Achieving durable disease resistance in cereals

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Towards an early warning system for wheat blast: epidemiological basis and model development

J. M. Fernandes, Embrapa Trigo, Brazil; E. M. Del Ponte and J. P. Ascarí, Universidade Federal de Viçosa, Brazil; T. J. Krupnik, International Maize and Wheat Improvement Center (CIMMYT), Bangladesh; W. Pavan*, Universidade de Passo Fundo and SensorOn – Estrada do Trigo, Brazil; F. Vargas, SensorOn – Estrada do Trigo, Brazil; and T. Berton, Universidade de Passo Fundo, Brazil

1 Introduction

Wheat blast is a relatively new disease to wheat (Triticum aestivum L.) caused by the fungus Pyricularia oryzae Triticum pathotype – PoT (syn. Magnaporthe oryzae B.C. Couch). The disease was first reported in the state of Paraná, south region of Brazil, in 1985 (Igarashi et al., 1986). During the following decades, wheat blast spread to almost all wheat regions in Brazil, and also to neighboring countries including Bolivia, Paraguay and northern Argentina (Kohli et al., 2011; Perelló et al., 2015). The impact of this disease to wheat production can be devastating; 100% yield losses have been reported multiple times in South America (Cruz et al., 2019; Gongora-Canul et al., 2020) and, more recently, large-scale outbreaks have occurred in Bangladesh (Islam et al., 2016; Malaker et al., 2016). However, significantly damaging wheat blast epidemics are sporadic

* International Fertilizer Development Center, Muscle Shoals, AL, U.S.A and Universidade de Passo Fundo - PPGCA, Rodovia, BR 285, Passo Fundo, RS, 99050-970, Brazil

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and tend to be limited to situations when exceptionally wet and warm weather occurs prior and during the season, in regions where inoculum is not limiting, more typical of the tropics of Brazil and Bolivia (Coelho et al., 2016; Fernandez et al., 2007; Gongora-Canul et al., 2020; Goulart and Paiva, 2000). However, the frequency of severe outbreaks has increased in the Cerrado region, central-western of Brazil, where the disease is currently a major constraint to the expansion of wheat production in this important agroecosystem (Pasinato et al., 2018).

Until 2016, wheat blast was restricted to South America and of concern to wheat farmers in the Americas, as a risk analysis study highlighted the potential to its introduction into North America (Cruz et al., 2012). Unexpectedly, instead of the anticipated northward movement, wheat blast caused by PoT was found to suddenly devastate over 15000 ha, from February to March 2016 alone, in Bangladesh (Malaker et al., 2016). To date, the explosive outbreaks have not re-occurred in that country. Bangladesh’s Department of Agricultural Extension (DAE) reported wheat blast-affected acreage ranging from 2 ha to 312 ha from 2016–2017 to 2019–2020 wheat growing seasons (DAE, Personal Communication). These numbers were backed by analyses conducted by the International Maize and Wheat Improvement Center (CIMMYT) and the Bangladesh Wheat and Maize Research Institute (BWMRI), in particular, by spore trapping efforts that confirmed the presence of airborne inoculum, though at low densities.

Another striking official report was the presence of the PoT fungus causing wheat blast in rain-fed wheat fields and experimental plots in Zambia, Africa (Tembo et al., 2020). Summer wheat production in Zambia is rain-fed, grown primarily by small-scale and resource-poor farmers who typically attain low yields given a range of limiting factors including foliar diseases such as spot blotch (Bipolaris sativus) (Tembo, 2019). The presence of wheat blast in Africa places current agricultural policies that have focused on increasing wheat acreage to reduce foreign currency expenditure on dependence on imports at risk (Tembo, 2019; Tembo et al., 2020).

