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Molecular genotyping revealed the gene flow of *Puccinia striiformis* f. sp. *tritici* clonal lineage from Uzbekistan of Central Asia to Xinjiang of China

Muhammad Awais[1], Jinbiao Ma[2], Wenbing Chen[1], Bingbing Zhang[1], Khurshid S. Turakulov[3], Li Li[2], Dilfuza Egamberdieva[4,5], Meliev Sodir Karimjonovich[3], Zhensheng Kang[1*] and Jie Zhao[1*]

Abstract

Wheat stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is an air-borne fungal disease, and its spores can be spread far away from its origin to colonize in new territory, causing inter-regional epidemics. Xinjiang not only is an important and independent epidemic region from other stripe rust epidemiological regions in China but also has distinguished *Pst* genetic structure and spatial features. However, the inoculum source of the rust in Xinjiang has remained unknown. It is not clear whether inocula in Central Asian countries migrate to Xinjiang and whether mutual gene flows possibly occur between both regions. We conducted a comparative population study of *Pst* populations in Xinjiang and Uzbekistan to better understand the *Pst* migration pattern and inoculum source of the rust in Xinjiang. Our results revealed high genetic diversity in Xinjiang (0.86, 63 MLGs out of 207 samples), compared with the Uzbekistan population (0.76, 47 MLGs out of 255 samples). Our analyses uncovered the clear migration of Uzbekistan *Pst* populations to Northwest Xinjiang, which is in proximity to Central Asia. The migration of clonal lineage could cause genetic drift and potential threat changing the genetic structure and virulence pattern of *Pst* in China. Further studies need to be conducted in the Xinjiang region to understand and evaluate the behavior of foreign genotypes in the local environment and their overall impact on local wheat crops.

Keywords Wheat, Stripe rust, Inter-regional spread, Genotyping, Inoculum source

Co-first authors: Muhammad Awais and Jinbiao Ma

*Correspondence:
Zhensheng Kang
kangzs@nwafu.edu.cn
Jie Zhao
jiezhao@nwafu.edu.cn
[1] State Key Laboratory for Crop Stress Resistance and High-Efficiency Production, College of Plant Protection, Northwest A&F University, Yangling 712100, Shaanxi, China
[2] State Key Laboratory of Desert and Oasis Ecology, Key Laboratory of Ecological Safety and Sustainable Development in Arid Lands, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830000, Xinjiang, China
[3] Institute of Genetics and Plant Experimental Biology of Academy Science of Uzbekistan, Tashkent, Uzbekistan
[4] Faculty of Biology, National University of Uzbekistan, 100174 Tashkent, Uzbekistan
[5] Institute of Fundamental and Applied Research, National Research University TIIAME, 100000 Tashkent, Uzbekistan

Background

Determining the intra- or inter-regional spread of a plant pathogen is crucial to prepare and mitigate the disease severity impact proactively. Previous epidemiological studies have proven that addressing threats from unfamiliar alien pathogens is more challenging than dealing with native adversaries (Torchin and Mitchell 2004; Crowl et al. 2008). The same scenario is related to plant diseases, as reported in Europe, where a substantial outbreak of wheat stripe rust occurred when non-European invasive races displaced the existing population of the pathogen (Patpour et al. 2022).

Wheat stripe rust, caused by *P. striiformis* f. sp. *tritici* (*Pst*), has an extremely serious impact on wheat crops worldwide (Line 2002; Chen 2005; Zhao and Kang 2023). *Pst* is an air-borne plant fungal pathogen. It is renowned for its long-distance migration and swift adaptation to new territories to become a major issue in wheat-growing regions (O'Brien et al.1980; Gaunt and Cole 1987; Boshoff et al. 2002; Brown and Hovmøller 2002; Ali et al. 2014). It was exemplified that the stripe rust pathogen migrated to Australia in 1979, subsequently spread rapidly across the main wheat production areas of the country, and later to New Zealand (Gaunt and Cole 1987). The intricacy of examining the migration patterns of *Pst* across diverse ecological zones is due to its ability to exploit multiple hosts including wheat, barley, and grasses (Hendrix et al. 1965; Stubbs 1985; Line 2002; Chen 2005). This adaptability could be influenced by several known ecological factors, i.e., temperature (Bryant et al. 2014; Ma et al. 2015), and rainfall (Sache et al. 2000). As previous studies described that pathogen population structures were correlated with different environmental factors, it is crucial to understand the behavior of ecological factors shaping the population structure of *Pst* and how it helps alien lineages to their adaptability to a new region.

Long-distance spread of air-borne plant pathogens, with significant random characteristics, can bring about founder effect in local plant pathogen populations in new territories where susceptible wheat cultivars are grown for harboring the survival and expanding population of the spreading pathogen (Brown et al. 2002). When *Pst* spread to a new region, potential outcomes based on an evolutionary perspective should be considered. The fungus may fail to establish and subsequently perish due to resistant hosts or unfavorable environmental conditions. If colonized in a new territory, it could successfully establish and develop in the area, possibly displacing the native pathogen population and causing the latter's extinction or coexisting stably with the local pathogen population. Global studies have identified several genetic groups of the *Pst* populations (Ali et al. 2014; Schwessinger 2017). In Europe, as reported by HovmØller et al. (2016), *Pst* races 'Warrior', 'Kranich', and 'Triticale aggressive' were identified. These races migrated from the near-Himalayan region to Europe, replaced local clonal populations, and became predominant due to rapid accumulation and dispersal. Within northwest Europe, long-distance migration of a single, clonal *Pst* population in four countries, 1700 km apart, is responsible for the low genetic diversity of the pathogen populations in these regions (HovmØller et al. 2002). In the United States, the 1958's epidemic of wheat stripe rust had likely resulted from a long-distance (~2400 km) migration of *Pst* spores from northern Mexico to North Dakota (Zadoks 1961). In China, recent studies showed that the spread of inoculum from northwestern and southwestern regions accounted for epidemics of wheat stripe rust in eastern regions (Awais et al. 2022; Ju et al. 2022). Therefore, spore migration of *Pst* can influence population structure and the level of population genetic diversity, as well as the occurrence of the disease.

China is the largest epidemic zone of wheat stripe rust in the world and has a unique stripe rust epidemiological pathogen system distinguishable from other regions of the world (Stubbs 1985; Zeng and Luo 2006). According to the spatiotemporal spread of inoculum (Li and Zeng 2002), multiple comprehensive factors are involved (Zeng and Luo 2006). China is subdivided into different epidemiological regions for stripe rust. Among the sub-epidemiological regions, Xinjiang is a relatively independent epidemiological region distinguishable from other regions in China, which was proven by molecular marker studies in relation to the Xinjiang *Pst* populations. More importantly, there was no significant gene flow between Xinjiang and other epidemic regions of China (Wan et al. 2015; Zhan et al. 2016; Zhang et al. 2024). In this region, the pathogen can over-summer and overwinter to complete the disease cycle all year round (Li and Zeng 2002). Therefore, we hypothesized that *Pst* migrations occur between Xinjiang and Central Asian countries.

To date, there have been only a few studies in relation to *Pst* populations of Uzbekistan, a Central Asian country, i.e., stripe rust incidents in 2004–2016 (Gulmurodov et al. 2016), evaluations of wheat germplasm resistance to stripe rust (Kokhmetova et al. 2017), and fungicide application for preventing yield losses of wheat from stripe rust (Sharma et al. 2016). In addition, only a small number of isolates from Uzbekistan were used for assessing the level of population genetic diversity in some countries worldwide (Sharma-Poudyal et al. 2020). However, so far, the migration of *Pst* populations between China and Central Asian countries has not been studied, limiting the understanding of population dynamics and population genetic lineage and gene flow, as well as the utilization of genetic resistance for controlling stripe rust in Xinjiang,

Uzbekistan, and other Central Asian countries. The present study aimed to determine the genetic diversity and relationship of *Pst* populations in Xinjiang and Uzbekistan using simple sequence repeats (SSR) markers and to analyze gene drift among regional *Pst* populations to track the early migration footprint in these regions.

