### RESEARCH

### **Open Access**

# Re-delimiting oversummering regions of *Puccinia striiformis* f. sp. *tritici* in China



Jiguang Zhang<sup>1</sup>, Yuxiang Li<sup>1</sup>, Di Liu<sup>1</sup>, Junjie Zhang<sup>1</sup>, Zhibo Zhang<sup>1</sup>, Qiang Yao<sup>2</sup>, Xiangming Xu<sup>3</sup> and Xiaoping Hu<sup>1\*</sup><sup>1</sup>

### Abstract

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is one of the most important diseases on wheat, causing severe yield losses. The pathogen can only survive the summer in the cooler areas of northern and western regions in China. Compared to the main wheat-growing region, the oversummering region is relatively small. Therefore, managing stripe rust in the oversummering region is crucial for controlling the disease nationwide. In this study, we conducted experiments to determine the survival of the predominant *Pst* races in China under high temperatures and used the data to predict potential *Pst* oversummering regions. The predominant races (CYR32, CYR33, and CYR34) were able to survive and reproduce at an average temperature of up to 27 °C. Disease incidence and the number of uredinia decreased with increasing temperatures of 24–27 °C during incubation. The results from re-delimiting oversummering regions suggested that *Pst* is able to oversummer in the east of Gansu province and the south of Shanxi province, which were previously considered unsuitable for *Pst* oversummering. Based on the present study, the east of Inner Mongolia and north of Heilongjiang could provide the oversummering condition for *Pst*. Three major oversummering regions, the Liupan Mountain range, the highlands in the south of Gansu province, and the east of Qinghai province were identified. The results should be useful for adjusting strategies to manage stripe rust in China.

Keywords Puccinia striiformis f. sp. tritici, Oversummering, Urediniospores, Epidemic

\*Correspondence:

Xiaoping Hu

xphu@nwsuaf.edu.cn

<sup>1</sup> State Key Laboratory for Crop Stress Resistance and High-Efficiency Production, Key Laboratory of Plant Protection Resources and Pest Management of Ministry of Education, Key Laboratory of Integrated Pest Management On the Loess Plateau of Ministry of Agriculture and Rural Affairs, College of Plant Protection, Northwest A&F University, Yangling 712100, China

<sup>2</sup> Key Laboratory of Agricultural Integrated Pest Management, Qinghai Province, Academy of Agriculture and Forestry Science, Qinghai University, Xining 810016, China

 $^{\rm 3}$  Pest and Pathogen Ecology, NIAB East Malling, West Malling, Kent ME19 6BJ, UK

### Background

*Puccinia striiformis* f. sp. *tritici* (*Pst*), the causal agent of wheat stripe rust, is a biotrophic fungus and one of the major threats to wheat production worldwide (Wellings 2011). *Pst* can infect wheat plants throughout the entire growth season, causing yield losses of up to 100% in highly susceptible cultivars under extremely favorable weather conditions (Chen and Kang 2017). China is widely regarded as the largest epidemic region in the world (Stubbs 1985; Li and Zeng 2002). In China, *Pst* has caused yield losses of approximately 6.0, 3.2, 1.8, 1.3, and 0.24 million tons in 1950, 1964, 1990, 2002, and 2020, respectively (Wan et al. 2007; Chen et al. 2009; Liu et al. 2022).

Monitoring the survival of *Pst* in summer is important for managing stripe rust. *Pst* is adapted to relatively



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

cool climate conditions, with low temperatures favoring its infection and summer survival. Sharp (1965) reported that urediniospores can germinate in the range of 2 to 15 °C, with the optimum temperature of 7–11 °C for infection. Temperature above 20 °C may drastically reduce *Pst* infection. Infection declines from 100% at 15.4 °C to 0.8% at 20.5 °C under controlled conditions (Park 1990). Zeng (2003) reported that regions with an average daily temperature during a period of ten consecutive days exceeding 22 °C are not suitable for *Pst* oversummering. However, with changing climate conditions, it remains unclear whether the *Pst* population in China has adapted to high temperatures.

The identification of *Pst* survival regions in both summer and winter has been instrumental in managing stripe rust in China (Kang et al. 2010). Based on previous studies, Li and Zeng (2002) defined five Pst oversummering regions: (1) the northwest region including south of Gansu, south of Ningxia, and east of Qinghai provinces; (2) the Yunnan region, mainly the central Yunnan province; (3) the northwest of Sichuan province; (4) the north China region including the areas bordering between Hebei, Inner Mongolia, and Shanxi province; and (5) the Xinjiang region. Ma et al. (2004) classified the potential Pst oversummering regions in China based on the criterion of the average temperature not exceeding 22 °C during periods of ten consecutive days. However, given the changing wheat growing systems in China, changing climates, and the potential adaptation of Pst to high temperatures, there is a need to redefine potential Pst oversummering regions in China.

