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LETTER

Transmission pathways for the stem rust pathogen into Central and East Asia and the role of the alternate host, barberry

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Supplementary material for this article is available online

Abstract

After many decades of effective control of stem rust caused by the *Puccinia graminis f.sp. tritici, (hereafter Pgt) the reported emergence of race TTKSK*/Ug99 of *Pgt* in Uganda reignited concerns about epidemics worldwide because ∼90% of world wheat cultivars had no resistance to the new race. Since it was initially detected in Uganda in 1998, Ug99 variants have now been identified in thirteen countries in Africa and the Middle East. Stem rust has been a major problem in the past, and concern is increasing about the risk of return to Central and East Asia. Whilst control programs in North America and Europe relied on the use of resistant cultivars in combination with eradication of barberry (*Berberis spp.*), the alternate host required for the stem rust pathogen to complete its full lifecycle, the focus in East Asia was principally on the use of resistant wheat cultivars. Here, we investigate potential airborne transmission pathways for stem rust outbreaks in the Middle East to reach East Asia using an integrated modelling framework combining estimates of fungal spore deposition from an atmospheric dispersion model, environmental suitability for spore germination, and crop calendar information. We consider the role of mountain ranges in restricting transmission pathways, and we incorporate a representation of a generic barberry species into the lifecycle. We find viable transmission pathways to East Asia from the Middle East to the north via Central Asia and to the south via South Asia and that an initial infection in the Middle East could persist in East Asia for up to three years due to the presence of the alternate host. Our results indicate the need for further assessment of barberry species distributions in East Asia and appropriate methods for targeted surveillance and mitigation strategies should stem rust incidence increase in the Middle East region.

1. Introduction

Stem rust caused by *Puccinia graminis f. sp. tritici* (hereafter *Pgt*) is one of the most serious fungal diseases of wheat and barley. It is a major global concern for food security because in the most severe cases it can cause 100% crop loss (Saari and Prescott 1985, Singh *et al* 2015). *Pgt* is the most destructive of the three wheat rust diseases (the others being stripe rust caused by *Puccinia striiformis f. sp. tritici* and leaf rust caused by *Puccinia triticina*), because it affects all above-ground plant parts (Eversmeyer and Kramer 2000). Historically, *Pgt* was a major problem in East Asia (Saari and Prescott 1985). In China, nine severe epidemics occurred between 1920 and 1970 (Wu *et al* 2020), and *Pgt* was widely distributed across Japan in 1950–1960 (Yamada *et al* 1961). *Pgt* was also a major problem in other wheat-growing regions such as Europe and North America (Stakman 1923, McKay 1957, Singh *et al* 2007). As a result, two main approaches for its control have been adopted: development of *Pgt*-resistant cultivars, and barberry (*Berberis spp.*) eradication programmes. Barberry is the alternate host required for full lifecycle involving sexual reproduction completion, which can lead to new recombinant strains of the pathogen. Direct wheat-wheat transmission only occurs through the uredinial (asexual) spore stage, and the longevity of an outbreak is limited in regions without barberry because the uredinial stage on wheat (i) cannot persist without a host, (ii) cannot overwinter in very cold conditions and (iii) cannot over-summer in very hot, humid conditions.

Pgt is not currently considered a disease of concern in Central and East Asia, and focus has turned instead to stripe rust (now regionally more problematic). However, after many decades of effective control, *Pgt* is reemerging as a major pathogen of wheat (Lewis *et al* 2018, CIMMYT 2024). The spread of a highly virulent race group, Ug99, out of Africa into the Middle East is of particular concern because ∼90% of the wheat and barley cultivars grown worldwide have no resistance (Pretorius *et al* 2000, Singh *et al* 2011, Steffenson *et al* 2017) and extensive breeding efforts for resistant cultivars are underway (Bhavani *et al* 2019).

China has been identified as one of the most vulnerable regions for *Pgt* (Radici *et al* 2022) and East Asia as a region with a high risk of *Pgt* infection on barberry (Sinha and Chen 2021). However, as well as excluding the role barberry plays in the disease cycle, previous work modelling transmission pathways for *Pgt* has seldom considered how mountain ranges restrict airborne dispersal of the fungal spores. To investigate the potential for Ug99 or other virulent *Pgt* races to spread from the Middle East into Central and East Asia, we therefore use and extend the integrated modelling framework of Bradshaw *et al* (2022) to consider these aspects and address the following questions:

i. Can *Pgt* reach East Asia from the Middle East via a northern pathway through Central Asia?
ii. Can *Pgt* reach East Asia from the Middle East via a southern pathway through South Asia?
iii. What is the risk of reciprocal spread into the Middle East or South Asia from Central and East Asia?
iv. Can simulated *Pgt* outbreaks extend beyond a single cropping year as the uredinial spore stage?
v. How are simulated *Pgt* outbreaks impacted by the presence of the alternate host, barberry?

2. Description

2.1. The integrated modelling framework

We use a simple Susceptible-Exposed-Infectious-Removed epidemiological framework to combine data from the Lagrangian particle dispersion model, NAME (Jones *et al* 2007) configured for the simulation of *Pgt* fungal spores, a meteorology-driven environmental suitability model and crop calendar information as shown in figure S1. The integrated model is described in Bradshaw *et al* (2022) and summarised in supplementary note S1. Our NAME model setup is higher resolution than many studies have used (e.g. 59 vertical levels as compared to six; Isard *et al* 2005) and includes processes such as UV decay of fungal spores, sedimentation/dry deposition, and a meteorology-dependent release rate, that many do not (e.g. Isard *et al* 2005, Pfender *et al* 2006, Prank *et al* 2019).

