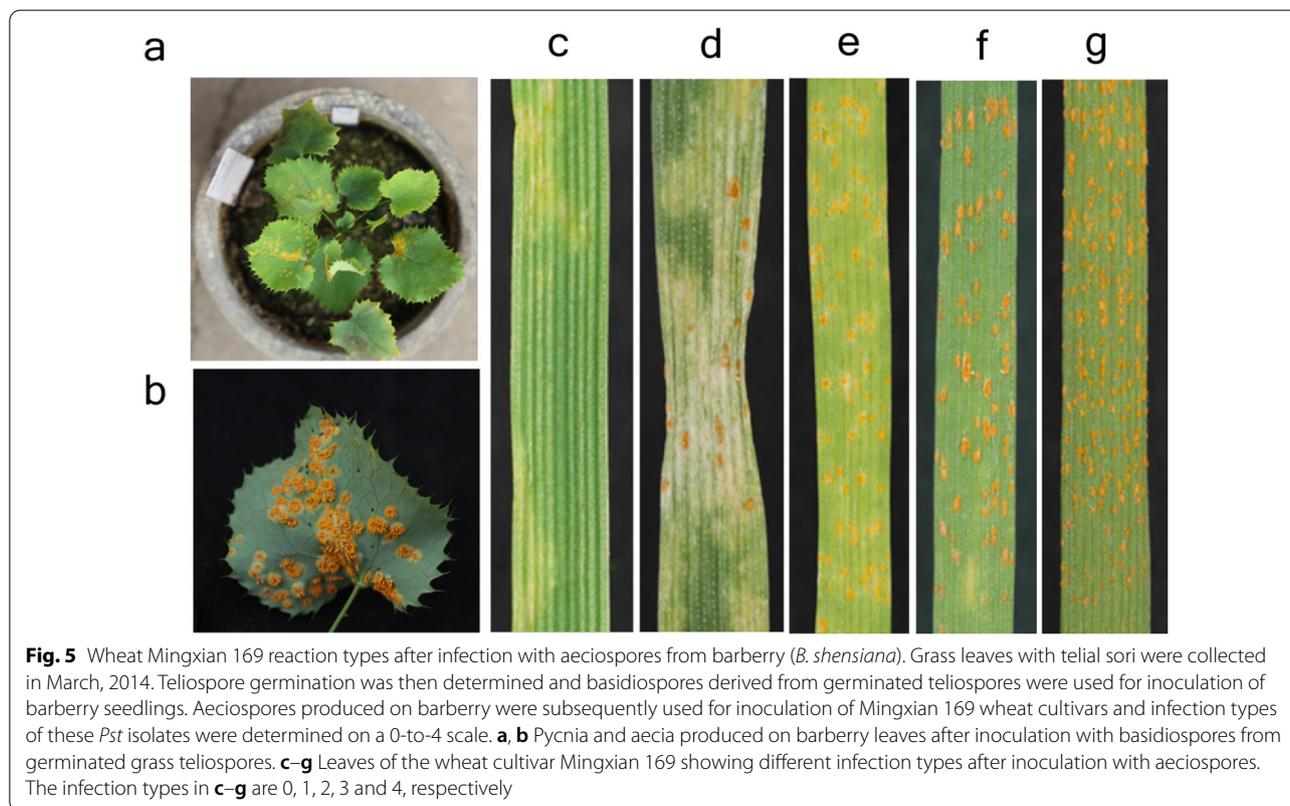
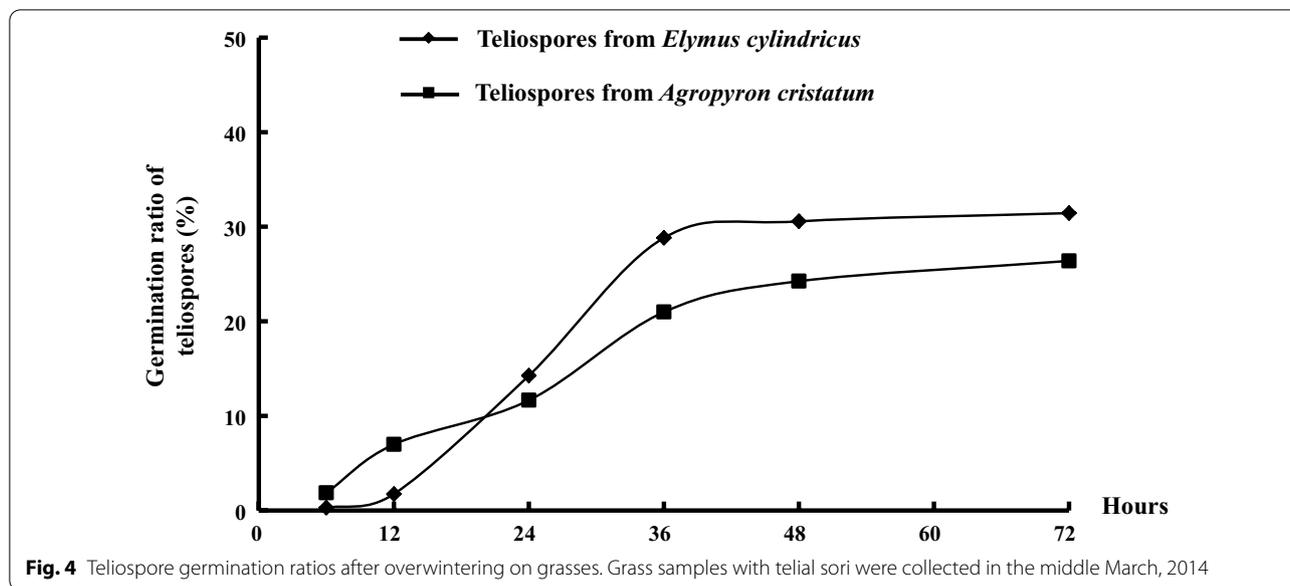