Results

Suitability of selected SSR markers

In this study, we used 17 SSR markers to genotype 255 Uzbekistan *Pst* isolates from 23 sampling sites and 207 Xinjiang isolates from 21 sampling sites (Fig. 1). Among these markers, NRJN12 and NRJN9 were monomorphic, while the markers NUW6 and NRJ6 had a low number of alleles, so we considered these two markers as low polymorphic (Table 1), and the remaining 15 markers were polymorphic. Markers NWU12, NRJN4, NRJN2, NRJN11, NRJO27, NRJN5, NRJO21, NRJO20, and NRJN10 showed high polymorphism ($He \geq 0.41$). The maximum number of alleles (≥ 4) were found in NRJO27, NRJN2, NRJN11, NRJN13, NRJN4, NWU12, NRJO20, NRJN5, and NRJO21 (Table 1). Results showed that the markers were suitable for detecting different multilocus genotypes (MLGs; Fig. 2a, b) and were used to determine different diversity parameters (Fig. 2c). These markers showed various levels of linkage disequilibrium among the Uzbekistan and Xinjiang populations (Fig. 2d).

Genetic diversities of *Pst* in the Xinjiang and Uzbekistan populations

Based on genotyping data analyses, a high gene diversity ($He = 0.28$; Fig. 3a) and an average allele count (3.64; Table 2) were observed in the Xinjiang *Pst* population. In comparison, the Uzbekistan *Pst* population had a lower gene diversity ($He = 0.223$) and lower average allele count (2.7). The Xinjiang *Pst* population had a high genotypic diversity (0.86; Table 2) with 63 MLGs out of 207 samples (Table 2), whereas the genotypic diversity (0.76) and MLGs (47 out of 255 isolates) of the Uzbekistan *Pst* population were relatively low compared with the Xinjiang population.

In Xinjiang, the highest gene diversity was found in North Xinjiang ($He = 0.26$; Fig. 3b) with an average number of alleles (Avg allele = 2), and the lowest gene diversity was found in Northwest Xinjiang ($He = 0.191$) and East Xinjiang ($He = 0.195$). However, the maximum genotypic diversity was found in West Xinjiang (0.85; Table 2) with 54 MLGs out of 127 samples. The pathogen populations from the other regions of Xinjiang exhibited low genotypic diversities (0.36 to 0.66), suggesting that the West Xinjiang region could be the center of diversity in Xinjiang for *Pst* for emerging new multilocus lineages. In Uzbekistan, the highest genotypic diversity of *Pst* population was found in southern Uzbekistan (0.88), with 26 MLGs out of 55 isolates. The lowest genotypic diversity was found in Central Uzbekistan (0.70, with 19 MLGs out of 90 Isolates) and Fergana Valley (0.73, with 15 MLGs out of 80 isolates).

Population genetic structures of *Pst* in Xinjiang and Uzbekistan

We used structure-based analysis software to compare the genetic structures of *Pst* populations in Uzbekistan and Xinjiang and to identify shared genetic groups. From structure analysis, we found the optimum clustering level at $K = 3$ for the overall population. At cluster $K = 2$, we observed two main groups. Group G1 was predominant in the Uzbekistan population. This group was also dominant in the Northwest Xinjiang population but was found in trace levels in the West Xinjiang population (Fig. 4a, b). On the other side, G2 was prevalent in the East Xinjiang, West Xinjiang, and North Xinjiang populations. At $K = 3$, interestingly, the G2 group contained a subgroup G3 that was predominant in the North Xinjiang population and separated this region from the other regions in Xinjiang. The F_{ST} value between the two groups showed that the G1 group, predominant in Uzbekistan and Northwest Xinjiang, has less genetic divergence than the group G2, which was prevalent in West and East Xinjiang ($F_{ST} = 0.457$). Interestingly, high genetic divergence was found between groups G2 and G3 ($F_{ST} = 0.517$), which was observed within the Xinjiang *Pst* population.

The population genetic structure was further confirmed on a spatial scale through discriminant analyses of principal components (DAPC; Fig. 4c). The overall log genotype probability value was determined using the saddle point assessments method (Fig. 4d) and the GENELAND program (Fig. 4e, f). In the GENELAND program, we used Markov chain Monte Carlo inference of clusters. This method revealed three cluster groups: the Uzbekistan (UZ) and the Northwest Xinjiang (NX) populations were grouped together; another cluster group was shared between West and East Xinjiang. North Xinjiang, interestingly, had a separate cluster group (Fig. 4f). These results are consistent with the findings from the structure analysis.

Genotype fitness among the Xinjiang and Uzbekistan *Pst* populations

Population genetic structures of *Pst* in Xinjiang and Uzbekistan were evaluated through STRUCTURE, *Nei's* genetic distance, and F_{ST} analyses. Although these methods were effectively used for determining the population genetic structures, they did not provide insights into individual fitness (whether good or poor) within and between the populations of Uzbekistan and Xinjiang. We used

