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RESEARCH ARTICLE

Genotypic and virulence dynamics of *Phytophthora infestans* populations in southwestern China

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Highlights

- *Phytophthora infestans* populations in southwestern China comprise three lineages, with the EU lineage being dominant.
- The predominant genotype MLG24 significantly contributes to the pathotypic diversity of the EU lineage.
- Two highly virulent MLG24 isolates could be controlled by two wild potatoes and three fungicides.

Abstract

The oomycete pathogen *Phytophthora infestans* causes late blight disease that severely reduces potato production worldwide. Monitoring the genotypic and virulence dynamics of *P. infestans* populations is vital for management of late blight. *Phytophthora infestans* populations in southwestern China diversify in genotypes and virulence, but the most recent status of these populations remains elusive. In this study, 218 isolates collected from six locations in southwestern China from 2019 to 2022 were analyzed for genotypic and virulence dynamics as well as effective management strategies. Phylogenetic analysis of simple sequence repeats-classified multi-locus genotypes (MLGs) revealed that these populations comprise three lineages, of which the EU lineage is dominant. These populations had overcome the resistance mediated by *R3a*, *R3b* and *Rpi-blb3* and had an increased trend in overcoming the resistance mediated by *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1*. The EU lineage consisted of 19 MLGs and the predominant genotype MLG24 significantly contributed to the pathotypic diversity of the EU lineage. In addition, two independent MLG24 isolates, CQ-22-16-1 and CQ-22-20-1, overcame the resistance mediated by all seven resistance genes and were virulent on 30 potato cultivars. Notably, two *Solanum candolleanum* relatives were highly resistant to these two highly virulent isolates. Furthermore, these two isolates could be controlled by three fungicides. In summary, this study elucidates the genotypic and virulence dynamics of *P. infestans* populations in southwestern China and provides valuable insights into effective control measures.

Keywords: potato, *Phytophthora infestans*, genotypic dynamics, virulence dynamics

1. Introduction

Potato (*Solanum tuberosum*) is the fourth most important crop in the world while China is the largest potato producer (FAOSTAT 2020; Naumann *et al.* 2020). There are four potato-growing regions in China, namely the northern, central, southern and southwestern regions (Jansky *et al.*

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2009). The southwestern region, including Chongqing Municipality as well as provinces of Guizhou, Hubei, Hunan, Sichuan and Yunnan, has recently become the largest potato production zone in China (Wang J *et al.* 2023). However, potato production in southwestern China is severely reduced by late blight, which is the most devastating disease of potato production worldwide and caused by the oomycete *Phytophthora infestans* (O'Beirne 2000). *Phytophthora infestans* evolves rapidly and newly emerged isolates with enhanced virulence on hosts or reduced sensitivity to fungicides often become predominant, leading to an altered genotypic and virulence structure of *P. infestans* populations (Dong and Zhou 2022). Therefore, monitoring the genotypic and virulence dynamics of *P. infestans* populations is vital for preventing potential outbreaks of late blight and breeding highly resistant germplasm (Cooke *et al.* 2012).

Population genotypes of *P. infestans* have been studied by various methods, including mitochondrial DNA, restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism and simple sequence repeats (SSR) (VanderLee *et al.* 1997; Cooke and Lees 2004; Fry 2016; Roy *et al.* 2021). To date, SSR has been used for genotyping *P. infestans* populations in different countries (Guo *et al.* 2009; Li *et al.* 2009, 2012, 2013b; Cooke *et al.* 2012; Fry *et al.* 2013; Han *et al.* 2013; Chmielarz *et al.* 2014; Chowdappa *et al.* 2015; Zhu W *et al.* 2015; Tian *et al.* 2016). *Phytophthora infestans* populations in China comprise three SSR lineages, namely CN01, CN02 and CN03, with the first two being the dominant lineages (Li *et al.* 2013b; Roy *et al.* 2021). CN01 is widespread in both northern and southern China and is represented by the RFLP genotype SIB-1 originally identified in Siberia (Elansky *et al.* 2001; Akino *et al.* 2004; Guo *et al.* 2010; Li *et al.* 2013b). CN02 is widespread in southwestern China and is represented by the SSR genotype B13, which originated from the Netherlands and has dominated Europe since 2004 (Cooke *et al.* 2010; Yoshida *et al.* 2013; Fry 2020; Beninal *et al.* 2022). This genotype was first recorded from Yunnan Province in China in 2005 and has become the dominant genotype in southwestern China (Li *et al.* 2013b; Wu *et al.* 2024). CN03 is mainly distributed in Fujian Province and is represented by the RFLP genotype US-11, which caused late blight in Taiwan Province of China in 1997 (Jyan *et al.* 2004; Chen *et al.* 2009). Meanwhile, these three lineages are also present throughout China (Li *et al.* 2013b; Li *et al.* 2020). With increased potato seed transportation and fast-evolving *P. infestans* genomes, it is necessary to annually examine the genotypic diversity of *P. infestans* populations aiming for late blight management.

The pathotypic diversity of *P. infestans* populations is always determined by race virulence on a combination of eleven Mastenbroek differential sets (Kim *et al.* 2012). In China, *P. infestans* populations from different regions always display distinct pathotypes and *P. infestans* populations from southwestern China are more complex than those from other regions (Li *et al.* 2013b). Highly virulent isolates, which are virulent on all these eleven Mastenbroek differential sets, are growing in recent years and are detected more frequently in southwestern region than other regions (Li *et al.* 2020; Zhang *et al.* 2021). Since these eleven Mastenbroek differential sets harbor identified and unknown resistance (*R*) genes, which were introgressed from wild potato relatives, and some of them harbor multiple *R* genes, it is impossible to use them to specify the pathotype of *P. infestans* isolates (Kim *et al.* 2012). Thus, near-isogenic lines, which individually express a single *R* gene in Desiree, offer a better choice to specify the specific pathotype of *P. infestans* isolates (Zhu *et al.* 2015).

Mutations in avirulence (*Avr*) genes, such as gene deletion, gene silencing and single nucleotide polymorphisms (SNPs), enable *P. infestans* to evade recognition by *R* genes (Vleeshouwers *et al.* 2011). For instance, *P. infestans* isolates lacking *Avr1* and *Avr3b* escape the resistance mediated by *R1* and *R3b*, respectively (Vleeshouwers and Oliver 2014). Likewise, *P. infestans* isolates silenced for *Avr3b*, *Avrblb2*, *Avr8* and *Avrvnt1* escape the resistance mediated by *R3b*, *Rpi-blb2*, *R8* and *Rpi-vnt1.1*, respectively (Yin *et al.* 2017; Pais *et al.* 2018; Zhang *et al.* 2021). Meanwhile, substitutions of lysine with glutamic acid at the 10th amino acid (AA) and of isoleucine with methionine at the 103rd AA abolish the recognition of *Avr3a* by *R3a* (Armstrong *et al.* 2005). Additionally, *Avr2-like* is homologous to *Avr2* and contains 25 SNPs that suppress *R2*-mediated recognition (Gilroy *et al.* 2011). Moreover, a frameshift mutation in *Avr4* produces a truncated protein, which suppresses *R4*-mediated recognition (van Poppel *et al.* 2008). Therefore, monitoring *Avr* polymorphisms can guide the deployment of functional *R* genes for germplasm breeding.