The threshold for the probability of infection (environmental suitability multiplied by the normalised log of fungal spore deposition, refer to supplementary note S1; hereafter PoIT) can be varied: in this study, we assume any value above 0 implies infection (i.e. 1 spore/ha, or more, landing on a susceptible site with a non-zero measure of environmental suitability leads to infection) and sensitivity tests are conducted with a PoIT value of 0.2, the value at which transmission pathways identified cease to be viable in other work (Bradshaw *et al* 2022). The latency period model used is the temperature-dependent model of Nopsa and Pfender (2014).

2.2. Extending the integrated model: mountains

Whilst the NAME model can simulate fungal spore transport over very high mountains, there is reason to believe it might not be a viable pathway. Firstly, the extreme low temperature limits for urediniospore viability are poorly studied, but there is a relationship between the duration of exposure to sub-zero temperatures and urediniospore survival (Eversmeyer and Kramer 1994) and it is likely there is a threshold below which urediniospores cannot recover (McCallum *et al*

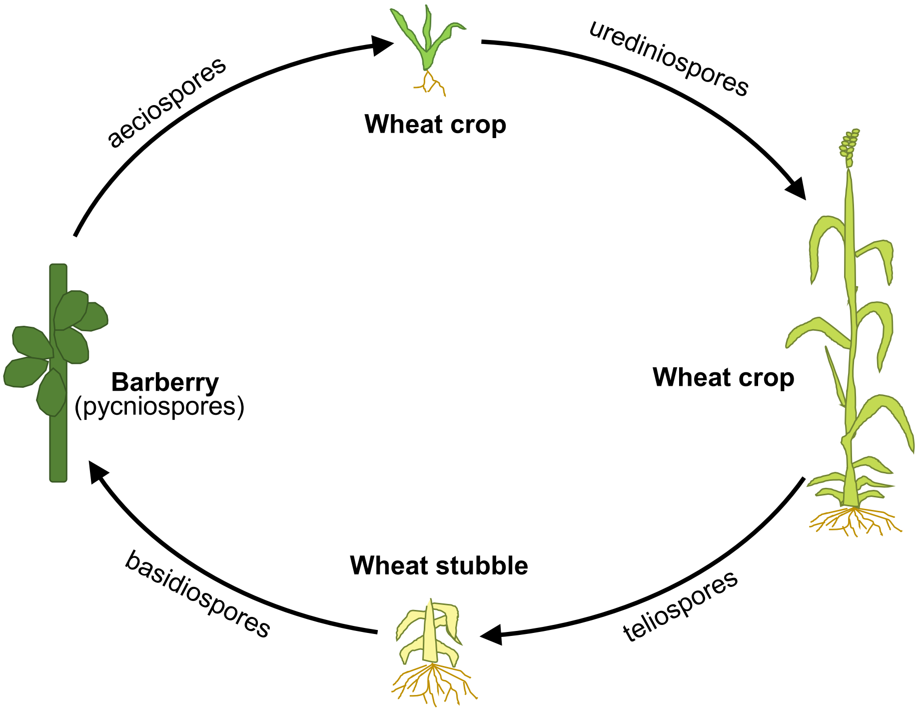

Figure 1. Stem rust lifecycle schematic. Note that the pycniospore stage is not considered in the integrated model.

1999). Secondly, it is likely spores transported to great heights in the atmosphere over the Himalayas can coalesce to form ice condensation nuclei, depositing out of the air column due to gravity (Morris *et al* 2013, Stopelli *et al* 2017). High genetic divergence between populations of stripe rust provide circumstantial evidence for the Himalayan mountains acting as a barrier to transmission (Khan *et al* 2019, Awais *et al* 2023). No other modelling setup currently includes extreme low temperature limits for fungal spore survival or fungal spore ice nucleation processes meaning that further study into the impact of high mountains on spore transmission is required, so here we computationally prohibit transmission between sites requiring transportation above 3000 masl (the elevation that captures most of the high mountain ranges in the region). The excluded pathways and a description of the impact of those exclusions is provided in supplementary note S2 and figures S2–S4.

2.3. Extending the integrated model: barberry (Berberis spp.), the alternate host

The *Pgt* pathogen has a complex lifecycle, with rapid cycles of asexual reproduction on wheat while sexual recombination requires the presence of an alternate host, barberry. Wheat-wheat infections can only occur in the urediniospore stage of the lifecycle (figure 1), which is dependent upon the continuous presence of green living tissue. Once wheat begins to senesce the fungus switches to the production of teliospores, which can over-winter on stubble (Agrios 2023). Teliospores are the only spore stage of *Pgt* that can survive without a living host. When teliospores germinate in spring, they produce basidiospores that infect the alternate host, barberry, but not wheat. The pathogen completes sexual reproduction on the alternate host within the pycniospore stage, after which aeciospores are released from the barberry and will infect new wheat crops (but not other barberry), repeating the cycle (Schumann and Leonard 2000).

We extend the framework of Bradshaw *et al* (2022) to include barberry in the *Pgt* lifecycle. Whilst we recognise there is great variability in the susceptibility of different barberry species to infection by basidiospores, subsequent abundance of aeciospores, and the infectiousness to wheat of those aeciospores (refer to Zhao *et al* 2015 and references therein), we consider only a 'generic' representation of all barberry species in this study.

There are likely some differences in the thresholds for the different spore stages, for example because teliospores germinate earlier in the year than urediniospores the temperature thresholds are likely to be lower, but there is not enough information in the literature to confidently prescribe different values. For our modelling, we therefore assume the same temperature and moisture thresholds for teliospore, basidiospore and aeciospore germination as for urediniospore germination (Pillai *et al* 1978, Schumann and Leonard 2000). Teliospore formation is also temperature-dependent, with production occurring between 5 °C and 30 °C (Kao and

Knott 1969, Pillai *et al* 1978, Roelfs and Groth 1988), and may also be associated with the presence of the hyphomycetous fungus *Aphanocladium album* (Biali *et al* 1972, Yaniv *et al* 1979). Telia formation may also be complicated by genetic adaptation to different environmental conditions (Wan *et al* 2019) and may form at all wheat growth stages (Chen *et al* 2021), though studies are limited to the stripe rust pathogen. In our study it is assumed that all uredinia progress to telia production one month before harvest.