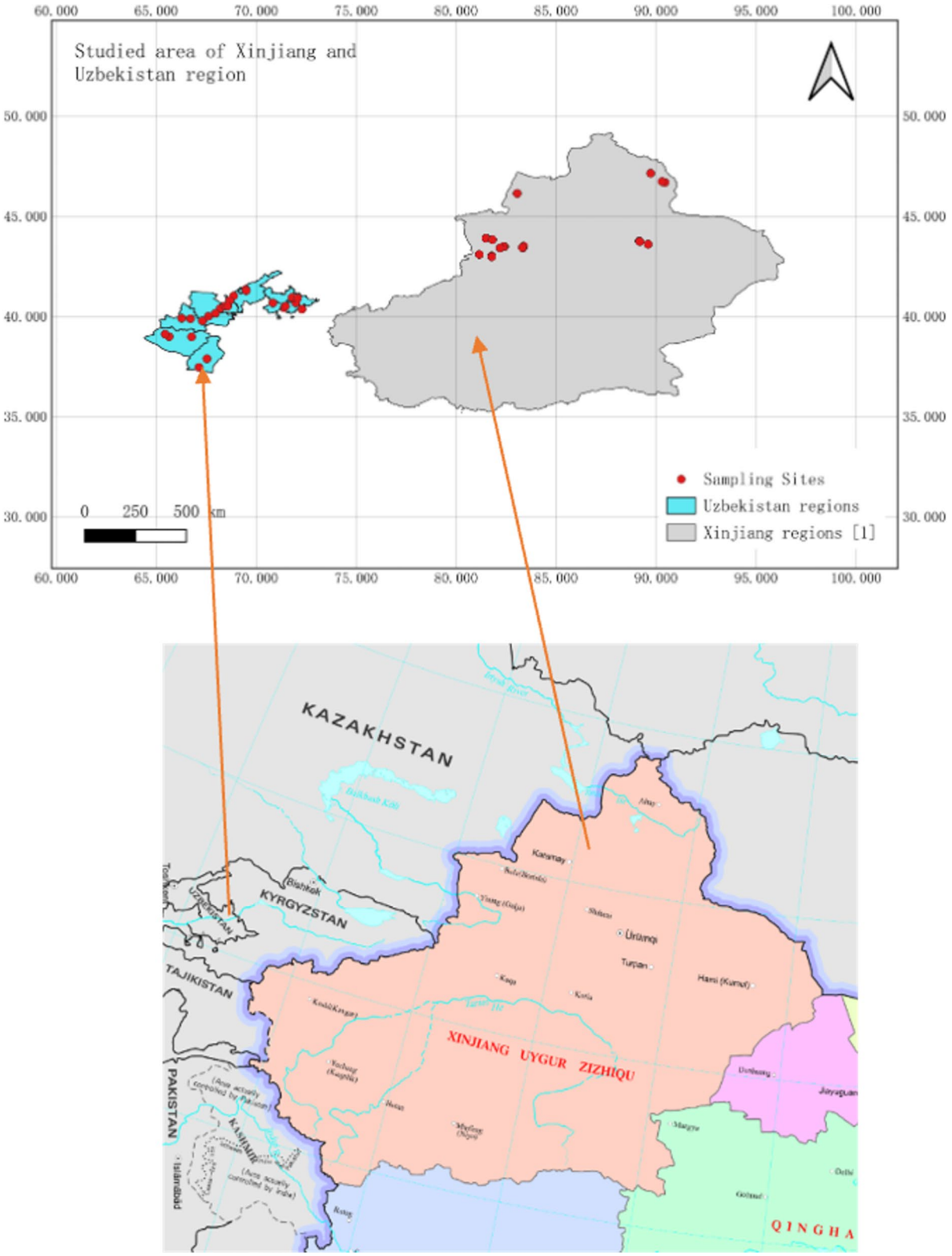

Fig. 1 Sampling sites of *Puccinia striiformis* f. sp. *tritici* isolates from Xinjiang, China and Uzbekistan, Central Asian region during the 2023 crop season**.** (basemap downloaded from http://bzdt.ch.mnr.gov.cn/)

Table 1 Allele richness, expected heterozygosity, and observed heterozygosity and allele range of SSR markers in *Puccinia striiformis* f. sp. *tritici* populations sampled in 2023 in different regions of Uzbekistan, Central Asia, and Xinjiang, China

Locus	No. of alleles	Expected heterozygosity (He)	Observed heterozygosity (Ho)	Allele range
NRJN12	1	0.00	0.00	196
NRJN8	3	0.09	0.10	303–309
NRJN13	7	0.09	0.09	131–159
NRJN3	3	0.38	0.32	338–344
NRJN11	7	0.52	0.97	174–186
NRJO27	9	0.48	0.11	200–241
NRJN6	3	0.07	0.06	315–355
NRJO21	4	0.44	0.60	173–182
NRJN10	3	0.41	0.56	227–263
NRJO18	3	0.38	0.40	334–360
NWU6	3	0.01	0.01	210–214
NRJO20	5	0.43	0.61	284–306
NRJN2	7	0.53	0.04	172–200
NRJN4	6	0.56	0.92	245–259
NRJN9	1	0.00	0.00	334
NRJN5	4	0.45	0.68	218–228
NWU12	5	0.61	1.00	323–332

the saddlepoint approximation method-based model approach to understand individual fitness among their reference populations (McMillan and Fewster 2017). We compared the overall genotype fitness values between both Uzbekistan and Xinjiang populations. So, for that purpose, we built a genetic profile utilizing the log posterior genotype probabilities (LPGs) for the Uzbekistan and Xinjiang populations to examine the genotype fitness with the ontology population and reference population (Fig. 5). The results indicated that the genotypes within the Xinjiang population demonstrated a high genetic diversity as genotypes scattered with some distance from each other (Fig. 5), and showed diversion among individual MLGs, while the Uzbekistan population genotypes appeared more tightly knitted. Some genotypes from the Xinjiang population scattered near the diagonal lines, and some overlapped with those of the Uzbekistan population (Fig. 5), suggesting that certain genotypes in the Xinjiang population shared a common ancestral background with those in the Uzbekistan population and should have population sub-divisions in Xinjiang.

Genotype fitness among the *Pst* populations of Uzbekistan and different Xinjiang epidemic regions

We compared the *Pst* populations in different Xinjiang regions (North Xinjiang, East Xinjiang, Northwest Xinjiang, and West Xinjiang) with the overall Uzbekistan population (Fig. 6a–d). The results displayed that the East Xinjiang population's MLGs scattered within some distance from each individual MLGs within the population, suggesting a unique MLG identity. A minimum log genotype probability of the East Xinjiang genotypes with the reference Uzbekistan population was observed (Fig. 6a), suggesting that either the populations or individual MLGs did not fit each other, and this was also validated through the maximum F_{ST} value (0.45). The Northwest Xinjiang population showed a unique pattern of dispersion, scattering near the diagonal line, and some of its genotypes overlapped with the Uzbekistan population, suggesting the maximum fitness of Northwest genotypes with the Uzbekistan population (Fig. 6b), which was also validated through the lowest F_{ST} value (0.07) between both populations. North Xinjiang and Uzbekistan genotypes showed the maximum genetic divergence between each other (Fig. 6c), which was also reflected by the maximum F_{ST} value (0.5). In contrast, some genotypes of the West Xinjiang population had close genetic relatedness with that of the Uzbekistan population, compared with those of the North Xinjiang and East Xinjiang populations (Fig. 6d). Although the overall F_{ST} value between West Xinjiang and Uzbekistan was comparatively lower than that of the two populations, it was still considerably high (0.43), which could be a result of the migration of some genotypes in the Uzbekistan population to the West Xinjiang region. Thus, the West Xinjiang region is likely to have a threat of potential stripe rust epidemic due to the ingress of foreign *Pst* genotypes, as a few genotypes showed high fitness values in the regions.

The individual genotype within the Uzbekistan *Pst* population (Central Uzbekistan, Fergana Valley, Southern Uzbekistan, and Zarafshan regions) exhibited substantial overlap, indicating that many individuals have a plausible fitness to multiple populations in Uzbekistan and thus cannot be conclusively assigned to a single population (Fig. 7aI–VI). This was further proved through F_{ST} values (0.002–0.01), suggesting no genetic divergence among populations in different Uzbekistan regions. In contrast, within the Xinjiang population, individual genotypes showed subpopulation structure.

Genotype fitness of Pst population within the Xinjiang epidemic regions

We further evaluated individual genotype fitness to the reference within the Xinjiang *Pst* population to check whether individuals have genetic differences. We first compared the *Pst* populations of Northwest Xinjiang with those of North Xinjiang, which showed an overall genetic divergence (F_{ST}=0.49; Fig. 7bI). The West Xinjiang and Northwest Xinjiang populations showed closeness as some individuals from the West Xinjiang population overlapped with the Northwest Xinjiang population