Fig. 3 Microscopic observations of germination of teliospores directly after sampling from leaves of two grass species. The grass plants with uredia were labelled in the autumn, 2013 and collected after overwintering in March, 2014. Observations of teliospore germination were performed with a light microscope. **a** Telial sori on *A. cristatum*. **b** Germination of teliospores from *A. cristatum*. **c** Telial sori on *E. cylindricus*. **d** Germination of teliospores from *E. cylindricus*. There was no significant difference in teliospore germination of telial samples between *A. cristatum* and *E. cylindricus* at the level of 0.05 ($P=0.277$)

Under natural conditions, the survival of *Pst* teliospores varies from one region to another worldwide. In China, in Gansu and other regions similar to Gansu, ecological and climatic conditions as well as cropping system (i.e. traditional agricultural model in some regions of northwestern China) are suitable for maintaining the validity of *Pst* teliospores until next spring. However, teliospore viability does not always overlap with the growth stage of the alternate host barberry, as is the case in the U. S. Pacific Northwest where teliospores usually degrade to inactivation prior to the appearance of new barberry shoots (Wang and Chen 2015). Additionally, another similar case was provided in Sweden where some *Puccinia* spp.,

including *P. graminis* f. sp. *avenae*, *P. graminis* f. sp. *tritici/secalis* and *P. graminis* f. sp. *arrhenatheri*, rather than *Pst* was detected in aecial samples from barberry species, (Berlin et al. 2013). The failure for *Pst* to complete sexual cycle in Sweden is most likely due to the unavailability of vigorous teliospores. Even if viable teliospores are presented, unfavorable climatic conditions for teliospore germination and barberry infection may not trigger initiation of sexual reproduction.

Viable teliospores are essential for initiating *Pst* sexual cycle. Because sexual stage of *Pst* has not been found until recently (Jin et al. 2010), teliospores as inoculum sources commencing sexual reproduction under field conditions



has not been investigated prior to this finding. Over the past decade, we have demonstrated that *Pst* sexual cycle on barberry regularly occurs in oversummering regions under field conditions in China (Zhao et al. 2013; Li et al. 2016; Wang et al. 2016). This fact hinted that in spring

viable *Pst* teliospores could act as inoculum for barberry infection. Our previous study testified that in China teliospore sources, which are responsible for sexual reproduction of the rust, originate from growing wheat plants, diseased wheat straws or debris (Chen et al. 2021). In

Table 3 Infection types (ITs) of *Puccinia striiformis* f. sp. *tritici* isolates recovered from aeciospores on barberry (*Berberis shensiiana*) seedlings

Grass species	Number of				
	Leaf segment	Aecia	Single aecium	Infection types ^a	
				1 and 2	3 and 4
<i>Agropyron cristatum</i>	26	60	227	4	4
<i>Elymus cylindricus</i>	9	339	1485	22	48
Total	35	399	1712	26	52