The global annual average temperature increased by 0.74 °C in the twentieth century and is projected to increase by another 1.1-6.4 °C by the end of the twentyfirst century (Pachauri and Reisinger 2007). The average temperature in July and August in China increased from 1960 to 2017, with a notable rise observed, particularly after 1980 (Additional file 1: Figure S1). The impact of increasing temperature is likely to vary among species and regions (Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004). Milus et al. (2006, 2009) demonstrated that new Pst races exhibit increased tolerance to warmer conditions. Isolates of Pst with high-temperature tolerance have also been reported in China (Zhang et al. 2013). However, it is not clear whether the current predominant Pst races in China, including CYR32, CYR33, and CYR34, are adapted to high temperatures. The epidemic frequencies of CYR32, CYR33, and CYR34 are 15.20%, 2.36%, and 38.51%, respectively, in Gansu province, the major initial inoculum provider for the broad wheat planting areas of China (Jia et al 2021).

If present, high-temperature tolerant *Pst* races could survive summer over larger areas than what was

previously assumed. They could become prevalent in summer and produce more urediniospores, initiating stripe rust on seedlings of wheat crops in the autumn. In this study, we conducted experiments under controlled conditions to test the hypothesis that the predominant *Pst* races in China can survive temperatures higher than the previously considered limit threshold. The objectives of this study were to (1) determine the maximum survival temperature for the predominant *Pst* races (CYR32, CYR33, and CYR34) in China; and (2) use the survival temperature along with the highest average air temperature over ten consecutive days to define areas where *Pst* can oversummer.

### Results

# The maximum survival temperatures of the predominant *Pst* races

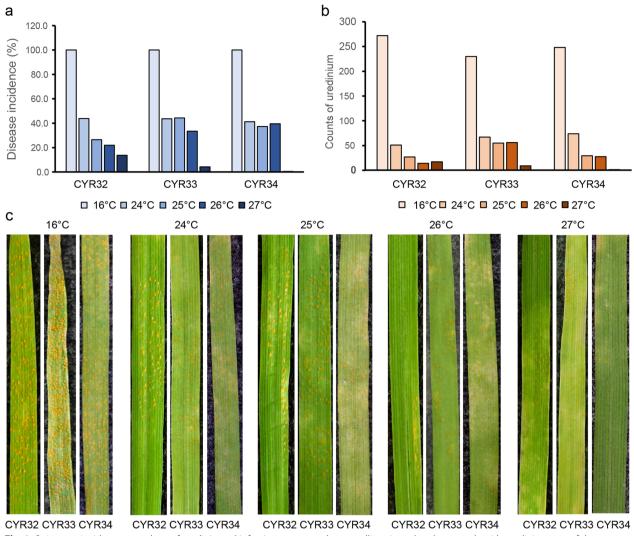
The disease incidence decreased from 100% to 13.7% for CYR32, 4.2% for CYR33, and 0.5% for CYR34 by increasing temperatures from 16 °C to 27 °C, 19 days after inoculation. The number of uredinia fell from 272 to 17 for CYR32, from 230 to 9 for CYR33, and from 248 to 2 for CYR34 (Fig. 1). At the 27 °C average temperature regime, the disease incidence and the number of uredinia for CYR34 were close to zero. Five additional races collected in 2023 from Yunnan, Sichuan, Hubei, Shaanxi, and Gansu provinces, respectively, can survive temperatures of up to 24 °C. The isolate from Yunnan province can survive up to 26 °C, while the isolate from Gansu province can survive up to 27 °C (Additional file 1: Figure S2).

### Highest average air temperature of ten consecutive days

The highest average air temperature is the decisive factor for the survival of *Pst.* To determine the highest temperature of ten consecutive days, the average air temperature was calculated for ten consecutive days from 1 July to 31 August for the years 2008–2017. The highest average air temperature typically occurs in late July in China, including regions such as Gansu, Qinghai, and Ningxia provinces, which are currently considered the main *Pst* oversummering regions. In the southwest of China, including Yunnan and Guizhou provinces, the average air temperature remains relatively stable from 1 July to 31 August (Fig. 2). Based on these results, the average air temperature of the last ten days in July, representing the hottest period, was selected as the threshold to delimit *Pst* oversummering regions.