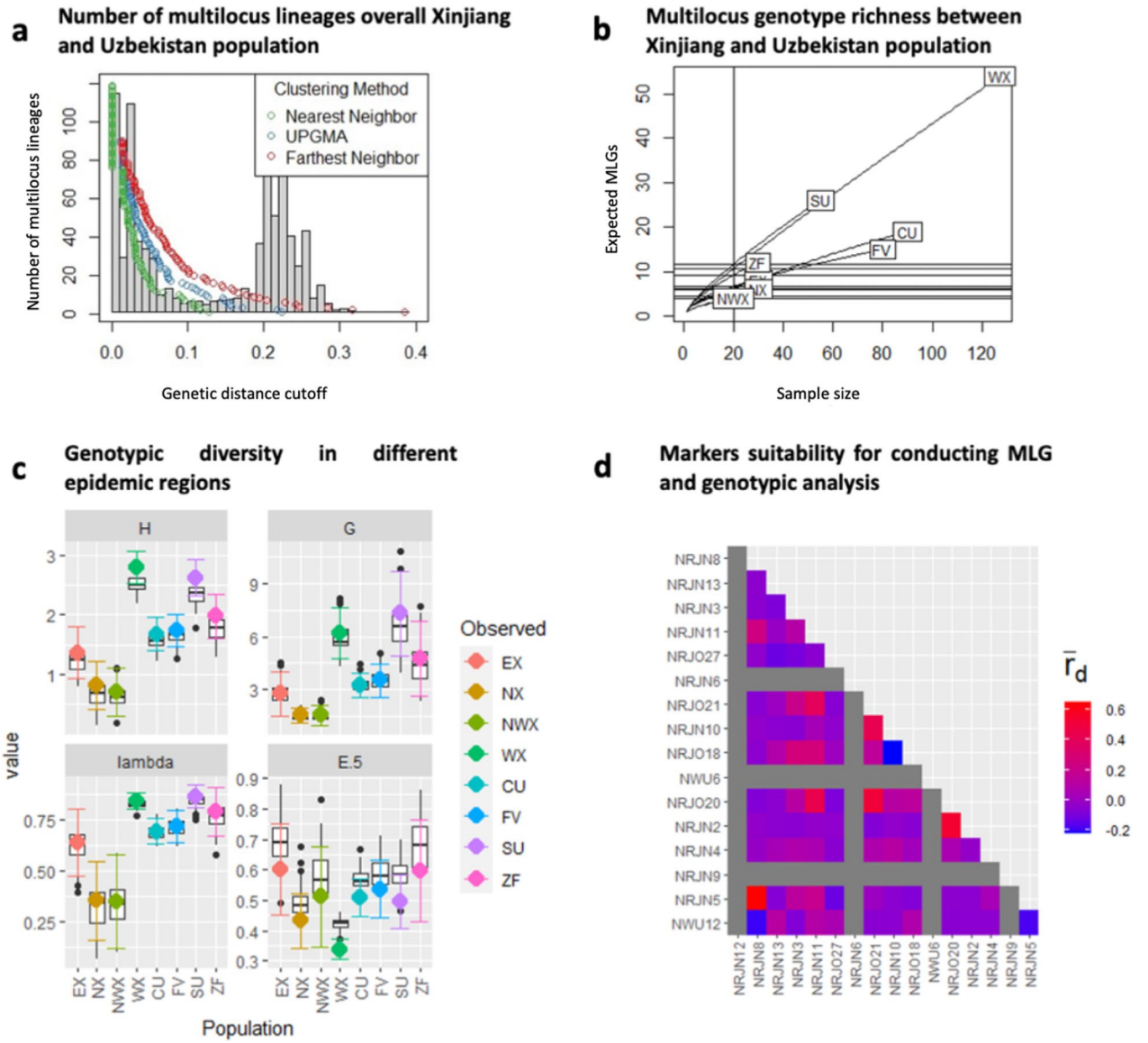

Fig. 2 Suitability of markers for detecting different multilocus genotypes (MLGs) of *Puccinia striiformis* f. sp. *tritici* from different regions of Xinjiang, China and Uzbekistan, Central Asia. **a** The minimum genetic distance at which two individuals would be considered from different clonal lineages (in our results, the optimum threshold level found at 0.007 bravo distance, detected overall 91 different genotype lineages in the dataset. **b** The total number of multilocus genotypes detected in the overall population. **c** Different genotypic diversity parameters. **d** Marker suitability based on linkage disequilibrium

(F_{ST} = 0.43; Fig. 7bII). Also, the Northwest Xinjiang population showed the lowest log probability value with the East Xinjiang population (Fig. 7bIII), indicating divergence among both populations (F_{ST} = 0.47). There was no significant divergence between the West Xinjiang and East Xinjiang populations, and both population genotypes scattered near the diagonal line (Fig. 7bIV), showing high similarity between both population genotypes (F_{ST} = 0.00). Genotypes in the North Xinjiang population showed some genetic divergence from those of the East Xinjiang population (Fig. 7V; F_{ST} = 0.47); likewise, a similar result was observed between North Xinjiang and West Xinjiang genotypes (Fig. 7VI; F_{ST} = 0.47).

Shared MLGs between Uzbekistan and Xinjiang

The gene-clone software was used to identify common MLGs from the 462 isolates between the Uzbekistan and Xinjiang populations. MLG-45 and MLG-47 were the most abundant (105 isolates) in the overall population, but were only detected in Uzbekistan. The most abundant

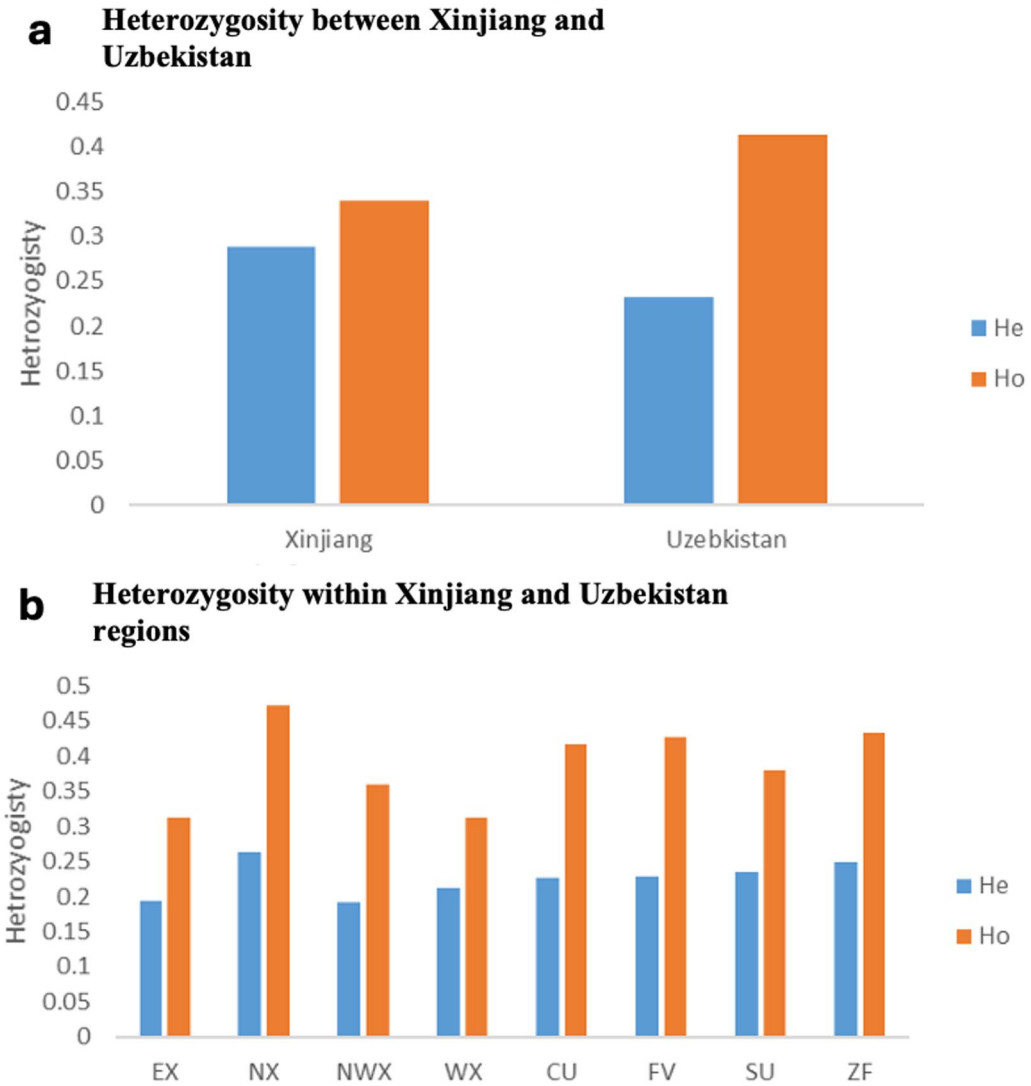

Fig. 3 Expected heterozygosity and observed heterozygosity of *Puccinia striiformis* f. sp. *tritici* isolates collected from different regions of Uzbekistan and Xinjiang during cropping season 2023. **a** Heterozygosity between Xinjiang and Uzbekistan. **b** Heterozygosity within Xinjiang and Uzbekistan regions