^a Infection types (ITs) were determined based on a 0-to-4 scale (Hungerford and Owens 1923). ITs 1 and 2 are considered as avirulent; and ITs 3 and 4 are considered as virulent

that study, it mentioned that *Pst* teliospores are produced during all stages of wheat growth in the field in China, and possess the capacity of germination from August to May of the next year. In addition, *Pst* teliospores inside wheat straw stacks after harvesting can survive until the next spring or later (Chen et al. 2021), which enables teliospores to potentially infect barberry young leaves and sometime other young tissues (petiole, thorn and berry). Our study of teliospores now shows that native grasses provide important sources for *Pst* sexual reproduction in spring in Gansu region of China. These results can be used to develop an integrated wheat stripe rust management strategy by combining grass and barberry control to reduce stripe rust genetic variability in the Gansu region, or even other overwintering regions of China.

Conclusions

Our study demonstrates that native grass species can contribute to the survival of *Pst* for overwintering and also provide potential teliospore inoculum for triggering sexual reproduction under natural conditions in China. Determination of production and viability of *Pst* teliospores is vital for understanding teliospore inoculum sources that cause occurrence of *Pst* sexual reproduction and preventing from this process of the rust to decrease the emergence of new *Pst* races that may be able to overcome resistance in established wheat varieties and recently released wheat lines. Therefore, the control of grass hosts and barberry bushes around wheat fields to reduce sexual recombination should be considered for integrated management of wheat stripe rust in China.

Methods

Sample collection

Based on previous studies in China, *Agropyron* and *Elymus* are more susceptible to *Pst* than other genera of gramineous grasses and were suggested as potential inoculum sources for stripe rust epidemics on autumn-sown winter wheat (Lu et al. 1956; Lin and Li 1990; Niu et al.

1991). During field investigations, we found that these two grass genera are widely distributed in the overwintering regions of Gansu and were commonly infected by stripe rust fungi. Thus, we concentrated our efforts on sampling and isolation of the pathogen from these two genera, and collected 864 stripe rust-infected leaf samples (with uredia) at 7 different sampling sites in Tianshui from September to October in 2012, and obtained 1320 stripe rust-infected leaf samples (with uredia) at 14 sites in Pingnan and Tianshui, Gansu from August to October in 2013. Thirty-five leaf samples with telia were collected from *A. cristatum* and *E. cylindricus* in March 2014 at uredial sampling sites labelled in the autumn 2013. Leaf samples were individually put into paper bags, which were dried in air at room temperature and kept in a silica gel desiccator, and then maintained under low temperature (4–5 °C) in a freezer until use.

Plant materials

Barberry (*B. shensiiana* Ahrendt) seeds collected from Xinjie, Baoji, Shaanxi Province were planted and grown as described by Zhao et al. (2013). The Wheat cultivar, Mingxian 169, which is highly susceptible to all known Chinese *Pst* races, and a set of wheat differential hosts consisting of 19 wheat genotypes used to identify *Pst* races were grown in plastic pots in a rust-free growth chamber under the same conditions used to cultivate barberry seedlings.

Inoculation of wheat seedlings with uredial samples from grasses

Individual grass leaves with stripe rust uredia were placed on clean glass slides in a petri dish containing 2–3 layers of wetted filter paper for 1–2 h. A single uredium was then transferred to seedling leaf surfaces of the Mingxian 169 wheat cultivar. The inoculated plants were misted with sterile deionized water, covered with a transparent plastic cylinder and incubated in a dew chamber (E-36L2, Percival, IA, USA) at 10 °C for 24 h in the dark.

Table 4 Avirulent (A) and virulent (V) patterns of uredia-derived 63 *Puccinia striiformis* f. sp. *tritici* (*Pst*) isolates (infection types 3 and 4) on a set of 19 Chinese differential hosts