In contrast to urediniospores, exposure to low temperatures has been found to condition teliospores for germination (Melhus *et al* 1920). We therefore prohibit teliospore germination if the teliospores have not been exposed to extended periods of cold temperatures (Schumann and Leonard 2000, Wang and Chen 2015). The duration for which exposure is required, however, is not well defined. Here we assume 30 d exposure to temperatures <4 °C based on findings from Anikster (1986) and typical treatments for vernalization experiments for a range of rust teliospores (e.g. Norquay 1992, Bruckart and Eskandari 2002). Teliospore viability is constrained to a single overwintering. Our adopted methodology therefore means the spread of *Pgt* to barberry is limited only by the ability to overwinter as teliospores and germinate in the spring. We assume all barberry and wheat stubble are rainfed.

Whilst urediniospores can be spread by the wind over long distances (for example, as far as 8000 km between southern Africa and Australia; Burdon *et al* 1982, Visser *et al* 2019), we assume barberry infections only happen close to stubble bearing teliospores. This is because basidiospores produced by germinating teliospores have a limited viability: they only survive for a few hours and require moisture so often dry out and die within a few kilometres from release (Roelfs 1985, Roelfs *et al* 1992, King 2015). We similarly assume wheat infections from aeciospores released from barberry only happen in close proximity as these spores usually only travel a few kilometres (Melhus *et al* 1920, Stakman *et al* 1957, Singh *et al* 2002, Bueno-Sancho *et al* 2021). In our simulations, transmission of basidiospores and aeciospores are therefore limited to the same representative wheat-growing region (9 model grid cells at 10 km resolution, refer to supplementary note S1) as the wheat site where uredinial sporulation first progressed to the formation of telia. Supplementary table S1 lists the key metrics used for each of the spore stages.

2.4. Sites and potential locations for Pgt infection

We take recent *Pgt* infection occurrences recorded in the RustTracker database (University of Aarhus 2022) for 2007–2022 (figure 2(a)) and consider only those sites within 200 km of an observed barberry occurrence to be suitable for barberry infection (refer to supplementary notes S1). This step was necessary because expert opinion is there is no barberry in the Bangladesh sites, western India or southern Pakistan and a consistent methodology for excluding barberry was desirable. We perform a sensitivity study of the impact of removing potential barberry sites (supplementary notes S3; figures S32 and S33).

The monthly crop calendar and wheat planting and harvest date assumptions are based on the references given in supplementary tables S2 and S3. The water regime assumptions are provided in supplementary table S4 and the main crop calendar assumptions in supplementary note S1. We assume two potential starting source locations: sites with confirmed Ug99 of Halabja, Iraq and Hamadan, Iran (University of Aarhus 2022), and simulations are conducted for the five-year period 2017–2021 with starting dates in each of the months the starting sources are both susceptible and infectious.

3. Results

3.1. Urediniospore lifecycle only

Pgt epidemics beginning in Iraq are very sensitive to the timing of the initial outbreak and PoIT. At PoIT = 0, a northern pathway of transmission from the Middle East across East Asia to Japan exists via Central Asia every year when the outbreak is early (figure 3(a)), whereas at PoIT = 0.2, the infection only reaches as far east as Japan in 2017, and then only for an early outbreak (figure 3(b)). For most years, later initial infections do not spread beyond Central Asia, and in many years does not leave the Middle East.

For one year, 2021, a southern pathway via Southern Asia materialises, spreading the infection very quickly to Japan (supplementary figures S55(a); March). In this scenario, sites in southern China and Japan are infected from Bangladesh (the only simulation where Bangladesh sites are infected) but only when PoIT = 0 and the outbreak is early. We therefore suggest this occurrence would be extremely rare and a southern pathway to East Asia an unlikely scenario.

In all cases, the infection dies out when the crops in all countries have been harvested. More detailed results can be found in figure S5.

Pgt epidemics beginning in Iran are similar to those beginning in Iraq, but northern sites are infected slightly more frequently and there is no southern pathway of transmission (figure 4). More detailed results can be found in figure S6.

We infer from these two sets of results that *Pgt* can reach East Asia from the Middle East via a northern pathway through Central Asia, but a southern pathway through South Asia is unlikely. We also conclude that *Pgt* outbreaks cannot extend beyond a single cropping year as the uredinial spore stage in this region with the assumptions used.

3.2. Full lifecycle

When the barberry alternate host is added, there is a huge jump in the frequency that sites become infected

