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Irrigation can create new green bridges that promote rapid intercontinental spread of the wheat stem rust pathogen

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Supplementary material for this article is available online

Abstract

Wheat stem rust epidemics caused by the obligate pathogenic fungus *Puccinia graminis* f.sp. *tritici* have historically driven severe yield losses on all wheat growing continents and, after many decades of control, stem rust is re-emerging as a disease of concern. In 1998, a highly virulent race able to overcome 90% of world wheat cultivars, Ug99, was identified in Uganda. Since initial detection, the pathogen has evolved many new variants and spread to many countries. The original variant spread from East Africa to the Middle East with three years between detection in Ethiopia and subsequent detection in Yemen. In 2014, another Ug99 variant (TTKTT), with one of the most complex virulence profiles, was detected in Kenya. This variant also spread from East Africa to the Middle East, but with only one year between detection in Ethiopia and subsequent detection in Iraq. Here we investigate potential airborne migration routes to account for the rapid spread of TTKTT in East Africa and beyond to the Middle East by using an integrated model combining the outputs from a meteorology-driven fungal spore dispersion model with epidemiological models to account for seasonal availability of susceptible crops and conditions for spore release and infectivity. We find viable pathways in the 2018/19 season that incorporate critical stepping-stone locations in Yemen or Saudi Arabia, but only in the presence of newly irrigated regions in Ethiopia. Our results indicate the potential and increasing importance of irrigated wheat areas in Ethiopia, Yemen and Saudi Arabia for inter-regional stem rust movements. Future movement of stem rust races out of East Africa is considered likely as irrigated areas expand. Targeted surveillance and the use of mitigation strategies including the use of durable resistant varieties in regions of irrigation are required to reduce the risks of enhanced dispersal of stem rust to other regions.

1. Introduction

Stem rust caused by the obligate pathogenic fungus *Puccinia graminis* f.sp. *tritici* (*Pgt*) is considered the most damaging of all the wheat rusts (Dean *et al* 2012), causing devastating stem rust epidemics in all wheat-growing continents. In sub-Saharan Africa, stem rust is responsible for ∼9% of wheat yield losses (Savary *et al* 2019) and during severe epidemics losses can be close to 100% (Olivera *et al* 2015). After decades of control stem rust is re-emerging as a disease of concern (Singh *et al* 2008, Lewis *et al* 2018, Saunders *et al* 2019). Diverse new stem rust races and lineages are now being detected and large outbreaks of disease

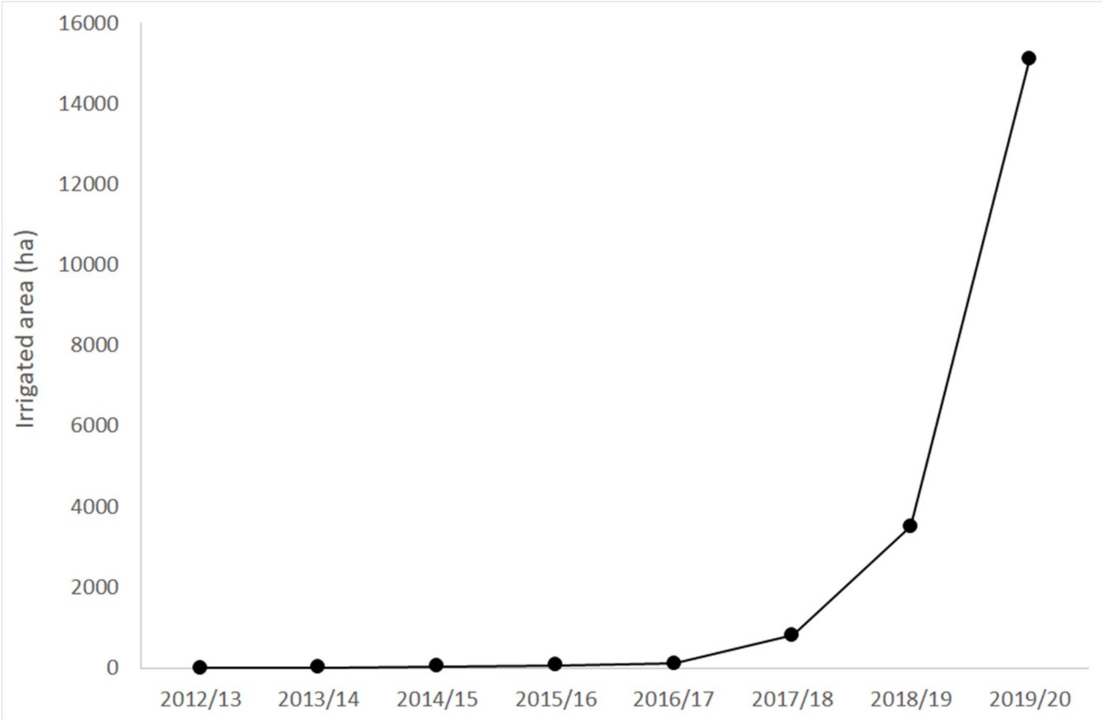

Figure 1. Area of irrigated wheat in Ethiopia planted by year. Data from the Ethiopian Institute of Agricultural Research (EIAR 2020).

are increasing (Singh *et al* 2015, Olivera *et al* 2019, Saunders *et al* 2019, Shamanin *et al* 2020).

Ethiopia is the largest wheat-producing country in sub-Saharan Africa (figure S1 in supplementary information) and wheat is the second most important crop in Ethiopia in terms of calorie intake (Wakeyo and Lanos 2019, FAO 2021). Cultivation is concentrated in the central highlands under rainfed conditions but there has been a large increase in the area of irrigated wheat grown in recent years (FAO 2021, EIAR 2020; see figure 1). The East African highlands are a 'hot-spot' for stem rust (Saari and Prescott 1985). Favourable environmental conditions permit year-round pathogen survival, but equally important is the continual presence of host plants. The pathogen is an obligate biotroph and requires green, living tissue for growth and survival. Overlapping cropping seasons and bimodal rainfall patterns in most East African countries result in green bridges that facilitate survival and build-up of inoculum between successive crops (Nagarajan *et al* 2012). Shifts from rainfed to irrigated wheat further augment the green-bridge effect by extending wheat crop cultivation and the type of irrigation system used can affect disease development (Swett 2020).

From its initial detection in Uganda in 1998, Ug99 race TTKSK took five years before detection in Ethiopia, eight years before detection in Yemen, and nine years before detection in Iran (see table 1 in Singh *et al* 2015). In contrast, since being first detected in Kenya in 2014 (Patpour *et al* 2016), and Ethiopia in 2018 (Hei *et al* 2020), race TTKTT was detected in Iraq in 2019, just one year later (Nazari *et al* 2021). Race TTKTT is now the second Ug99 variant to move into the Middle East, indicating a possible common migration route. Rapid spread of highly virulent stem rust races, such as TTKTT, from East Africa into major wheat producing regions of the Middle East is concerning (see supplementary information for the Ug99 lineage).

Here we investigate the likely pathways for the spread of race TTKTT using the historic meteorological data for 2018/19 and consider the role of changing wheat cultivation practices in Ethiopia, notably the expansion of irrigated wheat and the potential for extended green bridging at critical cropping periods. The impacts of policy changes in Saudi Arabia towards increased cultivation of wheat on disease risk and how to mitigate these risks are also discussed.