Isolate	Chinese differential hosts for <i>Pst</i> ^a																			Ph ^b
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
3-28-5	A	V	AV	A	AV	V	A	V	A	A	AV	A	A	V	A	A	A	A	A	Ph1
3-28-8-2	AV	AV	V	A	AV	VA	A	V	A	A	AV	A	A	V	A	A	A	A	A	Ph2
3-28-14-2	AV	V	A	V	V	V	A	V	A	V	A	A	A	V	A	A	A	A	A	Ph3
3-12-2	V	V	V	V	V	VA	A	V	A	VA	AV	A	A	V	A	A	V	A	A	Ph4
3-14-2	V	V	V	V	V	VA	A	V	A	VA	AV	A	A	V	A	A	V	A	A	Ph4
3-28-8	V	V	V	V	V	V	A	V	AV	VA	V	AV	AV	AV	A	VA	V	A	A	Ph5
3-14-1	VA	V	AV	V	V	V	A	V	A	V	AV	A	A	V	A	A	V	A	A	Ph6
3-13-1	VA	V	AV	V	V	V	A	V	A	V	AV	A	A	V	A	A	V	A	A	Ph6
3-28-20-2	A	V	AV	A	A	V	A	V	A	A	A	A	A	A	A	A	A	A	A	Ph7
3-28-11-2	V	V	AV	AV	V	V	A	V	A	V	AV	A	A	V	A	A	A	A	A	Ph8
1-31-1	V	V	V	V	V	V	V	A	V	VA	V	V	VA	V	A	V	V	A	A	Ph9
2-31-1	A	V	A	A	AV	V	VA	A	A	A	A	A	AV	V	A	A	A	A	A	Ph10
4-15-1	V	V	AV	V	V	V	AV	V	A	V	AV	A	A	V	A	AV	AV	A	A	Ph11
4-40-1	A	V	AV	V	V	V	A	V	A	V	A	A	A	V	A	A	AV	A	A	Ph12
2-56-1	VA	V	VA	V	V	V	VA	V	A	V	A	A	A	V	A	A	A	A	A	Ph13
3-28-7	A	V	AV	A	A	V	AV	V	A	A	A	A	A	A	A	A	A	A	A	Ph14
2-57-4	V	V	VA	AV	V	V	A	V	A	V	AV	A	A	V	A	A	A	A	A	Ph15
4-18-4	V	V	V	V	V	V	V	A	V	AV	V	V	VA	V	A	V	V	A	A	Ph16
4-15-2	A	V	AV	A	AV	V	VA	A	A	A	A	A	AV	V	A	A	A	A	A	Ph17
4-18-3	V	V	V	V	V	V	V	AV	VA	V	V	V	V	V	A	V	V	A	A	Ph18
4-18-2	V	V	V	AV	V	V	V	A	V	A	AV	V	V	V	A	V	V	A	A	Ph19
4-18-1	A	V	AV	A	AV	V	V	V	A	A	A	A	A	V	A	V	V	A	A	Ph20
3-12-2-2	V	V	V	V	V	V	V	AV	V	V	V	V	V	V	A	V	V	A	A	Ph21
4-14-1	V	V	V	V	V	V	V	AV	V	V	V	A	V	V	A	V	V	A	A	Ph22
3-30-1	A	V	VA	V	A	V	A	V	A	A	AV	A	A	V	A	A	A	A	A	Ph23
4-22-4	V	V	V	V	V	V	V	V	V	V	A	A	V	V	A	V	V	A	A	Ph24
3-28-31	A	V	A	A	A	A	A	A	A	A	A	A	A	V	A	A	A	A	A	Ph25
3-28-11	A	V	A	A	A	A	A	A	A	A	A	A	A	V	A	A	A	A	A	Ph25
3-28-1	A	V	V	V	A	V	V	A	A	A	A	A	A	V	A	A	A	A	A	Ph26
3-28-18	A	V	A	V	AV	V	VA	A	A	A	A	A	A	V	A	A	A	A	A	Ph27
3-28-28	A	V	A	V	V	V	A	AV	A	A	A	A	V	V	A	A	A	A	A	Ph28
3-28-21	A	V	A	A	A	AV	A	A	A	A	A	A	A	V	A	A	A	A	A	Ph29
3-28-14	A	A	A	A	A	A	A	AV	A	A	A	A	A	V	A	A	A	A	A	Ph30
3-12-4	A	A	A	A	A	A	A	A	A	A	A	A	A	V	A	A	A	A	A	Ph31
3-28-4	A	V	A	AV	A	V	A	AV	A	A	A	A	V	V	A	A	A	A	A	Ph32
3-28-1	A	AV	A	A	A	V	AV	AV	A	V	A	A	AV	V	A	A	A	A	A	Ph33
4-22-1	A	V	V	VA	VA	V	V	V	A	AV	V	A	A	V	A	A	A	A	A	Ph34
2-57-1	A	V	A	VA	A	VA	V	A	A	A	A	A	VA	V	A	A	A	A	A	Ph35
3-28-28-1	A	V	A	A	A	V	A	V	A	A	A	A	A	V	A	A	A	A	A	Ph36
3-28-9	A	V	A	A	A	A	A	V	A	A	A	A	V	V	A	A	A	A	A	Ph37
3-28-2	A	V	A	AV	AV	A	A	V	A	A	A	A	V	A	A	A	A	A	A	Ph38
13-1-7-1	A	A	AV	VA	A	V	A	VA	A	A	A	A	A	V	A	A	A	A	A	Ph39
13-1-6-1	A	A	A	V	A	V	VA	V	A	V	AV	A	A	V	A	A	A	A	A	Ph40
13-3-8-1	A	A	A	V	A	V	VA	V	A	V	AV	A	A	V	A	A	A	A	A	Ph40
13-2-4-2	V	A	V	V	V	V	AV	VA	A	V	A	V	AV	V	A	V	V	A	A	Ph41
13-3-6-4	V	A	VA	AV	A	AV	A	VA	A	A	V	AV	A	V	A	V	AV	AV	A	Ph42
13-3-6-5	V	A	VA	AV	A	AV	A	VA	A	A	V	AV	A	V	A	V	AV	AV	A	Ph42
13-3-8-3	V	V	V	V	V	V	V	V	A	V	V	V	V	VA	A	V	A	A	A	Ph43
13-1-3-3'	V	V	V	V	V	V	V	V	A	V	V	V	V	VA	A	V	A	A	A	Ph43

