Climate change impacts the spread potential of wheat stem rust, a significant crop disease

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Abstract

Long range atmospheric transport is an important pathway for the spread of plant pathogens, such as rust fungi which can devastate cereal crop health and food security worldwide. In recent years, serious concern has been caused by the evolution of new virulent races of Puccinia graminis f. sp. triticici, a pathogen causing wheat stem rust that can result in close to 100% yield losses on susceptible wheat cultivars in favourable weather conditions. We applied an Earth system model to compare the suitability of the current climate and a business-as-usual climate scenario (RCP 8.5) for 2100 for wheat stem rust. Although there are large uncertainties in modelling changes in disease spread, we focus in this paper on the changes which are likely to be robust to model assumptions. We show that the warmer climate with lower relative humidity and enhanced turbulence will lead to ~40% increase in the urediniospore emitting potential of an infected field as global average. The main predicted changes in the atmospheric long-range transport include reduced connections between Europe, Africa and South Asia, and increased frequency of spores crossing the mid-latitude oceans. Due to reduction in subfreezing conditions, the overwintering areas of the fungus will expand. On the other hand, projected drier conditions will reduce substantially the probability of an infection starting from deposited spores, except in irrigated fields.

Introduction

Phytopathogenic microbes with explosive epidemic potential represent a major threat to agriculture and, thus, food security and sustainability (Chakraborty and Newton 2011, Fisher et al 2012, Singh et al 2015, McDonald and Stukenbrook 2016). Rust fungi (Pucciniales) are a large group of plant pathogens that can infect a wide range of crops. Wheat can be infected by three different rust species: Puccinia triticina (leaf rust), Puccinia striiformis f. sp. tritici (stripe rust), and Puccinia graminis f. sp. tritici (stem rust). These three fungi are widely distributed around the world and are considered the most harmful wheat pathogens globally (Dean et al 2012, Huerta-Espino et al 2014), stem rust being the most destructive of the three.

Historically wheat stem rust has been a major disease in almost all wheat growing areas of the world (Saari and Prescott 1985). Currently the damage it can cause is limited by continuously breeding resistant cultivars and applying fungicides when necessary. However, severe yield losses (up to 50% regionally and over 90% on severely infected fields (Leonard and Szabo 2005, Huerta-Espino et al 2014)) can occur when new virulent races evolve, such as the wheat stem rust races of the Ug99 lineage discovered in Uganda in 1998 (Pretorius et al 2000) or race TKTTF that caused close to 100% yield losses on susceptible wheat cultivars during an outbreak in Ethiopia in 2013–14 (Singh et al 2015). Over 80% of the wheat of the world was highly susceptible to Ug99 (Ayliffe et al 2008).

While, in the modern connected world, human travel and transport of agricultural goods are increasingly
important for crop pathogens to reach distant locations, the relatively small size of wheat stem rust urediniospores (17–35 μm, Anikster et al 2008) makes atmospheric spore transport the most relevant vector for disease spread. Multiple events of rust fungi spreading from one continent to another through the atmospheric pathway, even crossing oceans, have been confirmed (supplementary table 1 is available online at stacks.iop.org/ERL/14/124053/mmedia; Brown and Hovmøller 2002), although more commonly the propagation happens as a series of shorter transport events, requiring the disease to get established in a new area before the next transport event expands the range further. For instance, the Ug99 lineage races have by now spread over large areas from South Africa (Pretorius et al 2012) to Iran (Singh et al 2015) and Russia (Sibikeev et al 2016), although have not reached India (Nagarajan et al 2014). The race TKTTF has been found in Germany, UK, Sweden, Denmark and Sicily (Lewis et al 2018), ending the practically wheat stem rust free decades in Europe.

The climate-related factors that control the success of the stem rust surviving and spreading by atmospheric urediniospore transport are shown on figure 1. The urediniospores are produced in repeating asexual reproduction cycles and are capable of re-infecting the primary cereal host. In suitable conditions the reproduction cycle takes 1–2 weeks from spore deposition to production of uredinia and release of a new generation of spores (Huerta-Espino et al 2014). Under optimal temperature (~30 °C) one uredinium produces 10 000 spores per day for 2–3 weeks (Katsuya and Green 1967, Huerta-Espino et al 2014). As a rough estimate based on 1% disease being defined as 10 pustules per culm (Kingsolver et al 1959) and up to ~1000 culms per square meter, there could be up to a million uredinia per square meter in a very heavily infected field.

