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RESEARCH ARTICLE

Identification of eight *Berberis* species from the Yunnan-Guizhou plateau as aecial hosts for *Puccinia striiformis* f. sp. *tritici*, the wheat stripe rust pathogen

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Abstract

Puccinia striiformis Westend. f. sp. *tritici* Erikss. (*Pst*) infects wheat and causes stripe rust. The rust is heteroecious with wheat as the primary uredinial and telial host and barberry (*Berberis* spp.) as the alternate pycnial and aecial host. More than 40 *Berberis* species have been identified to be alternate hosts for *Pst*, and most of these are Chinese *Berberis* species. However, little is known about *Berberis* species or their geographic distributions in the Yunnan-Guizhou plateau in southwestern China. The Yunnan-Guizhou plateau is considered to be an important and relatively independent region for evolution of the wheat stripe rust pathogen in China because the entire disease cycle can be completed within the region. In this study, we conducted a survey of barberry plants in the Yunnan-Guizhou plateau and identified the eight *Pst*-susceptible *Berberis* species under controlled conditions, including *B. julianae*, *B. tsienii*, *B. veitchii*, *B. wilsonae*, *B. wilsonae* var. *guhtzunica*, *B. franchetiana*, *B. lepidifolia* and *B. pruinosa*. These species were reported for the first time to serve as alternate hosts under controlled conditions for the wheat stripe rust pathogen.

Keywords: *Berberis* spp., alternate host, *Puccinia striiformis* f. sp. *tritici*, sexual reproduction, stripe rust, wheat, yellow rust

1. Introduction

Puccinia striiformis Westend. f. sp. *tritici* Erikss. (*Pst*) causes stripe rust (yellow rust) of wheat. *Pst* is a heteroecious rust fungus that infects wheat (*Triticum* spp.) as a primary host and barberry (*Berberis* spp.) and *Mahonia* as alternate hosts to complete the macrocyclic life cycle (Jin *et al*. 2010; Wang and Chen 2013; Zhao *et al*. 2013). Wheat stripe rust is a destructive disease threatening wheat productions in the wheat-growing regions throughout the world (Chen 2005; Wan *et al*. 2007; Ali *et al*. 2009; Hovmøller *et al*. 2010; Wellings 2011).

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China is the largest epidemic region of wheat stripe rust in the world. The Chinese epidemic region of the disease is subdivided into three zones consisting of the North-Northwest epidemic zone, Xinjiang epidemic zone and Southwest epidemic zone (Li and Zeng 2002). As an important region of the Southwest epidemic zone, the Yunnan-Guizhou plateau is a low-latitude highland located in the Southwest of China where wheat is grown in multiple seasons and wheat growth stages are overlapping in seasons around the year due to the mild local weather conditions. In this region, wheat stripe rust is an important factor affecting local wheat production and has caused massive yield losses in the past decades. Urediniospores produced in this region also contribute to stripe rust epidemics in other regions (Li and Zeng 2002; Zuo *et al*. 2009). The annual average area of infected wheat in Yunnan province reached 200 000 hectares from 1979–2003 (Lv *et al*. 2004; Li 2013), accounting for one third of the wheat growing area. In this region, *Pst* caused five large-scale epidemics from the 1960s to the 1980s, and the frequency of epidemics has increased since the late 1990s (Li 2004). Nine epidemics have been reported from 2001 to 2009 in this region, and in 2002, up to 50% of the planting wheat area was seriously infected (Li 2013). Similarly, Guizhou Province is also an important region with frequent wheat stripe rust occurrence. In 2017, wheat stripe rust affected 64 300 hectares, accounting for approximately 14% of the annual area of growing wheat (Huang *et al*. 2018).

China has more than 250 *Berberis* species, accounting for more than half of the number of species reported in the world (http://foc.iplant.cn/content.aspx?TaxonID=103816). The Yunnan-Guizhou plateau has nearly one hundred *Berberis* species. To date, the geographic distribution of *Berberis* species that can be alternate hosts for *Pst* in this region is largely unknown. Only ten *Berberis* species, including *B. ferdinandi-coburgii*, *B. phanera*, *B. aggregata* var. *integrifolia*, *B. davidii*, *B. wangii*, *B. platyphylla*, *B. jamesiana*, *B. vernalis*, *B. coryi*, and *B. guizhouensis*, have been reported to surveyed at four investigated sites in Yunnan and Guizhou provinces. Nine of which, the former nine *Berberis* species, were collected from three investigated sites in Yunnan, and the latter one from merely one investigated site in Guizhou. Eight of those *Berberis* species were identified as alternate hosts for *Pst*. Two *Berberis* species native to Yunnan, *B. vernalis* and *B. coryi*, showed highly resistant to *Pst* due to observations of no sign after triple inoculation tests using *Pst* basidiospores (Zhao *et al*. 2013). However, the lack of knowledge concerning additional *Berberis* species in major wheat production regions of the Yunnan-Guizhou plateau limits the understanding of potential roles of *Berberis* species as alternate hosts for *Pst* and their geographic distribution in this region. Therefore, the objective of this study was to determine the geographic distribution of *Berberis* spp. in the region and their susceptibility to *Pst*.