Table 2 Diversity parameters in *Puccinia striiformis* f. sp. *tritici* populations sampled in different regions of the Xinjiang and Uzbekistan

Location	No. of sample	No. of MLG	Max freq	Average allele	Diversity	PrCompat	IndAssoc	rBarD
East Xinjiang	30	8	16	2.00	0.66	1.00	4.39	0.46
North Xinjiang	30	6	24	2.06	0.36	1.00	4.80	0.56
Northwest Xinjiang	20	4	16	1.59	0.36	1.00	0.29	0.15
West Xinjiang	127	54	38	3.47	0.85	0.56	2.79	0.24
Overall Xinjiang	207	63	50	3.65	0.86	0.66	3.63	0.33
Fergana valley	80	15	38	2.00	0.73	0.99	0.03	0.00
Southern Uzbekistan	55	26	16	2.12	0.88	0.79	1.83	0.17
Central Uzbekistan	90	19	39	2.18	0.70	0.98	0.24	0.04
Zarafshan	30	12	12	2.06	0.82	0.98	0.84	0.11
Overall Uzbekistan	255	47	106	2.76	0.76	0.91	1.07	0.09

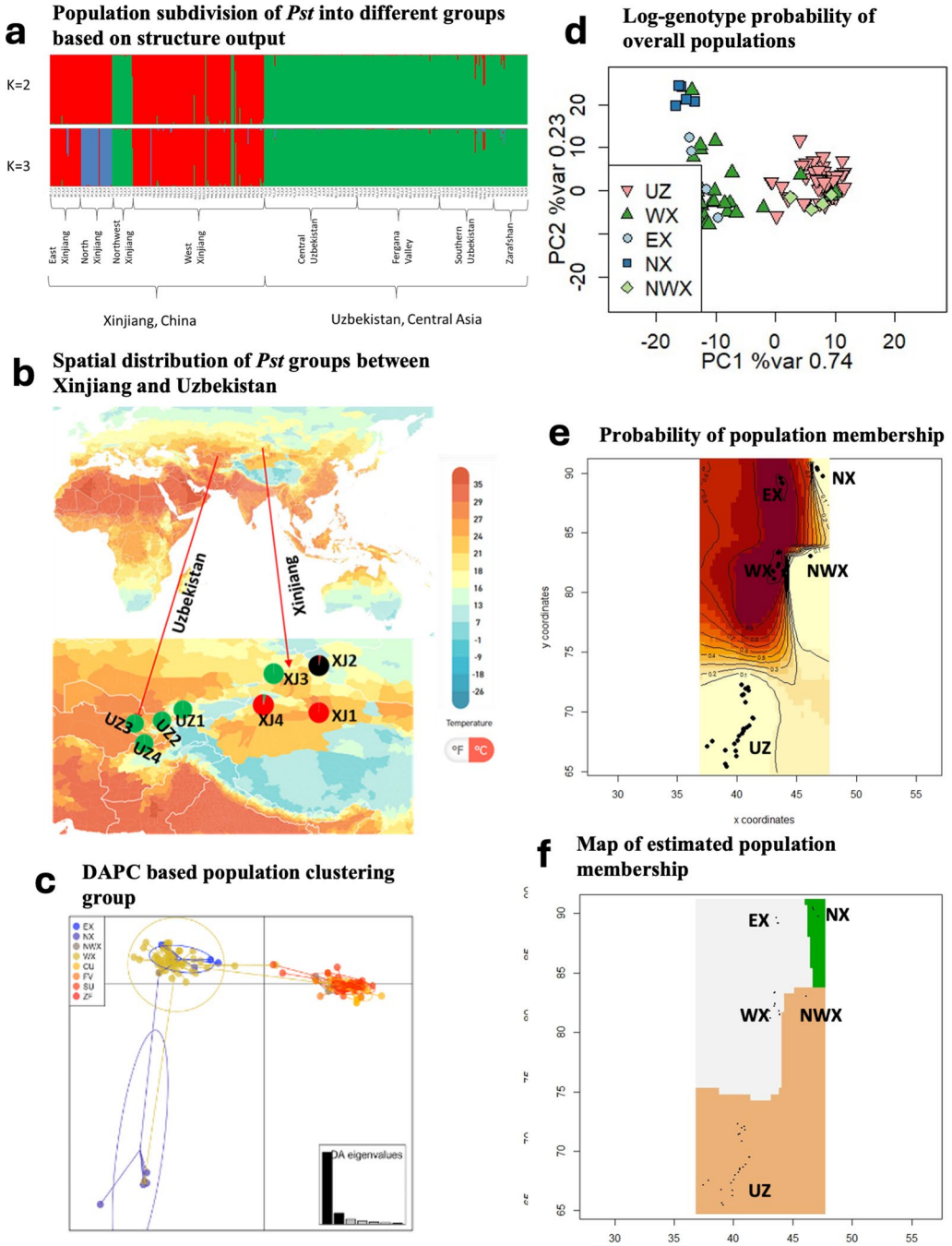

Fig. 4 Population structure of *Puccinia striiformis* f. sp. *tritici* isolates collected from the Xinjiang and Uzbekistan regions during the 2023 crop season. **a** Population subdivision based on Structure output.**b** Spatial distribution of *Puccinia striiformis* f. sp. *tritici* groups between Xinjiang and Uzbekistan. **c** Population genetic cluster group based on DAPC. **d** Log genotype probability of the overall population using the saddlepoint approximation method. **e** Spatial distribution of populations based on the Geneland program. **f** Map of populations using the spatial correlated model using Geneland. **Note:** XJ1 = East Xinjiang (EX), XJ2 = North Xinjiang (NX), XJ3 = Northwest Xinjiang (NWX), XJ4 = West Xinjiang (WX), UZ1 = Fergana Valley (FV), UZ2 = Central Uzbekistan (CU), UZ3 = Zarafshan(ZF) and UZ4 = Southern Uzbekistan (SU), and the geographical heatmap constructed through https://impactlab.org/map/ (Chen et al. 2023), based on mean temperature (June-Augst), at that time disease earlier appeared in north and northwest Xinjiang, a neighboring region of Central Asia

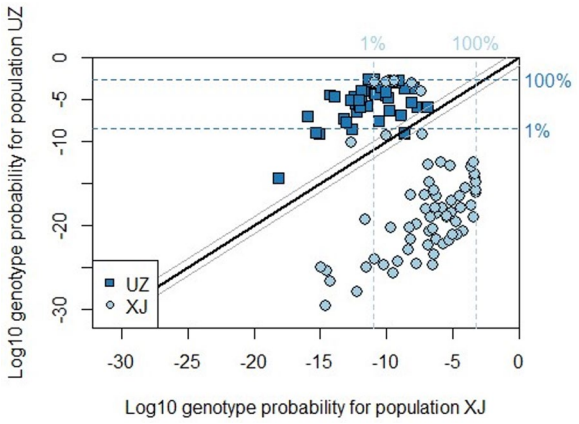

Fig. 5 Estimating Individual genotype fitness of *Puccinia striiformis* f. sp. *tritici* fitness between Uzbekistan and Xinjiang populations

MLGs in Xinjiang were MLG-99 (49 isolates) and MLG-97 (47 isolates). MLG-47 and MLG-29 were abundant in Uzbekistan and Xinjiang, which suggested potential *Pst* migration between Uzbekistan and Xinjiang (Additional file 1: Figure S1). This was supported by the results of STRUCTURE (Fig. 4A), DAPC (Fig. 4c), F_{ST} (Table 3), and phylogenetic analyses (Additional file 1: Figure S2).