Table 4 (continued)

Isolate	Chinese differential hosts for <i>Pst</i> ^a																			Ph ^b
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
13-1-3-1	V	V	V	V	V	V	V	V	A	V	V	V	V	V	VA	V	V	A	AV	Ph44
13-3-8-2	V	V	V	V	V	V	V	V	A	V	V	V	V	V	VA	V	V	A	AV	Ph44
13-1-7-1	V	V	V	V	V	V	V	A	A	V	V	A	V	A	A	V	A	A	A	Ph45
13-1-6-1	V	V	V	V	V	V	V	A	A	V	V	A	V	A	A	V	A	A	A	Ph45
13-3-8-1	A	A	A	VA	A	V	V	A	A	VA	AV	A	A	V	A	A	A	A	A	Ph46
13-2-4-2	A	A	A	VA	A	V	V	A	A	VA	AV	A	A	V	A	A	A	A	A	Ph46
13-3-6-4	A	A	AV	V	A	V	A	V	A	V	V	A	A	V	A	AV	A	A	A	Ph47
13-3-6-5	A	A	AV	V	A	V	A	V	A	V	V	A	A	V	A	AV	A	A	A	Ph47
13-3-8-3	V	V	V	V	V	V	V	A	A	V	V	V	V	V	V	V	V	A	V	Ph48
13-1-3-4	V	V	V	V	V	V	V	A	A	V	V	V	V	V	V	V	V	A	V	Ph48
13-1-3-1	A	A	AV	VA	A	V	A	AV	A	A	A	A	A	V	A	A	A	A	A	Ph49
13-3-8-2	V	A	V	V	V	V	V	VA	A	V	A	V	AV	V	A	V	V	A	A	Ph50
13-1-3-3	V	AV	A	V	A	V	V	AV	A	V	V	V	A	V	V	V	A	A	A	Ph51
13-3-6-2	V	V	V	V	V	V	V	VA	A	V	V	V	V	V	A	V	A	A	A	Ph52

The 63 *Pst* isolates were recovered from stripe rust-infected grass samples (with uredia) collected in autumns of 2012 and 2013