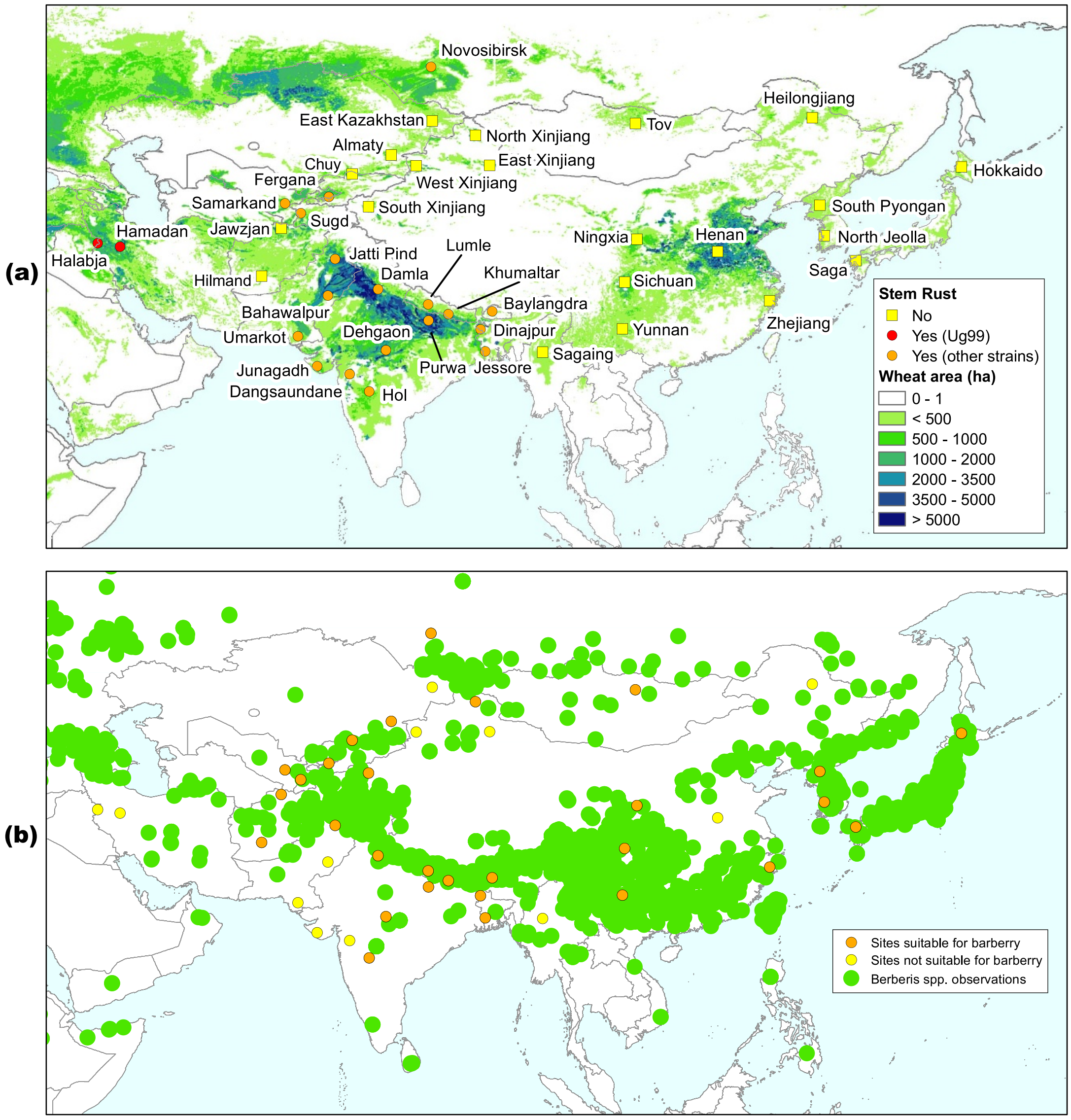

Figure 2. Site locations and crop types used in integrated modelling. (a): Sites in relation to wheat harvest area. Circles indicate confirmed disease locations (CDLs) and squares indicate representative disease locations (RDLs): red circles show sites with confirmed identification of Ug99 stem rust, orange circles show confirmed sites with identification of other strains of stem rust, yellow squares indicate areas of high wheat density where stem rust occurrences have not been recorded in the RustTracker database between 2007 and 2022 (University of Aarhus 2022). The wheat area shown is taken from the MapSPAM dataset for 2010 (International Food Policy Research Institute 2019). (b): Sites in relation to suitability for barberry. Green circles show occurrences of all barberry species (*Berberis spp.*) taken from the Global Biodiversity Information Facility (GBIF.org 2022). Orange circles show sites considered unsuitable for barberry according to the assumption of being located further than 200 km of an observation and yellow circles show sites considered suitable for barberry according to the assumption of being located within 200 km of an observation (refer to supplementary notes S1 for more details).

from Iraq over the five-year period (figure 5(a)). This is because the initial infection persists throughout Central and East Asia for the duration of the five-year period we assess (supplementary note S3 and figures S7(a)–S10(a)).

Sites where the rust can complete its full lifecycle with PoIT = 0 are in Afghanistan, Uzbekistan, Kyrgyzstan and Tajikistan (figure 5(b)); other sites do not meet the environmental suitability criteria for infection at the barberry stage. In some cases, infection spread in subsequent years is greater than the initial year of infection because the barberry transmission pathway allows local infections earlier in the crop calendar than the uredinial transmission pathway. This result is highly dependent upon the PoIT for urediniospores and the timing of the initial infection, however. At PoIT = 0.2, late initial infections are limited to the north (figures 6, S11–S14) because the environmental suitability for infection by basidiospores at the barberry stage of the lifecycle is not favourable enough to meet the higher threshold criteria (since the deposition of fungal spores remains the same in all PoIT scenarios) and only the number of sites experiencing barberry infections reduces.

The simulations beginning in Iran (figures S15–S22) are all very similar to those beginning in Iraq.

