Long-term surveillance suggests multiple hybridization events by nuclear reassortment and accelerated intercontinental spread of wheat yellow rust.

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Summary

- Drivers of evolution of crop pathogens leading to novel diversity and long-distance dispersal (LLD) may have strong implications on food security and sustainable plant

disease control at global scales. However, consolidated evidence is often lacking due to absence of regular pathogen surveys beyond national capacities.

- Our study documents world-wide connectivity between populations of *Puccinia striiformis*, causing yellow rust on cereals and grasses. Twelve cases of inter-continental spread of wheat yellow rust, including seven cases with major impact on disease epidemics in recipient areas, were detected from genotypic analyses of 3240 pathogen samples from 41 countries at six continents.
- In three cases, the most plausible mechanism for novel pathogen diversity was somatic hybridization via nuclear reassortment between co-existing lineages on shared host cultivars, spreading by LDD from Europe to South America and Australia, respectively, a few years after first detection. Several high-impact incursions from South Asia into East Africa were also observed, including a genotype with a dramatic impact on wheat breeding programs of global relevance.
- The present study stresses an urgent need for coordinated crop pathogens monitoring across borders. Only global efforts will enable prevention and control of pathogens that represent major challenges for food security at regional and global scales.

Key words

Puccinia striiformis, hybridization, world-wide spread, trajectory simulations, global surveillance, haplo-phased genome, SSR haplotype

Introduction

An increase in human travel and trade and the escalating speed of changing climate and weather patterns have renewed attention on disease epidemiology in humans, animals and crop plants, e.g., the US National Academies of Sciences (Olsen et al., 2011), the United Nations Food and Agriculture Organisation (FAO, 2024). This is exemplified by human vulnerability to pandemics as highlight by the coronavirus SARS-CoV-2 (Dillon et al., 2021; Chavda et al., 2022). Long distance dispersal (LDD) is an important epidemiological feature of many pathogens, including those affecting crops, because even rare LDD events can have a

major impact on crop production (Brown and Hovmøller, 2002; Carvajal-Yepes et al., 2019). Recent reviews suggest that LDD events of cereal rust pathogens are increasing in frequency at the intercontinental scale, possibly due to intensified crop production, climate change resulting in milder winters in temperate regions, and increased travel and commerce (Park, 2015; Jin et al., 2020; Hovmøller et al., 2023). The negative impact of more frequent LDD events may delay or prevent meeting the 70% increase in food and agricultural production by 2050 demanded by global population growth (van Dijk et al., 2021).

One major obstacle for the detection of LDD events in plant pathology is the lack of regular and extensive pathogen population surveys beyond national capacities (Jeger and Pautasso, 2008; Ristaino et al., 2021), including common sampling protocols, analytic tools and data sharing (Patpour et al., 2022). This makes it difficult to establish the exact geographical and evolutionary origins of a new pathogen variant as it spreads into recipient areas. Population genetic and genomic analyses are useful approaches to calculate distances and migration rates within and among pathogen populations (Zhan et al., 2003; Ali et al., 2014a; Bebber et al., 2014). At the same time, tracking of individual multi-locus genotypes (MLGs) represents a powerful strategy for the detection of LDD events especially in clonal populations, which tend to preserve haplotypes (Hovmøller et al., 2002).

The rust fungi (*Pucciniales*) are the most species rich and complex order of plant pathogens, consisting of almost 8000 species. They are characterized by a true biotrophic lifestyle and are individually adapted to their host plant at species and cultivar levels (Flor, 1971; Anikster, 1985; Aime et al., 2017). *Puccinia striiformis* f. sp. *tritici (Pst)*, causing yellow (or stripe) rust in wheat, is dikaryotic, heteroecious and macrocyclic requiring two taxonomically unrelated hosts to complete its life cycle (Jin et al., 2010). However, sexual reproduction on the alternate host, *Berberis spp.,* is observed rarely in nature, even in western China (Wang et al., 2016), despite multiple reports of signatures of sexual reproduction in populations in the near-Himalayan region, which are considered the center of diversity for *Pst* (Duan et al., 2010; Ali et al., 2014b; Thach et al., 2016; Huang et al., 2021). Somatic hybridization by fusion of hyphae, leading to nuclear reassortment which may preserve the entire haplotype, has so far only been reported under experimental conditions in *Pst* (Little and Manners, 1967; Little and Manners, 1969; Lei et al., 2017), unlike the wheat leaf rust pathogen *P. triticina* (Park and

88 Wellings, 2012; Sperschneider et al., 2023), the wheat stem rust pathogen *P. graminis* f. sp.
89 *tritici* (Li et al., 2019), and *P. coronata* causing oat crown rust (Henningsen et al., 2024).

90 The use of molecular markers in recent time has contributed significantly to the
91 understanding of the global landscape of wheat rust fungi. In North America, yellow rust was
92 first discovered in 1915, although the founder population is not known (Line, 2002), however,
93 random samples from the 1970s, 1980s and 1990s suggested a common origin of the North
94 American and the European PstS0 population (Markell and Milus, 2008; Ali et al., 2014a;
95 Thach et al., 2016). The initial spread of *Pst* from Europe to Australia in 1978, also PstS0, is
96 well documented (Wellings and McIntosh, 1990; Hovmøller et al., 2008; Ding et al., 2021).
97 The worldwide spread of two warm temperature-adapted strains of *Pst* in 2000 and following
98 years (termed PstS1 and PstS2, respectively), collectively represent one of the largest and
99 most rapid spread of a crop pathogen up until that time (Hovmøller et al., 2008). Timewise,
100 these large-scale dispersal events of *Pst* coincided with the emergence of *Pgt* race "Ug99" in
101 East Africa that was virulent on more than 80% of wheat lines developed by The International
102 Maize and Wheat Improvement Center (CIMMYT) (McIntosh and Pretorius, 2011). In
103 response, the Borlaug Global Rust Initiative (BGRI) was formed and laid the foundation for
104 more extensive and regular wheat rust disease and pathogen surveys. These included Africa
105 and Asia, which were connected with national rust survey programs in Europe and elsewhere
106 by the establishment of the Global Rust Reference Center in 2008 (Hovmøller, 2011). This
107 allowed analyses of the spread and evolution of *Pst* and *Pgt* across borders and continents,
108 including the return of *Pgt* into Europe and connectivity to epidemics elsewhere (Patpour et
109 al., 2022), including Western Siberia 2015-2016 (Shamanin et al., 2016) and East Africa
110 (Olivera et al., 2015). In addition, independent surveys have reported large scale
111 epidemiological consequences of new incursions of *Pst* into South America in 2017 (Anibal
112 Carmona et al., 2019; Riella et al., 2024) and Australia in 2017-2018 (Ding et al., 2021).

113 The present study investigated drivers of evolution of the *P. striiformis* population at the
114 global scale based on genotypic analyses of 3180 samples collected at four continents (37
115 countries) between 2009 and 2023, complemented by genotype information of additional 60
116 samples representing long-term surveillance efforts in Europe, North America (Milus et al.,
117 2015a) and Australia (Ding et al., 2021). LDD events were investigated by the potential
118 sharing of genotypes in putative source and recipient areas, considering the time of first

detection as well as accumulation of genetic diversity in the considered populations. Likely evolutionary origin of successful LDD migrants were explored in detail in specific cases, including hypothetical hybridization events by nuclear reassortment, which has not been demonstrated in *Pst* under non-experimental conditions. The plausibility of wind-dispersal along hypothesized transmission routes was explored by conducting trajectory simulations considering typical spore survival times and mean wind patterns. The prospects for prevention and mitigation efforts to reduce the increasing impact of crop pathogen spread at intercontinental scale are discussed.

