Wheat Blast: Past, Present, and Future

Paulo Cezar Ceresini,[1] Vanina Lilián Castroagudín,[1]
Fabrício Ávila Rodrigues,[2] Jonas Alberto Rios,[2]
Carlos Eduardo Aucique-Pérez,[2] Silvino Intra Moreira,[3]
Eduardo Alves,[3] Daniel Croll,[4]
and João Leodato Nunes Maciel[5]

[1]Department of Crop Protection, Agricultural Engineering, and Soils, São Paulo State University, 15385-000, Ilha Solteira, São Paulo, Brazil; email: paulo.ceresini@unesp.br

[2]Laboratory of Host–Parasite Interaction, Department of Plant Pathology, Federal University of Viçosa, 36570-900, Viçosa, Minas Gerais, Brazil

[3]Department of Plant Pathology, Federal University of Lavras, 37200-000, Lavras, Minas Gerais, Brazil

[4]Laboratory of Evolutionary Genetics, Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland

[5]Embrapa Wheat (Embrapa Trigo), Brazilian Agricultural Research Corporation, Passo 99050-970, Fundo, Rio Grande do Sul, Brazil

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Abstract

The devastating wheat blast disease first emerged in Brazil in 1985. The disease was restricted to South America until 2016, when a series of grain imports from Brazil led to a wheat blast outbreak in Bangladesh. Wheat blast is caused by *Pyricularia graminis-tritici* (*Pygt*), a species genetically distinct from the *Pyricularia oryzae* species that causes rice blast. *Pygt* has high genetic and phenotypic diversity and a broad host range that enables it to move back and forth between wheat and other grass hosts. Recombination is thought to occur mainly on the other grass hosts, giving rise to the highly diverse *Pygt* population observed in wheat fields. This review brings together past and current knowledge about the history, etiology, epidemiology,

physiology, and genetics of wheat blast and discusses the future need for integrated management strategies. The most urgent current need is to strengthen quarantine and biosafety regulations to avoid additional spread of the pathogen to disease-free countries. International breeding efforts will be needed to develop wheat varieties with more durable resistance.

THE HISTORY OF EMERGENCE AND SPREAD OF THE WHEAT BLAST PATHOGEN

Wheat blast caused by the hemibiotrophic ascomycetous fungal pathogen *Pyricularia graminis-tritici* (*Pygt*) (19) has been a major disease across central and southern Brazil since it was first described there in Paraná State in 1985 (71). Although it is highly likely that the disease was not widespread in the country before the first epidemic in 1985 (70, 71), an earlier report from 1936 (116) indicated that the pathogen was already present in the Brazilian agroecosystem. After emerging in Paraná, Brazil, the wheat blast pathogen spread to the neighboring states of São Paulo and Mato Grosso do Sul in 1986 (60) and Rio Grande do Sul in 1987 (70) (**Figure 1a,b**; **Supplemental Material 1**). The agriculture expansion to the warm cerrado areas of central-western Brazil enabled the invasion of *Pygt* into the new wheat agroecosystems in Minas Gerais in 1990 (M.A. de Souza, personal communication; 82), Goiás in 1992 (113, 114), and Brasília in 1993 (5). Severe wheat blast epidemics in 1987 limited further expansion of the tropical wheat cropping areas into the Brazilian cerrado. As a result of wheat blast, wheat fields are now rare in the cerrado, dropping by 95% from 428,000 ha in 1987 to fewer than 20,000 ha in 2016 (25) (**Supplemental Material 2**). The pathogen spread to eastern Bolivia in 1996 (9), eastern Paraguay in 2002 (158, 159), and northern Argentina in 2007 (2, 14, 108). *Pygt* is now firmly established in South America (**Figure 1a,b**; **Supplemental Material 1**). Starting from its origin in Paraná, the pathogen spread into warmer regions 1,200 km north toward Brasília; 1,700 km northwest toward Santa Cruz, Bolivia; and into cooler regions 1,200 km southwest toward the provinces of Chaco and Corrientes, Argentina.
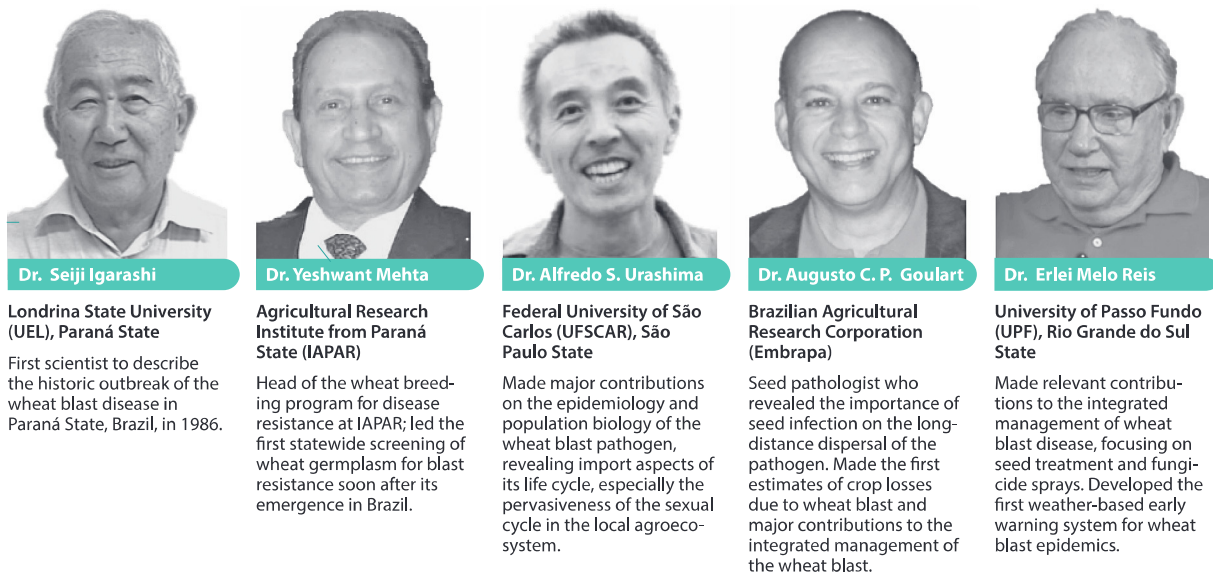
The pathogen conidia are not thought to spread far via wind (153), but seedborne inoculum (50, 53, 57) is likely to have facilitated the long-distance dispersal of the pathogen and enabled it to invade other agroecosystems in South America and now Southeast Asia. Despite the risk of introducing *Pygt* into their local agroecosystems, during the past 11 years (from January 2006 to September 2017), 10 countries with no history of wheat blast have repeatedly imported varying quantities (from 11 kg to 24.4 tons) of Brazilian bread wheat and durum wheat seed for sowing. Among these countries were Algeria, Angola, Belgium, Iran, Laos, Mexico, Mozambique, Pakistan, the Philippines, and even the United States (**Figure 1a**; **Supplemental Material 3**), which has particularly strict quarantine restrictions for wheat blast (154). A total of 65 countries imported Brazilian wheat or mixtures of wheat and rye, mostly during this period, with quantities as high as 0.82 to 1.14 million tons of grain exported to South Africa, Algeria, Vietnam, and the Philippines (**Supplemental Material 3**). A series of shipments in 2008, 2011, and 2015 totaled 426,840 tons (**Figure 1a**; **Supplemental Material 3**) of possibly contaminated mixtures of wheat and rye grains harvested from Brazilian wheat blast epidemic areas, preceding the recent emergence of *Pygt* in Bangladesh in 2016 (74).