# Relationship between average temperature and geospatial data

To delimit the oversummering areas for *Pst*, obtaining the average air temperature of any given location is essential. However, this task poses a significant challenge due to



**Fig. 1** Stripe rust incidences, numbers of uredinia, and infection types on wheat seedlings inoculated separately with urediniospores of three predominant races (CYR32, CYR33, and CYR34) of *P. striiformis* f. sp. *tritici* in China grown at various temperature regimes. **a** The disease incidences on wheat seedlings tested at five temperature regimes. **b** The numbers of uredinia on wheat seedlings tested at five temperature regimes. **c** The infection types on wheat leaves grown at five temperature regimes (pictures were taken 19 days after inoculation)

the vast geographic scale. Conventionally, spatial interpolation is employed as a method to approximate this data. Nevertheless, attempting spatial interpolation across the entire country using only 839 data points will inevitably result in significant errors. To address this complex issue, we analyzed the correlation between average temperature and geospatial factors such as latitude, longitude, and altitude using a backpropagation neural network. The results indicated a high correlation between average air temperatures and geospatial data (latitude, longitude, and altitude), with correlation coefficients (r values) of 0.987, 0.985, and 0.987 for the training, validation, and combined datasets, respectively (Additional file 1: Figure S3). The mean squared error of the predicted average temperature was 0.73. The discrepancy between the predicted and observed average temperatures was smaller than the annual fluctuations for the validation set (Fig. 3). Hence, using geospatial data to simulate average air temperature is both feasible and reliable.

**Delimitation of the oversummering regions for** *Pst* **in China** We predicted the potential *Pst* oversummering areas based on the maximum average air temperature required for the survival of the three predominant *Pst* races, as well as the wheat planting regions in each area. Although the predominant *Pst* in China can survive average temperatures up to 27 °C under controlled conditions, we selected 24 °C as the threshold to classify the

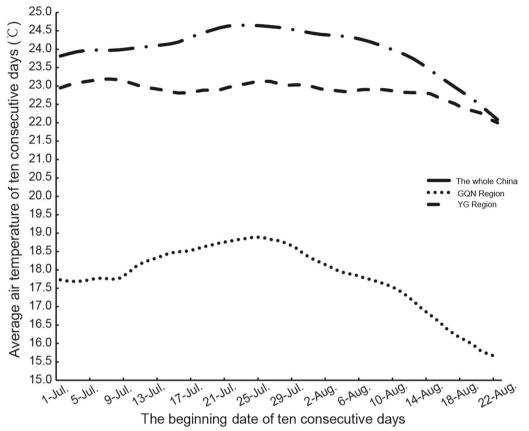


Fig. 2 Average air temperatures of ten consecutive days in China based on climate data from 2008 to 2017: GQN Region—Gansu, Qinghai, and Ningxia provinces; YG Region—Yunnan and Guizhou provinces

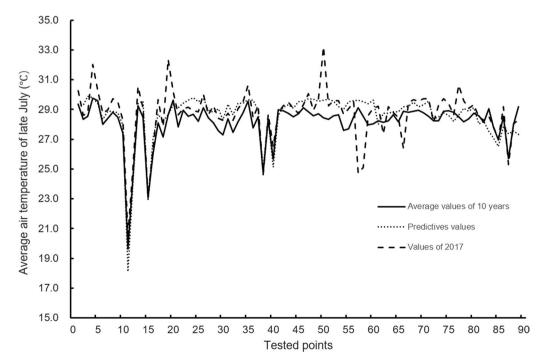


Fig. 3 Observed and predicted 2017 average air temperatures using the back propagation (BP) neural network model in comparison with the 10-year average temperatures for 89 weather stations in the validation set

oversummering regions, considering the actual natural conditions. When the inoculated wheat seedlings were incubated at 18 °C in dew chambers for 48 h, and then grown under the 24 °C average temperature regime, the disease incidence decreased to less than 3%, compared to the above 40% when incubated at 10 °C (Additional file 1: Figure S4); moreover, the disease incidence decreased to zero when the inoculated seedlings were incubated at 20 °C in the dew chamber. Hence, the average of 24 °C was selected as the threshold to delimit the oversummering regions.

Compared to the oversummering areas determined in 1965 using the average temperature of ten consecutive days < 22 °C (Wang et al. 1965) (Additional file 1: Figure S5), we observed prominent changes in the scope of the oversummering areas (Fig. 4). The east of Gansu province and the south of Shanxi province, once considered unsuitable for the survival of *Pst* in summer, have now been classified as oversummering regions. Our investigation on *Pst* oversummering in 2022 confirmed that *Pst* can infect and survive naturally in eastern Gansu (Additioanl file 2: Table S1). The northwest of Sichuan province, once considered an important location for Pst oversummering, has become less significant due to a sharp decline in wheat planting acreage. Regardless of whether using 22 °C or 24 °C as the upper limit temperature for classifying oversummering regions, large areas of oversummering regions were identified in the eastern part of Inner Mongolia and the northern part of Heilongjiang province. In the southwest oversummering region, including the west of Guizhou province, the south of Sichuan province, and almost the entire Yunnan province, no significant changes were observed, except for some expansion in the west of Guizhou. No significant change was observed in the area of the Xinjiang oversummering region when examined with either 22 °C or 24 °C as the upper limit temperature.