Materials and Methods

Collection and recovery of yellow rust samples

Pathogen sampling reflected the coordinated efforts in wheat rust surveillance facilitated by research programs within the Borlaug Global Rust Initiative, European Union research and network initiatives as well as national programs in Europe and Australia and recent studies in North America **(Fig. S1).**

A total of 3180 samples of yellow rust mainly from wheat (and occasionally other cereals and grasses) were collected in 37 countries on four continents between 2009 and 2023 (Table S1). The number of samples varied across years and locations, reflecting occurrence and sampling efforts of the yellow rust disease. Two hundred thirteen samples from the Middle East and West Asia were provided by The Regional Cereal Rust Research Center (RCRRC), ICARDA, Turkey. An additional pre-existing 60 isolates served as references of previously identified *Pst* groups, and *Pst* populations in USA (Milus et al. (2015b) and Australia (Ding et al. (2021).

Recovery of incoming samples and multiplication of urediniospores followed the procedure by Thach et al. (2025), after which they were harvested, dried, and stored in liquid nitrogen (-196°C) or freezer (-80°C) until further use. For analysis of diversity over time and space, samples were grouped in two time periods (2009-2016) and (2017-2023) and seven geographical regions, in addition to reference samples from North America, Australia and Europe.

148

149 **DNA extraction and SSR genotyping**

150 From 2009 to 2012, DNA was extracted from dried urediniospores (approx. 20 mg/sample)
151 according to Thach et al. (2016). Since 2013, extraction was based on dried leaf segments
152 with single rust lesions taken from multiplication plants or directly from incoming samples
153 according to Thach et al. (2025). Genotyping was done using 19 simple sequence repeat (SSR)
154 co-dominant markers and allele sizes were manually scored, allowing up to two missing
155 markers per sample (Thach et al., 2025). Samples with allele sizes and/or combinations
156 suggesting more than a single genotype were excluded from the dataset. Detection of novel
157 or exotic genotypes in a region/country was confirmed by additional independent DNA
158 extractions from original sample material and genotyping. Two hundred thirteen samples
159 from the Middle East (2018-2020) collected by Turkey-ICARDA Regional Cereal Rust Research
160 Center were SSR genotyped by EUROFINS, France. Scoring of allele sizes and data alignment
161 to existing format were carried out at the Global Rust Reference Center (GRRC). Assignment
162 of multilocus genotype identity (MLG #) was done for samples without missing data using
163 poppr package version 2.9.3 implemented in the R environment (Kamvar et al., 2014; Kamvar
164 et al., 2015); for samples with missing data at a maximum of two marker loci, new MLGs were
165 considered in case scored allele sizes revealed additional variability, whereas missing
166 observations were not taken into account for MLG identity. Duplicate MLGs derived from the
167 same bulk sample were removed from the dataset.

168

169 **Definition of genetic groups**

170 Nineteen previously defined genetic groups within *Pst* (PstS0-PstS18), each consisting of closely
171 related MLGs and associated races (Thach et al., 2025), were used to illustrate regional
172 pathogen differences and changes between two time periods, 2009-2016 and 2017-2023,
173 respectively. Historically, the definition and naming of a new group has been inspired by the
174 potential epidemic impact across large areas Hovmøller et al. (2010), and a diversification from
175 previous world-wide groups by a significant number of alleles (typically five SSR alleles or more)
176 and/or group-specific diagnostic markers (Walter et al., 2016; Ali et al., 2017). An updated
177 summary of named *Pst* groups is available at the GRRC website:

178 https://agro.au.dk/forskning/internationale-platforme/wheatrust/yellow-rust-tools-maps-
179 and-charts/definitions-of-races-and-genetic-groups.

180

181 **Phylogenetic analysis**

182 The dataset for phylogenetic analysis was compiled by including one representative sample
183 from each MLG (clone corrected). An unrooted phylogenetic Neighbor Joining tree was
184 constructed to visualize global diversity within *Pst*, including the positions of major genetic
185 groups defined as described above. The calculations were based on calculated genetic
186 distances using poppr package version 2.9.3 implemented in the R environment, 1200
187 bootstraps and cutoff at 50 (Kamvar et al., 2014), where Bruvo's distance for stepwise
188 mutation for microsatellites was calculated according to Bruvo et al. (2004).

189

190 **Population diversity and structure**

191 To investigate the power of discrimination of applied markers, a genotype accumulation curve
192 was calculated in the poppr R package based on samples without missing data (*n*= 2588), and
193 random resampling 10,000 times without replacement (Kamvar et al., 2014) (Fig. S2).

194 F_{st} values representing divergence between the geographic populations in two time periods (I:
195 2009-2016 and II: 2017-2023) were calculated based on the full dataset (3180 samples) and a
196 clone-corrected dataset with a single MLG representative per population and time period (283
197 samples) according to (Peakall and Smouse, 2006; 2012).

198

199 **Tests for somatic hybridization by nuclear reassortment**

200 Nuclear-specific haplotypes of hypothetical parental and hybrid isolates were inferred based
201 on the position of SSR markers and allele sizes on a chromosomal map derived from
202 haplotype-phased genome data of a PstS0 isolate (Plant Breeding Institute accession number
203 415 collected in 1982) (Schwessinger et al., 2018; Tam et al., 2025). The position of SSR
204 markers were determined by blast analysis (-word_size 12 -evalue 1 -dust no -outfmt 6) of 20
205 primer sequence pairs against the PstS0 genome (Table S2) and visualized by a phenogram
206 according to Wolfgang et al. (2013), including the lengths of individual SSR alleles (Fig. S3).

207 The analyses took advantage of multiple hypothetical hybridization events involving shared
208 SSR haplotypes, as well as time and geo-referenced sampling supporting both temporal and
209 spatial dimensions of evolution within the considered geographical populations.

210

211 **Whole genome confirmation of a somatic hybridization event**

212 The hypothesized hybridization resulting in PstS10 inferred by SSR and PstS0 genome data
213 were validated by two newly generated reference assemblies of isolates representing PstS7
214 and PstS10, respectively. The fully phased nuclear-assigned reference genome for an
215 Australian sampled PstS10 isolate (Ding et al. 2021) was generated as described previously for
216 PstS0 (Tam et al., 2025) with the exception of using PacBio HiFi and Oxford Nanopore
217 Technology (ONT) R10.4 based long-reads and Hi-C as input for Verkko genome assembler
218 (Rautiainen et al., 2023). The haplotype-phased reference genome of PstS7 used ONT R10.4.1
219 simplex reads and Hi-C with hifiasm --ont (Cheng et al., 2025). To expand upon the MLG
220 results at the genome level, we performed comparative alignments between the nuclear-
221 phased haplotypes of a proposed somatic hybrid, PstS10, and those of its two hypothetical
222 parental isolates, PstS0 (Tam *et al.*, 2025) and PstS7. Pairwise whole-genome alignments
223 were conducted using NUCmer v3.1 as part of the MUMmer package (Marçais et al., 2018)
224 with default settings. Only alignment blocks with >75% identity and longer than 500 bp were
225 retained. SNP counts and average identity were computed from 1-to-1 alignments using
226 MUMmer's DNAdiff v1.3. Dot plots were generated using a script adapted from paf2dotplot.r
227 (https://github.com/moold/paf2dotplot). The chromosomal locations and allele sizes for
228 PstS7 and PstS10 were also visualized in Table S2 and Fig. S3, respectively, and calculated
229 amplicon lengths were compared with SSR genotyping results.