Following the emergence of wheat blast in Bangladesh in 2016 (15, 74), *Pygt* came to the attention of Asian governments and the broader international community of plant pathologists, bringing to light an urgent need to develop plans to contain the spread of this destructive pathogen in Asia (74, 88, 91, 126, 127, 131, 136). Weather suitable for wheat blast coupled with susceptible
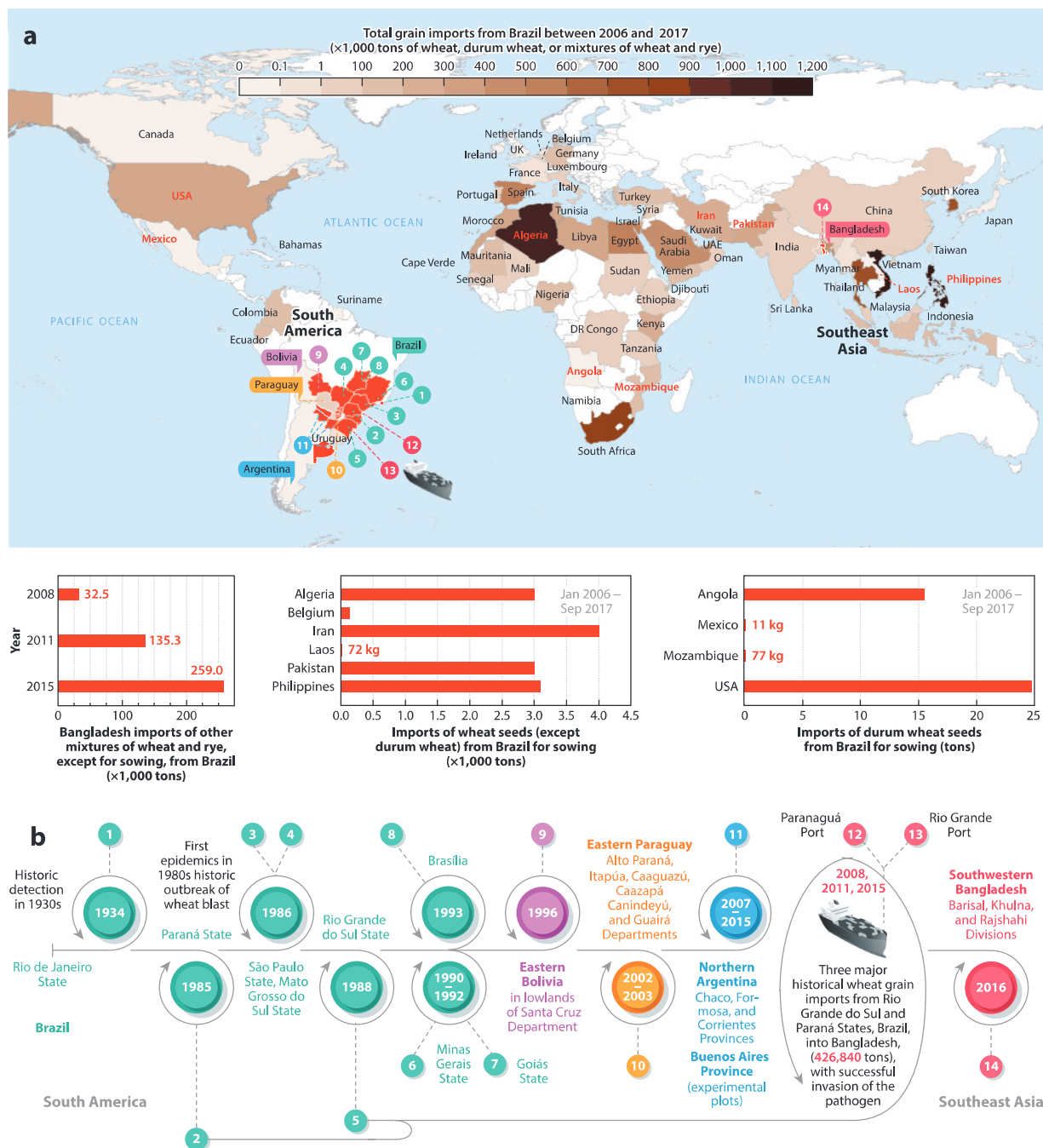
Figure 1