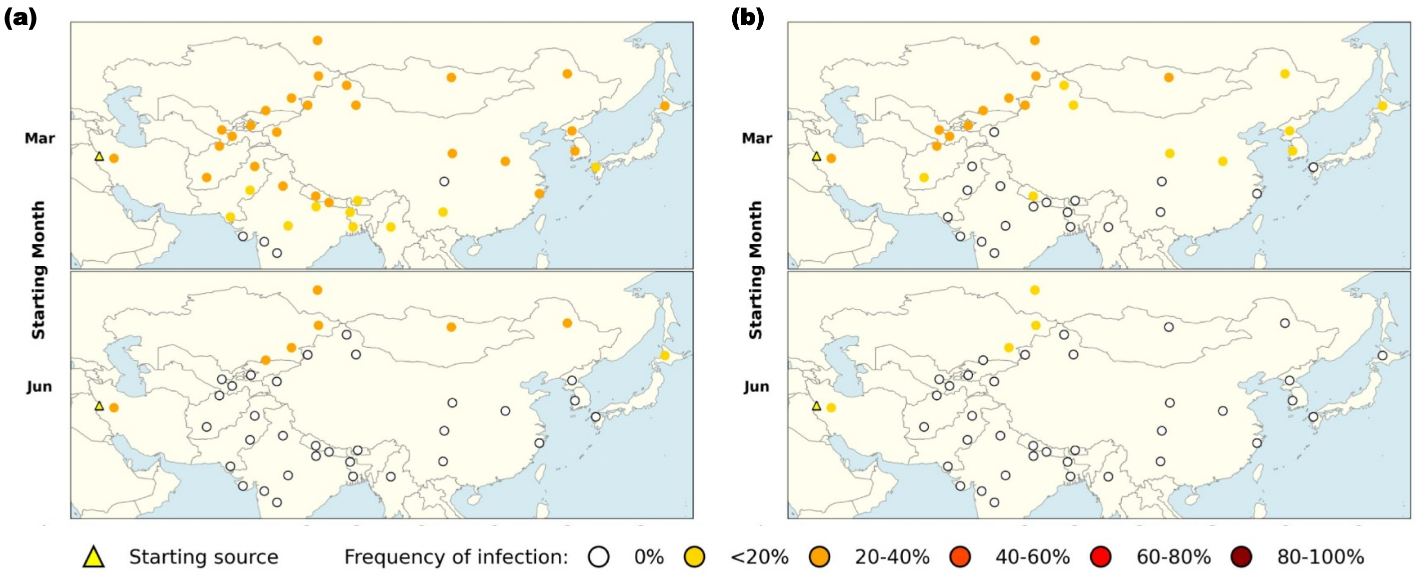

Figure 3. Simulation results for an outbreak in the starting source of Halabja in Iraq (urediniospore lifecycle only). (a): Probability of infection threshold 0.0; (b): probability of infection threshold 0.2. The frequency of each site being infected over the five-year period 2017–2021 is shown for an infection starting in March and in June each year. Note that the frequency of infection is calculated assuming 15 possible years of infection (2017–2021, 2018–2021, 2019–2021, 2020–2021 and 2021 alone).

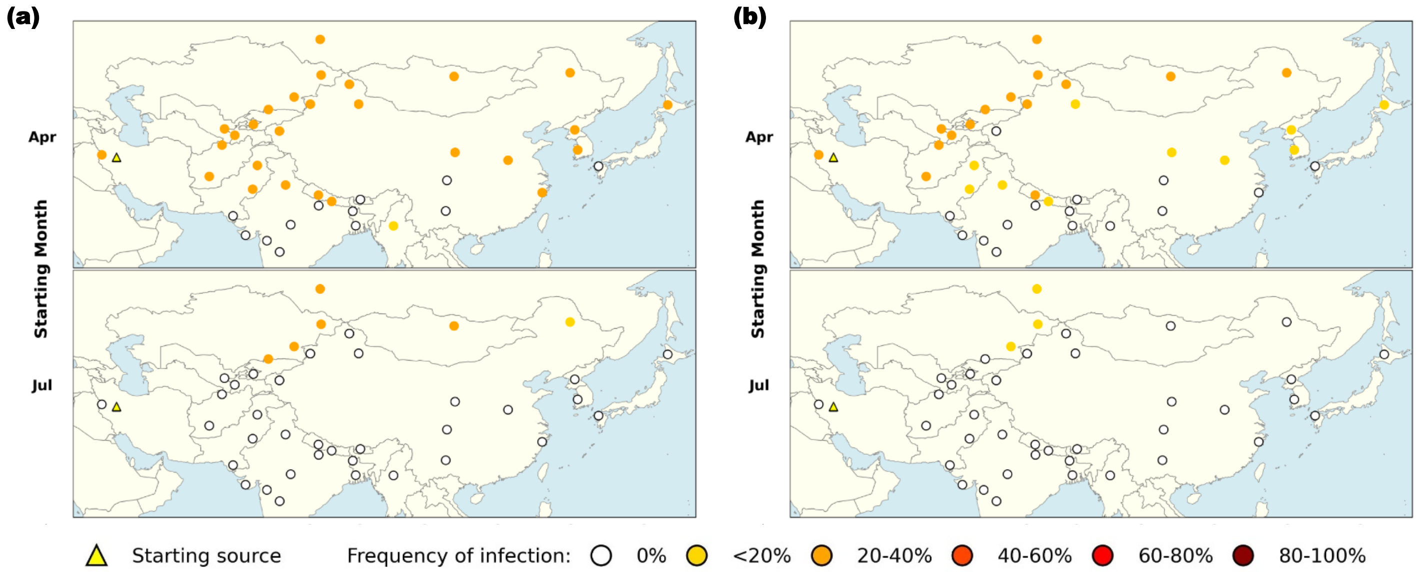

Figure 4. Simulation results for an outbreak in the starting source of Hamadan in Iran (urediniospore lifecycle only). (a): Probability of infection threshold 0.0; (b): probability of infection threshold 0.2. The frequency of each site being infected over the five-year period 2017–2021 is shown for an infection starting in April and in July each year. Note that the frequency of infection is calculated assuming 15 possible years of infection (2017–2021, 2018–2021, 2019–2021, 2020–2021 and 2021 alone).