230

231 **Virulence phenotyping for validation of recent common origin**

232 Successfully recovered migrant isolates from putative source and recipient areas were
233 virulence phenotyped to provide an independent assay for relatedness. An updated protocol
234 was followed using a 0-9 disease scoring scale according to (McNeal et al., 1971), where
235 infection types (IT) from 0-6 were generally considered incompatible (avirulent) and IT 7-9
236 compatible (virulent) (Thach et al., 2025). The interpretation of virulence/avirulence for each

237 isolate was generally based on two (or more) independent wheat lines carrying the
238 corresponding *P. striiformis Yr* resistance gene.

239

240 **Plausibility of wind-dispersal**

241 Plausibility of wind-dispersal was analysed by reviewing data from previous studies on related
242 fungal pathogens (Brown and Hovmøller, 2002; Isard et al., 2005; Meyer et al., 2017a; Meyer
243 et al., 2017b; Prank et al., 2019; Radici et al., 2022; Brodsky et al., 2023; Miedaner and
244 Garbelotto, 2024), analyzing long-term mean wind patterns, i.e., wind direction and speed for
245 times of overlapping wheat seasons at source and recipient areas based on the International
246 Research Institute for Climate and Society
247 (https://iridl.ldeo.columbia.edu/maproom/Global/Climatologies/Vector_Winds.html),
248 estimating typical spore survival times (Maddison and Manners, 1972; Rapilly, 1979; Aylor,
249 1986), and conducting a set of trajectory simulations using HYSPLIT (Stein et al., 2015) with two
250 different global-scale gridded meteorological datasets [NOAA's GDAS, 3-hourly temporal
251 resolution and 1 degree horizontal spatial resolution; ECMWF's ERA5, hourly temporal
252 resolution and 0.25 degree spatiol resolution (Hersbach et al., 2020) (see Fig. S4 for details).
253 Time-backwards trajectory simulations based on GDAS were conducted from locations in all
254 recipient areas to investigate origins of air masses that could have transported spores to
255 recipient areas where they were first detected. Time-forward simulations based on ERA5 were
256 conducted to analyze the plausibility of stepwise airborne transmission along two selected
257 pathways (Europe to South America via Northern Africa; and Central Asia to East Africa via the
258 Middle East).

259

260 **Results**

261 **Genotypic *Pst* diversity at global scales**

262 A total of 3483 samples collected from 41 countries on six continents were genotyped using
263 previously published procedures and SSR markers (Thach et al., 2025), which were all
264 polymorphic except for NRJN12. Of these samples, 136 were duplicates of identical
265 genotypes/races that had been sub-cultured from original bulk samples, and an additional 153
266 contained two or more genotypes per sample. The 289 duplicate and mixed samples were

267 excluded, leaving a total of 3180 for further analysis. An additional 60 reference samples
268 representing comprehensive long-term national rust surveys in Australia, North America and
269 Europe were included to illustrate genetic diversity at global scale (Fig. 1). A majority of the
270 samples (91.7%) grouped into previously defined genetic groups (PstS0-PstS18). The remaining
271 samples consisted of 74 highly diverse MLGs of distinct geographical origins, including areas in
272 South Asia, where high diversity has been reported previously. Samples from non-wheat hosts
273 in northern Europe, e.g., barley, wild grasses, and triticale, formed a distinct and diverse branch
274 in the phylogenetic tree, suggesting a different evolutionary origin. The 20 reference samples
275 from North America contained six MLGs grouping within PstS0, PstS1_2, PstS18, and two
276 unnamed groups. The 31 reference samples from Australia were contained in seven MLGs that
277 grouped within PstS0, PstS1_2, PstS10 and PstS13, and the six reference samples from Europe
278 and one from East Africa (1960-2006) represented PstS1_2, PstS3 and PstS4.

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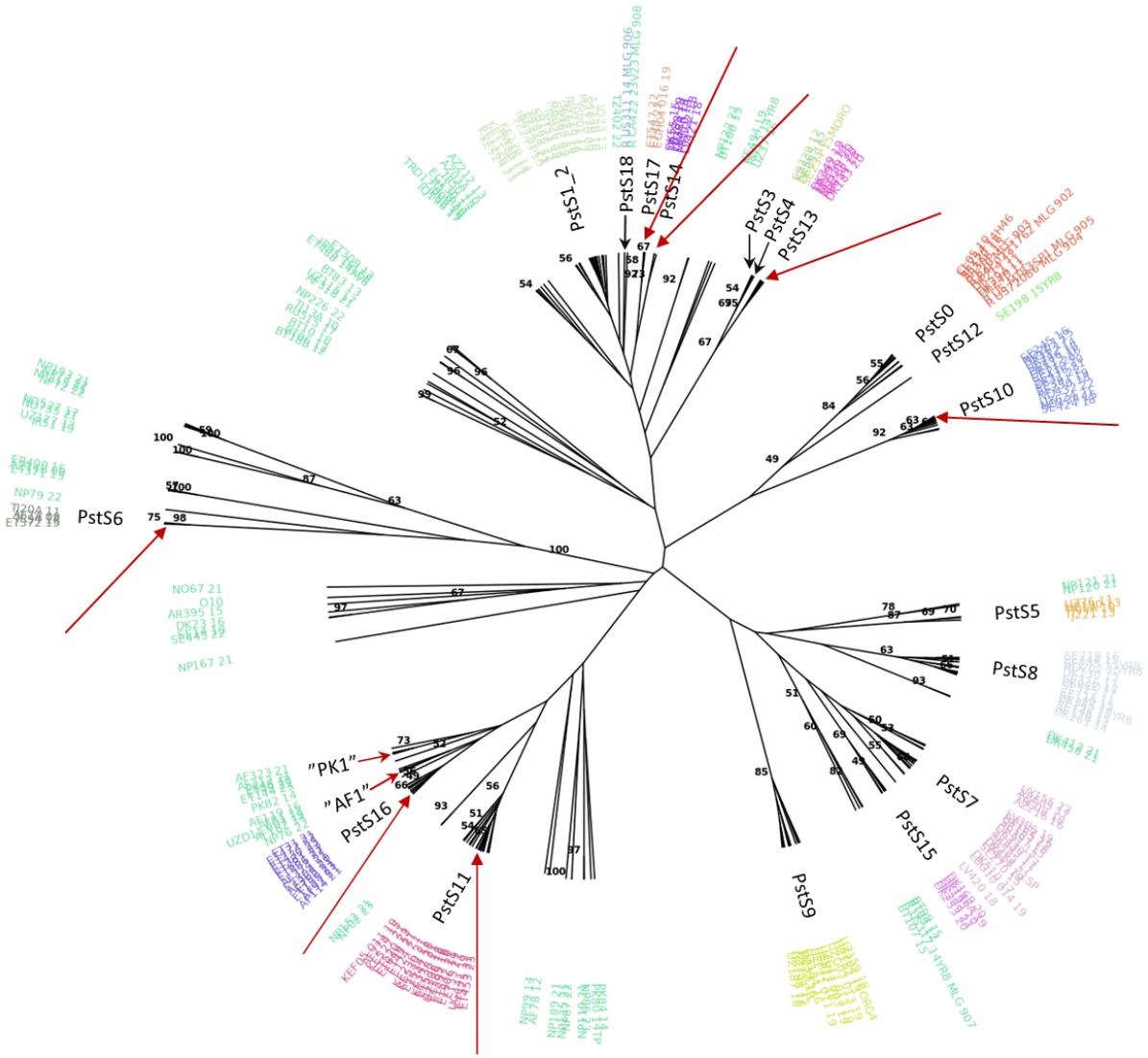

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281

282 Fig. 1. Unrooted Neighbor Joining tree (clone-corrected) using Bruvo's distance showing the
283 genetic relationship of 244 multi-locus genotypes (MLGs) representing world-wide sampling of
284 *P. striiformis* in 41 countries on six continents (2009-2023), including reference isolates
285 representing populations in Australia (1979-2021) and North America (1972-2023). Position of
286 named genetic groups (PstS0-PstS18) and two temporary named groups (AF1, PK1) are
287 indicated by different colours, typically consisting of clusters of multiple, closely related MLGs.
288 Additional 74 unnamed, diverse MLGs were shown in greenish blue. Intercontinental migrants
289 indicated by red arrows (within group position indicative).