During transport, the spores are exposed to sunlight and subfreezing temperatures that reduce their viability and thus limit the distances the pathogen can be transmitted in viable state in a single transport event. Schueller et al (2005) demonstrated that accurate knowledge of the parameters related to loss of viability is crucial for modelling the transport patterns—changing the UV sensitivity of oak pollen within its uncertainty limits changed the distance of gene transport several times. However, to the best of our knowledge, the study by Maddison and Manners (1972) is the only source of information on how the wheat stem rust spores are affected by sunlight. After 35 h of sunlight exposure the fraction of the spores able to germinate fell below the detection limit at 0.1%. Maddison and Manners (1973) demonstrate that the spores are sensitive to wide spectrum of UV radiation, and the sensitivity, shape of the germinability reduction curve and the effect of relative humidity differs between the wavelengths. However, this information is only available for germinability and not for final infectivity which they showed to be 3–6 times more sensitive to shortwave UV radiation (254 nm) emitted by a germicidal lamp, leaving large uncertainties to spore lifetime estimates.

The lifetime of the spores is also significantly reduced by subfreezing temperatures (Eversmeyer and Kramer 1995). While in storage conditions the spores can survive very low temperatures for long time, Huerta-Espino et al (2014) connected this cold tolerance with very low spore water content requiring proper drying of the spores. In nature one would expect the humidity to vary widely and freezing in
humid or wet conditions is probably the factor destroying the spore viability, causing water crystals to form inside the spores. Eversmeyer and Kramer (1995) showed a very short lifetime of spores in 30%–50% relative humidity for below freezing conditions.

After deposition onto a suitable host, the spores require suitable conditions to germinate and cause an infection – temperatures in a specified range (between +5 and +40 °C) and liquid water on leaves for at least 6, but ideally 8–12 h, followed by solar radiation exceeding 100 W m⁻² (Huerta-Espino et al 2014).

The sexual reproduction pathway of rust fungi can involve up to 5 different kinds of spores in successive stages and requires infecting an alternate host (Leonard and Szabo 2005) (Berberis vulgaris for wheat stem rust). The sexual reproduction is important to the fungus in providing genetic diversity, but also allows overwintering in colder climate. However, in majority of wheat growing areas it over-seasons in the asexual ure-dinial form due to the lack of alternate hosts near wheat fields (McCallum et al 1999). For instance, in North America the wheat stem rust overwinters in latitudes below 35° north, where temperatures mostly stay above freezing (McCallum et al 1999), though occasionally it can survive subfreezing temperatures on winter wheat under thick snow cover (e.g. Roelfs and Long 1987). Every spring it re-colonises the continent reaching the northernmost wheat growing areas by summer.

Previous modelling studies of rust fungi have successfully reproduced certain observed spore transport events and spread probabilities in selected regions in historical conditions (Isard et al 2005, Pfender et al 2006, Del Ponte and Esker 2008, Meyer et al 2017, Visser et al 2019). A recent study also highlighted an increasing climatic risk of stem rust re-emergence for the United Kingdom (Lewis et al 2018). In the current study we apply an earth system model to study the climate impact on various stages in the life cycle of the wheat stem rust fungus and atmospheric spore transport, and for the first time, look at this globally. As the amount of experimental data available in the literature is not sufficient to calibrate the model to accurately represent the whole life cycle of the fungus and we are not aware of any available data on wheat stem rust sporulation, spore concentration or deposition that could be used for quantitative model evaluation, our current study follows a highly idealized concept. Accurate representation of the spread of the infection is beyond the scope of the study, instead we focus on the changes which are likely to be robust to model assumptions and identify the most significant expected impacts and directions for future studies. We compare the current climate to the conditions of 2100 simulated following the business-as-usual (Representative Concentration Pathway or RCP8.5) scenario in regard to different stages of the wheat stem rust life cycle (sporulation, spore transport, infection and overwintering). Because future distribution of wheat is difficult to predict and is highly sensitive to the assumptions about human land use incorporated into the socio-economic pathways for the IPCC (Riahi et al 2017) we assume no change in land use for the future.