### Determination of core oversummering regions

In the process of delimiting oversummering areas, more important regions were revealed in the northwest region, which provides initial inoculum for the main

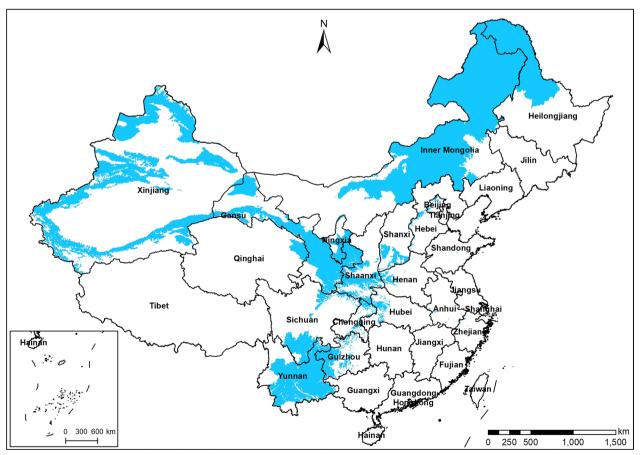
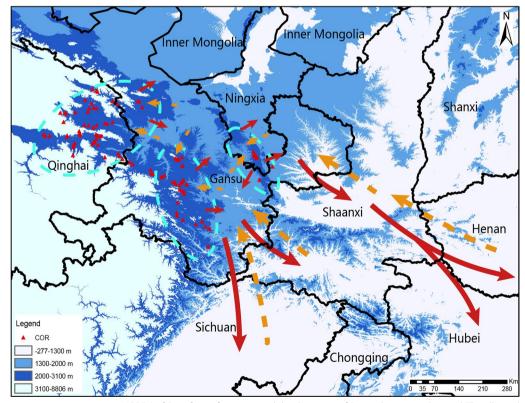


Fig. 4 Oversummering regions for *P. striiformis* f. sp. *tritici* in China were defined based on wheat acreage exceeding ten thousand hectares and the average air temperatures during the last ten days of July being less than 24 °C

oversummering regions. These regions are defined as core oversummering regions (CORs) and include the spring wheat planting areas and the late-maturing winter wheat areas with an altitude above 2000 m in the south of Gansu, south of Ningxia (the Liupan Mountain range), and east of Qinghai province (Fig. 5). In the CORs, wheat harvesting period lasts for a long time, from late July to September, depending on the altitude. Our survey on oversummering showed that, after mid-July, only the fields in the CORs have wheat in the growing stage. Wheat harvest period and the occurrence of stripe rust in the CORs were presented in Additional file 2: Table S2. The CORs play an important role in preserving and providing urediniospores for volunteer wheat seedlings in the main oversummering regions during summer. Hence, the CORs are essential in the annual epidemic cycle of wheat stripe rust and warrant increased attention on its management.

### Discussion

The pathogen of stripe rust prefers cool climatic conditions and exhibits tolerance to low temperatures. Temperatures between 0 and -10 °C inhibit the survival of the parasite but do not completely halt it (Rapilly 1979). Li and Zeng (2002) reported that Pst could successfully survive in winter, even when the monthly mean temperature is below – 10 °C, as long as wheat seedlings are covered with snow. Due to its adaptability to low temperatures, wheat stripe rust can emerge very early in the seedling stage, resulting in more severe damage in some areas than leaf rust (caused by *Puccinia triticina*) and stem rust (caused by Puccinia graminis f. sp. tritici) (Chen 2005). Compared to low temperatures, the pathogen is more vulnerable to high temperatures. Recent studies have confirmed that some Pst races exhibit tolerance to relatively high temperatures (Zhang et al. 2013). Our results also revealed that the prevalent races in China could survive and sporulate at an average temperature of 27 °C. However, both spore production and disease incidence were significantly lower compared to the optimum temperature. The adaptability of Pst to high temperatures expands its oversummering area, further increasing the supply of initial inoculum in the fall and exacerbating the epidemic of stripe rust in the following year.