290 The within-group diversity largely reflected time since first detection of the group, evolutionary
291 origin, and likely prevalence of the disease and sampling intensity (Table 1; Fig. S2). The highest
292 number of MLGs were observed in PstS1_2, first detected in East Africa in the 1970s, but

293 relatively high numbers were also observed for groups emerging from populations with high
294 genetic diversity in Asia, e.g., PstS7, PstS8, and PstS11, despite low diversity at time of incursion
295 into Europe (PstS7 and PstS8 in 2011) and East Africa (Psts11 in 2016) (data not shown).

296 Table 1. Diversity within world-wide genetic groups and geographic *Pst* populations defined
297 according to Table S1. Shaded values represent population, where each genetic group was
298 first detected.

	Overall diversity				**Number of MLGs per population**[1] (*n* =population size)						
Genetic group	Number of samples (n)	Number of MLG/ genetic	Shannon-Weiner index (H)	Frequency of prevalent MLG/ group	NEU (n=1086)	MEA (n=348)	EAF (n=914)	NWA (n=159)	SAS (n=283)	CWA (n=217)	SAM (n=173)
PstS0	57	7	1.95	54,4	5						4
PstS1_2	420	24	3.18	47,9		6	18	4	1	3	
PstS3	1	1	-	-						1	
PstS4	50	3	1.10	72,0	3	1					
PstS5	14	4	1.39	35,7						5	
PstS6	46	4	1.39	91,3			2		2	2	
PstS7	105	19	2.94	41,0	11	3		2		3	1
PstS8	128	15	2.71	51,6	15						
PstS9	139	14	2.64	53,2			1		1	14	
PstS10	600	16	2.77	82,2	15			1			1
PstS11	454	22	3.09	48,5		1	21		2	1	
PstS12	6	1	0.00	100,0	1						
PstS13	279	6	1.79	84,2	5			1			1
PstS14	239	6	1.79	72,0	5[2]	1		2[2]			1
PstS15	13	5	1.61	30,8	5						
PstS16	278	13	2.56	70,1			9		7		
PstS17	87	3	1.10	77,0	2	2	2				
Others	264	74	4.30		10	9	13		58	15	1
Total - named groups	2916	163			62	14	53	8	13	29	8
Grand total	3180	237	5.47		**72**	**23**	**66**	**8**	**71**	**44**	**9**

[1] Populations: NEU: Northern Europe, MEA: Middle East, EAF: East Africa, NWA: Northwest Africa, SAS: South Asia, CWA: Central-West Asia, SAM: South America.
299 [2] PstS14 first detected in NEU in 2015 (one single sample), where no surveys were conducted in NWA. PstS14 was highly dominant NWA from 2016 and onwards.

300

301 The distributions of isolates within the named genetic groups (PstS0-PstS17) were highly
302 divergent in the two time periods considered (2009-2016 and 2017-2023, respectively), and
303 across the considered geographical areas (Northern Europe, Middle East, East Africa,
304 Northwest Africa, South Asia, Central-West Asia, South America), which suggested dynamic
305 pathogen changes during time and significant geographic subdivisions since 2009 (Fig. 2).
306 Note that reference samples from North America and Australia, which represent historic key
307 isolates from these continents rather than systematic sampling in the two periods, were not
308 included in these analyses.

309

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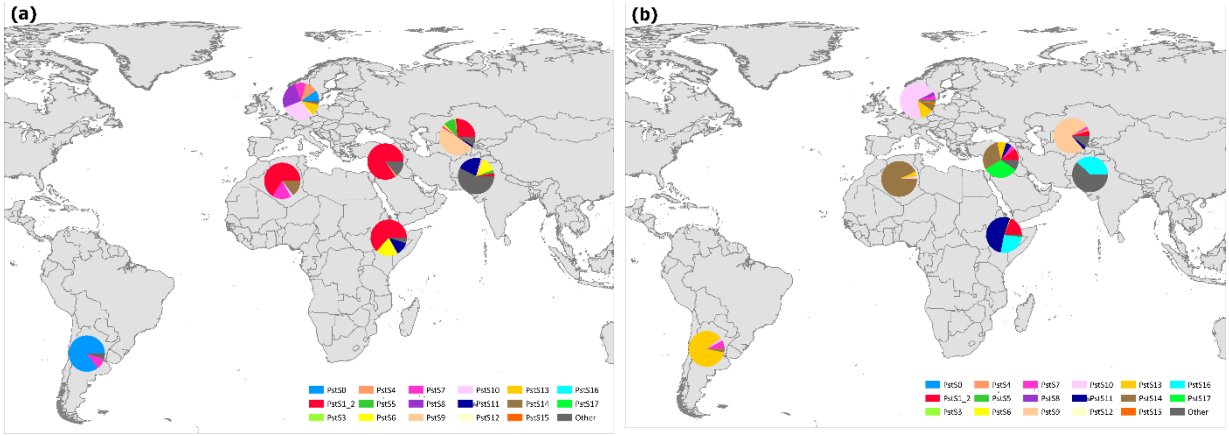

Fig. 2. Frequency of *P. striiformis* genetic groups in geographically distinct populations in two periods, a) 2009-2016 (n= 921) and b) 2017-2023 (n= 2259).

The distinct geographical distribution of genetic groups was striking. The aggressive and warm temperature-adapted group (PstS1/PstS2) was prevalent across Africa and the Middle East in the first period (2009-2016), but absent from South America, Europe and South Asia. PstS5 and PstS9 were only detected in Central Asia. PstS0, the prevalent genetic group in Europe up to 2010, was only detected in Europe, South- and North America and Australia. PstS8 was prevalent in northern Europe until 2016 and was not detected in other areas. PstS10 has been the most prevalent group in Europe since 2014 but has not been detected in East Africa and South- and Central Asia. These overall differences were reflected by corresponding F_{st} values based on an analysis where MLGs were grouped according to geographic population and sampling period (Table S2). Additional analyses based on clone-corrected data confirmed these trends but pointed towards additional connectivity between Central-West Asian populations and African and South Asian populations, respectively.

The limited differentiation between Middle East and East Africa/ NW Africa, and between South Asia and East Africa suggests sufficient migration to maintain low differentiation between these populations. The replacement of the prevalent PstS0 population in South America by a population dominated by PstS13 since 2017 represents the most dramatic temporal population shift between the two periods (Fst= 0.341).

333 The dataset also revealed several cases of emergence of novel, distinct genetic groups. For
334 example, PstS10 containing a single MLG was first detected in Europe in 2012 and became
335 widespread accounting for 82% of PstS10 samples (Table 1). This was followed by the
336 emergence of 14 additional, closely related MLGs in the European population. The
337 emergence of PstS13 and PstS14 in 2015-2016 in the European population represents two
338 additional, distinct genetic groups that were not readily explained by mutation or migration
339 events.