Breeding high resistance potato cultivars is one of the most effective strategies for controlling late blight (Nowicki *et al.* 2012; Dong and Zhou 2022). So far, more than 70 *R* genes have been identified from wild potato and tomato relatives and most identified *R* genes, including *R3a*, *R3b*, *Rpi-blb3*, *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1*, were cloned from wild potato relatives (Paluchowska *et al.* 2022). In addition, wild potato relatives also harbor a large number of unknown *R* genes that confer resistance to aggressive *P. infestans* isolates, which have escaped the recognition by identified *R* genes (Paluchowska *et al.* 2022). With decreasing resistance efficiency of a single *R* gene, stacking multiple *R* genes offers a promising approach to confer durable and broad-spectrum resistance to late blight (Berindean *et al.* 2024). Therefore, screening new *R* genes from wild potato relatives for further gene stacking in cultivated potatoes is vital for breeding highly resistant germplasm and preventing potential outbreaks of late blight.

To monitor the genotypic and virulence dynamics of *P. infestans* populations in southwestern China, 218 isolates, which were collected from Chongqing, Guizhou, Hubei, Hunan, Sichuan and Yunnan from 2019 to 2022, were analyzed for SSR genotypes and pathotypes. These *P. infestans* populations comprised three lineages, namely the EU, US and SIB lineages. The EU lineage was the major lineage, with MLG24 being the predominant genotype. Almost all isolates were virulent on the *R3a*, *R3b* and *Rpi-blb3* near-isogenic lines and these populations showed increased virulence on the *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1* near-isogenic lines. The EU lineage consisted of 19 MLGs and the predominant genotype MLG24 significantly contributed to the complex

pathotypic diversity of the EU lineage. In addition, two independent MLG24 isolates, CQ-22-16-1 and CQ-22-20-1, overcame the resistance mediated by all seven *R* genes and were virulent on 30 potato cultivars. Notably, these two highly virulent isolates could not infect two wild potatoes and could be controlled by three fungicides. In summary, this study elucidates the genotypic and virulence dynamics of *P. infestans* populations in southwestern China and provides valuable insights into effective control measures.

2. Materials and methods

2.1. Growth conditions for *P. infestans* strains and potatoes

Phytophthora infestans strains used in this study were cultured on rye-sucrose plates and incubated at 18°C in the dark. Rye-sucrose plates were prepared by sterilizing 60 g rye in 800 mL ddH_2O, homogenizing sterile rye and re-sterilizing the filtrate of homogenized rye together with 20 g sucrose and 15 g agar in ddH_2O, bringing the total volume to 1 L (Wang L *et al.* 2023). Mycelia of *P. infestans* strains were harvested from liquid cultures in pea broth medium. Approximately 10 discs of each *P. infestans* strain from rye-sucrose plates were placed into the pea broth and mycelia were harvested after 5 days of incubation at 18°C in the dark. Pea broth medium was prepared by sterilizing 120 g of peas in 1 L ddH_2O, filtering the sterile pea broth and re-sterilizing the filtrate with ddH_2O, bringing the total volume to 1 L. Potato near-isogenic lines and cultivar Desiree were preserved on Murashige and Skoog (Phytotech Labs, USA) medium at 20°C in an intelligent light incubator with a 16-h light and 8-h dark cycle.

2.2. Collection, isolation and purification of *P. infestans* isolates

In the potato-growing regions of Chongqing, Guizhou, Hubei, Hunan, Sichuan and Yunnan from 2019 to 2022, potato leaves with typical late blight lesions were collected from different plants, which were separated by at least two meters to avoid cross-contamination. Each leaf was separately wrapped in absorbent paper, which was subsequently placed in a kraft paper envelope that was immediately stored in a cool container. Importantly, these leaves were used for *P. infestans* isolation within 48 h post-collection under laboratory conditions. Leaves were washed with sterile ddH_2O five times to remove contaminants, slightly air-dried and subsequently placed upside down in humid infection trays. After 20–30 h of incubation, the aerial mycelium of *P. infestans* from each lesion area was collected with sterile dissecting needles and immediately transferred to a selective rye-sucrose plate containing ampicillin (50 mg L^{-1}), rifampicin (50 mg L^{-1}) and pentachloronitrobenzene (50 mg L^{-1}) at 18°C in the dark for 5 days. To further purify the isolates, *P. infestans* mycelium growing on the selective plates was re-grown on a new selective rye-sucrose plate at 18°C in the dark. After 8 days, five mycelium plugs from each isolate were suspended in milk in a 2 mL tube, which was subsequently stored in liquid nitrogen.

2.3. gDNA isolation

Mycelia from liquid cultures of *P. infestans* isolates grown in pea broth medium were used for gDNA isolation using the DNAsecure Plant Kit (Tiangen, China). gDNA was quantified by a NanoDrop One spectrophotometer (Thermo Fisher Scientific, USA) and subsequently diluted to 50 ng μL^{-1}. In addition, gDNA of US-11 and SIB-1 was provided by Philip Kear from the International Potato Center, China.

2.4. PCR and genotyping

B13, US-11, SIB-1 and collected *P. infestans* isolates were genotyped by SSR with 12 pairs of published primers, namely Pi02, Pi4B, Pi16, Pi33, Pi56, Pi63, Pi70, Pi89, SSR2, SSR6, SSR8 and SSR11 (Appendix A) (Knapova and Gisi 2002; Lees *et al.* 2006; Li *et al.* 2013a). Each primer pair was labeled with a fluorescent dye. Specifically, Pi02, Pi33 and SSR11 were labeled with TAMRA, Pi4B and SSR2 were labeled with ROX, Pi16, Pi63, Pi70 and SSR6 were labeled with HEX, while Pi56, Pi89 and SSR8 were labeled with FAM. Fragments were amplified in PCR tubes using a 12.5 μL reaction mixture, which included *P. infestans* gDNA (4 ng μL^{-1}), forward and reverse primers (0.16 μmol L^{-1}, Sangon Biotech, China), 4.25 μL of ddH_2O and 2× Taq Plus Master Mix II DNA polymerase (Vazyme, China). PCR was performed on a T100 thermal cycler (Bio-Rad, USA) with the following program: 94°C for 4 min, followed by 34 cycles of denaturation at 94°C for 30 s, annealing at 58°C for 30 s and extension at 72°C for 30 s. A final extension at 72°C for 10 min was performed, followed by incubation at 12°C. To check the quality of PCR products, 5 μL of product was loaded in a 2% agarose gel for electrophoresis and imaged by a Tanon 3500 (Tanon, China). PCR products were loaded onto a 96-well plate and sequenced by a 3730 DNA analyzer (Applied Biosystems, USA). The GeneMarker software (Applied Biosystems, USA) was used to read the fragment sizes of PCR products to obtain peak data. Each fragment was represented by a peak with a distinct color matching the fluorescent dyes used to label primers. In addition, an internal standard was used to determine the length of DNA fragments, and an allele ladder was used to identify and exclude fragments of unknown samples.