2. Materials and methods

2.1. Field surveys and collection of *Berberis* species

Field surveys of *Berberis* species were conducted in the flowering period (April-June) and the berry period (August-October) in Yunnan and Guizhou provinces in 2016 and 2018. During the surveys, information on latitude, longitude and elevation were recorded using GPSmap (60CSx, Garmin, USA). Leaves, flowers and berries or young plants of each *Berberis* sample were photographed and collected for identifying to species. The number of bushes for each *Berberis* species in an area of 0.5 km radius was visually estimated. *Berberis* species collected from the Yunnan-Guizhou region were identified by comparing with recorded species in genus *Berberis* using the Chinese botanical monograph *Flora of China* (e-version website: http://foc.iplant.cn/) based on the morphological characteristics of the leaves, flowers, and fruits.

2.2. Cultivation of barberry plants

Young plants of *Berberis* species without observed berries during the field surveys were transplanted in pots filled with potting mix (Inner Mongolia Mengfei Biotech Co., Ltd., Huhhot, Inner Mongolia, China). All plants were grown in a greenhouse at 20°C to 25°C with a routine 16-h light/8-h dark diurnal cycle. The light intensity was supplemented to 8 000 to 10 000 lux with high-voltage sodium lamps. After growing 2–3 new leaves, the barberry plants were inoculated with *Pst* basidiospores produced from germinated teliospores to test for susceptibility as described below.

For the *Berberis* species with berries collected during the surveys, the berries were peeled off to obtain seeds. The seeds were cleaned using tap water, placed on three layers of filter paper in a Petri dish, covered with a filter paper to prevent from floating on the surface of water and soaked over night in de-ionized water. After seeds fully absorbed water, water was discarded, and the Petri dish was moved to a growth chamber at 16°C to 20°C with a photoperiod of 16 h light/8 h dark until seeds germinated. When the first true leaves appeared, the barberry seedlings were transplanted into pots filled with potting mix and moved into the greenhouse with the same conditions as mentioned above. Four- to six-leaf barberry seedlings were used for inoculation.

2.3. Collection of wheat tissues bearing teliospores and growing wheat plants

Green wheat leaves containing *Pst* telia were collected from Yunnan Province and dried at room temperature for 2–3 days. The leaf tissues were put inside a plastic zip bag with blue silica gel (HG/t2765.4-2005, Qingdao Haiyang Chemical Co., Ltd., China) before sealing. The bag was placed in a desiccator and stored at 4°C for later use. About 10 seeds of wheat cultivar Mingxian 169, which is highly susceptible to known Chinese *Pst* races, were planted in a small plastic pot (7 cm×7 cm×8 cm) filled with potting mix. Pots were put in a plastic tray filled with water for subirrigation and kept in rust-free growth chamber under the same conditions mentioned above for growing barberry plants.

2.4. Tests of *Berberis* spp. for *Pst* susceptibility

Teliospore germination and barberry plant inoculations were carried out according to the method described by Zhao *et al*. (2013). The barberry plants were inoculated using basidiospores developed from germinated teliospores, incubated in a dew chamber (I-36DL, Percival, USA) at 100% relative humidity (RH) for 3-4 days at 16°C in an alternative condition of 16 h light/ 8 h dark prior to moving to a growth chamber. The inoculated plants were transferred to a growth chamber with a photoperiod of 16 h light/8 h dark at (13±3)°C. When pycnia at infected sites oozed visible liquid nectar (containing pycniospores) from ostioles (pycnial openings), fertilization was conducted by transferring nectar of one pycnium to another using a clean detached leaf segment of wheat. After the nectar transfers, the barberry plants were covered for 2 days with a transparent plastic cylinder made by rolling an A4-sized plastic film (0.2 mm thick, Deli Group Co., Ltd., Zhejiang, China) for continuous production of the nectar to ensure completion of fertilization, and then the plastic cover was removed from the barberry plants. The plants were observed for aecial formation on the abaxial surface of the inoculated barberry leaves.