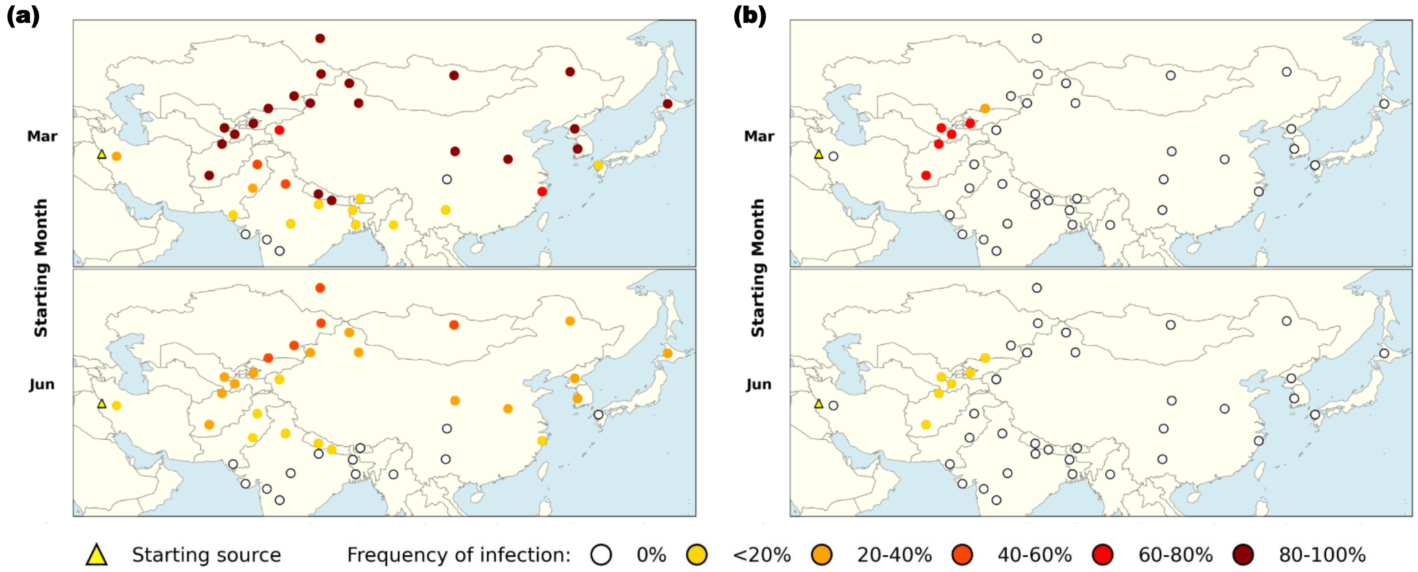

Figure 5. Simulation results for an outbreak starting source in Halabja (Iraq) with a probability of infection threshold of 0.0 (full lifecycle including the alternate host barberry). (a): wheat; (b): barberry. The frequency of each site being infected over the five year period 2017–2021 is shown for an infection starting in March and in June each year. Simulations begin on the first day of each starting month and continue for the full 5 year period.

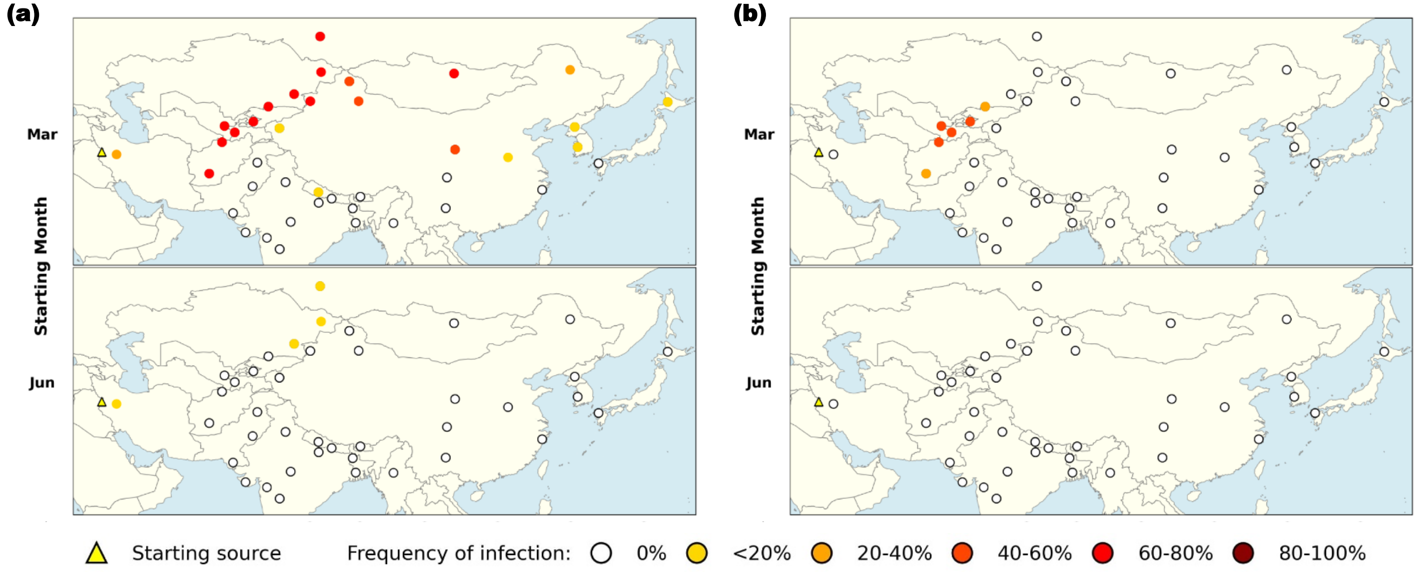

Figure 6. Simulation results for an outbreak starting source in Halabja (Iraq) with a probability of infection threshold of 0.2 (full lifecycle including the alternate host barberry). (a): Wheat; (b): barberry. The frequency of each site being infected over the five year period 2017–2021 is shown for an infection starting in March and in June each year. Simulations begin on the first day of each starting month and continue for the full 5 year period.

We conclude that *Pgt* outbreaks are profoundly impacted by the presence of barberry. Outbreaks ceasing in a single cropping year at the uredinial spore stage can persist for at least five years when barberry is present, and the spread can be greater in subsequent years than the initial year of infection.

3.3. Full lifecycle sensitivity test 1: starting sources in Ningxia in China, Hokkaido in Japan and Fergana in Uzbekistan

We conduct addition simulations with starting source locations in China, Japan and Uzbekistan. We do not find any potential for reciprocal spread of *Pgt* from Central and East Asia back to the Middle East or South Asia (figures S23–S34).