2.5. SSR data analysis

Before analysis, SSR data were corrected with the aim that the same genotype has only one representative per population by using the R package poppr (Kamvar *et al.* 2014). To further visualize groupings, discriminant analysis of principal components (DAPC) was performed using the R package of adegenet (Jombart 2008). Subsequently, a rooted neighbor-joining tree based on Bruvo's distance with a combination model was generated by using the R package of poppr with 1000 bootstrap iterations (Paradis 2010; Kamvar *et al.* 2014). To further examine distances among different MLGs, a minimum spanning network (MSN) diagram was generated for all MLGs. Poppr was also used to obtain population characteristics, including the number of MLGs, the basic parameters of expected MLGs at the smallest sample size of at least 10 (eMLG), the Shannon-Weiner index of

MLG diversity (H), the Stoddart and Taylor index of MLG diversity (G), the Simpson index corrected for sample size by multiplying the index value by N/(N-1) (λ), the E.5 measure of evenness, the Nei's unbiased gene diversity (Hexp) and the index of association (I_A) (Appendix B).

2.6. Virulence diversity of *P. infestans* isolates on potato plants

B13 and collected *P. infestans* isolates were both tested for virulence on Desiree and seven near-isogenic lines, which individually express *R3a*, *R3b*, *Rpi-blb3*, *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1* in the Desiree background. Specifically, a 10 μL aliquot containing approximately 3,000 zoospores of each isolate was inoculated onto detached leaves placed in a humid infection tray, which was kept at 18°C in the dark for 12 h and then transferred to an intelligent light incubator with a 16-h light and 8-h dark cycle. After 5 days, the disease index was recorded as immunity (IM), hypersensitive response (HR), medium resistance (MR), medium susceptibility (MS) and high susceptibility (HS). B13 and two highly virulent isolates, CQ-22-16-1 and CQ-22-20-1, were also tested for virulence on 30 potato cultivars and 30 *S. candolleanum* relatives with the same procedure described above.

2.7. RNA isolation

Phytophthora infestans zoospores were inoculated onto the detached leaves of Desiree with the same procedure described above. Infected samples were collected at 1-, 2- and 3-day post-infection (dpi) and subjected to RNA isolation by the Total RNA Extraction Kit (Pudi, China). RNA was quantified by a NanoDrop One (Thermo Fisher Scientific, USA) and subsequently reverse-transcribed to obtain cDNA.

2.8. Sequence and expression polymorphisms of *Avr* genes in *P. infestans* isolates

For sequence polymorphism analysis, the coding sequences together with 1 kb upstream and downstream flanking sequences of *Avr8* and *Avrvnt1* were amplified with their corresponding gDNA templates and primers (Appendix C). *Avrblb2* and *Avrblb1* were excluded as they have multiple copies and homologs in *P. infestans* (Thilliez *et al.* 2019). Subsequently, sequenced fragments were aligned and analyzed for the presence or absence of SNPs. For expression polymorphism analysis, RT-PCR was performed using cDNA from each *P. infestans* isolate and primers targeting *Avr8* and *Avrvnt1* (Appendix D). *PITG_11766* was used as a positive control (Actin), while *PITG_09823* was used as a negative control. Once finished, 5 μL of RT-PCR product was loaded on a 2% agarose gel for electrophoresis and imaged by a Tanon 3500 (Tanon, China).

2.9. Sensitivity of *P. infestans* isolates to fungicides

Rye-sucrose plates were supplemented with cymoxanil, dimethomorph and fluazinam at indicated concentrations (Suli Agro Science (Shanghai) Co., Ltd., China). These fungicides were dissolved in DMSO (Sigma-Aldrich, USA), which was also used as a control. A mycelium plug with a diameter of 5 mm was isolated from the edge of fresh colonies and placed in the center of fungicide-containing medium plates, which were subsequently incubated in the dark at 18°C for 7 days. Each treatment has three replicates and the diameter was measured twice for each colony by the cross method. Subsequently, the growth inhibition percentage and median effective concentration (EC_{50}) values inhibition were calculated.

3. Results

3.1. *Phytophthora infestans* populations in southwestern China comprise three lineages

From 2019 to 2022, a total of 218 *P. infestans* isolates were collected from Chongqing, Guizhou, Hubei, Hunan, Sichuan and Yunnan in southwestern China (Appendix E). All isolates were genotyped using 12 pairs of SSR molecular marker primers, which were previously established for *P. infestans* genotyping (Appendix A) (Knapova and Gisi 2002; Lees *et al.* 2006; Li *et al.* 2013a). Subsequently, SSR analysis categorized these isolates into 27 different MLGs (Appendix F). Among these MLGs, MLG1, MLG2, MLG3, MLG5, MLG8, MLG10, MLG11, MLG14, MLG15, MLG19, MLG20, MLG24 and MLG25 were detected multiple times. In addition, MLG24 accounted for 50.00% of the collected isolates and was dominant in southwestern China (Appendix F).

To investigate potential genetic relationships among collected isolates, a phylogenetic tree was constructed with all isolates as well as three reference strains, B13, US-11 and SIB-1, which represent the EU, US and SIB lineages, respectively. Phylogenetic and DAPC analyses revealed that *P. infestans* populations in southwestern China comprise all three lineages (Fig. 1-A and B; Appendix G). The EU lineage was the main lineage, which consisted of 19 MLGs that were further grouped into three sub-clades (Fig. 1-A). In addition, the EU lineage was represented by MLG24 (Fig. 1-A). Likewise, the US lineage consisted of MLG5, MLG6 and MLG7 (Fig. 1-A). Meanwhile, the SIB lineage consisted of MLG1, MLG2, MLG3, MLG14 and MLG15 (Fig. 1-A).

To examine the epidemic genotype of each lineage across different years and regions, the percentage of the main MLGs from each lineage and the rest MLGs, which were designated as others, was determined. Not all main MLGs were detected from 2019 to 2022, but MLG24 was consistently prevalent throughout these four years, accounting for 33.33%, 53.49%, 45.10% and 65.31% of the collected isolates, respectively (Fig. 1-C). Similarly, not all main MLGs were detected from Chongqing, Guizhou, Hubei, Hunan, Sichuan and Yunnan, but MLG24 was consistently prevalent in these six regions, accounting for 58.97%, 41.84%, 50.00%, 66.67% and 60.00% and 100% of the collected isolates, respectively (Fig. 1-D).