(*a*) Geographical distribution of wheat blast. Shown are countries with confirmed wheat blast (*areas highlighted in red*) and sixty-five countries that received significant imports of wheat from Brazil but have not officially reported wheat blast (*highlighted in varying shades of brown, with darker shades indicating greater imports*). Ten countries (*indicated with red lettering*) have imported wheat or durum wheat seeds for sowing. (*b*) Timeline of events spanning the emergence and spread of the pathogen in South America to the invasion into new areas in Southeast Asia. Data in panel *a* from Reference 61 and **Supplemental Material 3**.

Supplemental Material >

Dr. Seiji Igarashi	Dr. Yeshwant Mehta	Dr. Alfredo S. Urashima	Dr. Augusto C. P. Goulart	Dr. Erlei Melo Reis
Londrina State University (UEL), Paraná State	**Agricultural Research Institute from Paraná State (IAPAR)**	**Federal University of São Carlos (UFSCAR), São Paulo State**	**Brazilian Agricultural Research Corporation (Embrapa)**	**University of Passo Fundo (UPF), Rio Grande do Sul State**
First scientist to describe the historic outbreak of the wheat blast disease in Paraná State, Brazil, in 1986.	Head of the wheat breeding program for disease resistance at IAPAR; led the first statewide screening of wheat germplasm for blast resistance soon after its emergence in Brazil.	Made major contributions on the epidemiology and population biology of the wheat blast pathogen, revealing import aspects of its life cycle, especially the pervasiveness of the sexual cycle in the local agroecosystem.	Seed pathologist who revealed the importance of seed infection on the long-distance dispersal of the pathogen. Made the first estimates of crop losses due to wheat blast and major contributions to the integrated management of the wheat blast.	Made relevant contributions to the integrated management of wheat blast disease, focusing on seed treatment and fungicide sprays. Developed the first weather-based early warning system for wheat blast epidemics.

Figure 2

Late-1980s prominent Brazilian scientists who described the wheat blast pathogen and its disease biology and management.

cultivars may prompt severe outbreaks of the disease if it reaches India's northeastern plains and Pakistan, with the potential to cause high yield losses and seriously compromise regional food security (62, 127).

During the process of preparing this review, we interviewed a group of prominent Brazilian wheat blast scientists (**Figure 2**; **Supplemental Material 4**) who have worked on wheat blast since the original epidemic in 1985. They shared their thoughts on the likely impact and future prospects of wheat blast in Southeast Asia as well as their opinions on the origins of wheat blast and what knowledge will be needed to manage wheat blast more effectively in the future (**Supplemental Material 4**).

PYRICULARIA GRAMINIS-TRITICI: A DISTINCT, HIGHLY DIVERSE SPECIES WITH A BROAD HOST RANGE

The taxonomy of the *Pyricularia* species complex has long been disputed, oscillating between the names of the asexual (*Pyricularia*) or sexual (*Magnaporthe*) morphs to designate the genus (103, 167). Name changes in the Pyriculariaceae family have been extensively reviewed (77, 103, 125, 166, 167). These taxonomy disagreements have resulted in naming the rice blast pathogen as four different species during the last 17 years (143): *Pyricularia grisea*, *Pyricularia oryzae*, *Magnaporthe grisea*, and *Magnaporthe oryzae*. A similar multiname species confusion exists for the wheat blast pathogen (60, 70, 86, 147, 149).