^a The Chinese differential hosts: 1 = Trigo Eureka (*Yr6*), 2 = Fulhard (Unknown), 3 = Lutescenes 128 (Unknown), 4 = Mentana (*YrMen1*, *YrMen2*, *YrMen3*), 5 = Virgilio (*YrVir1*, *YrVir2*), 6 = Abbondanza (*YrAbb1*, *YrAbb2*), 7 = Early Piemium (Unknown), 8 = Funo (*YrA*, +), 9 = Danish 1 (*Yr3*), 10 = Jubilejina II (*YrJu1*, *YrJu2*, *YrJu3*, *YrJu4*), 11 = Fengchan 3 (*Yr1*, *YrFc1*, *YrFc2*), 12 = Lovrin 13 (*Yr9*, +), 13 = Kangyin 655 (*Yr1*, *YrKy1*, *YrKy2*), 14 = Suwon 11 (*YrSu*), 15 = Zhong 4 (Unknown), 16 = Lovrin 10 (*Yr9*), 17 = Hybrid 46 (*Yr3b*, *Yr4b*, *YrH46*), 18 = *Triticum spelta* var. *album* (*Yr5*), 19 = Guinong 22 (*Yr24*, = *Yr26*). Infection type data were scored based on a 0-to-4 scale (Hungerford and Owens 1923). A = Avirulent (infection types 0 to 2), V = Virulent (infection types 3 to 4), and AV/VA = Mixed infection types

^b Ph = Phenotype. Phenotype was used to determine types and virulence diversity of new races