Taken together, *P. infestans* populations in southwestern region comprise three lineages and the predominant EU lineage contains more MLGs than the other two lineages.

3.2. *Phytophthora infestans* populations in southwestern region become more aggressive and display distinct pathotypic complexity in different regions

To address the virulence type of these isolates, they were

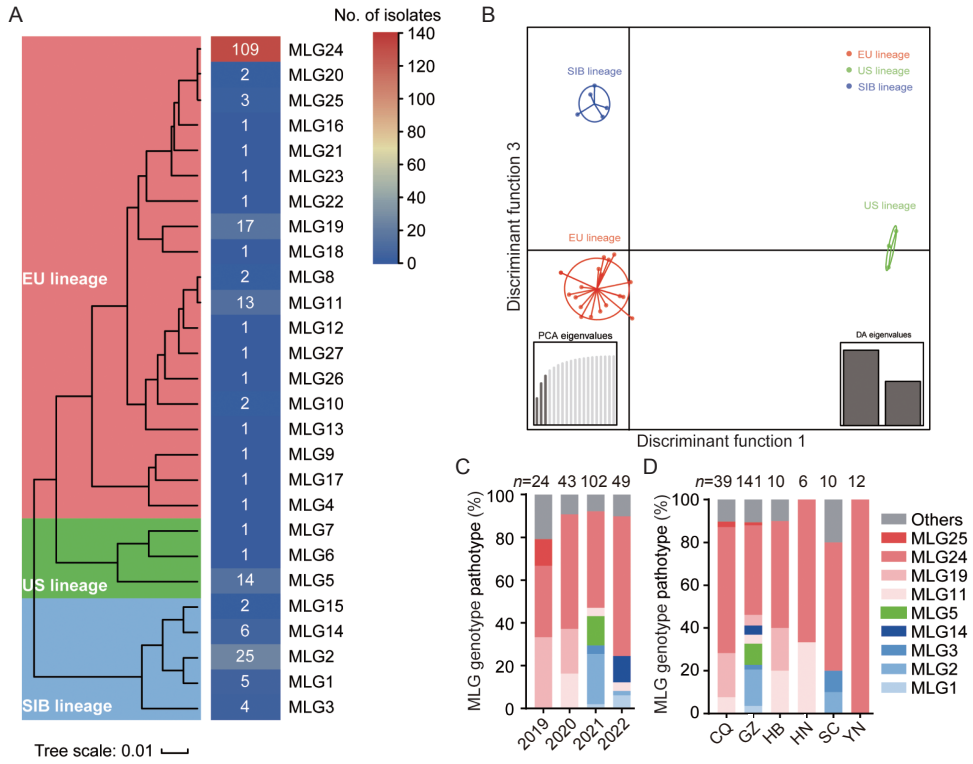


Fig. 1 *Phytophthora infestans* populations in southwestern China comprise three lineages with MLG24 of the EU lineage being the predominant genotype. A, a phylogenetic tree constructed by multi-locus genotypes (MLGs) reveals that *P. infestans* populations in southwestern China comprise three lineages. 218 isolates were genotyped by SSR and assigned as different MLGs, and the number of each MLG is highlighted by blue to red colors. B, DAPC analysis reveals that 218 isolates are classified into three groups. The inset panels for PCA and DA eigenvalues indicate the overall variability among individuals and the relative capture of variance for each discriminant function, respectively. The *X*- and *Y*-axes, respectively, indicate the first and third discriminant principal components, which best summarize the differences between clusters while neglecting within-cluster variation. C and D, the percentage of different MLGs in different years and locations. The *X*-axis represents years (C) and geographic locations (D), while the *Y*-axis represents the percentage of different MLGs. "Others" represents MLGs that were detected only once. CQ represents Chongqing Municipality, while GZ, HB, HN, SC and YN represent Provinces of Guizhou, Hubei, Hunan, Sichuan and Yunnan, China, respectively.

tested for virulence on seven near-isogenic lines, which individually express *R3a*, *R3b*, *Rpi-blb3*, *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1* in the Desiree background. The disease index of MS and HS were defined as virulence on potato. All isolates were virulent on Desiree and *R3a*, while 95.87% and 97.71% of the collected isolates were virulent on *R3b* and *Rpi-blb3*, respectively (Fig. 2-A and B). Meanwhile, 17.89%, 8.71%, 8.26% and 2.29% of the collected isolates were virulent on *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1*, respectively (Fig. 2-A and B). Taken together, these results suggest that *P. infestans* populations in southwestern region have overcome the resistance mediated by *R3a*, *R3b* and *Rpi-blb3*.

To examine the virulence diversity of these *P. infestans* populations, the virulence rate was analyzed by year and region. Almost all isolates, regardless of years and regions, were virulent on *R3a*, *R3b* and *Rpi-blb3* (Fig. 2-C and D; Appendix H). When sorted by year, 33.33% of the collected isolates were virulent on *Rpi-blb2* in 2019, while 9.30 to 22.45% of the collected isolates were virulent on *Rpi-blb2* from 2020 to 2022 (Fig. 2-C; Appendix H). Meanwhile, isolates of 2021 and 2022 were generally more virulent than those of 2019 and 2020 on *R8*, *Rpi-blb1* and *Rpi-vnt1.1* (Fig. 2-C; Appendix I). Notably, the resistance efficiency of *R8*, *Rpi-blb1* and *Rpi-vnt1.1* generally decreased from 2019 to 2022 (Fig. 2-C; Appendix H). When sorted by locations, 28.21%, 16.31% and 41.67% of the collected isolates from Chongqing, Guizhou and Yunnan were virulent on *Rpi-blb2*, respectively (Fig. 2-D; Appendix H). Likewise, 15.38%, 7.80% and 16.67% of the collected isolates from Chongqing, Guizhou and Yunnan were virulent on *R8*, respectively (Fig. 2-D; Appendix H). Meanwhile, 10.26%, 9.22% and 8.33% of isolates collected from Chongqing, Guizhou and Yunnan were virulent on *Rpi-blb1*, respectively (Fig. 2-D; Appendix H). Lastly, 5.13% and 2.13% of the collected isolates from Chongqing and Guizhou were virulent on *Rpi-vnt1.1*, respectively (Fig. 2-D; Appendix H). Notably, *Rpi-blb2*, *R8* and *Rpi-vnt1.1* conferred resistance to isolates collected from Hunan and Sichuan, while *R8*, *Rpi-blb1* and *Rpi-vnt1.1* showed intermediate resistance to isolates collected from Yunnan (Fig. 2-D; Appendix H). Taken together, these results suggest that *P. infestans* populations in southwestern region generally became aggressive from 2019 to 2022, with the population in Yunnan being more aggressive than those in Chongqing, Guizhou and Hubei, which are followed by Hunan and Sichuan.