Since the rice blast pathogen was first designated as *P. oryzae* in 1892 (143), many other *Pyricularia*-like isolates that were recovered from blast lesions on barley (*Hordeum vulgare*), millets (*Eleusine coracana*, *Pennisetum glaucum*, *Setaria italica*), oats (*Avena sativa*), perennial ryegrass (*Lolium perenne*), wheat (*Triticum aestivum*), and more than 50 other grass species were also classified under the same species name, converting *P. oryzae* into a species complex (26, 27, 98, 139, 151). Based on the assumption of host specificity, mating ability, and genetic relatedness, *P. oryzae*

was split into several subgroups (or pathotypes) to reflect a limited host range: *Oryza* pathotype, pathogenic on rice; *Setaria* pathotype, pathogenic on foxtail millet (*Setaria italica*); *Panicum* pathotype, pathogenic on common millet (*Panicum miliaceum*); *Eleusine* pathotype, pathogenic on finger millet (*Eleusine coracana*); *Triticum* pathotype, pathogenic on wheat; *Avena* pathotype, pathogenic on oats; and *Lolium* pathotype, pathogenic on perennial ryegrass (46, 77, 102, 144, 148). Despite becoming the status quo in plant pathology, this classification system, based on the assumption of host-specialized pathogen populations, did not reflect the biology of the blast pathogens on wheat, oats, and ryegrass because these *Pyricularia* have broader host ranges (77). For example, isolates of the *Triticum* pathotype can cause blast on barley, signalgrass (*Urochloa brizantha*), oats, rye (*Secale cereale*), and more than 10 other grass hosts (19, 149), whereas isolates of the *Avena* pathotype can infect oats and wheat (102) and some isolates of the *Lolium* pathotype can also infect wheat (45, 144).

Phylogenetic analyses based on multiple loci demonstrated that *Pyricularia* is indeed a species-rich genus in which different species seem to have emerged through repeated radiation events from a common ancestor (22, 69, 79). Since 2010, a series of comprehensive studies reexamined the relationships among *Pyricularia* spp. and *Pyricularia*-like species and led to significant changes in the order Magnaporthales (79, 84, 99). Most importantly, taxonomists eliminated the genus *Magnaporthe* and proposed the definitive name change from *Magnaporthe* spp. to *Pyricularia* spp. (79, 84, 99). During the past two decades, multilocus phylogenetic analyses also established that *P. oryzae* and *P. grisea* were independent phylogenetic species (27). A much more robust study using a maximum likelihood tree based on 859,067 single nucleotide polymorphisms distributed across entire genomes indicated that *Pyricularia* isolates from *Triticum* and *Avena* formed a single monophyletic clade that was clearly separated from the clade containing isolates from *P. oryzae* (163). These results were consistent with previous phylogenomic analyses (21).

A recent study including 10 housekeeping loci for 128 isolates of *Pyricularia* spp. sampled from sympatric populations of wheat, rice, and other grasses growing in or near wheat fields led to the identification of the new species *P. graminis-tritici* as the blast pathogen on wheat and several other hosts (19). The assignment of a new species that distinguished rice-infecting isolates from the broad host range clade *Pygt* has been subsequently challenged (49). Despite this challenge, it is evident from Gladieux et al. (49) that the rice- and wheat-infecting genotypes cluster into clearly distinct groups and that *Pygt* genotypes are highly diverse. Three arguments were presented against assigning the status of a new species to the wheat blast pathogen: (*a*) not all loci showed a concordant phylogeny, (*b*) genomes of rice- and wheat-infecting isolates showed evidence for gene flow at specific loci, and (*c*) the high diversity in deeply diverged lineages within the original *P. oryzae* made it inappropriate to assign all lineages into exactly two species. The requirement for concordance of phylogenetic signals at a specific set of loci is a well-established rule for evaluating the evidence of a new fungal species (140). The strength of this test is that it is highly conservative. However, recent genomic analyses of early stages of speciation in animals, plants, and fungi showed that phylogenetic concordance at conserved loci emerged significantly later than the emergence of reproductively isolated populations and reduced hybrid fitness (130).