**Fig. 5** The core oversummering regions (CORs) of *P. striiformis* f. sp. *triitici* and the directions of *Pst* urediniospore dispersal. The elliptical circles denote the core oversummering regions. Red solid line arrows indicate the directions of urediniospores dispersed from the CORs to the main oversummering regions in summer and then to the overwintering areas in the fall. Dashed orange line arrows indicate the directions of urediniospores transmitted from the overwintering areas to the main oversummering regions and then to the CORs in the following spring

Oversummering represents a bottleneck stage in the life cycle of *Pst.* Managing *Pst* oversummering area is considered the most cost-effective step for controlling wheat stripe rust. Therefore, re-delimiting the oversummering regions is of great significance for the control of the disease, especially given the increasing adaptability of *Pst* to high temperatures. In this study, we determined the maximum temperature that the predominant races of *Pst* in China can survive and pinpointed their oversummering areas. These results provide valuable guidance for monitoring and managing stripe rust in China. The expansion of the oversummering area suggests that we may face greater challenges in controlling wheat stripe rust in China.

Temperature and moisture are two important factors that affect the infection and occurrence of stripe rust. We only considered temperature as the parameter in delimiting the oversummering areas of Pst. This is because, in general, there is an abundance of precipitation in summer in most areas of wheat cultivation in China. Based on the climate data from the last ten days of July, precipitation ranged from 5 to 48 mm in the northwest oversummering region, including Gansu, Qinghai, and Ningxia provinces. In the southwest oversummering region, mainly comprising Yunnan and Guizhou provinces, the rainfall ranged from 29 to 158 mm according to the meteorological data from 2008 to 2017 (http://data.cma.cn/). Furthermore, the formation of dew at night during summer also provides the moisture needed for urediniospore germination and infection (Chen 2005). Therefore, moisture is generally not a limiting factor for oversummering in China.

The results of this study showed that there was a large area of oversummering region in the northeast, encompassing the east of Inner Mongolia and north of Heilongjiang. However, there have been no reports of large-scale outbreaks of wheat stripe rust in this region. Stripe rust can occur in this region, and it tends to manifest at low levels when the disease is severe in regions to the south and west, as observed in 2021 (Zhou et al. 2023). The winter in this region is generally too cold for *Pst* to survive. Spring wheat is grown as a relatively minor crop and harvested in late August. Airflow trajectory analysis showed that, during July and August, there is no airflow from this region to other oversummering regions (data not shown). Therefore, the role of this oversummering region in the epidemic of wheat stripe rust might be minor.

The grass species that can harbor wheat stripe rust fungus have been reported around the world (Arthur 1925; Newton 1936; Wahl et al. 1984; Holmes and Dennis 1985; Stubbs 1985; Line 2002; Cheng et al. 2016). In China, although several studies have reported on the grass hosts of *Pst* (Li and Zeng 2002; Niu et al. 1991; Qin et al. 2022), the role of grass hosts in China on the epidemic of wheat stripe rust is very limited (Li and Zeng 2002). Hence, in this research, the classification of oversummering region was based on the areas of wheat planting, while disregarding the influence of grass hosts.

Although we took the wheat planting area into account when classifying the oversummering regions, some areas with no wheat planting were still classified as oversummering regions due to the uneven distribution of wheat cultivation, for example, the south of Shaanxi, west of Hubei, and southeast of Xinjiang province. More accurate wheat planting areas from remote sensing images should be helpful to obtain more precise oversummering regions.

Disease management in the pathogen-oversummering areas is an economical and effective solution in the prevention and control of wheat stripe rust. The northwest oversummering region, with wheat planting areas totaling 0.86 million hectares (Chinese National Bureau of Statistics, https://data.stats.gov.cn), primarily encompassing Gansu, Qinghai, and Ningxia provinces, stands out as the most important survival region for Pst during the summer in China. In the past, measures have been proposed to eliminate volunteer wheat seedlings in the northwest oversummering areas to reduce the initial inoculum of Pst in the fall (Liu and Chang 1982). However, this strategy is difficult to implement in such a large region. In this study, we proposed the concept of CORs (Core Oversummering Regions) and defined its detailed scope. The CORs are essential and important in the annual epidemic cycle of wheat stripe rust because they serve as the main reservoir of *Pst* and supply the initial inoculum for the volunteer wheat seedlings in the main oversummering regions during summer. By controlling wheat stripe rust in the CORs, the initial inoculum for the volunteer seedlings should be greatly reduced. As a result, the incidence and affected area across the main oversummering regions, as well as the disease incidence on wheat seedlings in the fall, should be reduced. The epidemic cycle involving the CORs is as follows (Fig. 5). After almost all winter wheat is harvested, the CORs remain the only main reservoir of Pst in the northwest region and provide initial inoculum for the volunteer wheat seedlings across the main oversummering areas from July to September. After the emergence of earlysown winter wheat in the broad oversummering region (sown from early to mid-September), the urediniospores on the volunteer seedlings and some late-maturing spring wheat spread to the seedlings of early-sown winter wheat crop. When the urediniospores reproduce on the seedlings of early-sown winter wheat, they spread through airflow to the broad winter wheat areas, including

Shaanxi, Sichuan, Henan, and Hubei provinces, where the sowing time is usually from early to mid-October. In the following year, part of the inoculum in the main oversummering regions originates from the primary winter wheat regions, while another part comes from local overwintering *Pst*. After reproduction on the seedlings in the main oversummering regions, the urediniospores spread to the CORs, completing the annual epidemic cycle.