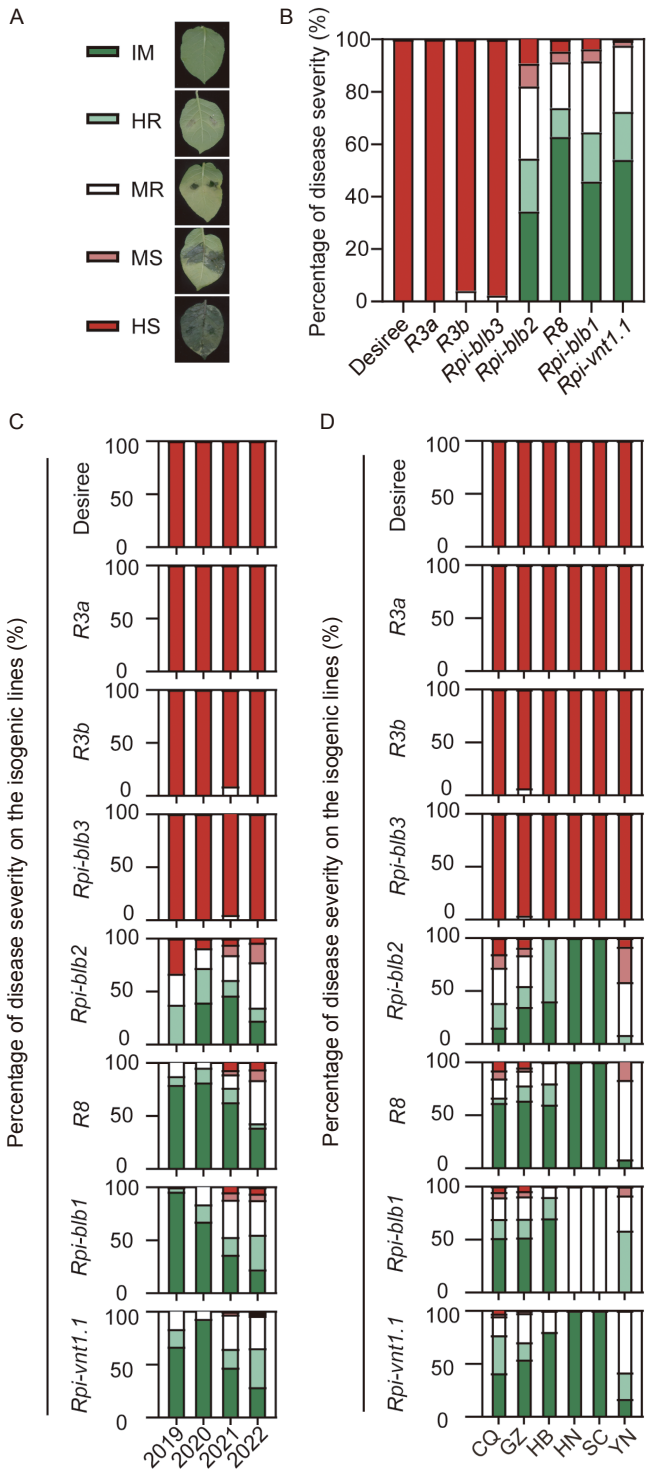


Fig. 2 *Phytophthora infestans* populations in southwestern region have become more aggressive over years. A, disease index was scored as immunity (IM), hypersensitive response (HR), medium resistance (MR), medium susceptibility (MS) and high susceptibility (HS). B, the percentage of disease index in Desiree and different potato near-isogenic lines. C and D, the percentage of disease index of the collected isolates on Desiree and different near-isogenic lines from 2019 to 2022 (C) and in different locations (D). CQ represents Chongqing Municipality, while GZ, HB, HN, SC and YN represent provinces of Guizhou, Hubei, Hunan, Sichuan and Yunnan, China, respectively. Representative results of at least three experiments with similar results were shown.

To assess the pathotypic complexity of these *P. infestans* populations, the virulence rate was analyzed by different combinations of these seven near-isogenic lines. A total of 15 pathotypes were detected, with 10 out of 15 pathotypes detected more than once (Fig. 3-A). The major pathotype, which accounted for 72.48% of the collected isolates, was virulent on *R3a*, *R3b* and *Rpi-blb3* (Fig. 3-A). Significantly, 0.92% of the collected isolates were virulent on all seven near-isogenic lines (Fig. 3-A). Analysis of pathotypes sorted by year and region revealed that the major pathotype that was virulent on *R3a*, *R3b* and *Rpi-blb3* is prevalent regardless of year and region (Fig. 3-B and C). However, pathotypes of 2021 and 2022 were higher than those of 2019 and 2020 (Fig. 3-B), while pathotypes of Chongqing, Guizhou and Yunnan were higher than those of Hubei, Hunan and Sichuan (Fig. 3-C). Likewise, analysis of the percentage of pathotypic complexity revealed that isolates that were virulent on three near-isogenic lines are dominant in these populations (Fig. 3-D). In addition, the pathotypic complexity, which is indicated by Shannon index, of 2021 and 2022 was higher than that of 2019 and 2020, while the pathotypic complexity

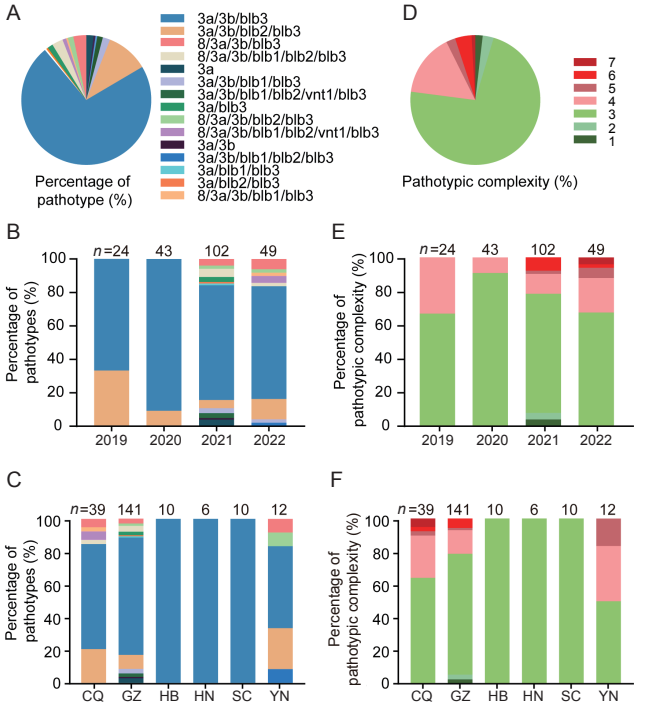


Fig. 3 *Phytophthora infestans* populations in southwestern region have a wide variety of pathotypes. A, the percentage of different pathotypes of all isolates. 218 isolates were grouped into 15 pathotypes and the major pathotype was virulent on *R3a*, *R3b* and *Rpi-blb3* (3a/3b/blb3). B and C, the percentage of different pathotypes of isolates from 2019 to 2022 (B) and in different locations (C). D, the percentage of pathotypic complexity of all isolates. Number of pathotypic complexity (1–7) represents the number of near-isogenic lines that a single isolate can infect. Disease index classified as both HS and MS was defined as virulence. E and F, the percentage of pathotypic complexity of isolates from 2019 to 2022 (E) and in different locations (F). CQ represents Chongqing Municipality, while GZ, HB, HN, SC and YN represent provinces of Guizhou, Hubei, Hunan, Sichuan and Yunnan, China, respectively.