In the case of MLG comparison between the Uzbekistan and Xinjiang *Pst* populations, we observed that MLG-45 was shared among all regions of Uzbekistan, i.e., Central Uzbekistan (39), Fergana Valley (38), southern Uzbekistan (16), and Zarafshan (12). MLG-47 was found in West Xinjiang and all Uzbekistan regions, and MLG-29 was shared among the populations of Northwest Xinjiang, Fergana Valley, and Zarafshan of Uzbekistan, suggesting that migration could occur

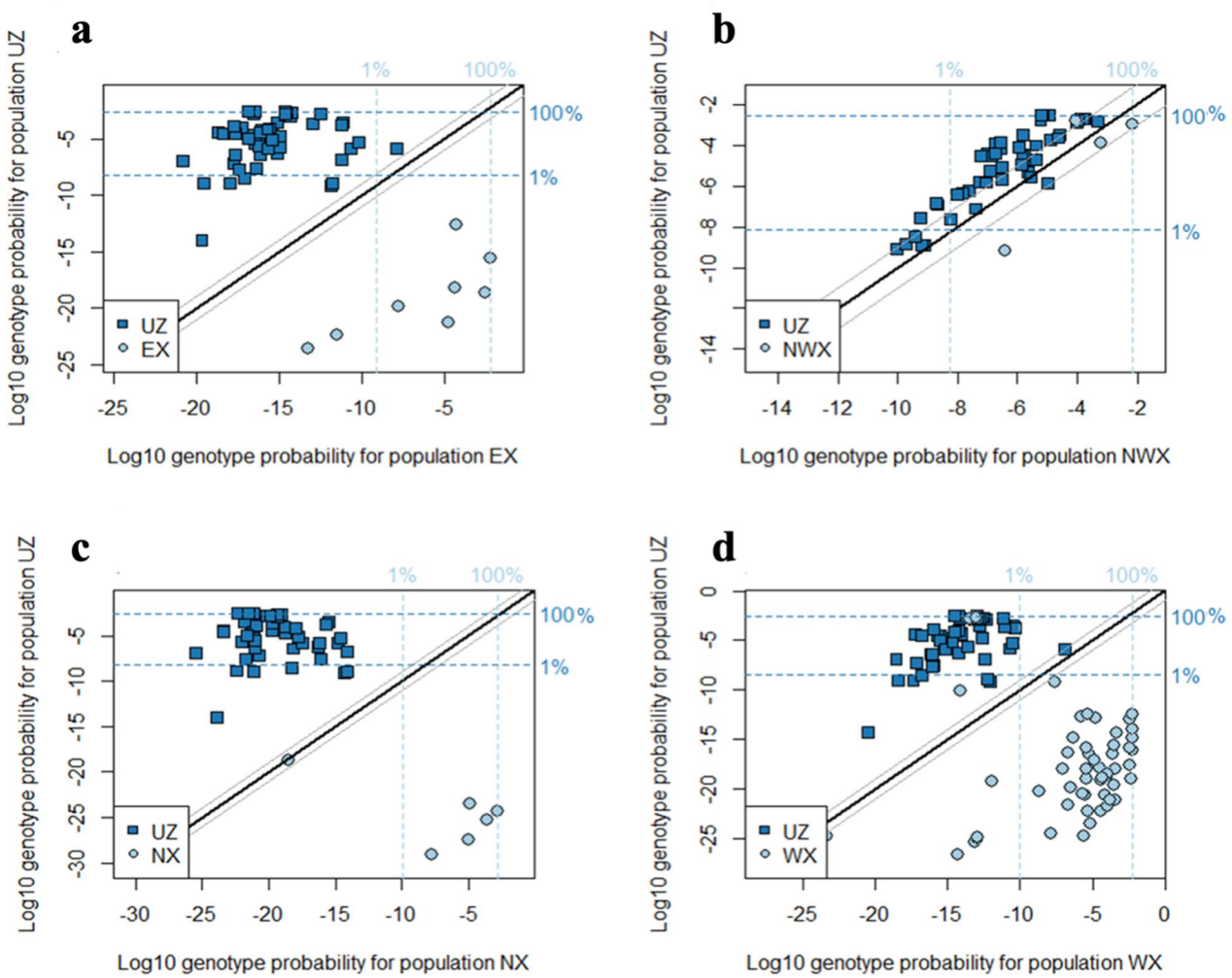

Fig. 6 Estimating individual genotype fitness of *Puccinia striiformis* f. sp. *tritici* among the Uzbekistan and Xinjiang regions **a** Comparison of the East Xinjiang and Uzbekistan populations. **b** Northwest Xinjiang and Uzbekistan populations. **c** North Xinjiang and Uzbekistan populations. **d** West Xinjiang and Uzbekistan populations

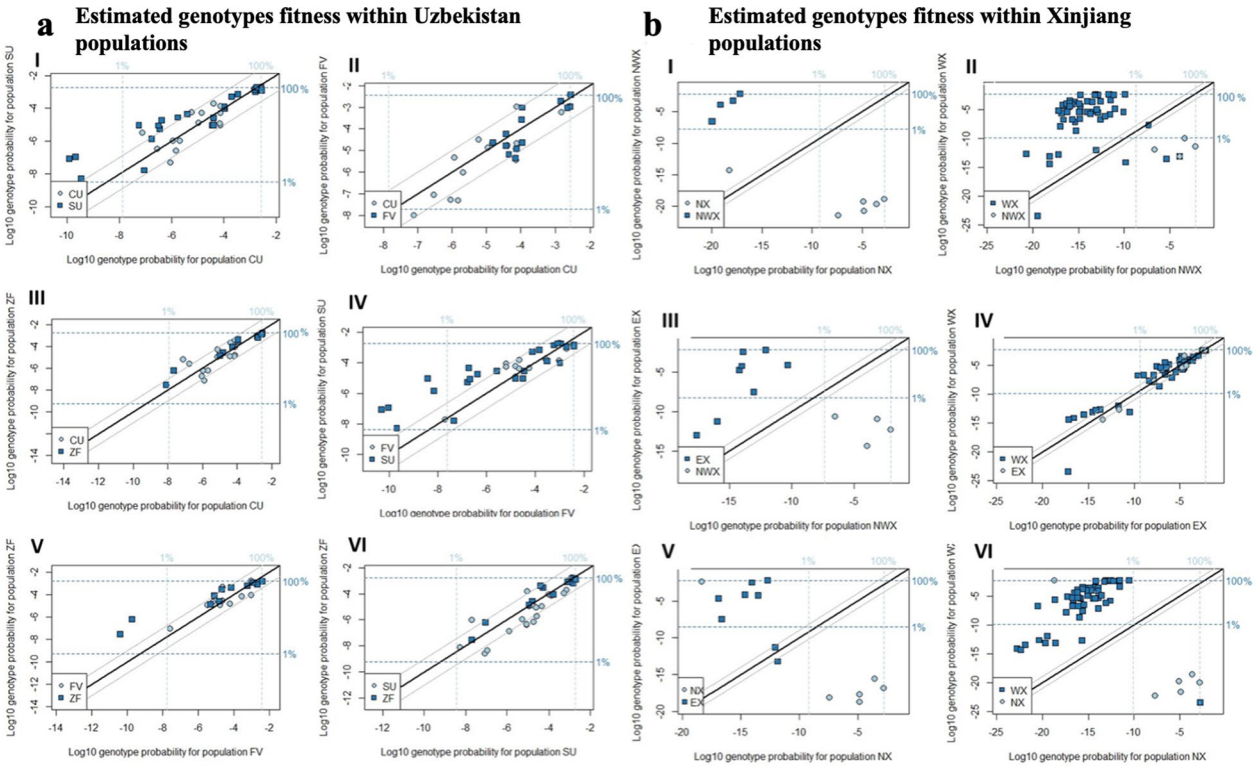

Fig. 7 Estimating individual genotype fitness of *Puccinia striiformis* f. sp. *tritici* within Uzbekistan and Xinjiang populations during cropping season 2023