### Conclusions

The predominant races CYR32, CYR33, and CYR34 in China are able to survive and grow at average temperatures as high as 27 °C under controlled conditions, but the disease incidence was reduced. The adaptability of *Pst* to high temperatures expands the range of its oversummering area. Compared to the oversummering areas determined using an average temperature of less than 22 °C for ten consecutive days, significant changes were observed in the extent of the oversummering areas. Three important regions in the northwest were identified as providing initial inoculum for the main oversummering regions. These regions were defined as core oversummering regions (CORs), including the spring wheat planting areas and the late mature winter wheat areas at altitudes above 2000 m in the south of Gansu, south of Ningxia (the Liupan Mountain range), and the east of Qinghai province.

### Methods

### Data sources

Meteorological data from 839 weather stations located in 34 provinces in China, covering the period from 1960 to 2017, were obtained from the Chinese Meteorological Science Data Center website (http://data.cma.cn). Data of the digital elevation model (DEM) were downloaded from the Geospatial Data Cloud website (https://www. gscloud.cn). The wheat growing area was obtained from the Chinese National Bureau of Statistics website (http:// www.stats.gov.cn).

### Pst races and wheat cultivar

The predominant races of *Pst* in China, including CYR32, CYR33, and CYR34, were provided by the Wheat Stripe Rust Collection Center (WSRCC) at Northwest A&F University. These races were used to study their tolerance to high temperatures. A susceptible wheat cultivar, Mingxian 169 (MX169), was used for reproducing urediniospores and the inoculation tests under different temperatures. Wheat plants at the two-leaf stage are dust-inoculated with a mix of fresh urediniospores with talcum at about 1:20 ratio (Chen and Kang 2017).

### Testing for maximum survival temperatures of the Pst races

To determine the maximum temperature for survival of each race, we inoculated six pots  $(9 \times 9 \times 9 \text{ cm})$  of wheat seedlings (8-10 seedlings in each pot) of cultivar MX169 with fresh urediniospores. The seedlings were misted with tap water and then incubated at 10 °C in a dew chamber for 48 h in the dark. The inoculated seedlings were transferred to growth chambers set to one of the five fluctuating temperature regimes (Additional file 2: Table S3) with the respective average temperature of 16 °C, 24 °C, 25 °C, 26 °C, and 27 °C, with a photoperiod of 16 h light and 8 h dark. In order to simulate natural conditions, another set of tests were conducted with the temperature in the dew chambers set at 18 °C, 20 °C, 22 °C, or 24 °C. After the inoculated seedlings were incubated in the dew chamber for 48 h, the seedlings were transferred to growth chambers at the average temperature of 24 °C. The photoperiod was the same as the above settings for the average temperature 24 °C regime. The number of leaves bearing Pst pustules (as incidence) and number of uredinia were recorded 19 days post inoculation (Chen and Kang 2017). The above experiments were repeated three times.

# Determination of the highest average air temperature of ten consecutive days

Zeng (2003) reported that the regions where the average daily temperature during a period of ten consecutive days exceeds 22 °C are not suitable for *Pst* oversummering. In order to find the maximum average air temperature of ten consecutive days for each weather station, we calculated the average air temperature of ten consecutive days from 1 July to 31 August using ten days as a sliding window based on the meteorological data of 839 weather stations from 2008 to 2017.

# Regression analysis of geospatial data and average air temperatures

Longitude, latitude, and altitude data across China were extracted from the digital elevation model (DEM, https:// www.gscloud.cn). To explore the relationship of geospatial data (longitude, latitude, and altitude) with average air temperatures, we performed regression analysis with a back propagation neural network using the geographical data and average air temperatures of the 839 weather stations. Of the 839 national climate stations across China, 750 were selected randomly as the training set and the remaining 89 stations as the validation set. Then, we used the regression model and the geospatial data to estimate the average air temperatures for the whole country. We resampled 1,048,575 data points from the digital elevation model across China, with a distance of 1800 m between adjacent points. Therefore, the spatial resolution of our final map for re-delimiting oversummering regions was 1800 m.

### Delimitation of the regions for Pst oversummering in China

To determine whether a particular area is significant for *Pst* oversummering, two criteria were used. First, the average air temperature for ten consecutive days in the given area is lower than the maximum temperature at which *Pst* (as represented by the three predominant races) can survive. Second, the total wheat-growing acreage in the area is more than 10,000 ha.