The urgent need to deal with this relatively recent and poorly studied disease has mobilized scientists from all over the world after major epidemics were reported in Brazil and Bolivia in the early 2000s, but especially its appearance in Asia (Cruz and Valent, 2017). Original research and review articles have been published in various venues (Ceresini et al., 2018; Inoue et al., 2017; Juliana et al., 2020). Much has been learned in several aspects including genetics and genomics of the pathogen (Gladieux et al., 2018; Inoue et al., 2017), genetics of host resistance (Cruppe et al., 2020; Goddard et al., 2020; Gruner et al., 2020; Juliana et al., 2020), host-pathogen interactions at both physiological and molecular levels (Aucique-Pérez et al., 2020, 2017; Cruz et al., 2015b, 2016; Farman et al., 2017), as well as fungicide resistance (Castroagudín et al., 2015;
Towards an early warning system for wheat blast (Dorigan et al., 2019; Oliveira et al., 2015) and biological control (Chakraborty et al., 2020).

Nevertheless, disease control is still a challenge for most farmers, and is complicated by two main factors, including (1) lack of genetic resistance in most wheat cultivars available commercially (Cruppe et al., 2020; Juliana et al., 2020) and (2) uncertainty in the profitability of fungicides that present inconsistent results with regards to efficacy and yield response (Cruz et al., 2019; Maciel, 2011). To counteract these challenges, shifting of sowing dates, particularly delaying planting in the Cerrado region, has been used as a disease avoidance measure (Coelho et al., 2016). Conversely, preliminary evidence in Bangladesh indicates that earlier sowing can help farmers to reduce disease risks by reducing the length of time that wheat experiences hotter temperatures favorable to infection later in the season (CSISA, 2020). Nonetheless, a close matching of disease-conducive factors over a large wheat production region is difficult to predict and can be devastating, such as the widespread severe epidemics of both leaf and head blast recorded in 2019 at the Cerrado region of Brazil (Fig. 1).

Much less research has, however, focused on crucially important and complex ecological interactions at the field, landscape or regional levels. Knowledge of disease epidemiology and ecology is a pillar of any integrated pest management (IPM) program, not only to refine management strategies, but also to develop and test models for risk analysis and prediction of the disease (Donatelli et al., 2017; Savary et al., 2018). During the season, fungicides are

![Figure 1](image-url)  
**Figure 1** Aerial view of the wheat fields (a) at the Cerrado region of Brazil, heavily affected on both (b) spikes and (c) leaves (with d) detail of lesions caused by wheat blast during the 2019 outbreak. Source: Embrapa (2019).
the last resort to minimize the impact of wheat blast, although the economic benefits of fungicides are questionable given the relatively low efficacy levels if improperly utilized (Cruz et al., 2019). Moreover, increase in production costs incurred with fungicide purchase limit the broad use of fungicides, especially for smallholder wheat farmers who may not be able to afford regular calendar-based applications. Nevertheless, a wheat blast warning system may be useful to indicate when and where the disease might occur, and thus preventative management advisories can be delivered to farmers several days in advance of potential disease outbreaks. This approach is aimed at rationalizing the use of fungicide, limiting it to locations and situations in which application is most likely to be necessary and economically rational (Shtienberg, 2013, 2000).

In this chapter, we review aspects of the epidemiology of wheat blast, mainly those related to inoculum and its role for the epidemics, which we believe are critical for more accurate predictions of wheat blast risk. We then describe the models that we have developed as well as the decision support system capable of operating at the global scale. Examples of the implementation of a warning system in Bangladesh and Brazil are illustrated.

2 Epidemiology and pathogen ecology

Epidemiology concerns the study of the change of the disease intensity in a population of host plants in space and time (Madden et al., 2007). In this context, epidemics are dynamic systems in which several different rates affect key processes that operate both at the ‘infection chain’ level (infection, colonization, sporulation) (plants) as well as at the landscape (fields) and regional (agroecosystems) levels. The latter two scales are affected by the spatial distribution and density of the main and the alternative hosts that harbor inoculum, seasonal weather patterns and source-sink relationships that influence the rate and severity of disease spread and infection (Plantegenest et al., 2007).