Specifically, we address the following key questions:

(a) What is the likely sequence of spread of race TTKTT within East Africa?
(b) Could stem rust caused by race TTKTT in Iraq in 2019 have originated by direct wind dispersal from infected sites in East Africa during the previous year?
(c) What is the evidence for indirect spread of race TTKTT from East Africa to Iraq via intermediate 'stepping-stone' sites during 2018 and 2019?

(d) How is the risk of spread between East Africa and the Middle East likely to be affected by irrigated wheat areas?
(e) What is the risk of reciprocal spread into East Africa from the Middle East?

2. Methods

2.1. The modelling framework

We use a meteorology driven Lagrangian particle dispersal model (NAME; Jones *et al* 2007) originally adapted by Meyer *et al* (2017a, 2017b) for dispersal of urediniospores (hereafter referred to as 'spores') *Pgt*. The NAME model is driven by 3D meteorological data from the UK Met Office Numerical Weather Prediction model the Unified Model (Walters *et al* 2019), with approximately 10 km horizontal and 3 h temporal resolution and up to 59 vertical layers. The model simulates the release, turbulent dispersal, wet and dry deposition and UV-induced death of spores (refer to supplementary information and Meyer *et al* (2017a, 2017b)).

We consider spore dispersal between donor sites (from which spores are dispersed from infected wheat) and receptor sites (where spores land on susceptible wheat). Amongst donor and receptor sites we distinguish confirmed disease locations (CDLs) in which TTKTT is confirmed and representative disease locations (RDLs; see Meyer *et al* 2017b) where *Pgt* is known to occur but TTKTT was not confirmed. Each CDL and RDL is represented by nine model grid cells (90 km $\times$ 90 km) and so characterises the broad wheat production region of the area.

We use a simple SEIR epidemiological framework (hereafter the integrated model) operating on a daily timestep to classify the infection status of the sites. A site moves into the susceptible (S) class after a period of initial growth. Infected sites move into the exposed (E) class, which accounts for the delay between initial infection and the site moving into the infected (I) class when capable of infecting other sites. The site remains infectious until leaf senescence prevents further spore production when it moves into the removed (R) class. Sites that pass into the removed class are not passed back to the susceptible class within the same cropping season because we do not define the length of the infectious period and we do not allow for chemical control in the current model. A meteorology-driven, environmental suitability model (see supplementary information) is used to assess whether temperature and moisture conditions are suitable for infection when spores land on a susceptible site.

Infected receptors remain in the exposed class until a crop latency period (the time between crop receptors being infected and themselves becoming infectious donors) has passed. A default version uses a temperature-dependent latency period based on the model of Nopsa and Pfender (2014), defined as:

$$\begin{aligned}&\text{Proportion of Lp50 completed}\\&\quad = \text{hours} \times (2.9 \times 10^{-4}) \times (T - 1.8)\\&\quad \times [1 - e^{(T-30.9)}],\end{aligned}$$

for values of T between 1.8 and 30.9 °C, where Lp50 is the time when 50% of the maximum number of pustules have erupted and T is the average temperature over the timestep. A second version using a fixed latency period of 30 d (Roelfs 1992) was examined as a sensitivity test.

A metric of the relative probability of infection was created as follows:

$$P(I) = \begin{cases} \text{if } D < 1 \text{ spore ha}^{-1}, \text{then } 0 \\ \text{if } D \geqslant 1 \text{ spore ha}^{-1}, \text{then ES} \times \text{Norm}[\log(D)] \end{cases}$$

where $P(I)$ is the probability of infection, ES is the environmental suitability value and Norm[log(D)] is the log of deposition values, normalised to between 0 and 1 with the upper limit of the deposition values calculated in a pre-processing step. The integrated model allows the user to specify the threshold for the combined suitability/deposition value above which a potential receptor becomes infected. Any value above 0 is assumed to imply infection, i.e. 1 spore ha^{-1}, or more, landing on a susceptible site with a non-zero measure of environmental suitability leads to infection (see also supplementary information for a sensitivity analysis).

2.2. Sites and potential locations of TTKTT infection

Simulations were performed for 2018–2019 under the following scenarios:

(a) **Scenario 1. 'CDLs'**: simulations restricted to sites with confirmed identification of TTKTT;
(b) **Scenario 2. 'CDLs + Ethiopia RDLs'**: simulations included sites with confirmed identification of TTKTT plus additional key wheat-growing locations in Ethiopia where *Pgt* is known to occur but TTKTT has not been confirmed;
(c) **Scenario 3. 'CDLs + Ethiopia RDLs + Stepping-stone RDLs'**: simulations include sites with confirmed identification of TTKTT plus additional key wheat-growing locations in Ethiopia and locations in theoretical stepping-stone countries of either Eritrea, Yemen, Saudi Arabia and Iran where TTKTT has not been confirmed.

The CDLs are shown in figure 2 for the years 2014–2019. However, with low frequency races like TTKTT it cannot be excluded that the race was present in additional sites, years or countries and went undetected in the field sampling (note: no sampling was undertaken in Yemen or Saudi Arabia).