3.4. Full lifecycle sensitivity test 2: excluding Kazakhstan, Turkmenistan, Kyrgyzstan, and Uzbekistan

We conduct an additional simulation where Kazakhstan, Turkmenistan, Kyrgyzstan, and Uzbekistan were excluded and find that the presence of sites with barberry in Afghanistan alone are sufficient to allow the infection to persist beyond a single cropping year (figure S37). When Afghanistan sites are additionally removed, no sites with barberry capable of infection remain and so spread is via urediniospores only and ceases when the crops are harvested.

3.5. Evaluation with observations

Only 8 of the 33 sites we have simulated are CDLs, so there are not many observations to use for evaluation. We have taken records for those CDLs (or sites close to those locations) from the RustTracker database (University of Aarhus 2022) for the years 2017–2021, as shown in figure 7. In agreement with observations and previous work (Meyer *et al* 2017b), most simulations do not infect Bangladesh in any year. *Pgt* was, however, recorded in Bangladesh in April/May 2014 and April 2015, the first recorded instances for three decades (University of Aarhus 2022). In all cases, the observed infections occurred very late in the growing season. In agreement, the single scenario where Bangladesh sites were infected in our simulations, they do so only at the end of the growing season in 2021 (figure S5) and this infection relies on an early initial infection in Iraq (which is not seen in the observations).

Pgt infection also occurred once in August 2017 in Novosibirsk in Russia. Our simulations suggest this late outbreak could have arrived via Iraq or Iran and that it is unlikely barberry can play a direct role in local *Pgt* infections here. This result is at odds with the collection of aeciospores from rust-infected barberry in nearby Omsk in 2018 (Skolotneva *et al* 2020) and the evidence for a sexual population infecting other regions in western Siberia and Kazakhstan between 2015 and 2017 (Shamanin *et al* 2018, Olivera *et al* 2022). The lack of barberry infection in our simulation is due to the environmental suitability, which suggests there were no days in August 2017 with favourable conditions in Novosibirsk because the free moisture requirements were not met. Given the localised nature of precipitation and humidity, we cannot be confident in using the observations from Omsk to compare to our results from Novosibirsk, especially as the incidence and severity of *Pgt* in the wheat in Novosibirsk in 2017 was notably lower than in Omsk (Hodson *et al* 2017), but the discrepancy highlights the need to better quantify the environmental requirements for barberry infection; we have assumed the same as urediniospores.

Finally, the observations document no *Pgt* infections in Fergana or Samarkand in Uzbekistan in 2018, a year where it was confirmed in Iraq in April. Our simulations show wheat in Uzbekistan being infected in 2018 from the outbreak starting in Iraq in April, regardless of the PoIT used (figure S5). In fact, our simulations suggest Uzbekistan sites are among those that could involve barberry in the *Pgt* infection cycle in 2021 when PoIT $= 0$ (figure S10(b)). For the period 2004–2016, *Pgt* was only recorded once in Uzbekistan, but this was in Fergana (Gulmurodov *et al* 2016). Unfavourable weather conditions in spring are cited as the reason why *Pgt* has not been a significant disease in Uzbekistan (Gulmurodov *et al* 2016), however other modelling work also considers Uzbekistan at risk (Sinha and Chen 2021). In areas with high levels of subsistence farming, landraces of wheat are still grown. These landraces have a high level of genetic diversity compared with varieties resulting from international breeding practices, and 23% of the landraces from Afghanistan, 14% of the landraces from Uzbekistan, and 11% of the landraces from Tajikistan tested are resistant to the Ug99 strain of *Pgt* (Newcomb *et al* 2013). It should be noted that since 2008, farm consolidation in Uzbekistan has taken place and in 2018 there would have been a dual system of smallholder farms (∼1 ha) and large individual farms (∼40–60 ha) (Zorya *et al* 2019). In 2019, Uzbekistan underwent extensive farm restructuring and land reallocations and now most wheat farms have doubled in size (∼100 ha) and are administered by the government (Zorya *et al* 2019). Farmers receive inputs, including seeds, from the state (Yigezu *et al* 2022), which may mean that any natural protection that was offered by landraces in the past will now be diminished. However, the Dostlik and Ulugbek 600 wheat genotypes from Uzbekistan also showed a high level of resistance to four other *Pgt* races (Kokhmetova *et al* 2011) and other countries in Central Asia also grow *Pgt*-resistant varieties of both wheat and barley (Kokhmetova *et al* 2011, Sallam *et al* 2017). It is therefore possible that the apparent model-data mismatch in Uzbekistan in our study could be due to resistant varieties in Uzbekistan

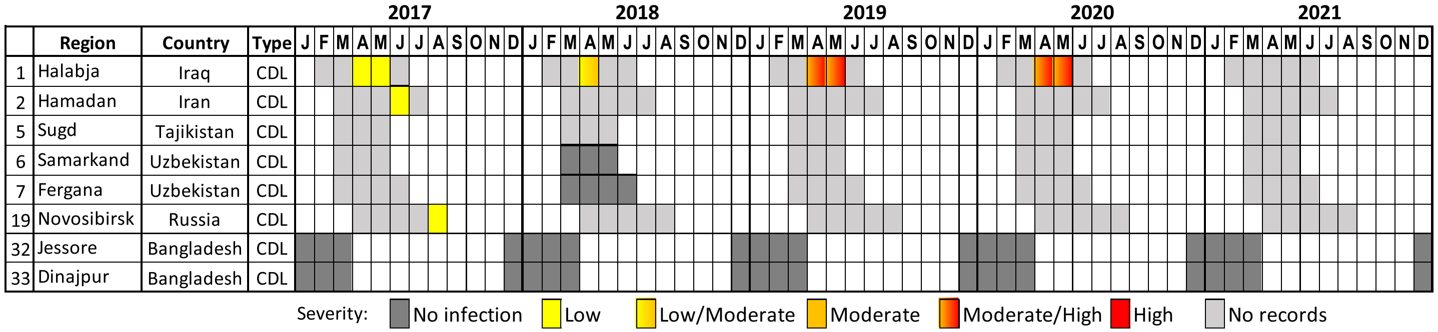

Figure 7. Month and severity of wheat stem rust infections in the CDLs. Data taken from the RustTracker database (University of Aarhus 2022). White boxes indicate the periods outside of the crop calendar assumptions used in this study. Note that the sites in Sugd, Jessore, and Dinajpur are classed as CDLs though they have a confirmed absence of infection, rather than presence, during the period of the study.