For wheat blast, the risk of severe attack and yield loss is increased when airborne inoculum is plentiful during the wheat heading period and the physical environment is wet and warm (Fig. 2). Therefore, knowledge of the presence and distribution of hosts of the wheat blast pathogen population, as well as factors that drive inoculum production and dispersal, are key not only to understand pathogen population genetics and evolution, but also and especially to predict current and future disease risks.

3 Inoculum sources and survival

Thus far, two sources of inoculum have been identified as important for wheat blast infection. These include (a) infected seeds (Gomes et al., 2018; Goulart and Paiva, 1990), which are responsible for the large distance (intercontinental)
Towards an early warning system for wheat blast spread (Cruz and Valent, 2017) and (b) infected grasses present in the surroundings of wheat crops, before wheat sowing. These alternative hosts can harbor and spread the wheat blast pathogen inoculum early in the season.

In South America, the most abundant blast-susceptible grass is signal grass (*Urochloa* spp.), present in all tropical regions where wheat is grown in Brazil (Jank et al., 2014). Together with other grass hosts, signal grass likely serves as a major reservoir of primary inoculum for both leaf and head blast epidemics in commercial wheat fields (Urashima et al., 2017). Under experimental conditions, where infected crop residues were amended to field plots, the earliest symptoms of disease were recorded on newly emerged and youngest wheat leaves; these early infected leaves can further serve as a source of newly produced conidia (secondary inoculum) that move upwards, further infecting wheat heads (Cruz et al., 2015b; Gongora-Canul et al., 2020). In Brazil, a study showed that the blast fungus was capable of surviving for up to five months (Pizolotto et al., 2019). Therefore, it is more likely that residue-borne spores will be available to infect grasses during the off-season, and not directly infect wheat in the following season.

### 4 Production, release and aerial transport of inoculum

It has been known for a long time that *P. oryzae* conidia are probably forcibly discharged, but at a very short distance, by the active bursting of the minute stalk-cell by which it is attached to the conidiophore (Ingold, 1964). Environmental factors may also play an essential role in the spore-release process. High-humidity conditions may be accountable for turgor pressure buildup inside the stalk-cell, which explains the high availability of conidia under moistened conditions (Ingold, 1964; Meredith, 1962). The conidia release of *P. oryzae* can be triggered by either increasing levels (from 24% to 100%) or decreasing levels (from 100% to 24%) of relative humidity; maximum conidia release has been found when relative humidity levels increase from 76% to 100% (Danelli et al., 2019; Leach, 1980). Short rains (less than 5 mm) also seem to favor spore

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**Figure 2** Generalization of the role of inoculum sources and key requirements of weather-based variables that lead to infection by *Pyricularia oryzae Triticum* (PoT) in wheat.
release, but intense rainfall events may also reduce *P. oryzae* conidia residence in sporulating lesions (Kim, 1994; Danelli et al., 2019). It is also plausible that under heavy rain, large raindrops vigorously damage conidiophores, releasing and washing off conidia, thereby reducing the amount of inoculum available for transport from plant to plant, field to field, and across regions. Silva and Prabhu (2005) also reported an inverse relationship between rainfall and trapped *P. oryzae* conidia. Another important factor for the release of *P. oryzae* conidia is light (Leach, 1980, 1962). Constant blue light and red light have been proven to induce higher conidia release than constant white light or darkness. The transition from a light to a dark period also induces the release of conidia (Lee et al., 2006).

Minimum wind speeds to induce spore release have been reported to vary among different fungi (Pasanen et al., 1991). However, there appears to be no evidence indicating that wind speed influences the conidia release of *P. oryzae*. Released spores can escape from the plant canopy (disease sources) and are dispersed or transported to different sites at various distances. Where they encounter a susceptible host, infections serve as a sink for the disease, in a pattern that is essential for the spread of the disease and perpetuation of an epidemic. Intermittent wind patterns also play a major role in spore removal and canopy escape, which in turn shape disease gradients for aerially dispersed fungal pathogens (Fitt et al., 2006; West and Kimber, 2015). One aerobiological study trapped *P. oryzae* conidia at distances as large as 1 km from a known source (Urashima et al., 2007).