### Data analyses

To verify that the average air temperature of any point in China is highly related to its geographical information (longitude, latitude, and altitude), we performed a regression analysis of the geographical data (longitude, latitude, and altitude) with average temperatures using the backpropagation (BP) neural network model run on Matlab (R2016a). Sigmoid function,  $f(x) = \frac{1}{1+e^{-x}}$ , was used as the activation function. Extraction of geospatial data and visualization of oversummering regions were performed using software ArcGIS version 10.8. The classification of the oversummering region was carried out based on the Mercator projected map of China.

#### Abbreviations

- CYR Chinese yellow rust
- COR Core oversummering regions
- f. sp. Formae specialis
- Pst Puccinia striiformis f. sp. tritici

### **Supplementary Information**

The online version contains supplementary material available at https://doi. org/10.1186/s42483-024-00308-y.

Additional file 1: Figure S1. Dynamics of average air temperature in July and August from 1960 to 2017 in China. Figure S2. The counts of uredinia and infection type on wheat seedlings inoculated with stripe rust isolates sampled in 2023 from Yunnan, Sichuan, Hubei, Shaanxi, and Gansu provinces and grown at various temperature regimes. a, b, c, d, and e The infection type on wheat leaves inoculated with different races and grown at five temperature regimes;  ${f f}$  The numbers of uredinia on wheat seedlings. 23-YN-KM-32, 23-SC-MS-04, 23-HB-ES-02, 23-SX-XY-02, and 23-GX-DX-11, represent races sampled in 2023 from Yunnan, Sichuan, Hubei, Shaanxi, and Gansu provinces, respectively. Figure S3. The correlation between geospatial information and the average air temperatures of the corresponding weather stations. Target denotes the observed values, and output indicates the predicted values. Figure S4. Disease incidences at different temperatures in dew chambers. Figure S5. Oversummering regions for P. striiformis f. sp. tritici in China were defined based on wheat acreage exceeding ten thousand hectares and the average air temperatures during the last ten days of July being less than 22°C

Additional file 2: Table S1. The occurrence of wheat stripe rust on volunteer wheat in Gansu and Ningxia province in 2022. Table S2. The occurrence of wheat stripe rust and wheat harvest period in the core oversummering regions. Table S3. Settings of the incubating temperatures and photoperiods.

### Acknowledgements

Not applicable.

### Author contributions

XH designed the research and revised the manuscript. JZ, JZ, DL, and ZZ performed the research. QY provided survey help. JZ wrote the manuscript, and YL and XH revised the manuscript. XX provided assistance in designing the research and revising the manuscript. All authors read and approved the final manuscript.

### Funding

This work was supported by the National Key Research and Development Program of China (2021YFD1401000), the National Natural Science Foundation of China (31772102), Major Science and Technology Project of Agricultural Collaborative Innovation and Promotion Association in Shaanxi Province in 2022 (LMZD202203), the Extension Project of Northwest A&F University (TGZX2021-13), International Cooperation Project of the Ministry of Science and Technology (G2023172013L), China Agriculture Research System of Wheat (CARS-03-37), and the Innovation Group of Crop Disease and Pest Prediction and Management (XYTD2023-04).

#### 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.

Received: 31 May 2024 Accepted: 27 December 2024 Published online: 27 February 2025

### References

- Arthur JC. The grass rusts of South America; based on the Holway collections. Proc Am Philos Soc. 1925;64:131–223.
- Chen XM. Epidemiology and control of stripe rust [*Puccinia striiformis* f. sp. *tritici*] on wheat. Can J Plant Pathol. 2005;27:314–37.
- Chen X, Kang Z. Introduction: History of research, symptoms, taxonomy of the pathogen, host range, distribution, and impact of stripe rust. In: Chen X, Kang Z, editors. Stripe rust. Dordrecht: Springer Netherlands; 2017. p. 1–33. https://doi.org/10.1007/978-94-024-1111-9\_1.

Chen WQ, Wu LR, Liu TG, Xu SC, Jin SL, Peng YL, Wang BT. 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;93:1093–101.

Cheng P, Chen X, See D. Grass hosts harbor more diverse isolates of *Puccinia striiformis* than cereal crops. Phytopathology. 2016;106:362–71.