### Methods

We included modules for modelling the emission and transport of fungal spores into the Community Earth System Model (CESM version 1.2.2, Hurrell et al 2013). The Community Atmosphere Model (CAM version 5.3, Neale et al 2012) in CESM was adapted to compute the global dispersion of the wheat stem rust urediniospores. The urediniospore emission parameterization includes three processes: temperature dependent spore production, removal from plant surface by air flow and escape from the crop canopy by turbulent mixing. Once emitted into the atmosphere, the model simulates the 3-dimensional transport, as well as wet and dry deposition processes. We compute the exchange of spores between 12 source-receptor areas, shown on supplementary figure 1. As a simplification due to the large uncertainty in the related parameters, we consider the loss of viability as a function of transport time, rather than UV exposure and track the time the spores spend airborne between their emission and deposition.

The probability of germination of the deposited viable spores is simulated considering the temperature, light and leaf wetness at the deposition area. Detailed description of the implementation of all above mentioned processes can be found in the supplementary information. The selected model parameter values are listed in supplementary table 2.

The model simulates four climate sensitive stages of the wheat stem rust life cycle (sporulation, spore transport, infection and overwintering), however, as a simplification, we do not model the spread of the infection and assume constant density of uredinia in all areas where wheat is growing according to the monthly data of MIRCA 2000 dataset (Portmann et al 2010).

In order to reduce the sensitivity of the results to the uncertain absolute values of the model parameters we present the differences between the future scenario and the modern climate relative to the current values. To further reduce the impact of the uncertain assumptions, we also present in the supplementary material the changes the weather parameters driving the processes and a limited set of sensitivity studies.

Although the current study concentrated on wheat stem rust, the developed model can be adapted to simulate other rust fungi with limited changes to the parameters.

Simulations were made for the modern (2000), and future (2100) climate conditions following the RCP8.5 scenario. The model was run in the fully coupled mode for 25 years for each period with daily output. The horizontal resolution was 0.9 \times 1.25 degrees. An additional simulation was made for the period
1980–2017 with meteorology forced by the MERRA2 reanalysis (Gelaro et al. 2017) which we refer to as the observed meteorology simulations.

To assess the statistical significance of the differences between the current and future conditions the p-values were computed for the sets of annual mean values for every model grid cell or source-receptor pair using the t-test of independent samples from scipy.stats library. To control against the multiple testing errors, the Benjamini–Hochberg procedure (Benjamini and Hochberg 2018) was applied with false detection rate 0.1.

**Results and discussion**

**Impact of climate change on spore production and emission**

The model simulations project that in the majority of regions, a warmer climate will lead to more days with suitable temperatures for sporulation (between +5°C and +40 °C) (supplementary figures 2(d)–(f)). Thus, shorter incubation stage and higher spore production rate will lead to more spores produced by a similarly infected field (supplementary figures 4(a) and 5(a)). Notable exceptions are the tropical areas, where high temperatures will reduce the spore production. Future simulations of drier and more turbulent conditions (supplementary figure 6) will also allow a larger fraction of the urediniospores escaping to the free atmosphere from the crop canopy (supplementary figures 4(b) and 5(b)). The result is a higher rate of spore emissions from the same level of infection (figure 2(a)).