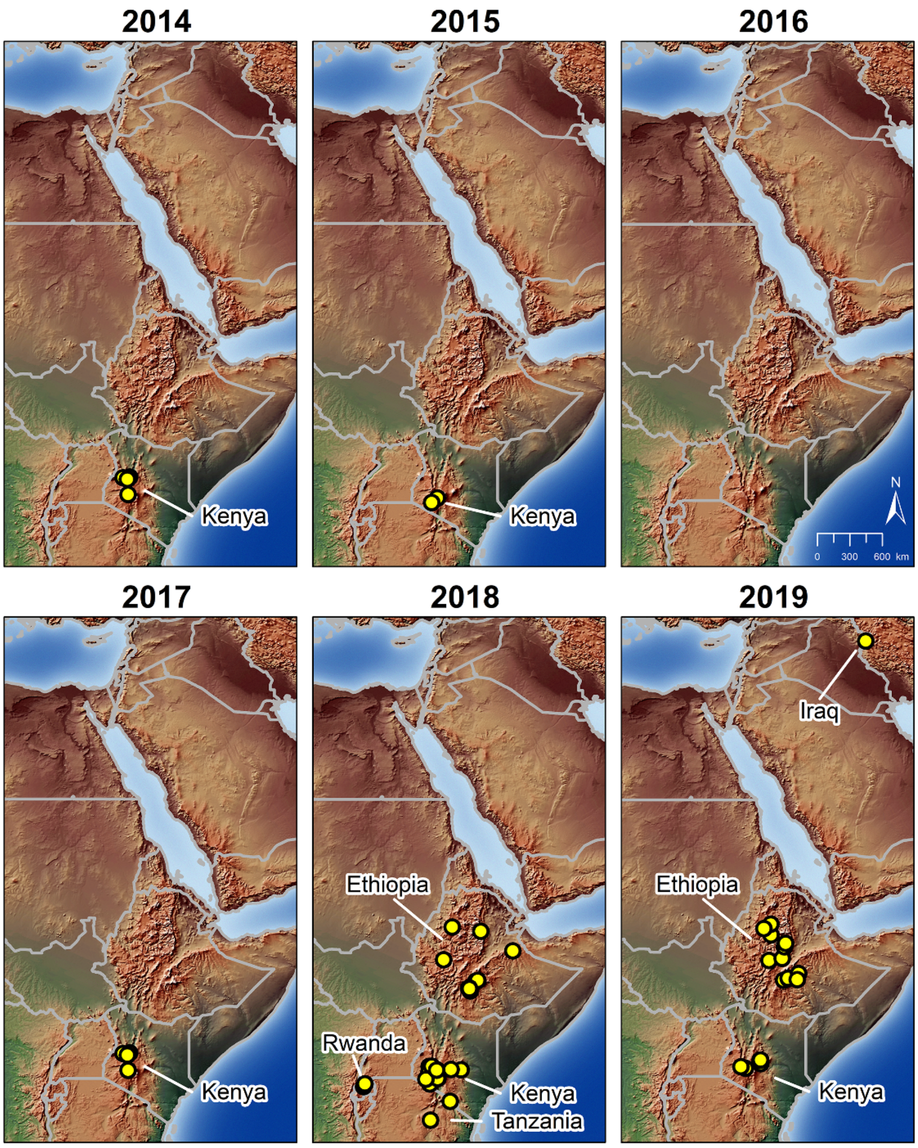

Figure 2. Confirmed disease locations for stem rust race TTKTT between 2014 and 2019 (yellow circles). Note that a new variant of race TTKTT with acquired virulence on resistance gene Sr8155B1 and given a temporary race name of TTKTT+ was detected at Njoro, Kenya in 2019 (USDA-ARS Cereals Disease Lab unpublished). Records of TTKTT+ have been excluded from the analysis.

Under Scenario 1, based on the timeline of dates in 2018 where the TTKTT race was identified, the initial donors are assumed to be CDLs in Kenya, Tanzania or Rwanda; note that due to the large number of confirmed sites in Kenya, all of the Kenyan sites are grouped together into the four CDLs shown in figure 3.

Under Scenario 2, additional wheat sites in Ethiopia are included where race TTKTT is not confirmed (but its presence in 2018 was possible because TTKTT was confirmed in later years):

(a) A representative site in Bale zone (figure 3: site #19)—the core wheat belt of Ethiopia and an area of double cropping. Wheat is grown both in the Belg (short rain) season (March/April–July/August) and the Meher (long rain) season (August–January), providing an important green bridge.
(b) Two representative sites in the newly furrow-irrigated regions along the Awash river (Gebul 2021)—Werer and Metahara (figure 3: sites #14, #15, respectively).

Under Scenario 3, potential stepping-stone sites in key wheat-growing regions of Eritrea, Yemen and Iran are included (figure 3 sites #1–3 and #7–10). The RDLs include locations where races other than TTKTT have been identified and RDLs used in Meyer *et al* (2017b); most RDLs are assumed to be rainfed but the East Yemen RDL is assumed to be flood-irrigated (Frenken 2009). Due to a change in government policy to re-support domestic wheat production in Saudi Arabia (USDA Foreign

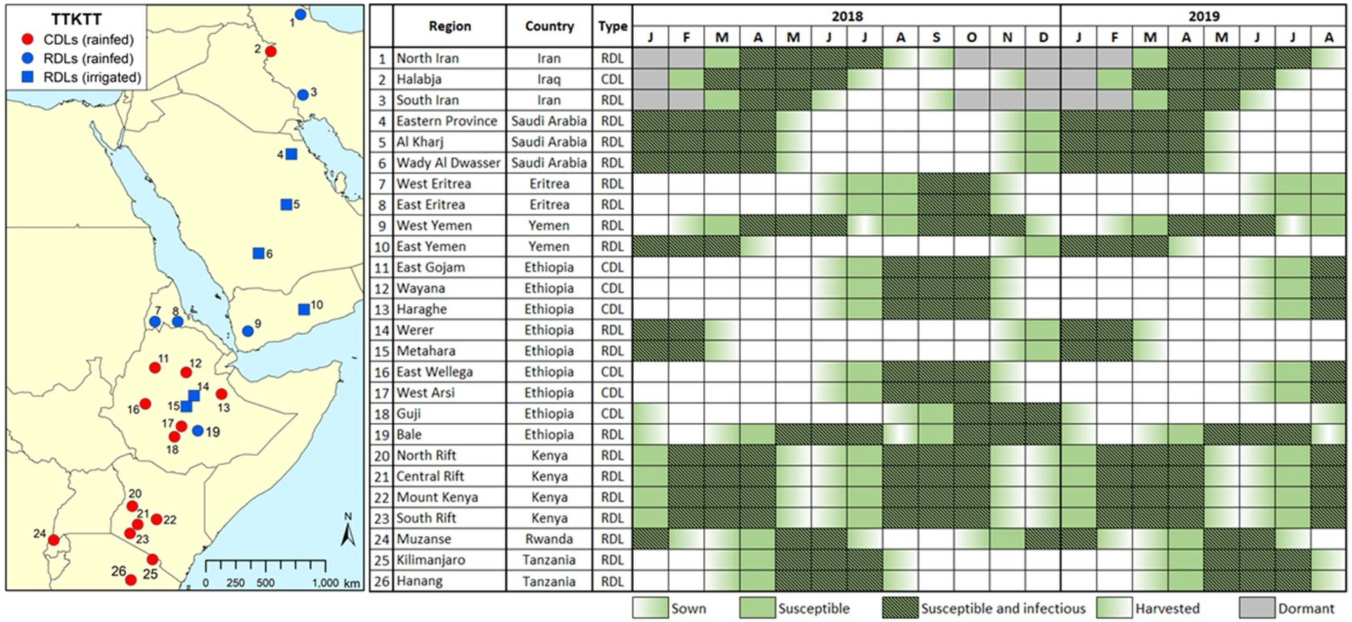

Figure 3. Site locations and crop calendar assumptions. CDLs = confirmed disease locations in which TTKTT is confirmed, RDLs = representative disease locations where *Pgt* is known to occur but TTKTT has not been confirmed. Sites are only considered receptive to stem rust from one calendar month after emergence (to allow for initial growth) until one month before harvest (when leaf senescence prevents further spore production). Sites are considered potential sources for stem rust according to a temperature-based 'latency period' (refer to section 2.1) or a 'latency period' of one month (shown here in dark green). Calendar months shown in grey indicate the dormant phase of winter wheat crops. The planting and harvest date assumptions for each site are based on those used in Meyer *et al* (2017b) according to expert opinion, with, additionally, Rwandan dates taken from the Seasonal Agricultural Survey for 2018 (National Institute of Statistics of Rwanda 2019) and Saudi Arabian sites using expert knowledge.

Agricultural Service 2019), we also include three additional sprinkler-irrigated locations (Frenken 2009) in Saudi Arabia: Wady Al Dwasser, Al Kharj and Eastern Province (figure 3: sites #4–6).