2.5. Inoculation of wheat plants with aeciospores

Aecial cups containing aeciospores were excised from inoculated leaves of *Berberis* plants using a scalpel, put onto a clean glass slide, and crushed gently with the scalpel to release aeciospores. Aeciospore suspensions were made by mixing with one or two drops of deionized water (approx. 50–100 μL). Each suspension was transferred onto wheat leaves (cv. Mingxian 169) using a hand-made metal inoculation tool with a flat end. The inoculated plants were moved into a dew chamber with 100% RH at 10°C in the dark for 24 to 36 h. After incubation, the plants were transferred to a growth chamber under the same conditions as mentioned above for the growth of barberry plants. At 18 to 20 days post inoculation, uredinial sporulation on the inoculated wheat leaves was observed and recorded.

3. Results

3.1. Distribution and species of *Berberis* in the Yunnan-Guizhou plateau

A total of 49 sites in the Yunnan and Guizhou provinces were investigated for species and distribution of barberry plants (Appendix A). Barberry plants were found at 43 sites and commonly grown on hillsides adjacent to crop fields including wheat fields. Of 14 sites investigated in Guizhou, 13 (93%) had barberry bushes. In Yunnan, 30 of 35 investigated sites (86%) had barberry plants. Eight *Berberis* species were identified and collected in both provinces (Table 1). In Guizhou, five of these *Berberis* species, including *B. julianae*, *B. tsienii*, *B. veitchii*, *B. wilsonae* and *B. wilsonae* var. *guhtzunica*, were found (Fig. 1), and *B. wilsonae* var. *guhtzunica* was the most widespread in this region (Fig. 2; Appendix A). In Yunnan, five *Berberis* species, *B. julianae*,

Table 1 Ten *Berberis* species distributed in Yunnan and Guizhou provinces, China based on field investigations in 2016 and 2018

Berberis species	Investigation site
	Guizhou Province
B. julianae	Shuichao Village, Hezhang County, Bijie City
B. tsienii	Haiga Village, Dawan Town, Shuicheng County, Liupanshui City
B. veitchii	Guji Village, Hezhang County, Bijie City
B. wilsonae	Haiga Village, Dawan Town, Shuicheng County, Liupanshui City
B. wilsonae var. *guhtzunica*	Dayi Village, Hezhang County, Bijie City
	Yunnan Province
B. franchetiana	Qingdong Village, Xizhou Town, Eryuan County, Dali City
B. julianae	Donghua Town, Lufeng County, Chuxiong City
B. lepidifolia	Heilongtan Park, Lijiang City
B. pruinosa	Ayoupu Village, Luliang County, Qujing City
B. wilsonae	Qingdong Village, Xizhou Town, Eryuan County, Dali City

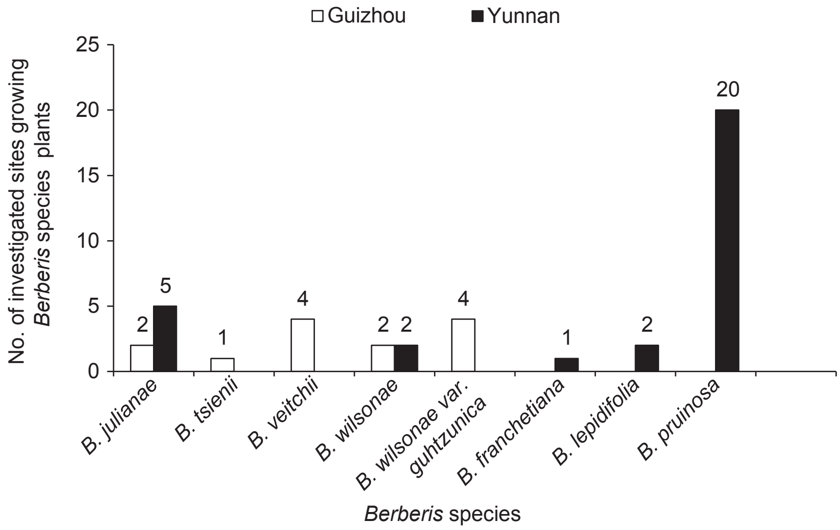

Fig. 1 The number of investigated sites growing *Berberis* species bushes in the Yunnan-Guizhou plateau, China.