Contrary to this finding, Damialis et al (2015a, 2015b) found in Thessaloniki, Greece a decrease in fungal spore concentrations from 1987 to 2005, which was also in contrast with the increase in pollen in the same location (Damialis et al. 2007). Sofiev and Prank (2016) analysed the ERA INTERM meteorological reanalysis for changes in parameters relevant for pollen emission, transport, and deposition in Europe (wind speed and direction, turbulence, precipitation, and relative humidity) for the period 1980–2013. The only significant change was the reduction of summertime precipitation and relative humidity in Southern Europe, which would lead to increasing bioparticle concentration due to reduction in wet deposition. Thus, the reduction in fungal spores must rather be related to the fungal biology. Damialis et al (2015a) showed that several fungal species grew faster at higher temperatures, but most of them produced fewer spores. The uredomyceum of *Puccinia graminis* indeed grows faster in higher temperatures (Mehta 1923, Kochman and Brown 1975), however, spore production of wheat stem rust has also been shown to increase with temperature up to 25 °C–30 °C (Prabhu and Wallin 1971) and thus the warming climate reduces it only in the tropical areas.

**Probability of deposited spores causing an infection**

At the same time the drier conditions reduce substantially the probability of germination of the deposited spores (figure 2(b)), as liquid water on the leaves is required for the fungus to successfully infect the plants (Huerta-Espino et al. 2014). Reduction in average wet canopy fraction together with reduced number of days in suitable temperature range (between +2 °C and +30 °C, supplementary figures 6(b) and 3(b)) leads to a lower chance for an infection in majority of the world, apart from mostly mountainous regions—the infection risk will be rising in western United States and Canada, Argentina, Western China and Central Asia, and also New Zealand. It is worth mentioning that in these simulations we have neglected the impact of irrigation on leaf wetness, which could enhance the ability of spores to infect the crops (Beddow et al. 2015). Our results are in good agreement with the predictions of Lewis et al (2018) about the reduction of infection risk in UK.
As exposure to UV radiation rapidly reduces the infectivity of urediniospores, the probability of the deposited spores being able to infect host plants will be further reduced by increasing levels of solar radiation reaching the surface in large parts of Europe, Eastern Asia, North and South America and South Africa because of a reduction in cloudiness (supplementary figure 7). The decrease in the solar radiation reaching the surface above the Atlantic Ocean may increase the chance of the spores remaining viable while crossing it.

**Changes in long range transport patterns**

We simulated the probabilities of the spores released in any of the 12 broad source regions (shown on the supplementary figure 1) to be deposited in any of the others. According to our computations, the spores that were transported across oceans spent majority of the travel time above the atmospheric boundary layer (supplementary figure 8), being exposed to direct sunlight and cold temperatures. Thus, we consider 3 d (representative of 35 h of sunlight) the longest transport time relevant for transmitting the pathogen and, alternatively, lifetime up to one day would also take into account the higher sensitivity of the infectivity (Maddison and Manners 1972, 1973). With strong winds, the distances travelled in one day can reach a few thousand kilometres, allowing frequent exchange of viable spores between, e.g., Europe and North Africa or Australia and New Zealand (figure 3, supplementary figure 9). Within 3 days spores can travel between North America and Europe, reach Australia from South America, Africa from South America and South America from New Zealand (figure 3, supplementary figure 10).

The modelled transport frequencies agree reasonably well with the small amount of information available from previous research (supplementary table 1). For instance, the model reproduces the low frequency of transport between South America and North America previously reported regarding the spread of soybean rust (Isard et al. 2005). Spores released in Colombia reached 30° north with a travel time below 3 d only in 7 out of the 38 years simulated with historical weather, making the frequency of potential transport events from South America to soy fields of USA once per 5–6 years. One of these modelled events coincided with the historic event that took place in 2004, when the hurricane Ivan introduced the soybean rust to USA.

According to the same simulations, an event which carries wheat stem rust spores in less than 3 days from South Africa to Australian wheat fields happens also once per 5–6 years. Although this frequency is substantially lower than simulated previously with a different modelling system (Visser et al. 2019), it agrees much better with the very low frequency of appearance of new wheat rust races in Australia reported in that study. As our study assumes constant infection levels on all wheat covered areas, certain overestimation is expected when comparing with historical records. According to our simulations the prevailing transport direction from South Africa narrowly misses Australia (blue contour on figure 3), making the frequency of transport events very sensitive to small differences in wind patterns from different circulation

![Figure 3. Areas influenced by spore transport from selected source regions: red—North America, turquoise—Europe, yellow—East Asia, green—South America, blue—Sub-Saharan Africa, pink—New Zealand. Contours and light shading—areas where below 3 d transport happens at least once per 5 years, darker shading—same for below 1 d transport. Gray shading—annual maximum wheat coverage. Based on 38 years long simulation forced with MERRA2 reanalysis.](image-url)
models, but potentially also to differences rising from changing climate.