Table 3 Pairwise divergence of *Puccinia striiformis* f. sp. *tritici* isolates sampled from Xinjiang and Uzbekistan (F_{ST}; upper diagonal) and *Nei*'s genetic distance (lower diagonal) based on 17 SSR markers and analyzed with Genetix 4.05 software

FST	EX	NX	NWX	WX	UZB
EX	–	0.47	0.47	0.00	0.45
NX	0.29	–	0.49	0.47	0.50
NWX	0.24	0.34	–	0.43	0.07
WX	0.00	0.29	0.22	–	0.43
UZB	0.27	0.38	0.02	0.25	–

from Uzbekistan to the Northwest and West Xinjiang regions.

Within Xinjiang, MLG-97 and MLG-99 were prevalent in the West Xinjiang population and shared with the East Xinjiang population, whereas MLG-97 was low in North Xinjiang, suggesting a strong migration pattern from West to East Xinjiang. MLG-30 was found abundant in Northwest Xinjiang but not observed in other parts of Xinjiang.

Migration events between the Xinjiang and Uzbekistan *Pst* populations

Gene flow among Xinjiang and Uzbekistan *Pst* populations was measured through the relative migration network of *Nm* value (Additional file 1: Figure S3). The results showed a high gene flow within the Uzbekistan populations, while the Northwest Xinjiang population had a high gene flow with the Uzbekistan populations. Within Xinjiang, high gene flow was observed between the West and East Xinjiang populations. No significant gene flow was observed among the North and other Xinjiang populations.

Discussion

In the present study, we determined the *Pst* population of Xinjiang, a stripe rust epidemic region isolated from other regions of China (Awais et al. 2022). Our results showed potential migration of *Pst* between Xinjiang and Uzbekistan. This is the first time to report gene flow of *Pst* populations between Xinjiang and Central Asian countries. Our result revealed the inoculum origin of the pathogen for the Xinjiang epidemic region, which provided an insight into understanding the evolution, population structure, and population genetic diversity of *Pst* in

this region and making a prospective strategy for stripe rust management by deploying resistant wheat cultivars.

Although Uzbekistan does not border Xinjiang, in this study, we found that significant gene flow could occur between the Xinjiang and Uzbekistan *Pst* populations. This finding hinted that spores of the pathogen in Uzbekistan were able to spread to Xinjiang by airflow and infect local wheat crops. These inoculum spores could expand its population and affect the local *Pst* population structure in Xinjiang. The Xinjiang region has varied topography and cropping patterns, which may influence the population structure. Based on previous disease outbreaks and geographical topography, we divided the Xinjiang population into four groups (North, Northwest, West, and East). During our field surveillance, we observed early disease infection in the seedling stage in the West Xinjiang region in December (2023). Disease symptoms appeared later in the Northwest Xinjiang (after May). We conducted sampling in the Uzbekistan region in May, while the disease samples were collected from the Northwest Xinjiang region in June. This supports our hypothesis that the disease first appeared in the Uzbekistan region and later spread to the Northwest part of Xinjiang. The disease infection in the western part of Xinjiang appeared earlier than in Uzbekistan, and our results also indicated that both populations had divergence. Spores in Uzbekistan mostly spread to the Northwest (Tacheng region) and limited to West Xinjiang, but not to other regions of Xinjiang (North and East Xinjiang), possibly due to the separation by the Tianshan Mountains located in West Xinjiang. Xinjiang borders Kyrgyzstan, Tajikistan, and Kazakhstan of Central Asia. However, there have been no reports on the association of the *Pst* population in Xinjiang with these countries, which is necessary for further investigation into the relationship of the wheat stripe rust disease epidemic between Xinjiang and other Central Asian countries. Additionally, we have recently demonstrated that the *Pst* population of China, including Xinjiang, was completely different from that of Pakistan, bordering China (Awais et al. 2023).

The adaptability of alien genotypes among the local Xinjiang population was studied further through the heatmap analysis. We spatially allocated genetic groups correlated with environmental factors such as temperature. A previous study identified different temperature-sensitive genes for resistance to specific races of *Pst* in host cultivars (Gerechter-Amitai et al. 1984). We found that the temperature ranges in Northwest Xinjiang and West Xinjiang are similar to those in the Uzbekistan region of Central Asia, which provides favorable conditions for foreign genotypes to nourish along with local populations. However, the temperature-specific genes in wheat cultivars related to the Uzbekistan and China *Pst* lineages need to be identified to develop resistant cultivars to control the disease. We also compared the air pressure data of Xinjiang with Central Asia (https://globalwindatlas.info/en) and noticed that the air pressure is relatively low in Northwest and West Xinjiang compared with the neighboring Central Asian regions, as wind flows from high pressure to low pressure, which could allow *Pst* migration from Central Asia to of the low air pressure areas of Xinjiang.

A relatively high level of genetic diversity has been observed in the Chinese *Pst* population of Xinjiang compared to Uzbekistan. Our previous study reported recombinant and high genetic diversity in Chinese epidemic regions (Awais et al. 2022). Ali et al. (2014) also mentioned that the Himalayas and nearby regions are the center of origin and diversity for *Pst*. Compared to other epidemic regions, the genetic diversity in the Xinjiang epidemic region is relatively low. However, the region is still important due to its proximity to Central Asia, Pakistan, and other epidemic regions of China, where high genetic diversity was previously reported. In this study, the maximum genetic diversity was reported in the West Xinjiang region. In previous years of field observations, we noticed a higher degree of disease severity in the West Xinjiang region than in other regions of Xinjiang. West Xinjiang region may be a center of diversity, and new emerging races migrate from this region to another part of Xinjiang. Low genetic diversity in north-northwest and east Xinjiang was noticed in this study during the 2023 crop season. The MLG results showed that the highest number of MLGs was in West Xinjiang, and some of the MLGs were shared by East and North Xinjiang. The migration network also confirmed high gene flow between the West and East Xinjiang populations and between the Northwest Xinjiang and Uzbekistan populations.

More importantly, the Chinese *Pst* population has triggered significant global attention due to its high level of population genetic diversity (Shan et al. 1998; Duan et al. 2010; Awais et al. 2022), and the occurrence of sexual reproduction under natural conditions (Zhao et al. 2013; Zhao et al. 2023). The environment in China provides conducive ecological and environmental conditions necessary for the evolution of *Pst* (Ma et al. 2015; Awais et al. 2022), promoting the development of more virulent races (Zhao et al. 2013; Zhao et al. 2023). With the particular emphasis on the Xinjiang region in this study due to its connectivity with Central Asian countries and Pakistan, our recent research that has been conducted through self-segregation progeny has shown that the Xinjiang population has a high evolving potential, capable of producing virulent races sexually on alternative host

barberry (Wang et al. 2024). A previous study comparing Chinese and Pakistani populations revealed a significant divergence between both countries' populations (Awais et al. 2023). However, a comparative study between the Chinese Xinjiang population and neighboring Central Asian countries had not been explored until the present study. Similar studies of the Xinjiang *Pst* population with other Central Asian countries are needed to understand the genetic relationships of the pathogen population for better-managing stripe rust in this vast wheat production region of the world.