of Chongqing, Guizhou and Yunnan was higher than that of Hubei, Hunan and Sichuan (Fig. 3-E and F; Appendix I). Taken together, these results suggest that *P. infestans* populations in southwestern region have more pathotypes in 2021 and 2022, and that the largest pathotypic diversity is recorded in Guizhou.

Collectively, *P. infestans* populations in southwestern region have overcome the resistance mediated by *R3a*, *R3b* and *Rpi-blb3*, and have become more aggressive and pathotypically diverse from 2019 to 2022. In addition, *P. infestans* populations in Chongqing, Guizhou and Yunnan are more aggressive and pathotypic diverse.

3.3. MLG24 harbors the most complex pathotypic diversity of the EU lineage in southwestern China

To explore the potential link between genotypes and pathotypes in these *P. infestans* populations, pathotypes were examined across different lineages. The EU lineage contained 10 pathotypes, while the US and SIB lineages contained four and seven pathotypes, respectively (Fig. 4-A). In addition, the pathotypic complexity of the EU lineage was significantly higher than that of the other two lineages (Fig. 4-B; Appendix I). Moreover, among the major MLGs of the EU lineage, MLG24 had a higher pathotypic complexity than other MLGs (Fig. 4-C; Appendix I). Furthermore, MLG24 isolates displayed various pathotypes, while the two most aggressive isolates, CQ-22-16-1 and CQ-22-20-1, were virulent on all seven near-isogenic lines (Fig. 4-D and E; Appendix H). Taken together, these results suggest that the EU lineage, especially the MLG24 genotype, contributes to the virulence diversity of *P. infestans* populations in southwestern region.

To investigate how specific *P. infestans* isolates from MLG24 evade resistance mediated by corresponding *R* genes, SNP and expression polymorphisms of *Avr8* (*PITG_07558*) and *Avrvnt1* (*PITG_16294*) were selected for analysis, because these two *Avr* genes are known to activate corresponding *R* genes-mediated resistance, and both corresponding *R* genes (*R8* and *Rpi-vnt1.1*) still confer durable resistance in southwestern China (Appendix I).

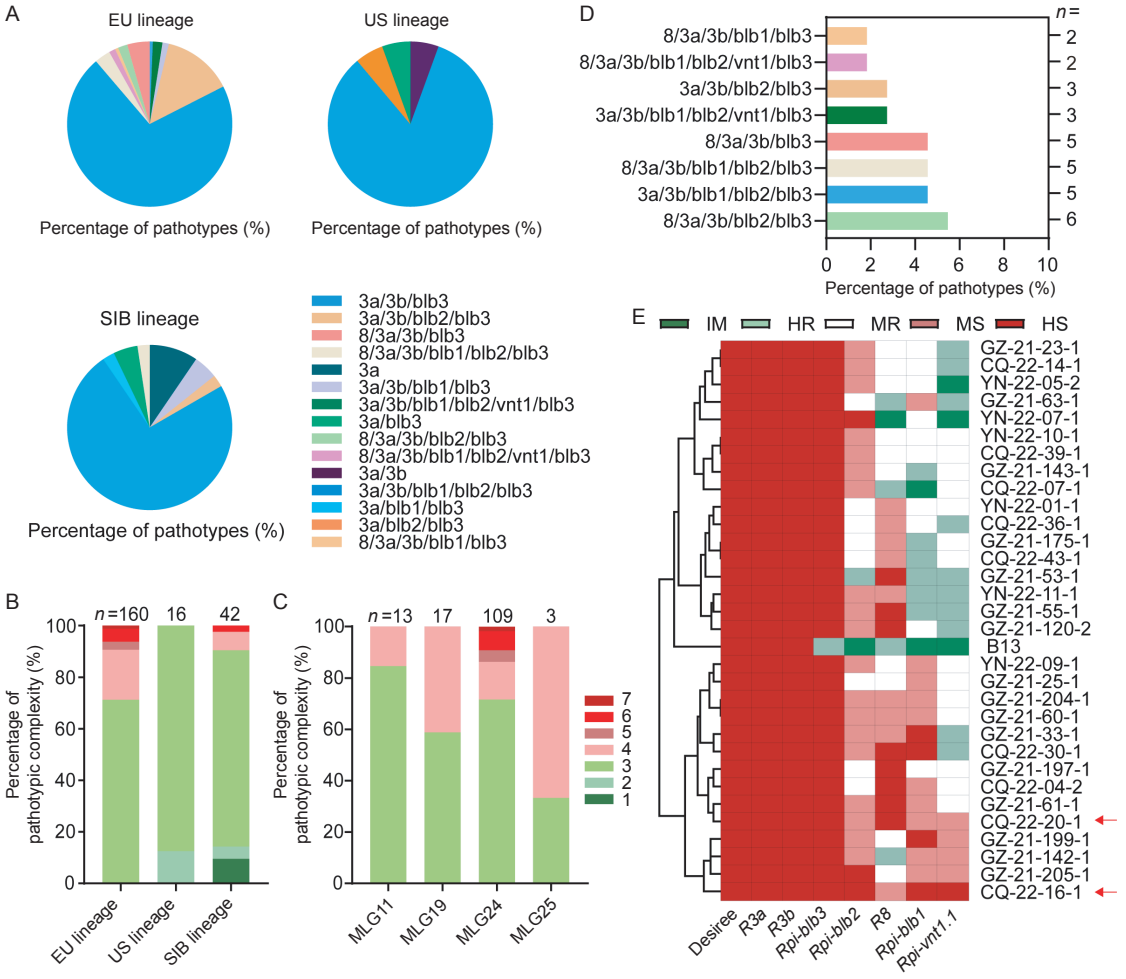


Fig. 4 The MLG24 genotype has the most complex pathotypic diversity of the EU lineage. A, the pathotypic percentage of isolates from three lineages. B, the percentage of pathotypic complexity of isolates from three lineages. C, the percentage of pathotypic complexity of MLGs detected for more than two times from the EU lineage. D, the pathotypic percentage of isolates with the MLG24 genotype. The number of isolates that overcome the resistance mediated by more than three *R* genes was shown. E, disease index of MLG24 isolates on different potato near-isogenic lines. CQ-22-16-1 and CQ-22-20-1 that overcome the resistance mediated by all seven *R* genes were indicated by red arrows. Representative results of at least three experiments with similar results were shown.