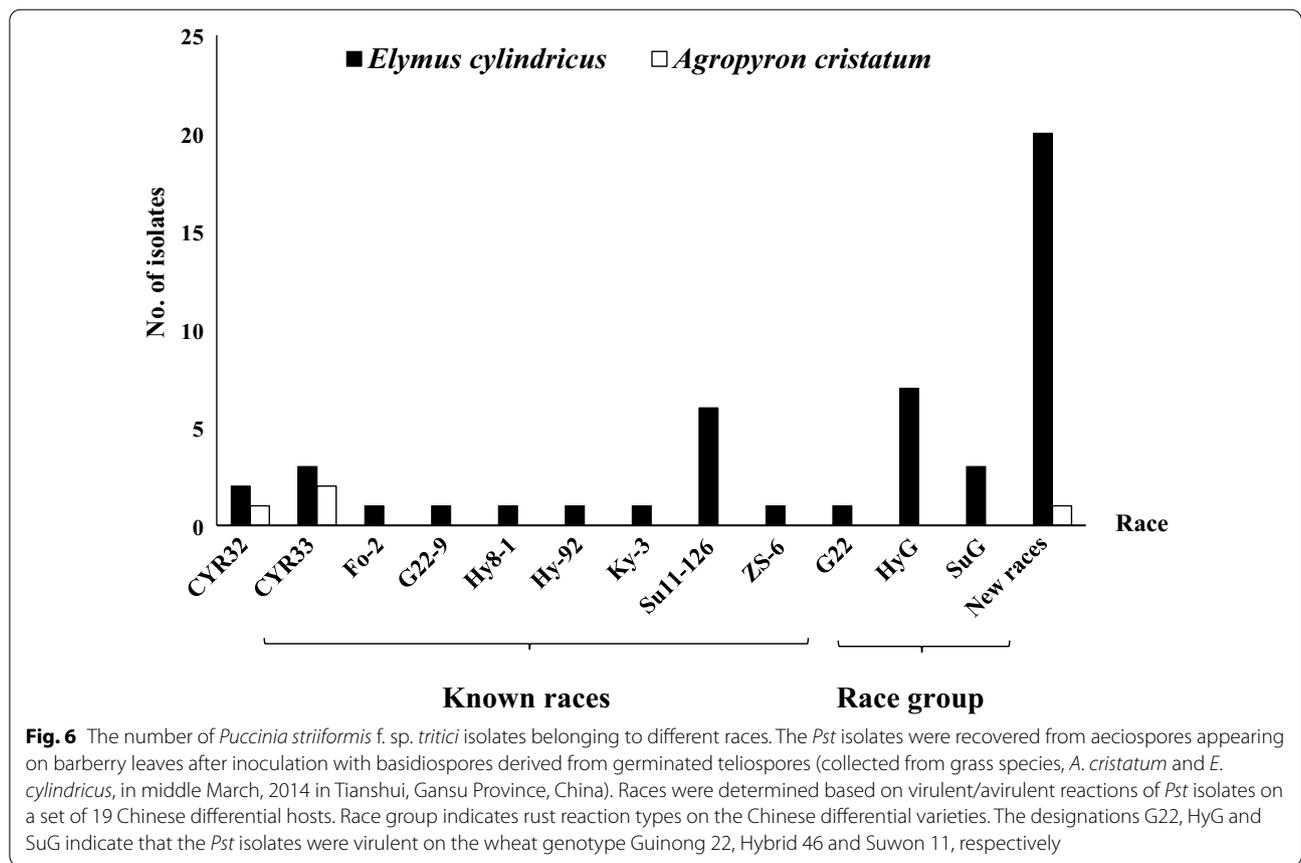


Fig. 6 The number of *Puccinia striiformis* f. sp. *tritici* isolates belonging to different races. The *Pst* isolates were recovered from aeciospores appearing on barberry leaves after inoculation with basidiospores derived from germinated teliospores (collected from grass species, *A. cristatum* and *E. cylindricus*, in middle March, 2014 in Tianshui, Gansu Province, China). Races were determined based on virulent/avirulent reactions of *Pst* isolates on a set of 19 Chinese differential hosts. Race group indicates rust reaction types on the Chinese differential varieties. The designations G22, HyG and SuG indicate that the *Pst* isolates were virulent on the wheat genotype Guinong 22, Hybrid 46 and Suwon 11, respectively

Table 5 Avirulence (A) /virulence (V) patterns of telia-derived *Puccinia striiformis* f. sp. *tritici* (Pst) isolates (infection types 3 and 4) based on a set of 19 Chinese differential hosts

No.	Avirulence and virulence on the Chinese differential hosts for Pst ^a																			Race	Type		
	Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18			19	20
<i>Agropyron</i>																							
B-I-4-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	A	V	V	A	A	V	CYR32	Known race
B-I-2	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	A	A	A	V	CYR33	Known race
B-I-1-7	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	A	A	A	V	CYR33	Known race
B-A-1-2	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	/	New race
<i>Elymus</i>																							
P-D-10-8	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	CYR32	Known race
P-M-3-3	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	CYR32	Known race
P-I-14-9	A	V	A	V	A	A	A	V	A	A	A	A	A	A	A	A	A	A	A	A	V	Fo-2	Known race
P-C-8-2	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	G22-9	Known race
P-H-21-3	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Hy8-1	Known race
P-H-15-3	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Hy-92	Known race
P-E-15-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Ky-3	Known race
P-D-2-2	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-C-1-7	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-K-59	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-K-6-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-C-12-3	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-L-8-2	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-A-13-2	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-A-13-6	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Su11-126	Known race
P-K-75	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	CYR33	Known race
P-G-18-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	CYR33	Known race
P-H-12-7	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	CYR33	Known race
P-K-78	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	Z5-6	Known race
P-J-26-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	G22 ^b	New race
P-K-73	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG ^c	New race
P-H-13-4	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG	New race
P-D-6-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG	New race
P-H-13-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG	New race
P-H-22-1	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG	New race
P-G-10-1	V	A	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	HyG	New race
P-D-7-14	V	V	A	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	SuG ^d	New race
P-K-10	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	SuG	New race

Table 5 (continued)

No.	Avirulence and virulence on the Chinese differential hosts for <i>Pst</i> ^a																				Race	Type
	Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
P-K-56	<i>E. cylindricus</i>	VA	VA	VA	A	VA	A	A	A	VA	A	A	VA	VA	A	A	VA	VA	A	A	V	New race
P-K-58	<i>E. cylindricus</i>	V	VA	A	A	A	A	VA	A	A	A	A	A	VA	A	A	A	VA	A	A	V	New race
P-A-13-4	<i>E. cylindricus</i>	V	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-B-8-2	<i>E. cylindricus</i>	AV	AV	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-K-55	<i>E. cylindricus</i>	A	A	A	A	A	A	A	V	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-K-24	<i>E. cylindricus</i>	A	A	A	A	A	A	AV	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-J-38	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-C-16-3	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-K-35	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-K-1-3	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-G-31-1	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-C-12-4	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-D-2-4	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-L-6-22	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-L-3-2	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-C-10-17	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	New race
P-L-10-1	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	V	A	A	A	A	A	A	A	A	A	A	New race
P-H-24-3	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	New race
P-M-12-3	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	New race
P-M-1-2	<i>E. cylindricus</i>	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	New race

The *Pst* isolates were from single aecial cups produced on barberry (*Berberis shensiiana*) after inoculation with basidiospores derived from germinated teliospores. The teliospores were collected from infected grass leaves in middle March, 2014