340

341 **Identification of hypothetical somatic hybrids**

342 Our genotypic data for PstS10, PstS13 and PstS14 were consistent with the hypothesis of
343 somatic hybridization by nuclear reassortment of isolates of pre-existing lineages within the
344 European population. First, allele sizes detected within samples representing MLGs of the
345 first detected cases of PstS10, PstS13 and PstS14 were compared with samples representing
346 all named genetic groups detected within Europe. This revealed that most MLGs and genetic
347 groups were excluded as potential parent(s) due to mismatching allele sizes (Table S3). The
348 next step involved inference of haplotypes of hypothetical parental pairs and hybrid MLGs by
349 alignment with the PstS0 haplotype-phased reference genome, and assignment of the
350 position of SSR markers on a genetic map, which revealed the genome derived SSR haplotype
351 of PstS0 (Table S2, Fig. S3) as well as the haplotype based on observed SSR allele sizes (Table
352 S6). Nucleus haplotype A of prevalent European races in PstS0 provided a 100% match with a
353 nucleus haplotype of PstS10, where the second haplotype (B) provided a 100% match with a
354 nucleus haplotype represented by the most prevalent MLG in PstS7. These results were
355 confirmed by independent genomic data of isolates representing the parental groups of PstS0
356 and PstS7, and the hybridization resulting in PstS10 (Fig. S5). Similarly, we obtained 100%
357 nucleus haplotype matches for PstS13 and PstS14, revealing that haplotype B in PstS7 was
358 involved in the three hybridization events, however, arising from two different MLGs within
359 PstS7. A schematic representation of the sequence and network of hybridization events is
360 presented in Fig. 3; supplementary dotplots of the pairwise genome alignments and total SNP
361 counts and average identity among the nuclear phased haplotypes of the PstS10 hybrid and
362 the likely parental isolates shown in Fig. S5.

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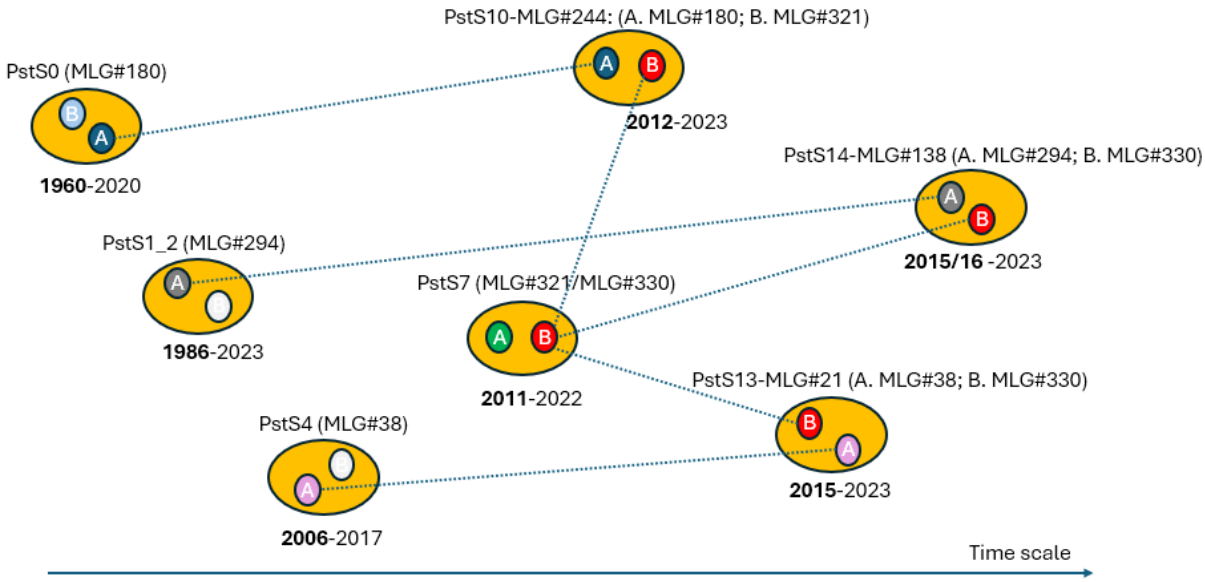


Fig. 3. Schematic representation of three independent hybridization events supported by observed SSR multilocus genotypes, pairwise genome alignments, and derived nuclear haplotypes. PstS10 was first detected in northern Europe (2012) in an area where the respective MLGs of PstS0 (#180) and PstS7 (#321) were prevalent on shared hosts of bread wheat. PstS13 was first detected in 2015, where a single MLG (#21) was detected at multiple locations in Europe, often on Triticale and rarely on winter wheat. The relevant MLG of PstS4 (#38) was detected almost exclusively on Triticale, while the MLG of PstS7 (#330) was detected widespread on triticale as well as bread wheat. PstS14 (MLG#138) was first detected in Europe in 2015/ NW Africa 2016 (not surveyed in 2015), the involved MLGs of PstS7 (MLG#330) and PstS1_2 (MLG#294) being prevalent in southern Europe/NW Africa at that time. First and last sampling years for individual genetic groups in the dataset are indicated (years before 2009 represented by historic reference samples).