A more recent study that included 95 entire genome sequences of the wheat blast pathogen and other *Pyricularia* species substantiated the identification of *Pygt* as a distinct, highly diverse pathogen species with a broad host range. *Pygt* is capable of causing blast on many important crop species, including wheat, signalgrass, barley, and oats as well as native and introduced grasses often found as invasive species (weeds) in commercial wheat fields (e.g., *Chloris distichophylla*, *Cynodon* spp., *Digitaria insularis*, *Equinochloa crus-galli*, *Panicum maximum*, *Rhynchelytrum repens*, and *Sorghum sudanense*) (18) (**Figure 3**).
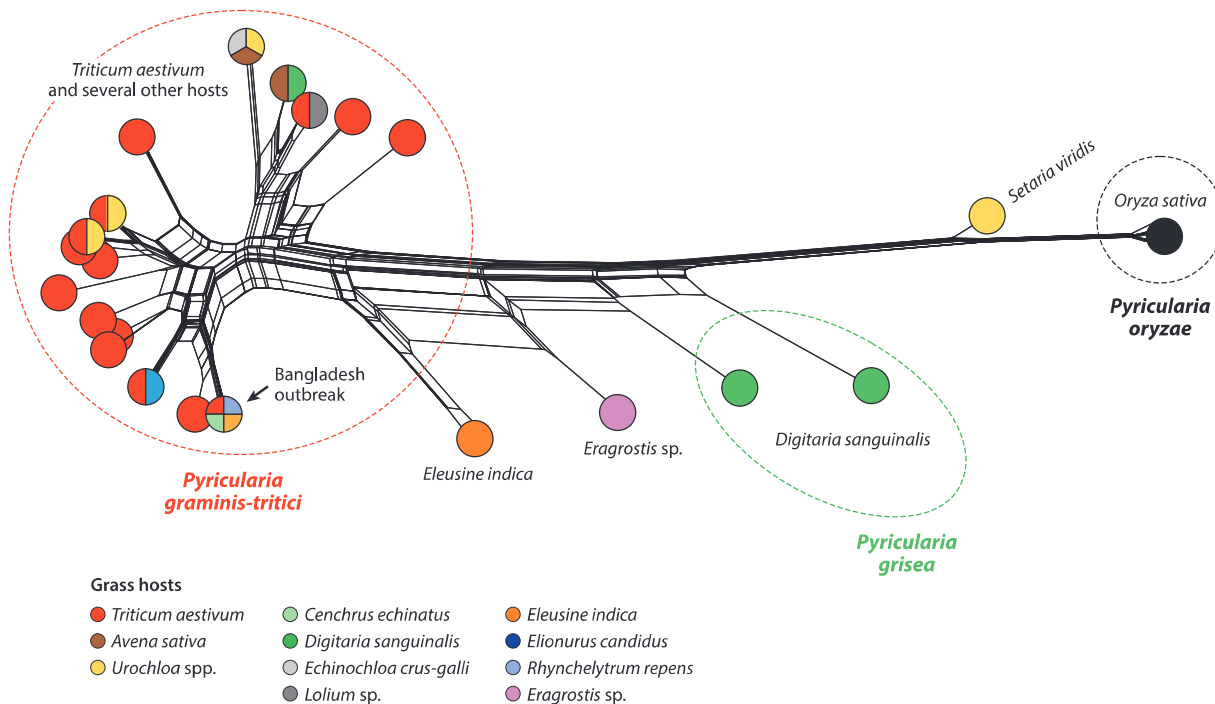
Figure 3

A phylogenomic analyses of 63 isolates of *Pyricularia* spp. from diverse grass hosts. Tips of the network are summarized with pie charts that identify the host from which the isolate was collected. The unrooted network was constructed with Splitstree based on genotypes at 27,961 single nucleotide polymorphism markers selected at ~1 kb distances across the genome. Isolates infecting rice and *Setaria viridis* form a distinct clade. Highly distinct lineages were found on *Digitaria sanguinalis*, *Eragrostis* sp., and *Eleusine indica* hosts. *Pygt* infects wheat (*Triticum aestivum*) and a wide diversity of other crops and grasses, including *Avena sativa* and *Urochloa* spp. The outbreak of wheat blast in Bangladesh was triggered by a *Pygt* genotype that was very closely related to a genotype found on wheat and other grasses (*highlighted by an arrow*). The network depicts only 63 genomes (from 95 originally) as the *P. oryzae* strains grouped together as a near-clonal genotype.

Regardless of any taxonomic considerations, the identification of genetically distinct *Pygt* genotypes has two important implications: (*a*) *Pygt* is not a wheat-specialized pathogen, and (*b*) the hypothesis of host-specific populations for the overall *P. oryzae* species complex is falsified (18).

The recognition of *Pygt* as a genetically distinct species has pressing implications for quarantine regulators worldwide (18). A lack of awareness that the geographically restricted wheat blast pathogen is not the same species as the widely distributed rice blast pathogen *P. oryzae* may account for the quarantine breach that led to the inadvertent introduction of *Pygt* into Bangladesh through a series of wheat grain imports from Brazil in 2008, 2011, and 2015 (61) (**Figure 1a**; **Supplemental Material 3**). The Bangladesh plant quarantine rules and guidelines [Destructive Insects and Pests Rules 1966 (Plant Quarantine), Amendment 1989 (63) and Plant Quarantine Act 2011 (64)] did not include the wheat blast pathogen as a potential threat to the country's agriculture. It is plausible that because of the confusing nomenclature and a lack of knowledge of the most recent findings, the wheat blast pathogen was thought to be the same species as the rice blast pathogen *P. oryzae*, which was already a well-established pathogen causing high yield losses in Bangladesh (78), raising no concerns from the national quarantine authorities.