Conclusions

Our molecular genotyping study revealed the invasion of *Pst* lineages of Uzbekistan, Central Asia, to the Northwest Xinjiang epidemic region of China. Genetic analysis of correlation with environmental factors such as temperature suggested that some Central Asian genotypes of *Pst* are suitable to nourish in the local environment and could be able to infect local wheat cultivars of Xinjiang, China. Comparative genetic analysis of *Pst* suggested no population subdivision in the Uzbekistan regions, while population subdivisions were observed within the Xinjiang region. High genetic diversity was found in Xinjiang, compared with Uzbekistan. The detected migration of the clonal lineages from Uzbekistan may be a threat to wheat production in China, especially in the Xinjiang region.

Methods

Sample collection

To compare the *Pst* populations between Xinjiang and Central Asia, we chose two specific regions: Uzbekistan, situated in the middle of Central Asia and surrounded by other Central Asian countries, and Xinjiang, which shares its borders with Central Asian countries and Pakistan. In Uzbekistan, the sampling sites were selected based on different wheat cultivation zones previously reported by Khalikulov et al. (2016). These regions included Fergana Valley, Central Uzbekistan, Zarafshan, and Southern Uzbekistan. In Xinjiang, we subclassified the sampling regions to East Xinjiang, West Xinjiang, North Xinjiang, and Northwest Xinjiang, according to the wheat stripe rust epidemic history (Fig. 1). Samples were collected from various regions in Uzbekistan in May 2023, and Xinjiang sampling was done during different intervals of time (December–July 2023). We ensured the maximum representation of samples from each epidemic region. For that purpose, a minimum distance of at least 15 km from one sampling field to another was maintained. An infected leaf with a single stripe of lesions (uredinia) longer than 5 cm, as shown in Additional file 1: Figure S4, was picked and put in a semitransparent paper envelope. All samples were then stored in a bag with silica gels at 4°C in a desiccator in a refrigerator after completely dried.

DNA extraction

Genomic DNA was extracted from a leaf sample or urediniospores (~5 mg) after single uredial spore multiplication following the CTAB method (Ali et al. 2017) in the case of insufficient stripe of lesions. Quality and quantity of DNA was measured using a spectrometer (NanoDrop 1000, Thermo Scientific, Waltham, MA, USA). The DNA solutions were stored at −20°C until use.

PCR amplification

Seventeen SSR primers were selected for genotyping *Pst* isolates from Xinjiang and Uzbekistan (Additional File 2: Table S1). Three different fluorescent dyes (HEX, FAM, and NED) were used for tagging. The PCR amplification was carried out using high-quality reagents, including *Tag* Plus DNA Polymerase (Sangon, B600090), 10×PCR buffer (with Mg^{2+}; Sangon, B600017), dNTPs (10 mM; Sangon, B500056), sterilized deionized water (E607017), 6×DNA Loading Dye (ThermoFisher, R0611), DNA Ladder Mix (100–3000 bp; B500437), 50×TAE (Sangon, B548101), Agarose H (Sangon, A500016), 1×TE (Sangon, B548106), POP-7TM Polymer (ThermoFisher, 4,363,785), and HiDi™ Formamide (ThermoFisher, 4311320). The conditions for PCR reaction were given in the Additional File 2: Tables S1, S2. A standardized PCR protocol was followed, and the PCR products were then detected through a 3730xl ABI sequencer.

Population genetic analyses

The SSR data were used to perform genetic analyses on different populations. The observed and unbiased expected heterozygosity, the estimation of F_{ST}, *Nei's* genetic distance, and linkage disequilibrium between loci using 1000 random permutations were done through the Genetix V4.05 Program (Belkhir et al. 2004). Visualization of multilocus lineage graph, multilocus genotype (MLG) in different regions of Xinjiang and Uzbekistan, and different diversity parameters were drawn through the R package POPPR (Grünwald et al. 2017). Principal coordinate analysis (PCoA) and network analysis of the neighbor-joining (NJ) tree were performed in the R adegenet package (Jombart et al. 2010). Model-based Bayesian clustering to identify genetic clusters among populations was done through STRUCTURE 2.3.4 (Pritchard et al. 2000). A Markov chain Monte Carlo (MCMC) simulation was performed using the Bayesian framework. The assignment to various clusters ranged from *K1* to *K10*; at each *K* value, 10 independent runs with 100,000 iterations and a burn-in

period of 100,000. CLUMPAK (Cluster Markov packager across *K*) was used to examine consensus among multiple separate runs at different *K* levels (Kopelman et al. 2015). The spatial structure was further assessed with the R package Geneland (Guillot et al. 2009). MLGs were determined using GENECLONE software, whereas their distribution was estimated across the different regions. POPULATION software (Langella 2002) was used to measure phylogenetic distance using the *Nei's* genetic distance approach (Nei 1972), and these genetic distance values were used to construct a phylogenetic tree using the Mega 7 software. Genotypic diversity, standardized index of association (rbarD), number of different genotypes, and frequency of most frequent genotypes were analyzed using the Multilocus software (Agapow and Burt 2001). Visualizations for genetic assignment analyses using the saddlepoint approximation method were done through R Geneplot package (McMillan and Fewster 2017). A migration network based on effective migrants (*Nm*, *N* is the effective population size of each population, and *m* is the migration rate between populations) was visually generated in the geneflow pattern network among Xinjiang and Uzbekistan regions using the 'diversity' Package in R (Bai et al. 2021).

Abbreviations

Pst	*Puccinia striiformis* f. sp. *tritici*
He	Expected heterozygosity
Ho	Observed heterozygosity
MLG	Multilocus genotype
LPGs	Log posterior genotype probability
EX	East Xinjiang
NX	North Xinjiang
NWX	Northwest Xinjiang
WX	West Xinjiang
FV	Fergana Valley (Uzbekistan)
CU	Central Uzbekistan
ZF	Zarafshan (Uzbekistan)
SU	Southern Uzbekistan
UZB	Uzbekistan

Supplementary Information

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Additional file 1: Figure S1 Distribution of multilocus genotypes of *Puccinia striiformis* f. sp. *tritici* collected during crop season 2023. **Figure S2** Relationship of Chinese *Puccinia striiformis* f. sp. *tritici* populations based on analysis of 17 SSR genotype data. **Figure S3** Relative migration network of *Puccinia striiformis* f. sp. *tritici* populations among the different regions of Xinjiang and Uzbekistan; the depth of the blue line shows the strength of gene flow, the green color represents the Xinjiang epidemic region, and the pink represents Uzbekistan regions. **Figure S4** A wheat stripe rust sample with a single stripe of uredinia selected for genotyping.

Additional file 2: Table S1 Seventeen sets of simple sequence repeat (SSR) markers used for genotyping of *Puccinia striiformis* f. sp. *tritici* populations of Xinjiang and Uzbekistan. **Table S2** PCR preparation. **Table S3** PCR amplification program.

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Author contributions
JZ and ZK conceptualized the study. MA, JM, KT, DE and MSK performed the sampling. MA, JM and LL performed the experiment and data analysis. BZ and WC curated the data. MA and JM wrote the manuscript.

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Availability of data and materials
The data supporting this publication are provided within this paper. Requests for materials relating to this paper should be made to Jie Zhao (jiezhao@nwafu.edu.cn) at Northwest A&F University, and Jinbiao Ma (majinbiao@ms.xjb.ac.cn) at Xinjiang Institute of Ecology and Geography.

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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