2.3. Crop calendar

Although complex models simulating the spread of rust epidemics have been developed (e.g. Eversmeyer *et al* 1973, Rossi *et al* 1997, Bregaglio and Donatelli 2015, Savary *et al* 2015, Naseri and Sabeti 2021, Salotti *et al* 2022), given the spatial extent of our study area (which covers a wide range of climatic regimes) and the lack of survey data available to calibrate a more complex model, we adopt a simpler approach in our study. The crop calendar is defined in terms of a monthly timestep and planting and harvest date assumptions for each site (figure 3) are based on those used in Meyer *et al* (2017b), the National Institute of Statistics of Rwanda (2019) and expert knowledge. The main assumptions are that new wheat plants only become receptive to stem rust one month after emergence (to allow for initial growth) and cease to be receptive one month before harvest (when leaf senescence prevents further spore production). Given that these are considered conservative estimates, sensitivity testing to these timings is also conducted.

3. Results

3.1. Scenario 1. 'CDLs'

The following initial donor sites and start dates for spore dispersal were used (see figure 3):

- Rwanda (Muzanse): 1st January 2018 and 1st May 2018,
- Kenya (North Rift, Central Rift, South Rift and Mount Kenya): 1st February 2018 and 1st August 2018
- Tanzania (Kilimanjaro and Hanang): 1st May 2018

The results show there is no meteorology-driven transmission pathway between CDLs in East Africa and the Middle East in the 2018/19 season. Spores released from Muzanse cannot infect any other CDLs. Although spores are deposited from Muzanse over the viable CDLs in Kenya for the January start date (figure 4), environment conditions are not suitable for infection before the crops in Kenya are harvested. For the May start date, the crop calendars do not overlap between the infected donor and susceptible receptor crops.

We find that Tanzanian donors can only infect Musanze in Rwanda, which causes no onward transmission of wheat stem rust, as previously described.

With the February start date, Kenyan donors do not infect any other CDLs. With the August start date, Kenyan donors infect all Ethiopian CDLs, but no onward transmission to Iraq is simulated.

Inspection of the crop calendar (figure 3) reveals that the only CDLs that can be infectious at the same time as the CDL in Iraq is receptive are Muzanse, the two Tanzanian CDLs and the four Kenyan CDLs. However, deposition (figure 4) indicates spores released from all these CDLs cannot be transported directly to Halabja, Iraq. This means other potential locations for wheat stem rust where TTKTT has not been identified must be considered as possible stepping-stones.

Given that spores from Muzanse in Rwanda and the two Tanzanian CDLs cannot infect any other CDLs, it is highly unlikely these were the origin of the confirmed TTKTT infections in Ethiopia in 2018 or the confirmed TTKTT infection in Iraq in 2019. For this reason, we confine all further analyses to Kenyan initial donors, and we assume an August start date only because the February start date assumption did not lead to any infections outside of Kenya.

3.2. Scenario 2. 'CDLs + Ethiopia RDLs'

The potential Ethiopian RDLs considered in Scenario 2 are Bale (two annual rainfed crops), Werer, and Metahara (both with single irrigated crops). The simulations assume Kenyan initial donors starting in August, as described in section 3.1.

Inclusion of the Bale RDL or the two irrigated Ethiopian RDLs (Metahara and Werer) result in infection at those sites (in September 2018, December 2018, and January 2019, respectively), but the infection does not reach Halabja. Spores from the Ethiopian sites could, however, reinfect the CDLs in Kenya and Rwanda before the crops are harvested in June 2019.

Inclusion of the additional Ethiopian RDLs cannot facilitate infection of Halabja because spore deposition from Bale (figure 5(A)) or Metahara/Werer (figure 5(B)) does not extend as far as Iraq. This means that other potential RDLs in key wheat-growing regions, in other countries, where sampling has not been undertaken and TTKTT has not been identified, must be considered as possible 'stepping-stones'.

3.3. Scenario 3. 'CDLs + Ethiopia RDLs + Stepping-stone RDLs'

The potential Ethiopian RDLs considered in Scenario 3 are the irrigated locations of Werer and Metahara; and Bale with two annual rainfed crops in both the Belg and Meher seasons. Other possible stepping-stone RDLs are located in Eritrea, Yemen, Saudi Arabia and Iran. Each potential stepping-stone RDL is considered individually, and, in each case, we consider the results both with and without the irrigated Ethiopian RDLs. The simulations assume Kenyan initial donors starting in August, as described in section 3.1.

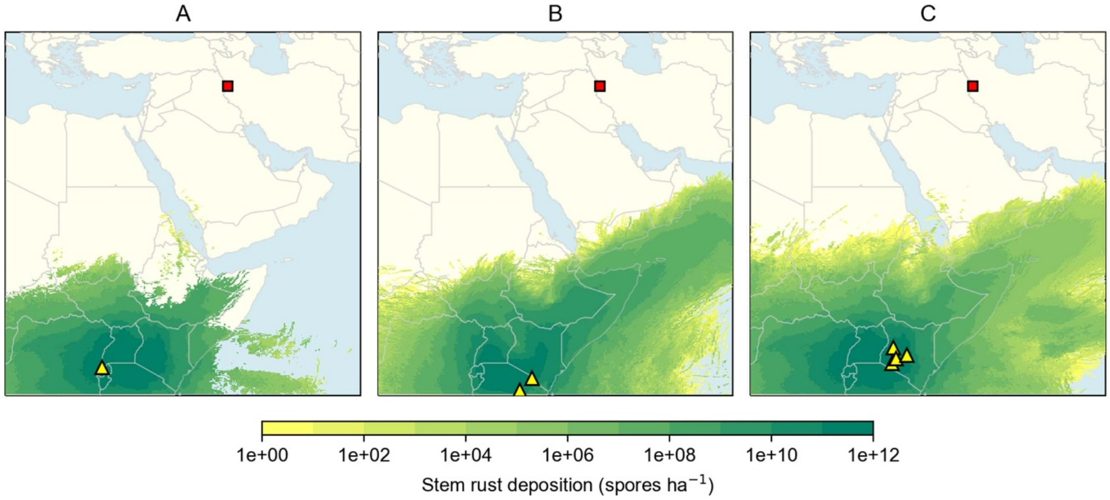

Figure 4. Scenario 1: Dispersion from confirmed TTKTT sites (CDLs): total reach of wheat rust deposition during 2018 and 2019 simulated using the NAME model. (A) From the Rwandan CDL Muzanse (yellow triangle) during periods in which crops are potentially infectious (December to January and May to June), (B) from the two Tanzanian CDLs: Kilimanjaro and Hanang (yellow triangles) during the assumed infectious periods of May to July, (C) from the four Kenyan CDLs North Rift, South Rift, Central Rift and Mount Kenya (yellow triangles) during the assumed infectious periods of February to April and August to October. The infected Iraqi CDL, Halabja, is shown as a red square.