The simulation results for the future climate show a larger fraction of spores having longer atmospheric lifetimes, and thus being transported further from their source. The transport patterns of the climate simulations are shown on supplementary figure 11. The statistically significant changes in the transport frequencies are shown in figure 4. The results indicate reduction in the fraction of days with connection between Europe, Africa, Arabian Peninsula and South Asia (the area on figure 4 with numerous the blue arrows, reaching from the Mediterranean to South Asia). There are two main reasons for this. Firstly, the regions around the Sahara Desert and Arabian Peninsula will get too warm for the fungus to successfully sporulate—a significant rise in the number of days with temperatures above 40 °C in this region is projected (supplementary figure 2(d)). Secondly, the increasing sea-land temperature differences could strengthen the sea breeze. The model projects significantly more days with winds blowing in the landward direction on the coasts of the Mediterranean, Red Sea and Gulf of Arabia, which reduces the number of days the spores can cross these barriers.

The number of potential transport days increases for eastward connections in the southern hemisphere, with the exception of South-Africa to Australia.

**Overwintering**
The ability of wheat stem rust to overwinter in uredinial stage is often reported to be limited to areas where the winter temperatures stay mostly above freezing (McCallum *et al* 1999). This definition of overwintering is supported by the fact that the urediniospores do not survive long in subfreezing temperatures. However, an experimental study of *Puccinia graminis subsp. graminicola*, a close relative to wheat stem rust, showed that once the fungus has infected the plant it can survive temperatures as low as −10 °C, and its survival only depends on the host tissue survival (Pfender and Vollmer 2007). The potential overwintering areas computed following this definition for current climate and their expansion due to global warming are shown on figure 5 and the alternative assumption on supplementary figure 12.

According to these results the overwintering areas are projected to expand northwards in the northern hemisphere and also increase in mountainous regions. The likelihood of overwintering is predicted to increase in parts of USA, Eastern Europe, Central Asia, China, and Argentina.

**Limitations and sensitivities**
Due to the limited available experimental data, large uncertainties exist in the values of model parameters. Extra uncertainties are introduced by simplifications in the model parameterizations that are needed to reduce the required computing time. The most important model parameters and estimated sensitivities are listed in supplementary table 2. While exhaustive sensitivity analysis of all the parameters is out of the scope of this study, a limited set of sensitivity analyses are shown in the supplementary material. We found moderate sensitivity of the climate related difference in sporulation to the shape of the assumed temperature sensitivity. The sensitivity of the overwintering areas to the assumptions regarding the
survival temperature was strongest in Europe. And the sensitivity of the long range transport patterns to the amount of spore produced was very low. As future direction we suggest further sensitivity studies for the following parameters: (i) sensitivity of climate suitability parameterizations for all phases in the wheat stem rust life cycle to parameter values and functions selected to describe the temperature, light and humidity and leaf wetness dependences, (ii) sensitivity of the long range transport patterns to the parameters describing the loss of spore viability in transport due to UV, temperature and humidity, (iii) sensitivity of the spread of the pathogen to wheat susceptibility, wheat phenology and sowing time, and the assumptions regarding the over-seasoning conditions.

In addition to uncertainties in the climate projections, the main limitations of this study are related to its simplified design. Firstly, the idealized study design assumes constant infection on all wheat areas and does not compute realistic spread of the disease. Secondly, we use the same fixed wheat area and timing for current and future period without considering the climate or land use change impacts. Thirdly, the four modelled phases in the life cycle of the fungus (spore germination, spore production and emission, atmospheric spore transport and over-season survival) are considered independently from each other, apart from spore emission and transport. Also, the model does not include any variation between wheat cultivars or rust races in terms of infectivity or susceptibility or any of the specific model parameters. As another limitation, the relative lack of experimental data has led to several simplifications in the model parameterizations, for instance the use of transport time as an indication of spore viability instead of UV exposure. And finally, the model considers only the fungal biology, while for accurate modelling the interactions of the host-parasite system should be taken into account.