A strong relationship between the number of conidia trapped in a volumetric sampler and rice blast disease progress was reported in a multiple-year study (Pinnschmidt et al., 1993). Increasing temperature may also be a factor leading to high airborne spore concentrations of *M. oryzae* during the rice-growing season in Southern Spain (Castejón-Muñoz, 2008). Daily spore release patterns for *P. oryzae* have been well described in the rice blast pathosystem. Among them is a nocturnal pattern of *M. oryzae* spore release that is observed in high concentrations at night (Leach, 1980; Meredith, 1962).

### 5 Infection and colonization

Detailed information on the effects of temperature and wetness duration period on infection by the wheat blast pathogen (PoT) is scarce (Cardoso et al., 2008). In their study conducted using PoT from Brazil, Cardoso and collaborators (2008) showed that a minimum of 10 hours was required for infection with an increase in infection efficiency positively correlated with an increase in wetness duration. Moreover, temperatures between 25°C and 30°C were more favorable for infection than 15°C (Cardoso et al., 2008). In the United States, temperature and leaf wetness duration models were fitted to data gathered
in experiments that inoculated the gray leaf spot pathogen (*P. oryzae Lolium* pathotype, PoL) on perennial ryegrass (Uddin et al., 2003) or wheat (Mills et al., 2020). For the PoL-wheat pathosystem, the mean levels of disease intensity and rates of its increase were higher at 25°C and 30°C, with 24 and 48 hours of relative humidity >95%, when compared with 20°C and < 12 hours of high relative humidity (Mills et al., 2020). Overall the effects of temperature and moisture on infection are quite comparable among PoT (*Triticum* pathotype), PoO (*Oryzae* pathotype) and PoL (*Lolium* pathotype).

Apart from the weather influence, the infection site has shown to be important to define the intensity. In fact, massive wheat yield losses occur when *P. oryzae* infects the rachis at the base of the spike, thereby limiting grain development and filling in addition to destroying the spikes completely (Kohli et al., 2011). Cruz and collaborators (2015b) reported that within 72 hours after infection, the fungal hyphae reach the rachis and spread upward and downward along the rachis. Within rachis tissue, fungal hyphae massively colonized the epidermis, collenchyma, cortical and pith parenchyma and vascular bundle at just 96 hours after infection (Cruz et al., 2015b).

## 6 Modelling wheat blast epidemics

Models of plant disease epidemics are mathematical simplifications that, in most cases, allow the prediction of epidemic risks or future behavior, depending on their objective and complexity (De Wolf and Isard, 2007; Hardwick, 2006; Magarey et al., 2005). Model predictions are useful for aiding decisions during planning of risk mitigation procedures, establishing management strategies as well as controlling the disease in the field to minimize the risk of yield losses (Gent et al., 2013).

Depending on the specific conditions, the models vary in complexity and their development is not without challenges, depending on the goals (Cunniffe et al., 2015). As far as models to warn disease risk are concerned, traditionally they are based on requirements for infection (Magarey et al., 2005). However, this is valid only when the inoculum can be assumed as not limiting. This seems not be the case for wheat blast where grasses in the landscape serve as large reservoirs for the inoculum, but its production and amount available to infect commercial wheat is dependent on the seasonal weather (Danelli et al., 2019; Fernandes et al., 2017). Therefore, our group has employed efforts to develop weather-driven wheat blast models that take both inoculum production and infection risk into account. Thus far, our modelling efforts have resulted in two generations of wheat blast models that have been improved together with the decision support systems where the models are embedded and predictions deployed as risk maps at the country level.
6.1 First-generation model