B. *wilsonae*, *B*. *franchetiana*, *B*. *lepidifolia* and *B*. *pruinosa*, were identified (Fig. 1), and *B*. *pruinosa* was the most widely distributed species (Fig. 3; Appendix A). Two species, *B*. *wilsonae* and *B*. *julianae*, were observed in both provinces (Table 1).

3.2. Susceptibility of *Berberis* species to *Pst*

After inoculation with *Pst* basidiospores developed from teliospores collected from wheat, all eight *Berberis* species collected from Yunnan and Guizhou were susceptible to *Pst*. The inoculated barberry plants produced obvious pycnia on the adaxial surface of leaves 9 to 11 days after inoculation (Fig. 4-A1–H1). Aecia (aecial cups) were observed on the adaxial surface of leaves 16 to 20 days post inoculation (Fig. 4-A2–H2). Various lengths and numbers of aecial cups were observed on the tested *Berberis* species (Fig. 4-A3–H3). After inoculation with aeciospores collected from each of all eight *Berberis* species, respectively, uredinia produced on the surface of leaves of Mingxian 169 wheat seedlings (Fig. 4-A4–H4). The results indicated that the eight tested *Berberis* species, *B*. *julianae*, *B*. *tsienii*, *B*. *veitchii*, *B*. *wilsonae*, *B*. *wilsonae* var. *guhtzunica*, *B*. *franchetiana*, *B*. *lepidifolia*, and *B*. *pruinosa* (Table 1), were susceptible to *Pst* and serve as alternate hosts for *Pst* under controlled conditions.

4. Discussion

Identification of *Berberis* species for susceptibility to *Pst* is the first step to determine if alternate hosts play any role in the pathogen variation and contributing to stripe rust epidemics in the wheat crop. Since the discovery that barberry species can serve as alternate hosts for *Pst* (Jin *et al*. 2010), 45 *Berberis* species collected from different countries, including the U.S. (Jin *et al*. 2010), China (Zhao *et al*. 2013, 2016; Du *et al*. 2019; Zhuang *et al*. 2019), and Pakistan (Mehmood *et al*. 2019), have been reported to be susceptible to *Pst*. In the present study, the eight *Berberis* species, *B*. *julianae*, *B*. *tsienii*, *B*. *veitchii*, *B*. *wilsonae*, *B*. *wilsonae* var. *guhtzunica*, *B*. *franchetiana*, *B*. *lepidifolia* and *B*. *pruinosa*, collected from the Yunnan-Guizhou

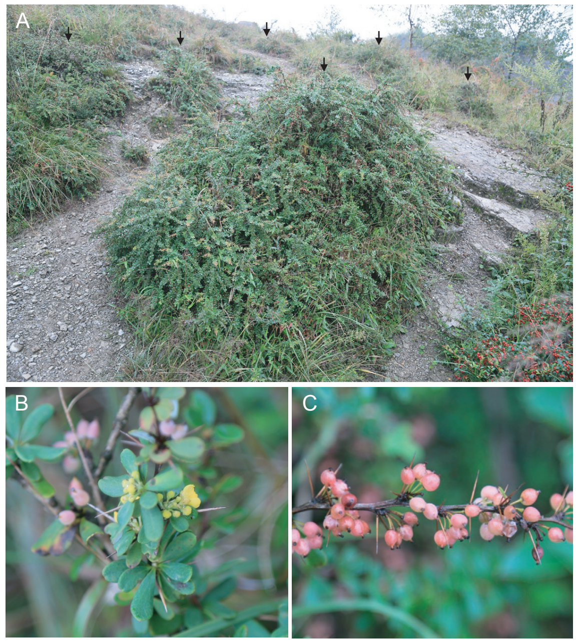

Fig. 2 Bushes of *Berberis wilsonae* var. *guhtzunica* growing near Shabao Town, Nayong County, Guizhou Province , China observed in October, 2018. A, bushes (indicated by black solid arrows). B, shoots with flowers. C, berries.