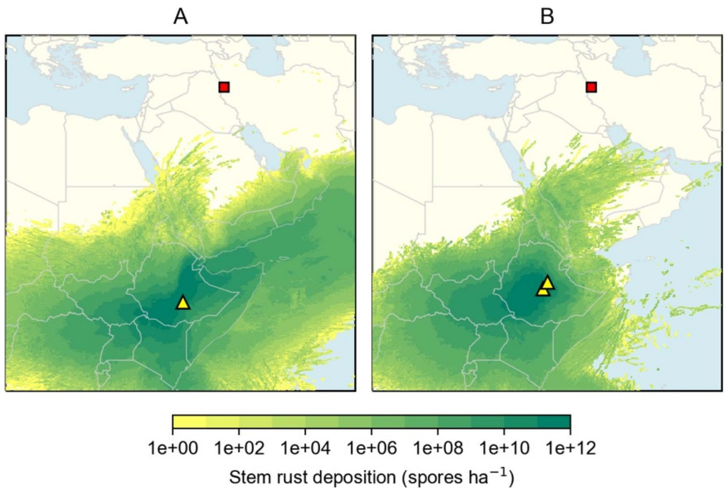

Figure 5. Scenario 2: Dispersion from Ethiopian representative disease locations (RDLs): total reach of wheat rust deposition during 2018 and 2019 simulated using the NAME model. (A) From the Ethiopian RDL Bale (yellow triangle) during periods in which crops are potentially infectious (May to July and October to December), (B) from the irrigated Ethiopian RDLs Metahara and Werer (yellow triangles) during periods in which crops are potentially infectious (January to February). The infected Iraqi site, Halabja, is shown as a red square.

In all cases, when the two irrigated Ethiopian RDLs are excluded from the analysis, the crop is harvested before the infection reaches Halabja. When the irrigated RDLs in Ethiopia are included, stepping-stone RDLs in either Saudi Arabia or Yemen are necessary to facilitate infection at Halabja. We now describe these two simulations in more detail.

3.3.1. Yemen

The West Yemen RDL is infected from the Hararghe CDL in August 2018 (figure 6(A)). Spores from West Yemen in November 2018 are deposited over Halabja when there is no susceptible wheat. The Guji CDL and/or the Bale RDL (infected in September 2018 from Meher Ethiopian CDLs) infect the Metahara RDL, which then infects the neighbouring Werer RDL (figure 6(B)). The irrigated Ethiopian RDLs infect the irrigated East Yemen RDL (figure 6(C)) and then East Yemen infects Halabja in March 2019 (figure 6(D)). East Yemen also reinfects West Yemen in March 2019 and the infection spreads back into Bale in April 2019, and the cycle repeats.

3.3.2. Saudi Arabia

The simulation is identical to that described for Yemen until the two irrigated Ethiopian RDLs have

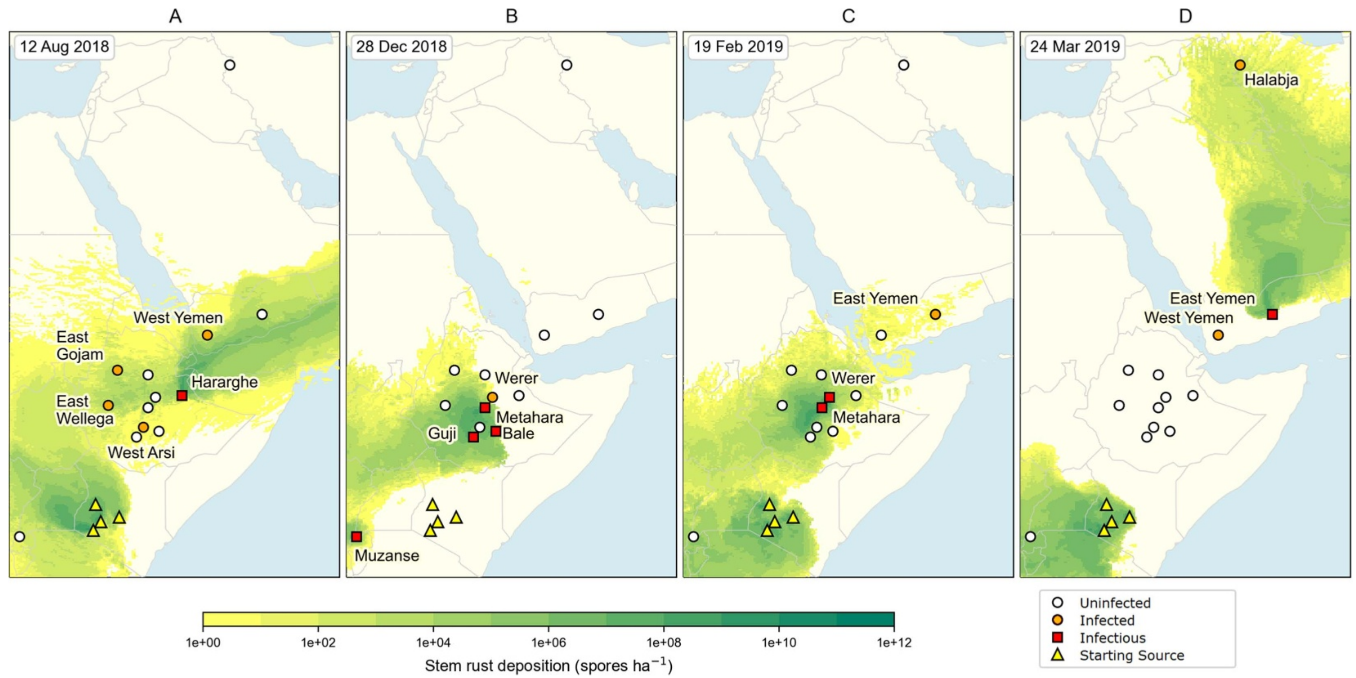

Figure 6. Scenario 3: Ethiopian, and Yemen stepping-stone representative disease locations (RDLs): Yemen, wheat stem rust infections simulated with the August 2018 start date and starting sources in Kenya (North Rift, South Rift, Central Rift and Mount Kenya). (A) Initial infection of the rainfed Meher season Ethiopian CDLs and the rainfed RDL of West Yemen, (B) infection of the irrigated RDLs Metahara and Werer, (C) infection of the irrigated RDL East Yemen, (D) infection of the rainfed CDL Halabja in Iraq.

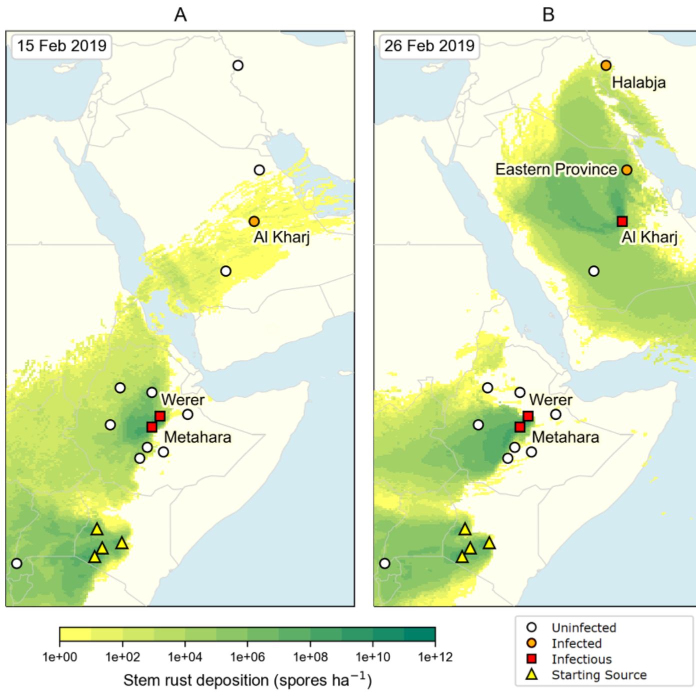

Figure 7. Scenario 3: Ethiopian and stepping-stone representative disease locations (RDLs): Saudi Arabia, wheat stem rust infections simulated with the August 2018 start date and starting sources in Kenya (North Rift, South Rift, Central Rift and Mount Kenya). (A) Infection of the irrigated Saudi Arabian RDL of Al Kharj, (B) infection of the irrigated Saudi Arabian RDL of Eastern Province and the rainfed Halabja CDL in Iraq.

been infected. In February 2018, those irrigated Ethiopian RDLs then infect the central irrigated Saudi Arabian RDL of Al Kharj (figure 7(A)), which then infects Halabja (and the other two Saudi Arabian RDLs) in March 2019 (figure 7(B)). Unlike the East Yemen route, though, no reinfection of the Ethiopian sites occurs in this scenario and the infection transmission ceases in July 2019.