The first dynamic wheat blast model that considered inoculum production on the primary sources (grasses) was parameterized a model to predict inoculum buildup and availability (Fernandes et al., 2017). The authors adapted the approach used in a previous study (Bregaglio and Donatelli, 2015) on the development of a simulation model for predicting the seasonal progress of rice blast (*Magnaporthe oryzae* Oryzae) based on relative humidity requirements for conidia production. The parameters in the wheat blast model were defined based on expert knowledge and observations of wheat blast outbreaks in Brazil. This model was purposely designed to be relatively simple in structure so as to be flexible and easy to use in practice. It was the first attempt to input variables which were limited to hourly temperature, relative humidity and precipitation observations or forecasts in the prediction of wheat blast.

The wheat blast model developed by Fernandes et al. (2017) has four components. The first component assumes that spores are present and estimates the rate of conidiophore development as a function of temperature and relative humidity, both of which are integrated to estimate blast inoculum potential by solving Equation 1 for the hourly sum of inoculum potential (IP) over the season:

\[
IP = \begin{cases} 
14.35 - 0.25 \times T & 15^\circ C < T < 27^\circ C \text{ and } RH \geq 93% \\
-8.5 - 0.59 \times T & 27^\circ C < T < 35^\circ C \text{ and } RH \geq 93% \\
0 & \text{otherwise}
\end{cases}
\]

(1)

where T and RH are air temperature and relative humidity, respectively. Where RH is below the threshold in Equation 1, the model does not accumulate thermal time. The model also calculates the development of a spore cloud subject to assumptions of air current uptake, atmospheric diffusion and wind shear that affect spore longevity. Survival of spores while airborne may also be affected by temperature, solar and ultraviolet radiation, in addition to relative humidity. Spore cohorts were therefore assumed to have a half-life of three days within any seven-day window.

The model also determines the number and timing of days with weather favoring blast infection using a conditional ruleset. Days favoring infection were consequently declared following spore cloud development when the daily maximum temperature exceeded 23°C and temperature amplitude (calculated daily minimum temperature subtracted from daily maximum temperature) was > 13°C, with mean daily RH above 70%.

6.2 Second-generation model

The second generation was built on a previously developed generic plant disease model structure (Pavan et al., 2009). The model parameters were
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defined using values obtained from the literature or expert knowledge of wheat blast epidemics. In this model, hourly values of weather variables (such as temperature, relative humidity and precipitation) are the main drivers of wheat blast progress. The model assumes that alternative hosts (grasses) are presented at the surrounding of a wheat field. A submodule, parameterized for each region, predicts the host leaf area assumed to be a potential infection site. Spores originating from nearby sources that are deposited over the wheat canopy remain viable for a certain time that varies as a function of age and a cloudiness factor. Wheat crops are infected when a threshold value for airborne inoculum concentration is estimated, and lesions are formed and expand over time. At the end of the latency period, the lesion becomes infectious and newly produced spores produced are distributed over three spatial hierarchy layers, respectively, auto-deposition, allo-leaf-deposition and allo-plant-deposition (Willocquet and Savary, 2004).

The simulations are run for 200 days with a time step of one day. The model uses numerical weather model forecast outputs on a three-hourly timescale for precipitation, relative humidity and temperature as input. These represent environmental conditions for inoculum buildup expressed by continuous periods favoring sporulation (represented by a spore index) and the density of spores in the air (a spore cloud). The latter is simulated as the density of spores in a 1 m$^3$ area over the crop canopy, subject to assumptions of air current uptake, atmospheric diffusion and wind shear, all of which can affect and reduce spore longevity (Mousanejad et al., 2009). Importantly, this model also assumes the geographically uniform presence of PoT inoculum in the environment for which simulations are run. It therefore does not yet account for source-sink and spore dispersal mechanisms, but instead simulates the development of conidia and lesion cohorts from an assumed uniform base population.