^aThe Chinese differential host set genotypes: 1 = Trigo Eureka (Yr6), 2 = Fulhard (Unknown), 3 = Lutescens 128 (Unknown), 4 = Mentana (YrMen1, YrMen2, YrMen3), 5 = Virgilio (YrVir1, YrVir2), 6 = Abbondanza (YrAbb1, YrAbb2), 7 = Early Piemium (Unknown), 8 = Funo (YrA, +), 9 = Danish 1 (Yr3), 10 = Jubilejina 2 (YrJul1, YrJul2, YrJul3, YrJul4), 11 = Fengchan 3 (Yr1, YrFc1, YrFc2), 12 = Lovrin 13 (Yr9, +), 13 = Kangyin 655 (Yr1, YrKy1, YrKy2), 14 = Suwon 11 (YrSu), 15 = Zhong 4 (Unknown), 16 = Lovrin 10 (Yr9), 17 = Hybrid 46 (Yr3b, Yr4b, YrH46), 18 = *Triticum spelta* var. album (Yr5), 19 = Guinong 22 (Yr24, = Yr26), 20 = Mingxian 169, used as a susceptible check. A = Avirulence (infection types 0 to 2), V = Virulence (infection types 3 to 4), and AV/VA = Mixed infection types

^{b,c,d} G22, HyG and SuG indicate three different races virulent to wheat genotypes Guinong 22, Hybrid 46 and Suwon 11, respectively. "/" indicates that isolates are not virulent to any of major genotypes (Guinong 22, Hybrid 46 and Suwon 11)

After incubation, the plants were placed in a controlled growth chamber with a photoperiod of 16 h light at 16 °C and 8 h dark at 13 °C. Infection types (ITs) were recorded 18–20 days post-inoculation based on a scale of 0–4 (Hungerford and Owens 1923). This scale is: ITs 0=healthy appearance without necrotic and chlorotic foci. ITs 1–2 necrotic to chlorotic foci without uredia. IT 3=small chlorotic foci containing small amounts of urediospores. IT 4=foci with abundant urediospores surrounded by bright green tissue islands. Isolates with IT 3 or 4 reactions on Mingxian 169 wheat were used for virulence tests.

Inoculation of barberry seedlings with teliospores from telial samples of grasses

Grass plants with stripe rust uredia were labelled at collection sites in the previous autumn, from which telial samples were collected after overwintering, and the germination of teliospores was evaluated during the following spring by inoculation of barberry seedlings. Grass leaf samples with telia were cut into 5-cm-long segments and soaked in sterile deionized water at room temperature for 24 h. The leaf segments were put onto a clean glass slide to abraded until telia were broken to expose teliospores, after which the segments were placed onto 2% (m/v) water agar plates and incubated at 16 °C in a condition-controlled growth chamber. After the teliospores began to germinate, the leaf segments were used to inoculate barberry seedlings as described by Zhao et al. (2013). After inoculation, the barberry plants were incubated for 3–4 d days at 16 °C and then were transferred to a condition-controlled growth chamber under the same conditions mentioned above until pycnial nectar appeared. Pycnial fertilization was conducted by transferring nectars from one pycnium to another with a clean plastic inoculation loop. Individual emerging aecia were excised, placed on a clean glass slide disinfected with 75% ethanol solution, and broken to expose aeciospores by gentle pressure with a clean scalpel. The aeciospores were then suspended in 50 µL of sterile deionized water and misted onto seedlings of wheat cultivar Mingxian 169.

Virulence tests on differential hosts

To characterize avirulence and virulence responses of *Pst* isolates recovered from the grass telial samples, uredia of ITs 3 and 4 were inoculated to Mingxian 169 seedlings and evaluated for avirulence and virulence patterns on a set of 19 Chinese differential host genotypes as described by Zhao et al. (2013). Mingxian 169 was used as a susceptible control in all tests. The scale of 0 to 4 described by Hungerford and Owens (1923) was used to score infection types on the differential varieties. ITs 0 to 2 were considered to be avirulent, and ITs 3 and 4 were designated as virulent.

Abbreviations

Pst: *Puccinia striiformis* f. sp. *tritici*; IT: Infection type; Ph: Phenotype.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42483-022-00129-x>.

Additional file 1. Figure S1: Timeline skeleton illustrating growing and harvesting periods of winter wheat in Tianshui, Gansu, China.

Authors' contributions

JZ, ZK and JQ conceived and designed the project and wrote the manuscript. JQ, ZW and YL performed the experiments. JZ, JQ and ZW wrote and modified the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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