However, SNPs detected in the CDS as well as the upstream and downstream flanking sequences of *Avr8* and *Avrvnt1* did not differentiate virulence from avirulence (Appendices C and J). In addition, *Avr8* and *Avrvnt1* were constitutively expressed in all virulent isolates and reference strains (Appendices D and K). Taken together, these results suggest that neither SNPs nor expression of *Avr8* and *Avrvnt1* contributes to the virulence of MLG24 isolates, and the elucidation of the evading mechanisms requires further investigation.

3.4. Management of highly virulent isolates by two wild potatoes and three fungicides

Since the southwestern region contributes around 40% to potato production in China (Jansky *et al.* 2009), potential threat mediated by CQ-22-16-1 and CQ-22-20-1 was examined by testing their virulence on potato cultivars. A total of 30 potato cultivars were collected and tested for their resistance against CQ-22-16-1 and CQ-22-20-1 with B13 serving as a control. When inoculated with B13, 16.67% and 16.67% of cultivars were MS and HS, respectively. In addition, 46.67%, 10.00% and 10.00% of cultivars were IM, HR and MR, respectively (Fig. 5-A; Appendix L). When inoculated with CQ-22-16-1 and CQ-22-20-1, only Qianyu 8 displayed MS, while the rest were HS (Fig. 5-A–C). Taken together, these results suggest that CQ-22-16-1 and CQ-22-20-1 are much more virulent than B13 in infecting tested potato cultivars.

To provide resistance resources for preventing potential pandemic of CQ-22-16-1 and CQ-22-20-1, a total of 30 *S. candolleanum* relatives were tested for their resistance against these two isolates with B13 serving as a control. When inoculated with B13, 20.00%, 23.33%, 6.67%, 3.33% and 46.67% of wild potatoes were HS, MS, MR, HR and IM, respectively (Fig. 5-C; Appendix M). When inoculated with CQ-22-16-1, 73.33%, 20.00%, 3.33% and 3.33% of wild potatoes were HS, MS, MR and HR, respectively (Fig. 5-C; Appendix M). When inoculated with CQ-22-20-1, 60.00%, 16.67%, 10.00% and 13.33% of wild potatoes were HS, MS, MR, and HR, respectively (Fig. 5-C; Appendix M). Notably, two wild potatoes were resistant to B13, CQ-22-16-1 and CQ-22-20-1 (Fig. 5-D–F; Appendix M), suggesting that these two resources might contain unidentified *R* genes beyond these seven tested *R* genes.

Given that resistance breeding against *P. infestans* is time-consuming, CQ-22-16-1 and CQ-22-20-1 were tested for sensitivity to three main fungicides. Although significant differences in EC_{50} values were observed between these two isolates and B13 under fungicide treatments, cymoxanil, dimethomorph and fluazinam could still effectively inhibit the growth of B13, CQ-22-16-1 and CQ-22-20-1 (Appendix N), suggesting that these three fungicides could be an emergency strategy to effectively prevent the potential epidemic of these two isolates.

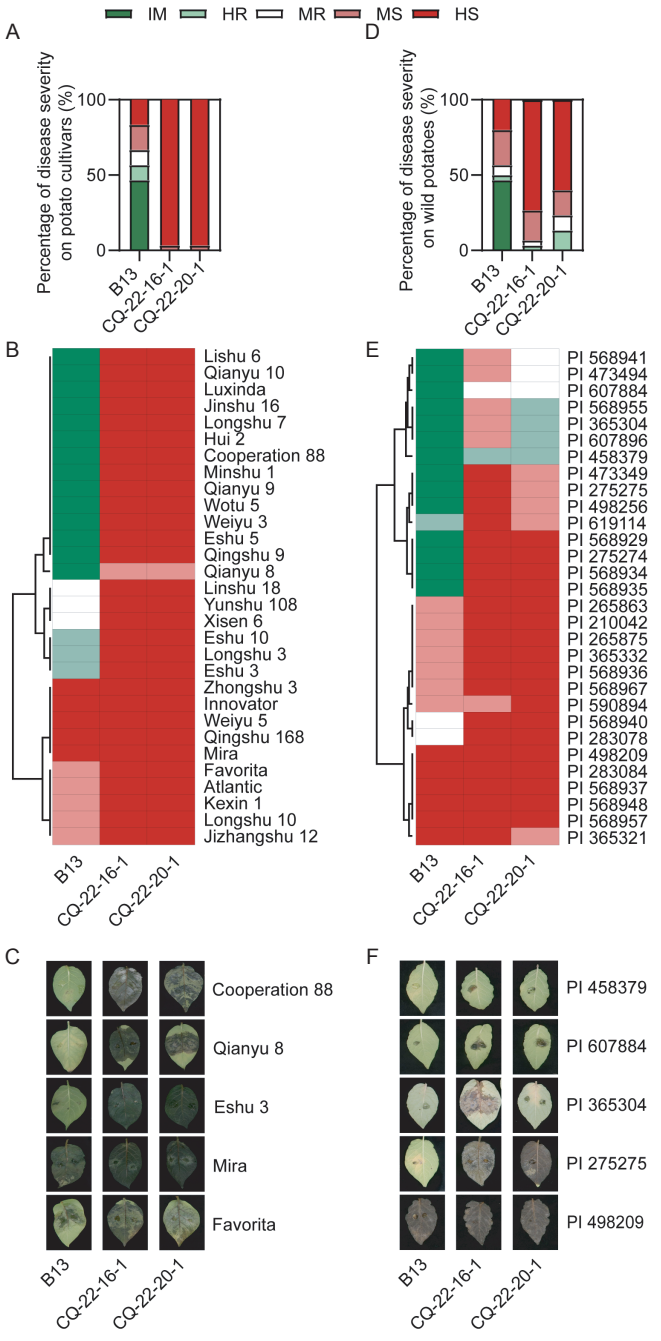


Fig. 5 Two wild potatoes confer resistant to highly virulent *Phytophthora infestans* isolates. A, the percentage of disease index of B13, CQ-22-16-1 and CQ-22-20-1 as well as the control strain B13 on 30 potato cultivars. B, the detailed disease index in (A). C, pathogenesis of B13, CQ-22-16-1 and CQ-22-20-1 on five selected potato cultivars. D, the percentage of disease index of B13, CQ-22-16-1 and CQ-22-20-1 on 30 wild potatoes. E, the detail disease index in (D). F, pathogenesis of B13, CQ-22-16-1 and CQ-22-20-1 on five selected wild potatoes. Representative results of at least three experiments with similar results were shown.