7 Early warning system for wheat blast

Considering the strong dependence of wheat blast epidemics on seasonal weather, which varies across regions and seasons within a region, a prediction system that operates at large may be useful not only to anticipate the risk of outbreaks in the early season. In addition, such systems - when well-designed - can be used to map risk areas using historical data (Savary et al., 2012) or conduct risk analysis in regions where a pathogen has not been introduced (Hyatt-Twynam et al., 2017). Whatever the case, an early warning system (EWS) is a computerized framework that integrates several layers of geographic, climatic and biological information, which are processed and the results communicated via textual and graphical outputs to target users (Pavan et al., 2011).

The wheat blast early warning system (WB-EWS) uses weather data for simulating inoculum buildup during the vegetative growth stage of wheat which is key to estimate the risk of infection. The WB-EWS was developed
by EMBRAPA and CIMMYT for Brazil and Bangladesh and is available at ‘http://beattheblastews.net’. The current implementation of the WB-EWS integrates weather databases and scripts for specific submodules developed using different programming languages. For example, the spore index was implemented using the R programming language (R Core Team, 2020) based on previous work (Fernandes et al., 2017), and the spore cloud model was implemented using C++ based on a generic disease model (Pavan et al., 2009). All the submodules are integrated, and information on infection risks and crop management advisories are delivered to end users via e-mail, SMS and the web. The model diagram is presented in Fig. 3.

The WB-EWS has been made operational in Bangladesh and Brazil. In Bangladesh, to more accurately identify and map risk areas, three-hourly Weather Forecasting Research (WRF) model outputs are supplied by the Bangladesh Meteorological Department (BMD) at a 18-km² grid resolution for all wheat-growing areas of Bangladesh. WRF forecasts are generated on a three-hourly rolling basis for five days into the future, and combined with an automatic weather station network for observed data, advisories are generated at this spatial and temporal resolution. In Brazil, the Eta Model (Mesinger et al., 2012) output is provided by CPTEC/INPE ‘https://www.cptec.inpe.br/’ at 20-km² grid resolution for all wheat-growing areas. These are used to generate time- and location-specific advisories on a five-day forecast basis. The model adequately described the observed epidemic and non-epidemics years in Brazil and Bangladesh (Figs 4 and 5).

![Figure 3](image)

**Figure 3** A relational diagram for the wheat blast-early warning system (WB-EWS) operational in Brazil and Bangladesh.
Figure 4 Procedural flow of information generating early warnings for wheat blast in Bangladesh and Brazil.
Figure 5 Graphical outputs generated by the WB-EWS (http://beatheblastews.net) using historical weather data from epidemic and non-epidemic years in Bangladesh.
This system results in the triggering of an automated alert system deploying email and SMS warnings to extension agents and lead farmers that is operational during the corresponding typical phenological range from early heading to maturation for wheat in both countries (Fig. 5).

8 Model uses and future developments

In contrast to advisories that encourage calendar-based preventative sprays without field scouting, a data-driven approach can be used to adaptively advise farmers how to take effective and safe preventative action through the intelligent use of fungicides for disease control. The WB-EWS was approved for use in extension in Brazil in 2018 and in Bangladesh in 2019, and uses numerical weather model forecast outputs to map favorable areas and identify critical periods for wheat blast epidemics, which are currently being tested and improved with regard to accuracy. These are used to generate time- and location-specific advisories on a five-day forecast basis (Fig. 6).

We are also considering options for delivering blast warnings directly to farmers using interactive voice response (IVR) technologies for at-risk locations prior to potential infection. In contrast recommendation for standard sprays deployed as a function of the number of days after seeding and without field verification of disease, this data-driven approach can be used to adaptively advise farmers how to take effective and safe preventative action through the intelligent use of appropriate fungicides for disease control. In coupling a wheat growth model with the wheat blast model, our future objective is to provide

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**Figure 6** Graphical outputs generated by the WB-EWS (http://beattheblastews.net) using historical weather data from epidemic and non-epidemic years in Brazil.
farmers not only with forecast advisories, but also estimates of potential yield loss if they do not take preventative action to control blast.

9 References


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