ORIGIN AND DIVERSIFICATION OF THE WHEAT BLAST PATHOGEN

Unlike some other *Pyricularia* species, isolates of *Pygt* recovered from wheat can infect a wide range of hosts, including grasses from the tribes Hordeae, Festuceae, Avenae, Chlorideae, Agrosteae, and Paniceae (149). Physical proximity between cultivated grasses (e.g., wheat) and weedy grasses (i.e., weeds or invasive grass species) under natural field conditions could facilitate genetic exchange among the *Pyricularia* populations, infecting different hosts and enabling host shifts. Cross-infection and interfertility between fungal strains from different grass hosts were hypothesized to have played a role in the emergence of wheat blast in Brazil (19, 107, 149). Evidence to support this hypothesis came from a recent study that analyzed genetic variation in the avirulence genes *PWT3* and *PWT4* (72). This study proposed that wheat blast emerged via a host shift from a *Pyricularia* population infecting *Lolium*. In the model presented in that study, *Lolium*-derived isolates carrying the *Ao* avirulence allele at the *PWT3* locus infected a susceptible wheat cultivar carrying the *rwt3* susceptibility allele. This model further proposes that the spread of the wheat blast pathogen during the 1980s outbreak in Brazil was enabled by the widespread cultivation of susceptible wheat cultivars carrying *rwt3*. Selection occurring on less common *Rwt3* wheat cultivars then favored the emergence of pathogen strains with nonfunctional *PWT3* alleles, and the authors proposed that it was these *pwt3* strains that ultimately became the epidemic wheat blast population prevalent in South America (72).

Population genomic analyses that included 36 *Pygt* strains originating from many different hosts in Brazil and 59 strains of other *Pyricularia* species did not unambiguously resolve whether there were multiple origins or a single origin for the wheat blast pathogen. The absence of strict host specialization among the major *Pygt* subclades suggests that the ability to infect wheat may have originated multiple times (18). The findings from Castroagudín et al. (17, 18) were consistent with the emergence of wheat blast in Brazil through a host shift from the *Pygt* population infecting other grasses growing near wheat fields. The authors provided strong evidence that gene flow still occurs between the *Pygt* population infecting wheat and the *Pygt* population infecting other grasses, but not from the rice-derived population of *P. oryzae* (18) (**Figure 3**). Furthermore, the most common virulence groups were shared between the grass- and wheat-infecting *Pygt* populations, providing additional evidence for movement of *Pygt* between wheat fields and nearby grasses (18, 86). This recurring gene flow may enable *Pygt* populations to maintain significant genetic variation on multiple hosts, a finding that stands in stark contrast to what is found for populations of *P. oryzae* causing rice blast (18, 128).

The high number of associated hosts and the apparent genetic diversification of *Pygt* raised important questions about the functional roles of polymorphism within *Pygt*. The escape from recognition through mutations in the avirulence genes *PWT3* and *PWT4* is the only clearly demonstrated genetic factor in the adaptation of *Pygt* to its host (72). However, recent studies detected hundreds of presence/absence gene polymorphisms both within *Pygt* and between wheat- and rice-infecting isolates (21, 163). In particular, genes located in proximity to transposable elements were more likely to segregate deletion polymorphisms (163). Interestingly, the gene categories that were most strongly affected by gene deletion polymorphisms included genes encoding effectors and key secondary metabolite enzymes (163). Recent analyses of other plant pathogens demonstrated that such standing genetic variation fuels rapid adaptation to new host genotypes (67, 68). Genomic monitoring of the spread of *Pygt* to Bangladesh proved highly informative about the origin of the outbreak and its evolutionary potential. Genomic analyses of the *Pygt* strains collected in Bangladesh in 2016 and 2017 showed that all genotypes clustered tightly into a single clone. Hence, the Bangladesh *Pygt* populations likely consist still of a single genotype, which is in striking contrast to the genetic diversity discovered at the pathogen's center of origin in South America (74). Furthermore, the finding of a single Bangladesh genotype means that quarantine

efforts to prevent any further introduction should be of the highest priority. Limiting the evolutionary potential of the Bangladesh wheat blast outbreak population by preventing immigration of additional, sexually compatible strains will prove a successful strategy if it prevents the Asian *Pygt* population from undergoing the rapid diversification through recombination that happened in South America (164).

POPULATION BIOLOGY AND EPIDEMIOLOGY

A recent comprehensive study on the population biology of *Pygt* included more than 500 strains collected from across the wheat-growing regions of Brazil in 2012 and 2013. An important and novel aspect of this study was to include many *Pygt* strains taken from nonwheat grasses growing in or nearby the infected wheat fields. This nonwheat collection of strains provided important insights into the origins, genetic structure, epidemiology, and disease cycle of the wheat blast pathogen. Contemporary populations of *Pygt* carry high genotypic diversity for genetic markers and virulence diversity on a set of wheat differentials, including 198 multilocus microsatellite genotypes (MLMGs) and 25 virulence groups. These populations exhibited a genetic structure consistent with a mixed reproductive system in which cycles of sexual reproduction are followed by the dispersal of locally adapted clones (18). Similar genetic structures were detected in earlier populations of *Pygt* from central-southern Brazil (86). Morphological evidence supporting the hypothesis of sexual reproduction was the formation of protoperithecia and perithecia (sexual fruiting bodies) of *Pygt* on autoclaved wheat stems and on senescing stems of wheat and other grasses, suggesting that sexual reproduction occurs mainly during the saprotrophic phase of the disease cycle on crop residues or within senescent tissues of the alternative hosts (18, 97). *Phalaris canariensis* (canarygrass) supported the fullest development of perithecia, suggesting that it is a promising candidate for identifying the teleomorph in the field.