We have shown that both Yemen and Saudi Arabia can act as stepping-stone locations between East Africa and the Middle East, but only when we include the irrigated wheat RDLs in Ethiopia, as summarised in figure 8. We find that infection of Halabja from spores released from East Yemen, though, can only happen on three days in March and a single day in April 2019. Conversely, infection of Halabja from spores released from the Saudi Arabian (irrigated) RDLs can happen on 29 d between February and April 2019 and therefore we consider the route through Saudi Arabia more likely. Infection of West Yemen by spores released from East Yemen, however, is necessary for the infection to return to Ethiopia.

3.4. Sensitivity tests

Several sensitivity tests evaluate the robustness of the results for these two Scenario 3 simulations (see supplementary information). The **'Control scenario'** consists of CDLs + irrigated Ethiopian RDLs + Bale RDL + Stepping-stone RDLs in Saudi Arabia and Yemen, initial donors in Kenya and an August start date.

The results are sensitive to the latency period (refer to section 2.1): with a 30 day latency period, only a pathway through Saudi Arabia provides a viable transmission route from East Africa to the Middle East. The Saudi Arabian pathway is also the only viable route found when the probability of infection threshold is increased above 0 but ceases to be a viable pathway when the threshold is raised above 0.1. The results are also sensitive to the timing of receptiveness to infection, but only to the time at which crops become susceptible after sowing. A one-month delay in susceptibility at receptor locations results in no infection of the irrigated RDLs. Extending the period of susceptibility closer to harvest does not change the results from the Control scenario.

The sensitivity tests confirm that it is not just the overlap in the crop calendar that is important in creating a green bridge between the Guji CDL and/or the Bale RDL and the irrigated Ethiopian RDLs, but also the fact that those RDLs are irrigated: spore deposition does not coincide with environmental suitability for infection when those RDLs are not irrigated. Future work should consider sensitivity of the environmental suitability model to the type of irrigation system used (Swett 2020).

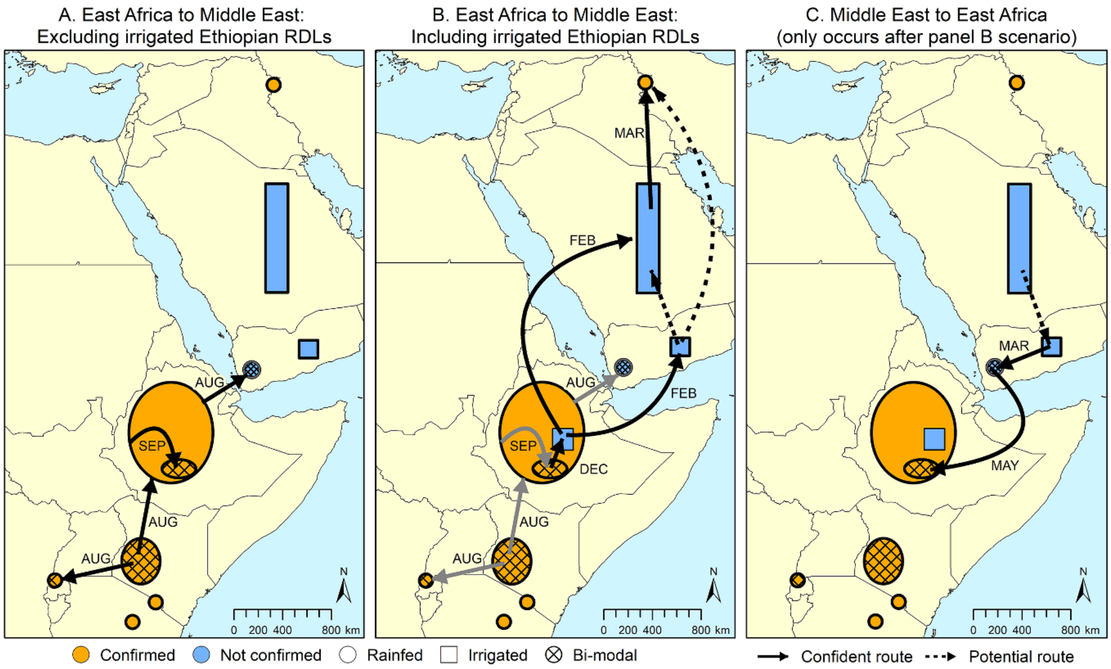

Figure 8. Outline of potential wheat stem rust infection pathways between Kenya and Iraq simulated by the integrated model for Scenario 3: Saudi Arabia and Yemen with the August 2018 start date and starting sources in Kenya (North Rift, South Rift, Central Rift and Mount Kenya). (A) Excluding irrigated Ethiopian RDLs only leads to infection transmission to Ethiopia and Yemen; (B) including irrigated Ethiopian RDLs leads to infection of Halabja. For clarity, the same transmission pathways occurring as panel (A) are shown in grey; (C) including irrigated Ethiopian RDLs and the Bale RDL leads to reinfection of Ethiopia.

4. Discussion and conclusions

Wheat stem rust spore deposition simulations have been combined with crop calendar information and estimates of environmental suitability for infection to simulate whether an outbreak of the TTKTT variant in East Africa could have reached Iraq in the single year 2018/19. We find that an outbreak beginning in Rwanda was highly unlikely to have been able to reach Iraq. Evidence is found, however, to suggest that an outbreak beginning in Kenya could reach Iraq in a single year via stepping-stones in Ethiopia, Yemen and Saudi Arabia, but likely only when facilitated by the recent expansion of irrigated Ethiopian wheat areas in e.g. in the Awash valley. The timing and presence of irrigated wheat in East Yemen and Saudi Arabia also appears to be critical to the transmission, confirming that Yemen is an important stepping-stone between East Africa and the Middle East (Meyer *et al* 2017b). Furthermore, we find the outbreak can reinfect sites in Ethiopia and Kenya from Yemen, potentially repeating the cycle the following year. However, our results indicate a low risk of reciprocal spread of spores into East Africa from the Middle East, in agreement with other work (Meyer *et al* 2017b).