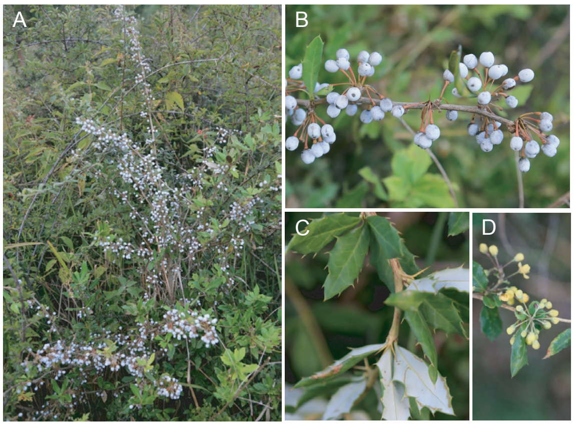

Fig. 3 A typical example of *Berberis* species (*B. pruinosa*) naturally growing and widely distributed in Yunnan Province, China. A, barberry bushes. B, berries covered with waxy bloom. C, the adaxial surface and abaxial side of leaves. D, inflorescence.

plateau, were reported here for the first time and added to the list of susceptible *Berberis* species that have been reported previously.

Wheat stripe rust is a major disease in the Yunnan-Guizhou plateau. The disease has occurred seriously in the past several decades since 1940s in this area, especially Yunnan where *Pst* is apt to generate genetic variation and produce various virulent races (Li 2013). However, whether epidemics of wheat stripe rust are related to the presence of susceptible barberry plants is unknown. The present study and a previous study (Zhao *et al*. 2013) identified 17 *Berberis* species susceptible to *Pst* in this region. Natural rust infections on plants of barberry species, *B. pruinosa* in Yunnan and *B. wilsonae* var. *guhtzunica* in Guizhou, were observed in early spring in 2016 based on our field surveys. However, we failed to obtain *Pst* isolate from aeciospores produced on naturally infected *Berberis* plant tissues. So far, no evidence has been showed that the presence of widespread susceptible barberry plants is associated with epidemics of wheat stripe rust and the high genetic diversity in the Yunnan-Guizhou plateau.

Appropriate temperatures and continual high relative humidity are very important for teliospore germination of *Pst*. It had been reported that teliospore germination of *Pst* can commence at a wide temperature range of 5–22°C under laboratory conditions (Wang and Chen 2015). The Yunnan-Guizhou plateau is located in southwestern part of China and also mountainous in which weather conditions is mild of cool temperature in summer and warm in winter. Average temperature is ranged from 19–22°C in Yunnan and 22–25°C in Guizhou in July that is the hottest month and 6–8°C in Yunnan and 3–6°C in Guizhou in January that is the coldest month, respectively. Thus, temperatures in the most