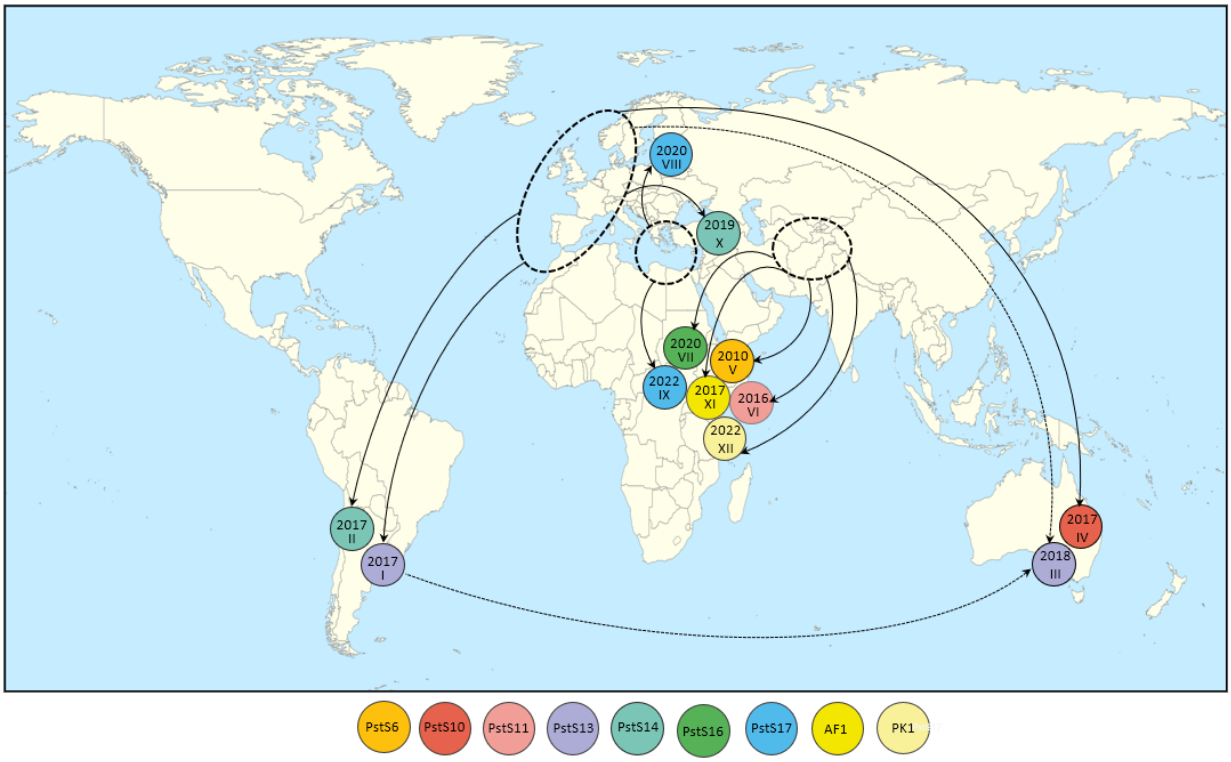
Long distance dispersal events

The hypothesis of migration events at intercontinental scale was investigated by analyses of first detection of specific genetic groups and distinct MLGs within these in the seven geographical populations (Fig. 4). In three cases, first detection was associated with novel evolutionary origin by hybridization of pre-existing MLGs of divergent genetic groups within the considered geographical population, i.e., PstS10 (PstS0 and PstS7), PstS13 (PstS4 and

384 PstS7), and PstS14 (PstS1_2 and PstS7). These were first detected in Europe and NW Africa
385 between 2012 and 2016 (Fig. 4).

386 We documented 12 cases of exotic incursions of *Pst* at intercontinental scales (I-XII). Migration
387 direction and events were hypothesised based on year of first detection / hybridization event
388 in source and recipient areas, as well as prevalence and diversity within considered genetic
389 group (Table 1, Table 2, Figure 4).

390



391

392 **Figure 4.** Documented inter-continental incursions of *P. striiformis* 2009-2023, based on
393 sequential resampling of multilocus SSR genotypes/pathogen races on different continents.
394 Dotted circles represent putative source areas, where considered *Pst* group and MLGs
395 defined by 18 polymorphic SSR markers were first detected, arrows represent putative
396 transmission routes, colored circles represent first year of detection on the recipient
397 continent and the corresponding ID of individual MLGs. Details of individual dispersal events
398 and individual migrant MLGs are presented in Table 2. Dotted arrows: PstS13-MLG #21
399 present at two continents at time of incursion into Australia. The positions of circles and
400 arrows on the map are indicative.

401

402 Table 2. Inter-continental *Puccinia striiformis* dispersal events (I-XII) within a 15-year period
403 (2009-2023) documented by source and recipient areas of unique multi-locus genotypes
404 (MLGs), genetic groups and race phenotype.

Dispersal event (cf. Fig. 4)	Migrant (MLG #)	SSR genetic group	First detected (population and year)	Reference	Recipient population and year	Race confirmation in source and recipient population)[3]
I	21	PstS13	Europe (2015)	Ali et al. 2017	South America (2017)[2]	**Confirmed** : -,2,-,-,-,6,7,8,9,-,-,-,-,-,-,-,-,-,AvS,-
II	134	PstS14	Europe (2015)	Hovmøller et al. 2017 [1]	South America (2017)[2]	-
III	21	PstS13	Europe (2015)	Ali et al. 2017	Australia (2018)[2]	-
IV	244	PstS10	Europe (2012)	Ali et al. 2017	Australia (2017)[2]	-
V	8	PstS6	Central Asia (2009)	Ali et al. 2017	East Africa (2010)[2]	**Confirmed**: 1,2,-,-,-,6,7,-,9,-,-,17,-,-,27,-,-,AvS,-
VI	78	PstS11	Central Asia (2012)	Hovmøller et al. 2018 [1]	East Africa (2016)[2]	**Confirmed**: -,2,-,(4),-,6,7,8,-,-,-,17,-,-,27,32,-,AvS,-
VII	205	PstS16	South Asia (2017)	Hovmøller et al. 2023 [1]	East Africa (2020)[2]	**Confirmed**: 1,2,3,(4),-,6,7,8,9,-,-,17,-,25,27,32,-,AvS,-
VIII	170	PstS17	Middle East (2018)	Hovmøller et al. 2019 [1]	Europe (2020)	**Confirmed:** -,2,-,-,-,6,7,8,-,-,-,17,-,-,-,32,(Sp),AvS,Amb
IX	170	PstS17	Middle East (2018)	this paper	East Africa (2022)	**Confirmed:** -,2,-,-,-,6,7,8,-,-,-,17,-,-,-,32,(Sp),AvS,Amb
X	138	PstS14	Northwest Africa (2016)/ Europe (2016)	this paper	Middle East (2019)	-
XI	103	AF1	Central Asia (2012)	this paper	East Africa (2017)	**Confirmed**: 1,2,-,-,[-],6,7,8,9,-,-,17,[-],-,27,-,-,AvS,-
XII	185	PK1	South Asia (2017)	this paper	East Africa (2022)	-

[1] Annual reports from Global Rust Reference Center (accessible: www.wheatrust.org)

[2] High impact event in recipient areas

[3] Figures and symbols designate virulence and avirulence (-) corresponding to Pst resistance genes: *Yr1, Yr2, Yr3, Yr4, Yr5, Yr6, Yr7, Yr8, Yr9, Yr10, Yr15, Yr17, Yr24, Yr25, Yr27, Yr32* , and the resistance specificity of Spalding Prolific (Sp), Avocet S (AvS) and Ambition (Amb).

405

406

407 In all cases, we were able to detect likely geographical source areas, including two specific
408 MLGs spreading from Europe into South America in 2017 (I and II, Table 2), i.e., PstS13 (MLG
409 #21) and PstS14 (MLG #134), MLG #21 spreading into Australia (III, Table 2) and detected the
410 following year (2018). PstS10 (MLG #244), the most common genotype in Europe since 2016,
411 was also detected as an exotic incursion in Australia in 2017 (IV, Table 2). MLGs within three
412 additional and highly divergent genetic groups, PstS6 (MLG #8), PstS11 (MLG #78) and PstS16
413 (MLG #205), detected in Central/South Asia in 2009, 2012 and 2017, were observed for the
414 first time in East Africa (Ethiopia) in 2010, 2015 and 2020, respectively (V, VI, VII, Table 2).
415 PstS17 (MLG #170), first detected in the Middle East in 2018 and since then prevalent in this
416 region, was first detected at low frequency in northern Europe (Latvia, 2020, VIII, Table 2) and
417 in East Africa (Ethiopia, 2022, IX, Table 2). PstS14 (MLG138), first detected in Europe and NW
418 Africa in 2015/2016, was detected in the Middle East in 2019 (X, Table 2), later becoming
419 dominant in local areas in West Asia, e.g., Iraq, where a single MLG in PstS14 made up 100%
420 of samples from multiple locations and host cultivars (2021, 2022). Two MLGs, which have not
421 yet been assigned a named genetic group, detected in Afghanistan, 2012 (temporary
422 designation AF1, MLG #103) and Pakistan, 2017 (temporary designation PK1, MLG #185),
423 respectively, were observed in East Africa in 2017 (Kenya) and 2022 (Ethiopia), respectively

424 (XI, XII, Table 2). These genetic groups, including PstS17, have remained at low frequency to
425 date in recipient areas in Northern Europe and East Africa.