As one example of wheat biology influencing the fungal development, Yirgou and Caldwell (1968) related the observed light and CO₂ dependence of the leaf penetration probability to wheat metabolism. The light requirement of this process is fulfilled in daytime outdoor conditions on majority of weather conditions (Huerta-Espino et al 2014), and thus we are not expecting it to cause differences in future climate. However, the higher CO₂ concentrations in future might reduce the infection probability.

More relevant from the point of view of climate change is that higher temperatures would change the phenology of the host plant. For example, Gange et al (2013) relates the earlier and longer fungal spore seasons in Europe (Gange et al 2007, Kauslerud et al 2012) to resource availability from the host plants that has changed due to the changing climate. Higher temperatures would lead to faster phenological development in wheat, shortening the overall growth period (Wheeler et al 1996, Sadras and Monzon 2006). As the period between inoculation and pustule emergence of wheat stem rust also shortens in higher temperatures (Mehta 1923, Kochman and Brown 1975), the shortening of wheat growth period would compete with the shortening of the pathogen cycle and the number of cycles completed during the wheat growth period might change in either direction, depending on the temperature sensitivities of the host and the parasite. Additionally, some of the resistance genes are only functional in the adult plants, leading to higher susceptibility of the seedlings (Ellis et al 2014). Shortening the seedling phase would reduce the window of increased susceptibility at seedling state. This is an interesting direction for future studies that would become possible.

Figure 5. Climatically suitable regions for wheat stem rust overwintering in uredinial stage, computed as areas where the minimum annual surface temperature stays above −10 °C for majority of years. Green—overwintering areas in current climate, orange— increase of overwintering areas by 2100 s (RCP 8.5).
after fully integrating the fungal model with the crop model in the land component of CESM.

There are a number of other directions the developed model could be used to explore. Extending the model to take into account various host-parasite interactions would allow to investigate impacts of increasing CO2 concentrations and also the impact of the disease on the wheat yield, thus connecting the biological processes to socioeconomic impacts. The model could be applied to study the impact of different agricultural practices such as fungicide use, different types of irrigation, fraction of susceptible wheat varieties, timing of sowing etc.

Expanding the timescale of the study to cover the whole period from now to 2100 and considering different climate scenarios would allow to identify periods with highly favorable conditions. While future crop cover is uncertain and the projected changes are limited, it would be interesting to investigate how the much the smaller extent of wheat in preindustrial era impacted the spread of the pathogen. Finally, the model can be applied to study other similar pathogens, such as wheat leaf and stripe rust.

Conclusions

While there are large uncertainties in describing the life cycle of the wheat rust simulated here, the relevance of this topic to global food security justifies a first look at how climate change may impact the spread of wheat rust diseases. Here we have focused on the results which are likely to be robust to underlying uncertainties, and also present a section which highlights future research areas to constrain the uncertainties.

Although the warmer and drier climate is predicted to benefit the urediniospore production and escape to free atmosphere, leading to more spores being released from a similarly infected field, the same factors significantly inhibit the germination of the spores. The availability of liquid water on the leaves becomes the limiting factor for the fungus infecting the crops in large parts of the world, notable exceptions being the mountainous regions. Better chances of overwintering can further worsen the outcome in these areas, leading to earlier initiation of epidemics and resulting in more severe disease and disease-induced yield loss, especially if the farmers in these areas switch to growing more winter cultivars, providing the fungus with available hosts for the winter months.

Changes in extent and type of irrigation can negate the impacts of dryer climate in the tropical and subtropical areas where we are predicting the infection probability to decrease due to reduction in availability of liquid water on crop leaves.

Thus, the net effect of climate change on the ability of devastating fungal diseases to spread by long range transport is not yet known but could be substantial.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request. Selected subset of the model output at annual temporal resolution is available at http://geo.cornell.edu/eas/PeoplePlaces/Faculty/mahowald/dust/Pranketal2019/.

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