Infection of the East Yemen and Saudi Arabian RDLs from the two irrigated Ethiopian donors in February 2019 was restricted to just the few days when spores were deposited, with no equivalent suitable days occurring in the 2017/18 season. This indicates dispersal into East Yemen or Saudi Arabia may be a relatively low probability event, thereby suggesting targeted control measures in February in these regions could reduce the risk of new races passing between East Africa and the Middle East. These irrigated RDLs were identified as critical stepping-stones for subsequent spread into the Middle East, but without additional dispersal modelling it is not clear how representative 2019 is of the mean climatology or whether 2019 was unusual. A study that quantified likely spore deposition for many countries in Africa and Asia between 2003 and 2014 (Meyer *et al* 2017b) did not include the irrigated wheat RDLs in February and therefore this requires future research. Meyer *et al* (2017b) confirm, however, that the number of viable spore deposition days from Saudi Arabia to Iraq is far greater than the equivalent from East Yemen to Iraq. The limited number of sites used in our simulations could also hide other opportunities for infection spread, but we suggest that the inclusion of other sites would only increase the likelihood of reaching the Middle East in a single year, rather than reducing it. For example, whereas the simulated dispersion of spores from Metahara and Werer are predominantly to the west of the locations in February, recent modelling of other newly irrigated sites in Afar shows instead stable deposition to the north and into Saudi Arabia (figure S2 in supplementary information). Information on stem rust status in irrigated wheat areas in Saudi Arabia is currently unavailable and our results suggest that these areas may play an important role. Old reports indicate the occasional presence of stem rust (El-Meleigi *et al* 1996), and wheat production in Saudi Arabia has increased in recent years due to a change in government policy (FAO 2020). We recommend increased surveillance and sampling of wheat rusts in both Saudi Arabia and Yemen as a high priority.

Our results raise some important questions regarding the implications of increasing areas of irrigation. Ethiopian agriculture currently consists primarily of smallholder subsistence farming with rainfed cropping. The area of wheat harvested has increased by ∼2.5% per year since 2005 (FAO 2021) and the irrigated area has increased exponentially in recent years, with further extensive expansion planned (figure 1; EIAR 2020). Irrigation is a vital strategy for adaptation to the impacts of climate change and to improve food security in many regions (Muluneh *et al* 2017, Tack *et al* 2017, Zaveri and Lobell 2019, EIAR 2020). Wheat stem rust is already a cause for concern for irrigated wheat production in northern Iraq and Kurdistan (Al-Maaroof 2017). In Ethiopia, the incidence and severity of stem rust is increasing rapidly at the lowland irrigated sites considered in this study (Yesuf *et al* 2021). Other studies have shown that irrigation can lead to increased meteorological suitability for a wide variety of pests and diseases (e.g. Menzies 1967, Rotem and Palti 1969, Dixon *et al* 2015, De Villiers *et al* 2017, Avila *et al* 2019, Swett 2020) through increased canopy moisture, changes in stomatal conductance, and microcracking, although in some instances reduced water stress may also enhance disease resilience (Swett 2020). Potential mitigation strategies include more targeted fungicide use and the extensive use of durable rust-resistant varieties and drip irrigation systems in regions where irrigation is to take place (Sanogo 2004, Daugovish *et al* 2012, Maldaner *et al* 2015, Swett 2020). Given the importance of irrigation as an adaptation strategy for climate change and improved food security, it is recommended that irrigation expansion plans be accompanied by risk assessment analyses to identify any associated mitigations also required. More initiatives such as the Early Warning System in operation in Ethiopia (Allen-Sader *et al* 2019) will also be fundamental for effective targeted fungicide use.

Our study finds overlapping wheat crop seasons that connect East Africa and the Middle East, between which spore dispersal is feasible, if perhaps a low probability event in 2018/19. Expanding, lowland irrigated wheat areas in Ethiopia provide a green bridge to Yemen and Saudi Arabia that can subsequently act as sources for the Middle East and the low probability event witnessed in 2018/19 could become a more frequent occurrence in the future. The short rain Belg season wheat areas in southern Ethiopia also provide a bridge connecting Yemen back to Ethiopia and the main Meher season crops. Effective control of stem rust in the expanding lowland, irrigated areas of Ethiopia and in Yemen is therefore seen as high priority to limit the spread of virulent new races into important wheat growing regions. The potential role of increasing wheat production in Saudi Arabia, due to government policy changes, also needs further investigation.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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References

Al-Maaroof E M 2017 Identification of physiological races of *Puccinia graminis* f. sp. *tritici* in Iraq *J. Wheat Res.* **9** 47–53

Allen-Sader C, Thurston W, Meyer M, Nure E, Bacha N, Alemayehu Y, Stutt R O J H, Safka D, Craig A P, Derso E and Burgin LE 2019 An early warning system to predict and mitigate wheat rust diseases in Ethiopia *Environ. Res. Lett.* **14** 115004

Avila G A, Davidson M, Van Helden M and Fagan L 2019 The potential distribution of the Russian wheat aphid (*diuraphis noxia*): an updated distribution model including irrigation improves model fit for predicting potential spread *Bull. Entomol. Res.* **109** 90–101

Bregaglio S and Donatelli M 2015 A set of software components for the simulation of plant airborne diseases *Environ. Model. Softw.* **72** 426–44

Daugovish O, Bolda M, Kaur S, Mochizuki M J, Marcum D and Epstein L 2012 Drip irrigation in California strawberry nurseries to reduce the incidence of *Colletotrichum acutatum* in fruit production *HortScience* **47** 368–73

De Villiers M, Kriticos D J and Veldtman R 2017 Including irrigation in niche modelling of the invasive wasp *vespula germanica (Fabricius)* improves model fit to predict potential for further spread *PLoS One* **12** e0181397

Dean R *et al* 2012 The top 10 fungal pathogens in molecular plant pathology *Mol. Plant Pathol.* **13** 414–30

Dixon G 2015 Water, irrigation and plant diseases *CAB Rev.* **10** 1–18

EIAR 2020 Irrigation—based Wheat Production: a transformation from Import to Export (Addis Ababa) (available at: www.moa.gov.et/documents/20181/35819/2020+Wheat+Brochure+PM+V8.pdf/21a2d4d3-e91c-464f-9a1b-2204da439569)

El-Meleigi M A and Al-Rokibah A A 1996 Survey of wheat diseases in central Saudi Arabia *Bull. Fac. Pharm. Cairo Univ.* **47** 499–512

Eversmeyer M G, Burleigh J R and Roelfs A P 1973 Equations for predicting wheat stem rust development *Phytopathology* **63** 348–51

FAO 2020 *Saudi Arabia Country Brief* (Food Agriculture Organization United Nations) (available at: www.fao.org/giews/countrybrief/country.jsp?code=SAU&lang=en)

FAO 2021 *FAOSTAT Database* (Food Agriculture Organization United Nations) (available at: www.fao.org/faostat/en/)

Frenken K 2009 Irrigation in the Middle East region in figures AQUASTAT Survey-2008 *FAO Water Reports* No. 34 (Rome)

Gebul M A 2021 Trend, status, and challenges of irrigation development in Ethiopia—a review *Sustainability* **13** 5646

Hei N B *et al* 2020 First report of *Puccinia graminis* f. sp. *tritici* race TTKTT in Ethiopia *Plant Dis.* **104** 982

Jones A, Thomson D, Hort M and Devenish B 2007 The UK Met Office's next-generation atmospheric dispersion model, NAME III *Air Pollution Modeling and Its Application XVII* (Boston, MA: Springer) pp 580–9

Lewis C M *et al* 2018 Potential for re-emergence of wheat stem rust in the United Kingdom *Commun. Biol.* **1** 1–9