4. Discussion

In this study, the population diversity of *P. infestans* from southwestern China was examined in order to better understand the genotypic relationship within these pathogens. We identified all three reported lineages in southwestern region, namely the EU, US and SIB lineages (Li *et al.* 2013b; Roy *et al.* 2021). In this study, SSR-based genotyping revealed that *P. infestans* populations in southwestern region consist of all these three lineages (Fig. 1-A and B).

Consistent with previous studies (Li *et al.* 2013b; Roy *et al.* 2021), the EU lineage is the dominant lineage in this region (Fig. 1-A, C and D; Appendix G). This lineage was detected across all surveyed areas and years, suggesting it has firmly established in southwestern China. We speculated that the increased virulence and aggressiveness contributed to the widespread distribution of this lineage (Cooke *et al.* 2012). Specifically, 19 MLGs were found in the EU lineage across all six locations in this study (Fig. 1-A; Appendix G). In addition, two MLGs (MLG20 and MLG25) relatively close to MLG24 were detected more than once, suggesting that the EU_13 lineage contains novel genetic variants. Further virulence and fitness tests are required to determine whether these sub-genotypes are more aggressive or not. These observations suggest that the EU lineage is both expanding and diversifying in this region. Contrary to previous reports indicating low frequencies of US and SIB lineages in this region (Li *et al.* 2013b; Roy *et al.* 2021), the prevalence of these lineages is increasing in southwestern China. Notably, the US lineage was only detected in Guizhou Province in 2021 (Fig. 1-C and D), raising questions about its emergence and potential fluctuations. We hypothesized that the large-scale trade of potato seed tubers has facilitated the spread of these lineages, and that the year-round cultivation of potatoes by smallholder farmers using saved seed tubers may provide a favorable niche for rare *P. infestans* lineages in this mountainous area.

We used genetically modified potato late blight *R* gene differential set for virulence monitoring, offering a more accurate approach compared to traditional Mastenbroek differential sets and the simple monitoring of *Avr* polymorphisms. Despite promising prospects of *R* genes in resistance breeding and deployment, resistance based on a single *R* gene has frequently been overcome (Berindean *et al.* 2024). Isolates from specific geographical areas can be used to predict the durability of specific *R* genes and provide effective *R* genes for stacking in resistance breeding (Zhu *et al.* 2012; Zhang *et al.* 2021). In this study, we present potential guidance for the use of the seven *R* genes. *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1* remain durable, but *R3a*, *R3b* and *Rpi-blb3* should not effectively manage late blight in southwestern China (Fig. 2-B and C). It is notable that the percentage of virulent isolates is increasing, highlighting the need for integrated pest management to extend the effective lifespan of these *R* genes. Collectively, these findings provide a foundation for the effective deployment of specific *R* genes.

Pathogens evolved a variety of strategies to evade *R* gene-mediated host immunity. In our result, neither SNPs nor the expression of *Avr8* and *Avrvnt1* contributes to the virulence of MLG24 isolates (Appendices J and K). Recent reports showed that variation of virulence factors at the sequence, transcriptional, post-transcriptional and biochemical modification levels enable pathogens to defeat the host immunity (Chen *et al.* 2021). Furthermore, the research of effector epistatic interaction in *Phytophthora* is still limited. As such, the evading mechanisms require further investigation.

Recent surveys revealed that aggressive isolates, which overcome resistance in multiple resistant lines, have been increasing in southwestern region (Yang 2007; Zhao 2007; Li *et al.* 2013b, 2020; Yang 2016) as well as other regions (Guo *et al.* 2007, 2009; Jin 2009; Tian *et al.* 2016). Notably, a certain *P. infestans* population may contain multiple pathotypes, while different *P. infestans* populations consistently exhibit distinct pathotypes (Yang 2007; Zhao 2007; Jin 2009; Yang 2016, 2019; Li *et al.* 2020). Spatiotemporally, pathotypes of *P. infestans* populations in southwestern region are becoming more complex, especially for those in Chongqing, Guizhou and Yunnan (Fig. 3; Appendix I). Southwestern China is characterized by extremely complex and geographical habitats due to the huge altitudinal and climate differences. Mountainous terrain, frequent fog and rainfall, cool temperatures and year-round potato cultivation favor different potato cultivars growth and late blight development. We speculated that the complex geographical habitats and a diverse variety of potato cultivars enable evolution of pathogens.

A large-scale survey of pathogen phenotypes provides theoretical support and technical guidance for rational disease control. Compared to cultivated potatoes, wild species tend to have tremendous resistance gene to late blight. In this study, although two highly virulent isolates were aggressive on 30 potato cultivars, further resistance evaluation experiments provided two elite wild potatoes from *S. candolleanum* (Fig. 5-D and E; Appendix M). Crossing barriers between cultivated potato and most wild species can pose challenges in utilizing wild genetic resources. *Solanum candolleanum* is the progenitor of cultivated potato from south American (Li *et al.* 2018; Tang *et al.* 2022). However, *S. candolleanum* can cross relatively easily with cultivated potato and relative species, making it a valuable source of genetic material for breeding programs (Jackson and Hanneman 1999). Interestingly, these two isolates exhibited different infection ability among 30 *S. candolleanum* relatives, suggesting large resistance variation within *S. candolleanum* species. No cloned *R* genes have been reported in this species to our knowledge, suggesting additional zig-zag evolutionary events beyond characterized Avr-R interactions are ongoing, and that several *R* genes may have been overcome before cloned (Dong and Zhou 2022; Paluchowska *et al.* 2022; Hadiarto and Ambarwati 2024). Besides, these two highly virulent isolates were still sensitive to three fungicides (Appendix N), which highlights fungicide application as an emergency strategy to control late blight. Because of the increasing complexity of the genotype and pathotype of *P. infestans* populations in southwestern China, it is necessary to annually assess the virulence and fungicide resistance of *P. infestans* populations to facilitate sustainable control of late blight.

5. Conclusion

In this study, 218 isolates collected from Chongqing, Guizhou, Hubei, Hunan, Sichuan and Yunnan in southwestern China from 2019 to 2022 were analyzed for genotypic and virulence dynamics as well as effective management strategies. These *P. infestans* populations comprise three lineages, with the MLG24 genotype of the EU lineage being dominant. In addition, these *P. infestans* populations have become more aggressive, leading to inefficacy of *R3a*, *R3b* and *Rpi-blb3* and reduced efficacy of *Rpi-blb2*, *R8*, *Rpi-blb1* and *Rpi-vnt1.1*. Notably, two highly virulent isolates, CQ-22-16-1

and CQ-22-20-1, of the predominant genotype MLG24 of the EU lineage have overcome the resistance mediated by all seven resistance genes and are virulent on 30 potato cultivars. Nevertheless, these two highly virulent isolates can be controlled by two *S. candolleanum* relatives and three fungicides. Taken together, this study elucidates the genotypic and virulence dynamics of *P. infestans* populations in southwestern China and provides valuable insights into effective control measure.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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