providing adequate protection against *Pgt* not captured by our model setup. Our sensitivity test (refer to section 3.4), however, suggests that barberry in Afghanistan alone is sufficient to permit infections to persist beyond a single cropping year.

4. Conclusions

We have used an integrated modelling framework combining fungal spore dispersion modelling with *Pgt* environmental suitability and crop calendars to simulate outbreaks.

4.1. Research questions i, ii and iii: can Pgt reach East Asia from the Middle East via a northern pathway through Central Asia, via a southern pathway through South Asia, and what is the risk of reciprocal spread into the Middle East or South Asia from Central and East Asia?

We find transmission pathways to East Asia via Central Asia and South Asia but consider the southern pathway an unlikely route because it only occurs once in our simulations and relies on an early infection in the Middle East combined with the lowest PoIT.

We do not find a transmission pathway back to the Middle East or South Asia from Central or East Asia. Only early outbreaks in the Middle East could be widespread across East Asia; late outbreaks are generally restricted to more northerly sites, especially when only the urediniospore stage is considered. All results are sensitive to the PoIT.

4.2. Research question iv: can simulated Pgt outbreaks extend beyond a single cropping year?

Outbreaks do not extend beyond the same cropping year in the urediniospore lifecycle because there is not enough overlap in the crop calendars to sustain the infection. If crops are grown outside of our crop calendar assumptions (e.g. by the use of irrigation), they could be vulnerable to *Pgt* because other work suggests year-round survival in southwest China (Beddow *et al* 2015).

4.3. Research question v: how are simulated Pgt outbreaks impacted by the presence of the alternate host, barberry?

Outbreaks persist in East Asia for up to five years, but this is sensitive to the PoIT. Persistence beyond five years may be possible because interannual weather variability might mean different results are found for alternative five-year periods. To test the longevity of infection and assess the probability of the infection risk, we recommend future work extends the study over a longer period using data such as ERA5 (Hersbach *et al* 2020).

4.4. Limitations

Our analyses are based on sites for which wheat stem rust had been reported in the RustTracker database. It is possible that there may have been additional transmission steps but we do not test that possibility here because of the lack of data to support the choice of where those additional locations should be. Lack of data at potential intermediate sites highlights the need for more surveillance and recording efforts. Due to limitations in our modelling framework, spore transmission pathways above 3000 m have been excluded outside of the NAME model. Future work should implement a low temperature-dependent kill-off for spores within NAME, as is currently done for UV (Meyer *et al* 2017a, 2017b), and an ice nucleation processes for high elevation.

We have assumed barberry at all sites 200 km from an observed barberry occurrence and *Pgt* spread to barberry limited only by teliospore overwintering ability and spring germination. Future work should assess suitability for respective barberry species (since different barberry species are known to thrive in different conditions, e.g. Davlatov and Baikova 2011) because different species have varying levels of *Pgt* resistance (Roelfs 1985, Zhao *et al* 2015). Sometimes, even when highly susceptible, barberry has not infected wheat (Zhao *et al* 2015). Better quantification of barberry species' distributions in the current climate and under projected climate change will help aid removal programmes if necessary.

Barberry increases the genotypic diversity of the *Pgt* pathogen (Jin 2011, Berlin *et al* 2012) and there are hundreds of different species with differing levels of *Pgt* resistance, and hundreds of distinct races have evolved (though most will be avirulent). For example, in Tajikistan, small genetic differences were found between populations collected in May/June and those collected later in the season (Berlin *et al* 2015). Whilst this high evolutionary potential is concerning and only a few hosts carrying highly aggressive strains are required, many of these genotypes will have low levels of aggressiveness (Lehtinen *et al* 2009). Growing a wide variety of wheat cultivars with varying resistance to differing *Pgt* races might reduce the potential for largescale spread—the devastating outbreak in Ethiopia in 2013 spread through Digalu monocultivar crops (Olivera *et al* 2015). In fact, it is hypothesised the persistent presence of many different races of *Pgt* over long periods may have contributed to the evolution of *Pgt* resistance in the Central Asian cultivars (Steffenson *et al* 2017). In contrast to Central Asia, only 2% of the 700 Chinese wheat cultivars tested were resistant to Ug99 (He *et al* 2008)—meaning if this race group were to arrive in China, the impacts could be devastating.

4.5. Recommendations for further work

If *Pgt* makes a notable return to Asia, future work should test the sensitivity to the water regime employed (rainfed or irrigated), crop calendar assumptions, and targeted fungicide applications to assess possible adaptation and mitigation measures. Our results highlight the need for quantification of barberry species distributions, better understanding of the environmental conditions for *Pgt* to pass to/from barberry, and appropriate methods for targeting surveillance (spatially and temporally) of *Pgt* on barberry.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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Author contributions

C B and D L H conceived and designed the study in collaboration with M S, D E, T-G L, B T, J D, S U, F Z, and H L. C B performed the NAME model simulations and the integrated model simulations. T M performed the environmental suitability modelling. W T provided technical assistance. D P H, C A G, J S, T M provided expert guidance. C B wrote the manuscript. All authors discussed the results, assisted in the interpretation of the results, and reviewed the manuscript.

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