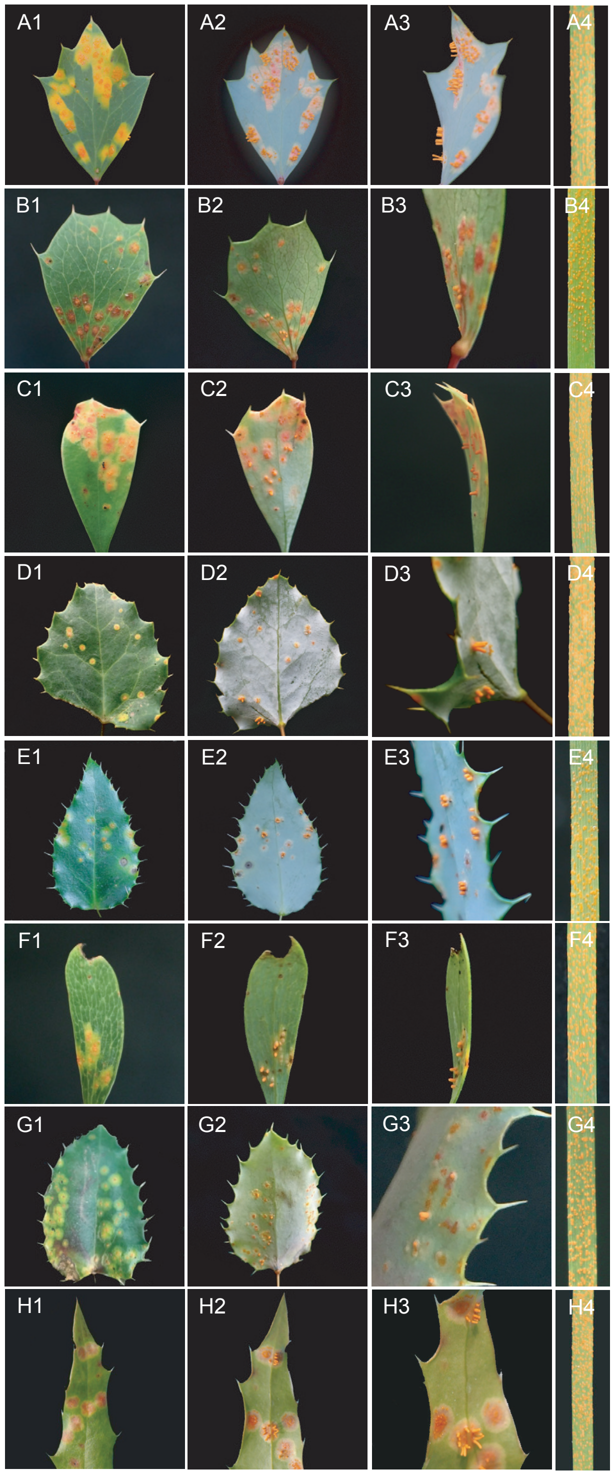

Fig. 4 Evidence of *Pst* susceptibility for the eight *Berberis* species collected from Yunnan and Guizhou provinces, China. A, *B. wilsonae*. B, *B. wilsonae* var. *guhtzunica*. C, *B. lepidifolia*. D, *B. pruinosa*. E, *B. veitchii*. F, *B. franchetiana*. G, *B. tsienii*. H, *B. julianae*. 1, pycnial stage; 2, aecial stage; 3,side of aecial cups; 4, uredinia on wheat *cv*. Mingxian 169.

months in the Yunnan-Guizhou are suitable for teliospore germination. Based on our tests in laboratory, *Pst* teliospore can germinate at lower than 5°C and beyond 22°C but a low germination rate (data not shown). The Yunnan-Guizhou plateau belongs to subtropical humid zone and has a plenty of rainfall all the round year, especially April to November, providing a long term of humid climatic condition.

Overlap of vital teliospores and regrowth of young tissues of barberry bushes (mainly young leaves) are necessary for occurrence of *Pst* sexual reproduction under natural conditions. According to previous study by Zhao *et al*. (2013) and the present study, many of *Berberis* species distributed in the Yunnan-Guizhou plateau were known to serve as alternate hosts for *Pst* and are deciduous or evergreen, which are widely spread in the Yunnan-Guizhou plateau. Based on our field investigations in this region in recent years, regrowth of young shoots on either deciduous *Berberis* species or evergreen ones in early spring and evergreen *Berberis* species in autumn is quite common in this region. Moreover, teliospore formation in wheat field in the Yunnan-Guizhou plateau can be observed easily in early February and teliospores were of germinability (data not shown). Thus, overlapping of vital teliospores and regrowth of young leaves of barberry is presented, which is potentially possible for causing occurrence of sexual reproduction of *Pst*.

Widespread of susceptible *Berberis* species and routine occurrence of *Pst* sexual reproduction under natural conditions has been demonstrated to contribute to generation of new races and high genetic diversity of *Pst* population in some regions of China, including southern Gansu as a hot-spot for *Pst* (Duan *et al*. 2010; Mboup *et al*. 2010; Zhao *et al*. 2013; Li *et al*. 2016; Wang *et al*. 2016), and *P. graminis* (Berlin *et al*. 2012). Previous studies revealed that the *Pst* populations from Yunnan and Guizhou present high genetic diversity (Li 2013; Liu *et al*. 2016; Jiang *et al*. 2018), similar to those from southern Gansu. The Yunnan *Pst* population also exhibited diverse haploid genotypes, possessing shared haploid genotypes with southern Gansu *Pst* population (Li 2013). Presumably, *Pst* sexual reproduction could occur on susceptible *Berberis* species under natural conditions and contribute to high genetic diversity.

5. Conclusion

This study carried out field surveys of geographic distribution of *Berberis* species at 49 sites in the Yunnan-Guizhou plateau and 43 of which were found barberry plants. Eight *Berberis* species, *B. julianae*, *B. tsienii*, *B. veitchii*, *B. wilsonae*, *B. wilsonae* var. *guhtzunica*, *B. franchetiana*, *B. lepidifolia* and *B. pruinosa*, were reported here for the first time to serve as alternate hosts for *Puccinia striiformis* f. sp. *tritici*. This provides useful information for further studies to determine the role of *Berberis* species on stripe rust epidemics under natural conditions.

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Appendix associated with this paper can be available on http://www.ChinaAgriSci.com/V2/En/appendix.htm

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