Given that fungal strains capable of infecting both wheat and other grasses can move back and forth between hosts, recombination may occur mainly on the other grasses, giving rise to the highly diverse *Pygt* population observed today. Support for this scenario can be found in previous reports of cross-infection and interfertility between isolates from wheat and other poaceous hosts (13, 48, 149) as well as in the lack of differentiation among wheat- and other Poaceae-adapted populations (18), the sharing of genotypes and virulence groups between the two host groups (18), and the finding of gametic equilibrium consistent with sexual recombination in most populations, including those from other grasses (18).

There is also evidence for extensive gene flow between populations of *Pygt* sampled from wheat and those sampled from other grasses, including signal grass (*U. brizantha*) and 12 other grass hosts (18). Because *U. brizantha* is a widely grown pasture grass occupying more than 90 million ha in Brazil (75) and often found next to wheat fields, it may function as a major reservoir of wheat blast inoculum and provide a temporal and spatial bridge that connects wheat fields across Brazil. These findings suggest that nonwheat hosts may play an important role in the epidemiology of wheat blast, further complicating control efforts.

Pygt populations separated by more than 2,000 km were very similar, consistent with a high degree of gene flow across large spatial scales and/or high levels of genetic diversity, which would reduce the impact of genetic drift and maintain similar allele frequencies over longer periods. The high gene flow could reflect efficient wind-dispersal of conidia and/or ascospores over short distances (153) as well as long-distance dispersal on infected seed of wheat and *Urochloa* (50, 55–57).

Among the more important findings reported in a study from Castroagudín and collaborators (18) is the discovery of a superrace called virulence group A that is capable of causing blast on the entire set of tested wheat cultivars (**Figure 4**; **Supplemental Material 5**). Virulence group

a

HVGs	N	(%)	Wheat										Barley	Total of resistant (R) reactions
			Anahuac 75	BR 18 Terena	BR 24	BRS 220	BRS 229	BRS 234	BRS Buriti	CNT 8	MGS 3 Brilhante	Renan 2NS	PFC 2010123	
A	138	79.8	S	S	S	S	S	S	S	S	S	S	S	0
B	25	14.5	S	S	S	S	S	S	S	S	S	R	S	1
C	2	1.2	S	S	S	S	S	S	S	S	S	S	R	1
D	2	1.2	S	S	S	S	S	S	S	S	S	R	R	2
T	1	0.6	S	R	R	R	R	R	R	R	R	R	S	9
AA	2	1.2	S	S	R	S	S	S	S	S	S	S	S	1
BB	1	0.6	S	S	R	S	S	S	R	S	S	R	S	3
CC	1	0.6	S	S	S	S	S	R	S	S	S	R	R	2
DD	1	0.6	S	R	S	R	R	R	R	S	R	R	S	7
Total	173	100.0												
Total of R reactions			0	2	3	2	2	3	3	1	2	6	3	–
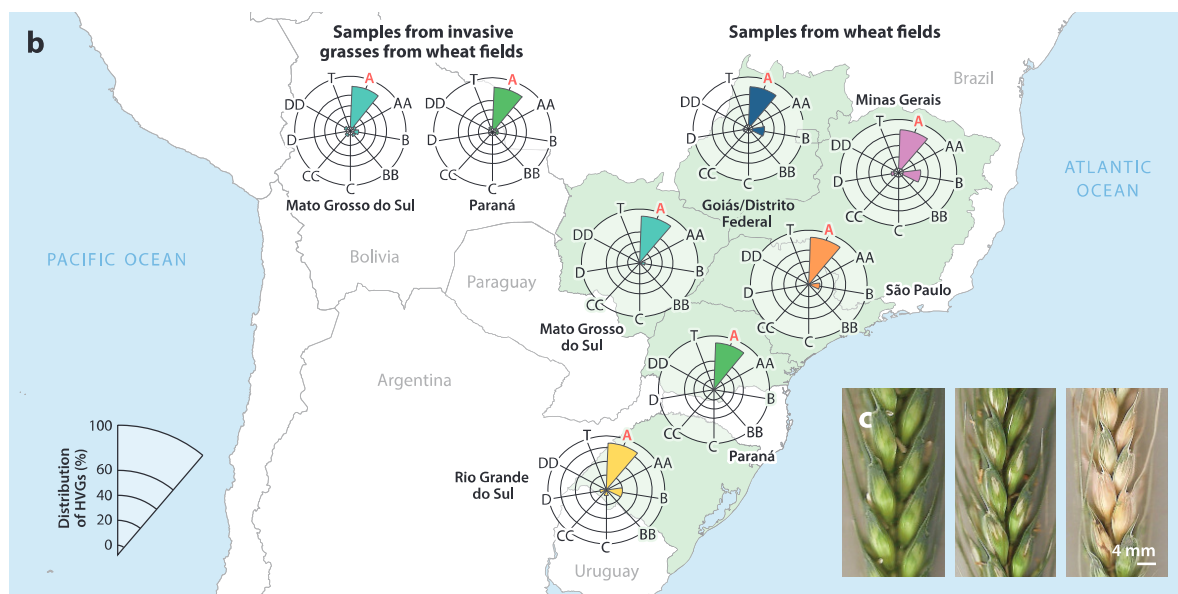
Figure 4