Maldaner I C, Heldwein A B, Bortoluzzi M P, Loose L H, Lucas D D and Silva J R D 2015 Irrigation and fungicide application on disease occurrence and yield of early and late sown sunflower *Rev. Bras. de Eng. Agricola E Ambient.* **19** 630–5

Menzies J D 1967 Plant diseases related to irrigation *Irrig. Agric. Lands* **11** 1058–64

Meyer M, Burgin L, Hort M C, Hodson D P and Gilligan C A 2017a Large-scale atmospheric dispersal simulations identify likely airborne incursion routes of wheat stem rust into Ethiopia *Phytopathology* **107** 1175–86

Meyer M, Cox J A, Hitchings M D T, Burgin L, Hort M C, Hodson D P and Gilligan C A 2017b Quantifying airborne dispersal routes of pathogens over continents to safeguard global wheat supply *Nat. Plants* **3** 780–6

Muluneh A, Stroosnijder L, Keesstra S and Biazin B 2017 Adapting to climate change for food security in the Rift Valley dry lands of Ethiopia: supplemental irrigation, plant density and sowing date *J. Agric. Sci* **155** 703–24

Nagarajan S, Kogel H J and Zadoks J C 2012 Epidemiology of *Puccinia graminis* f. sp. *tritici*-Ug99 in the Rift Valley "Flyway" from Uganda-Kenya to Yemen *Plant Health Prog.* **13** 31

Naseri B and Sabeti P 2021 Analysis of the effects of climate, host resistance, maturity and sowing date on wheat stem rust epidemics *J. Plant Pathol.* **103** 197–205

National Institute of Statistics of Rwanda 2019 *Seasonal Agricultural Survey–2019 Annual Report* (Kigali City) (available at: www.statistics.gov.rw/publication/seasonal-agricultural-survey-2019-annual-report)

Nazari K, Al-Maaroof E, Kurtulus E, Kavaz H, Hodson D and Ozseven I 2021 First report of Ug99 race TTKTT of wheat stem rust (*Puccinia graminis* f. sp. *tritici*) in Iraq *Plant Dis.* **105** 2719

Nopsa J F H and Pfender W F 2014 A latent period duration model for wheat stem rust *Plant Dis.* **98** 1358–63

Olivera P D, Sikharulidze Z, Dumbadze R, Szabo L J, Newcomb M, Natsarishvili K, Rouse M N, Luster D G and Jin Y 2019 Presence of a sexual population of *Puccinia graminis* f. sp. *tritici* in Georgia provides a hotspot for genotypic and phenotypic diversity *Phytopathology* **109** 2152–60

Olivera P *et al* 2015 Phenotypic and genotypic characterization of race TKTTF of *Puccinia graminis* f. sp. *tritici* that caused a wheat stem rust epidemic in southern Ethiopia in 2013–14 *Phytopathology* **105** 917–28

Patpour M, Hovmøller M S, Justesen A F, Newcomb M, Olivera P, Jin Y, Szabo L J, Hodson D, Shahin A A, Wanyera R and Habarurema I 2016 Emergence of virulence to SrTmp in the Ug99 race group of wheat stem rust, *Puccinia graminis* f. sp. *tritici*, in Africa *Plant Dis.* **100** 522

Roelfs A P 1992 *Rust Diseases of Wheat: Concepts and Methods of Disease Management* (Mexico: CIMMYT)

Rossi V, Racca P, Giosue S, Pancaldi D and Alberti I 1997 A simulation model for the development of brown rust epidemics in winter wheat *Eur. J. Plant Pathol.* **103** 453–65

Rotem J and Palti J 1969 Irrigation and plant diseases *Annu. Rev. Phytopathol.* **7** 267–88

Saari E E and Prescott J M 1985 World distribution in relation to economic losses *Diseases, Distribution, Epidemiology, and Control* (New York: Elsevier) pp 259–98

Salotti I, Bove F and Rossi V 2022 Development and validation of a mechanistic, weather-based model for predicting *Puccinia graminis* f. sp. *tritici* infections and stem rust progress in wheat *Front. Plant Sci.* **13** 1761

Sanogo S 2004 Response of chile pepper to *phytophthora capsici* in relation to soil salinity *Plant Dis.* **88** 205–9

Saunders D G O, Pretorius Z A and Hovmøller M S 2019 Tackling the re-emergence of wheat stem rust in Western Europe *Commun. Biol.* **2** 1–3

Savary S, Stetkiewicz S, Brun F and Willocquet L 2015 Modelling and mapping potential epidemics of wheat diseases—examples on leaf rust and *septoria tritici* blotch using EPIWHEAT *Eur. J. Plant Pathol.* **142** 771–90

Savary S, Willocquet L, Pethybridge S J, Esker P, McRoberts N and Nelson A 2019 The global burden of pathogens and pests on major food crops *Nat. Ecol. Evol.* **3** 430–9

Shamanin V P, Pototskaya I V, Shepelev S S, Pozherukova V E, Salina E, Skolotneva E S, Hodson D P, Hovmoller M S, Patpour M and Morgounov A I 2020 Stem rust in Western Siberia-race composition and effective resistance genes *Vavilov J. Genet. Breed.* **24** 131–8

Singh R P, Hodson D P, Huerta-Espino J, Jin Y, Njau P, Wanyera R, Herrera-Foessel S A and Ward R W 2008 Will stem rust destroy the world's wheat crop? *Adv. Agron.* **98** 271–309

Singh R P, Hodson D P, Jin Y, Lagudah E S, Ayliffe M A, Bhavani S, Rouse M N, Pretorius Z A, Szabo L J, Huerta-Espino J and Basnet B R 2015 Emergence and spread of new races of wheat stem rust fungus: continued threat to food security and prospects of genetic control *Phytopathology* **105** 872–84

Swett C L 2020 Managing crop diseases under water scarcity *Annu. Rev. Phytopathol.* **58** 387–406

Tack J, Barkley A and Hendricks N 2017 Irrigation offsets wheat yield reductions from warming temperatures *Environ. Res. Lett.* **12** 114027

USDA Foreign Agricultural Service 2019 *Saudi Arabia: Grain and Feed Annual* (Riyadh) (available at: www.fas.usda.gov/data/saudi-arabia-grain-and-feed-annual-4)

Wakeyo M and Lanos B 2019 Analysis of price incentives for wheat in Ethiopia for the time period 2005–2012 *Gates Open Res.* **3** 278

Walters D, Baran A J, Boutle I, Brooks M, Earnshaw P, Edwards J, Furtado K, Hill P, Lock A, Manners J and Morcrette C 2019 The Met Office Unified Model global atmosphere 7.0/7.1 and JULES global land 7.0 configurations *Geosci. Model Dev.* **12** 1909–63

Yesuf N S, Getahun S, Hassen S, Alemayehu Y, Danu K G, Alemu Z, Tesfaye T, Hei N B and Blasch G 2021 Distribution, dynamics, and physiological races of wheat stem rust (*Puccinia graminis* f. sp. *tritici*) on irrigated wheat in the Awash River Basin of Ethiopia *PLoS One* **16** e0249507

Zaveri E and Lobell D B 2019 The role of irrigation in changing wheat yields and heat sensitivity in India *Nat. Commun.* **10** 1–7