- Holmes RJ, Dennis JI. Accessory hosts of wheat stripe rust in Victoria Australia. Trans Br Mycol Soc. 1985;85:159–60.
- Jia QZ, Cao SQ, Wang XM, Huang J, Sun ZY, Zhang B, Luo HS, Li QQ. Monitoring the variation of physiological races of *Puccinia striiformis* f.sp. tritici in Gansu province during 2017–2018. Plant Prot. 2021;02:214–8 ((in Chinese with English abstract)).
- Kang ZS, Zhao J, Han DJ, Zhang HC, Wang XJ, Wang CF, Han QM, Guo J, and Huang LL 2010. Status of wheat rust research and control in China. Pages 50–69 in: BGRI 2010 Technical Workshop Oral Presentations. Full papers and abstracts. May 30–31, 2010, St Petersburg, Russia.
- Li ZQ, Zeng SM. Wheat Rusts in China. Beijing: China Agricultural Press; 2002. p. 379.

- Line RF. Stripe rust of wheat and barley in North America: a retrospective historical review. Annu Rev Phytopathol. 2002;40:75–118.
- Liu HW, Chang LY. A study on strategies for reducing the amount of stripe rust on the seedling of Longdong early sowing winter to protect the main wheat planting area. Shaanxi J Agri Sci. 1982;1982:1–6 ((in Chinese with English abstract)).
- Liu WC, Wang BT, Zhao ZH, Li Y, Kang ZS. Historical review and countermeasures of wheat stripe rust epidemics in China. China Plant Prot. 2022;42:21–7 (**(in Chinese with English abstract)**).
- Milus EA, Seyran E, McNew R. Aggressiveness of *Puccinia striiformis* f. sp. *tritici* isolates in the South-Central United States. Plant Dis. 2006;90:847–52.
- Milus EA, Kristensen K, Hovmøller MS. Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis* f. sp. *tritici* causing stripe rust of wheat. Phytopathology. 2009;99:89–94.
- Newton M, Johnson T. Stripe rust, *Puccinia glumarum*. Canada Can J Res. 1936;14:89–108.
- Niu YC, Li ZQ, Shang HS. The new discovery on geographic distribution of *Puccinia striiformis* West, f. sp. *hordei* in China. Acta Univ Agric Boreali-Occident (Suppl). 1991;19:63–5 ((in Chinese with English abstract)).
- Pachauri RK, and Reisinger A. Climate change 2007: Synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC; 2007.
- Park RF. The role of temperature and rainfall in the epidemiology of *Puccinia striiformis* f.sp. *tritici* in the summer rainfall area of eastern Australia. Plant Pathol. 1990;39:416–23.
- Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003;421:37–42.
- Qin J, Wang Z, Lv Y, Kang Z, Zhao J. Grasses are able to harbor the oversummering of urediospores and the overwintering of teliospores of *Puccinia striiformis* f. sp. *tritici* in China. Phytopathol Res. 2022;4:1–15.
- Rapilly F. Yellow rust epidemiology. Annu Rev Phytopathol. 1979;17:59–73. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. Fingerprints
- of global warming on wild animals and plants. Nature. 2003;421:57–60. Sharp EL. Prepenetration and postpenetration environment and development
- of *Puccinia striiformis* on wheat. Phytopathology. 1965;55:198–203. Stubbs, R. W. 1985. Stripe rust. Page 61–101 in: The Cereal Rusts, Vol. II,
- Diseases, Distribution, Epidemiology, and Control. A. P. Roelfs and W. R. Bushnell. eds. Academic Press, Orlando, Florida.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. Extinction risk from climate change. Nature. 2004;427:145–8.
- Wahl I, Anikster Y, Manisterski J, Segal A. Evolution at the center of origin. In: Bushnell WR, Roelfs AP, editors. The Cereal rusts: origins, specificity, structure, and physiology, vol. I. Orlando: Academic Press; 1984. p. 39–77.
- Wan AM, Chen XM, He ZH. Wheat stripe rust in China. Aust J Agric Res. 2007;58:605–19.
- Wang JQ, Lu JX, Liu SJ, Dai SK, Liu RZ. A preliminary study on the trend of oversummer of stripe rust of wheat in Gansu province. Acta Phytopathol Sin. 1965;8:1–10 ((in Chinese with English abstract)).
- Wellings CR. Global status of stripe rust: a review of historical and current threats. Euphytica. 2011;179:129–41.
- Zeng SM. Simulation study on oversummering process of wheat stripe rust caused by *Puccinia striiformis* in China. Acta Phytopathologica Sinica. 2003;33:267–78 (**(in Chinese with English abstract)**).
- Zhang JQ, Liu B, Chen WQ, Liu TG, Gao L. Temperature-sensitivity of population of *Puccinia striiformis*. Acta Phytopathologica Sinica. 2013;43:88–90 ((in Chinese with English abstract)).
- Zhou A, Wang J, Chen X, Xia M, Feng Y, Ji F, Huang L, Kang Z, Zhan G. Virulence characterization of *Puccinia striiformis* f. sp. tritici in China using the Chinese and Yr single-gene differentials. Plant Dis. 2023;183:671–83.

### **Publisher's Note**

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.