426 We grouped the dispersal events according to similarities in source and recipient areas,
427 resulting in seven potential intercontinental atmospheric transport routes (see Table S6).
428 Results from HYSPLIT trajectory simulations, analyses of mean wind patterns in combination
429 with wheat growth timing and spore survival times, as well as previous evidence from related
430 fungal pathogens lead us to hypothesize that (i) wind dispersal was not plausible for the two
431 dispersal events, i.e., "Europe to Australia" (route 3) and "South America to Australia" (route
432 2), where accidental human-mediated transmission seems more likely; (ii) wind dispersal was
433 highly unlikely for direct movement from Europe to South America (route 1) and from
434 Central/South Asia directly to East Africa (route 4), although the data does not exclude the
435 possibility of indirect, stepwise airborne transmission (via northern Africa and the Middle
436 East/Arabian Peninsula, respectively); (iii) wind dispersal was plausible for the three dispersal
437 routes, Middle East to Europe (route 5), Middle East to East Africa (route 6) and Europe/North
438 Africa to the Middle East (route 7).

439

440 **Discussion**

441 The potential impact of rare events of long-distance dispersal (LDD) of plant pathogens on
442 plant health has been known for decades, e.g., Brown and Hovmøller (2002), Smart and Fry
443 (2001), Ristaino et al. (2021), Jones (2021). Despite this, in the vast majority of cases the exact
444 source and recipient areas are not known. The focus has often been on high impact examples,
445 e.g., overview for *Pst* on wheat by Jin et al. (2020), rather than cases with insignificant impact,
446 which may be overlooked and thereby contribute to an underestimation of the true
447 frequency of LDD in crop pathogens.

448 The present study was based on unique and systematic wheat rust surveillance efforts over
449 15 years facilitated by the formation of the Borlaug Global Rust Initiative (BGRI) and the
450 Global Rust Reference Center in 2008. This network approach has taken advantage of the
451 engagement of multiple collaborators across the world in coordinated wheat rust sampling
452 efforts (Table S7), the use of standardized pathogen phenotyping and genotyping
453 methodologies (Thach et al., 2025), as well as application of commonly agreed data

454 management and analytical tools (Hovmøller, 2011). Altogether, the sampling covered major
455 wheat growing regions in 37 countries across seven broad geographical areas in Africa, Asia,
456 Europe, and South America, and was further connected to North America and Australia
457 through reference samples from major long-term national rust surveillance initiatives. This
458 study may, therefore, represents the largest and most comprehensive spatiotemporal survey
459 of a major crop pathogen to date (Savary et al., 2019).

460 We confirmed at least 12 intercontinental LDD dispersal events of Pst on wheat, each
461 supported by distinct multi-locus genotype data, and in many cases also phenotypic virulence
462 data, suggesting a recent common evolutionary origin for samples in both source and
463 recipient areas. In seven cases, the dispersal events resulted in severe and widespread
464 disease epidemics in recipient areas (Anibal Carmona et al. (2019) Riella et al. (2024); Ding et
465 al. (2021), whereas five cases had only minor epidemiological impact (i.e., rare detection of
466 the corresponding genetic groups in following years). In three cases, PstS10, PstS13, and
467 PstS14, the first detected and most prevalent MLGs within each of these groups were
468 hypothesized to originate asexually by somatic hybridization and nuclear reassortment. This
469 provided a unique opportunity to identify the evolutionary mechanism and source of
470 migrants, in addition to identifying the geographical area of first detection. Our conclusions
471 concerning the hypotheses of LLD dispersal in the latter three cases, versus an alternative
472 hypothesis of hybridization of "local" strains in recipient areas, were in all cases supported by
473 lack of detection of matching parental isolates of the hypothesized hybrids in recipient areas
474 (Australia and South America), despite extensive and widespread surveillance efforts
475 (www.wheatrust.org; (Anibal Carmona et al., 2019; Ding et al., 2021; Riella et al., 2024).

476 Additional LDD events were also identified, although the exact source areas were not
477 confirmed. For instance, the emergence of MLG #321 (PstS7) in Argentina in 2018 following
478 first detection in Europe (2011) and Northwest Africa (2013-2014), MLG #247 (PstS10) in
479 Uruguay in 2021, and MLG #175 (PstS17) in Northern Europe and East Africa. However, these
480 observations most likely followed the dispersal paths already established by related MLGs
481 with documented source origin, e.g., PstS7-MLG #321 and PstS10-MLG #247 (route 1), and
482 PstS17-MLG#175 (route 5), but final conclusions would require additional sampling efforts
483 from potential source areas that were not represented in the dataset.

484

485 Our findings represent previously undocumented aspects of yellow rust epidemiology. Unlike
486 other cereal rust fungi, somatic hybridization in *Pst*, involving nuclear reassortment, and
487 hypothesized parasexual exchange of genetic material has only been reported under
488 experimental conditions. Already in the 1960s, mixtures ofurediniospore isolates of different
489 races suggested that somatic hybridization by fusion of hyphae and subsequent nuclear
490 reassortment was the likely source of new race variants. More recently, cross infection
491 studies on wheat and barley using paired experimental isolates supported the occurrence of
492 somatic hybridization, however, these results could only be explained by assuming
493 chromosome reassortment and crossovers between parental isolates (Lei et al., 2017).
494 Earlier, Park and Wellings (2012) concluded that somatic hybridization was likely in many rust
495 species and *formae speciales*, the process being observed in nature within and between rust
496 species on *Linum*, *Populus*, *Senecio*, several grass species, and leaf rust on wheat. However,
497 the exact mechanisms were generally not well understood.

498 Our data suggest that somatic hybridization may be a more significant source of
499 agriculturally-relevant genetic diversity in yellow rust than sexual recombination. This may
500 help explain why the pathogen is rarely detected on the alternate host *Berberis vulgaris* (Jin
501 et al., 2010; Wang et al., 2016), even in the near Himalayan region or elsewhere, despite high
502 genetic diversity (Duan et al., 2010; Ali et al., 2014a; Thach et al., 2016; Huang et al., 2021).

503 In the present study, putative hybridization events in *Pst* were identified by positioning SSR
504 markers and allele sizes on a chromosomal map based on a haplotype-phased genome of a
505 PstS0 isolate (Tam et al., 2025). This was combined with careful analysis of MLGs generated
506 using consistently applied methodologies (Thach et al., 2025), which revealed three major
507 hybridization events giving rise to PstS10, PstS13 and PstS14. Importantly, the hybrid origin of
508 PstS10 was confirmed by comparing haplotype-phased nuclear assigned genomes of the
509 potential parents. The prevalence of matching MLG haplotypes in PstS0 and PstS7 suggested
510 a hybridization event resulting in PstS10 somewhere on bread wheat in Europe. In contrast,
511 the inferred parental origin of PstS13 was a relatively rare MLG in PstS7 (#330, <10%),
512 sampled from both bread wheat and Triticale, and a frequent MLG in PstS4 (#38, > 95%),
513 almost exclusively associated with Triticale. This suggests that hybridization most likely took
514 place on Triticale. The resulting MLG (# 21) of PstS13 was frequently detected on Triticale,
515 durum wheat, and spring wheat, but rarely on winter wheat. For PstS14, one of the putative

516 parents, PstS1_2 MLG #294, was detected only in NW Africa, coinciding with the presence of
517 a matching second parent (PstS7 MLG #330 in the same region in 2014. Interestingly, PstS14
518 made up 100% of samples in surveys in three consecutive years in NW Africa since 2016, i.e.,
519 2016 (six samples), 2017 (38 samples) and 2018 (54 samples), whereas this group was
520 observed only sporadically elsewhere. This spatial and temporal pattern strongly support the
521 emergence of PstS14 through somatic hybridization in Northwest Africa. In addition to these
522 three major hybridization events, our data revealed two additional cases of 100% matches
523 between hypothesized parental pairs and hybrids, which remained at low prevalence in the
524 European *Pst* population, and one case of hybridization in the North American population
525 (data not shown).

526 In four high-impact and three low-impact cases, the conclusion of recent dispersal events
527 was supported by identical virulence phenotypes in source and recipient areas based on
528 assays comprising wheat experimental lines representing more than 25 different host
529 resistance specificities (Thach et al., 2025). Because mutation from avirulence to virulence in
530 plant pathogenic fungi, including *Pst,* may be significantly higher than average mutation rates
531 (Hovmøller and Justesen, 2007), the existence of an exact match in virulence phenotype is an
532 additional indication of direct connection between such populations in an evolutionary time
533 perspective.

534 Based on the 12 confirmed dispersal events, we hypothesized seven putative transmission
535 routes, where the plausibility of wind dispersal was investigated through HYSPLIT trajectory
536 simulations based on high-resolution global meteorological data, testing different spore
537 survival times in the atmosphere, and also through analyses of wheat growing timing, monthly
538 mean wind patterns during those periods where the empirical data suggested that LDD could
539 have taken place. This integrative analysis along with recent evidence from related fungal
540 pathogens, indicates that both human mediated and windborne dispersal playing important
541 roles in intercontinental dispersal of wheat yellow rust.

542 Airborne dispersal appears especially plausible between the Middle East and East Africa as well
543 as Europe. This aligns with observed, genetic similarities between *Pst* populations in the Middle
544 East and East Africa (Table S3) that also indicates frequent gene flow between these regions
545 and help explain several of the reported incursion events (Fig. 4, Table 2). The recent detections
546 of Pst6, Pst11, Pst16, Pst17, AF1 and PK1 in East Africa after previous detections in the Middle

East and Central/South Asia, provide supportive evidence for the previously proposed Rift Valley Incursion pathway for rust fungi (Meyer et al., 2017a). While direct dispersal from Central/South Asia to East Africa seems highly unlikely, the possibility of stepwise airborne dispersal via the Middle East cannot be ruled out. However, the latter scenario is less supported since PstS6 and PstS16 were not detected in the Middle East, and PstS11 appeared in the region only three years after first detection in East Africa, although relatively low sampling intensity in critical areas on the Arabian Peninsula and the Horn of Africa should be taken into account, as well as the stochastic nature of these LDD events.

Direct airborne dispersal from Europe to South America or from Central/South Asia to East Africa were highly unlikely, and a more comprehensive modelling study is required to test the hypothesis of stepwise airborne transmission. Similarly, for the two dispersal events from Europe to Australia and South America to Australia, wind dispersal was not plausible, indicating human mediated transport and emphasizing the importance of quantifying risks due to unintended human-mediated transmission via trade and travel. The trajectory simulations presented here were intended at developing initial hypotheses about which dispersal mechanisms might be plausible for each incursion event. Testing as part of future work would require large-scale modelling efforts incorporating detailed spore dispersion simulations that include environmental and epidemiological conditions at source and target regions, along with sensitivity analysis covering spore survival times, releasing times and locations. To advance such efforts, two key components are essential. First, the collection of more detailed experimental data on spore survival times during atmospheric transport obtained from large samples of viable spores, to estimate more reliably the fraction of spores, out of extremely large numbers released during outbreaks, and a continued extension of global surveillance networks are essential for further improving our understanding and capacity to predict and mitigate risks from long-range exotic incursion events.

Altogether, our study has documented a high degree of connectivity world-wide between populations of one the most epidemic crop pathogens, yellow rust infecting cereals and grasses, geographically as well as genetically. Incursions from the Himalayas and elsewhere into Europe and the Mediterranean basin 10-20 years ago (Hubbard et al., 2015; Hovmøller et al., 2016; Walter et al., 2016) hybridized with isolates of pre-existing genetic groups, e.g., PstS0, PstS1_2, PstS4, the new hybrids replaced to a large extent existing population(s),

578 spreading onwards to new continents (Hovmøller et al., 2023), where the immigrant strains
579 rapidly became dominant (Anibal Carmona et al., 2019; Ding et al., 2021; Riella et al., 2024).

580 Such a connectivity between populations of airborne pathogens is probably particularly evident
581 in global cropping systems like wheat, which is grown on six continents. This widespread
582 cultivation underscores the need for coordinated pathogen surveillance and early-warning
583 systems at both regional and global levels. Access to reference laboratories and testing facilities
584 is crucial as these enable timely assessment of the vulnerability of breeding material and
585 deployed cultivars to new and aggressive pathogen strains before they become widespread.

586 We show here that somatic (asexual) hybridization both takes place and seems to be common
587 in natural populations of *Pst* despite previously only reported under experimental conditions.
588 The rapid raise of hybrids such as PstS10, PstS13 and PstS14, which to a large extent replaced
589 pre-existing pathogen populations in Europe, Australia and South America, suggests that new
590 epidemiological insights into the actual mechanisms of hybridization at both cellular and
591 genetic levels are required. While not all hybridization events necessarily lead to increased
592 fitness or persistence, the widespread success of these particular hybrids suggests that these
593 may be potentially superior in fitness to their parents taking the entire epidemiological disease
594 cycle into account, which may involve changed interactions with various components and
595 mechanisms of host resistance.

596 Our data suggest that the risks and pace of pathogen evolution driven by mutation and somatic
597 hybridization may correlate positively with the size and areas affected by ongoing epidemics. In
598 turn, this may influence the probabilities of further hybridization and risks of unintentional
599 pathogen spread at local, regional and global levels. Thus, there is an imminent and urgent need
600 to sustain research and development within the area of plant breeding and disease
601 epidemiology including both experimental as well as modelling approaches to better anticipate
602 and prevent future epidemics. In parallel, greater awareness is needed around the risks of
603 unintentional crop pathogen spread via human activity to enhance food security in
604 agroecological settings with rapidly changing climate and weather patterns and increasing
605 political instability.

606

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Competing interests

None declared

Author contributions

DH and MSH conceived and designed the surveillance program; TT carried out the experimental SSR genotyping work under the supervision of AFJ, including data alignment and quality check and population genetic analyses; VR assisted in genotyping of samples from South America; JRA performed virulence phenotyping of hypothetical migrant isolates and assisted in SSR genotyping ; JGH developed the web-based data management and display system for world-wide prevalence of *Pst* genetic groups; KN supplied raw SSR data for Middle East samples 2018-2020; RP was curator of reference samples representing the Australian *Pst* population 1979-2021, undertook race analysis, and was responsible for associated funding; RT and MM performed the sequencing and genomic data analyses of PstS10 hybrid and parental isolates; BS and JR contributed to genomic data analysis, supervised and secured funding for the genomic work and provided extensive feedback on the manuscript; PS RT and MM performed the sequencing and genomic data analyses of PstS10 hybrid and parental isolates; BS and JR supervised and secured funding for the genomic work; PS supervised the PhD work of VR in South America; MME conducted trajectory simulations of the plausibility of wind dispersal of spores based on meteorological datasets; MSH was curator of samples hosted by the GRRC, supervised project activities anchored at GRRC, wrote the first draft of the manuscript; all authors revised and accepted the final manuscript.

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674

675 **Data availability**

676 All raw sequencing data generated in this study have been submitted to NCBI BioProject
677 database under accession number PRJNA1256629. The SSR genotypic data of the 3180 isolates
678 included in the present study are available at https://doi.org/ (pending)

679

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