(*a*) Pathogenicity spectra of head virulence groups (HVGs) of isolates of *Pyricularia graminis-tritici*. (*b*) Distribution of HVGs of the wheat blast pathogen in central-southern Brazil, including the association with other grass species. "Superrace A" (*indicated in red*), the most frequent virulence group in the country, was capable of infecting all wheat differential cultivars tested, including "Renan," carrier of the *2NS* insertion element. (*c*) Variable levels of head blast on wheat. Abbreviations: BR, Trigo Brasil from Embrapa (Empresa Brasileira de Pesquisa Agropecuária); BRS, Brasil Sementes from Embrapa; CNT, Centro Nacional de Trigo from Embrapa; MGS, Minas Gerais Sementes from EPAMIG (Empresa de Pesquisa Agropecuária de Minas Gerais); PFC, Passo Fundo Cevada from Embrapa; R, resistant; S, susceptible.

A is not a clone (this virulence phenotype is found in many different genetic backgrounds), but it occurs at a high frequency on Brazilian wheat and was also found on several grass species invading wheat fields, including *A. sativa*, *U. brizantha*, *Caulerpa distichophylla*, *Echinochloa crus-galli*, *R. repens*, *Digitaria sanguinalis*, *Eleusine indica*, *Eragrostis plana*, *Cenchrus echinatus*, *Cynodon* spp., *D. insularis*, *P. maximum*, and *S. sudanense* (18). The most common virulence groups were shared between the

grass- and wheat-infecting *Pygt* populations, providing additional evidence for movement of *Pygt* between wheat fields and nearby grasses.

Knowledge of the infection process by *Pygt* on wheat leaves and spikes remains limited, but some very recent studies combining scanning electron, laser confocal, and bright field microscopy have greatly increased our understanding of this process (35, 36, 65). The leaf infection process was studied on plants from the wheat cultivar BRS-Guamirin inoculated 30 days after sowing (35). *Pygt* conidia landing on the adaxial leaf surface began to germinate six hours after inoculation (hai) (**Figure 5a**) from both the basal (**Figure 5a,b,d**) and apical cells (**Figure 5c**). From the germ tube, a dome-shaped appressorium initiated its differentiation at 12 hai (**Figure 5b**). From 12 to 24 hai, the wax on the leaf surface was removed at the appressorium attachment sites (**Figure 5c**). Conidia and appressoria became withered between 36 and 72 hai, in a process called autophagy (**Figure 5d**), which is thought to enable the release of nutrients to the infection peg and is a common phenomenon described for other fungi (80), including other *Pyricularia* species (157). The first leaf blast symptoms were observed at 48 hai. Abundant fungal hyphae and conidia production were observed on the leaf surface at 120 hai (**Figure 5e**).

Airborne *Pygt* conidia produced on and released from infected wheat seedlings are thought to provide an important source of inoculum for spikes infection (28). The infection process on spikes was studied by inoculating plants from wheat cultivar BR-18 halfway through anthesis (35). At 72 hai, abundant fungal hyphae reached the rachis from the nodes and spread upward and downward along the rachis, causing intense discoloration (**Supplemental Material 2**). Within the rachis, *Pygt* hyphae were able to massively colonize the epidermis, parenchyma, cortex, and vascular bundles (**Figure 5f–j**). At 120 hai, the extensive hyphal colonization of the rachis tissues extended to the cortical and pith parenchyma (**Figure 5f**) as well as the xylem vessels and phloem sieves (**Figure 5g**). At 168 hai, the *Pygt* hyphae colonized the xylem vessels, parenchyma tissues (**Figure 5h**), and epidermis (**Figure 5i**). Fungal hyphae grew both inter- and intracellularly in the rachis tissues and also breached the cell walls (**Figure 5j**), destroying the spike completely.

Another study, based on laser scanning confocal microscopy, revealed that early (12 hai) colonization of the spikelets occurred similarly on plants from both Milan (resistant) and Sumai 3 (susceptible) cultivars (65). Germinated conidia and hyphae of *Pygt* were found on the anther, stigma, filament, and palea of plants from both cultivars. However, the pathogen grew much faster in the rachilla of plants from the susceptible cultivar rather than the resistant cultivar, indicating that host resistance is probably expressed in the pedicel (65).

PHYSIOLOGICAL CHANGES ON WHEAT PLANTS DURING INFECTION BY *PYRICULARIA GRAMINIS-TRITICI*

Changes in the Primary Metabolism

Infection by *Pygt* affects the physiology of wheat plants by changing metabolic processes such as carbon assimilation, stomatal function, and the source:sink ratio (e.g., the ability of the leaves to produce photosynthates versus the capacity of the grains to accommodate the assimilates) (10). Knowledge of the biochemical and physiological changes caused by wheat blast came from experimental infections of leaves, flag leaves, and/or spikes (summarized in **Figure 6**).
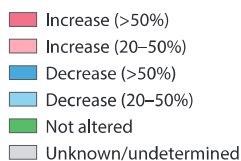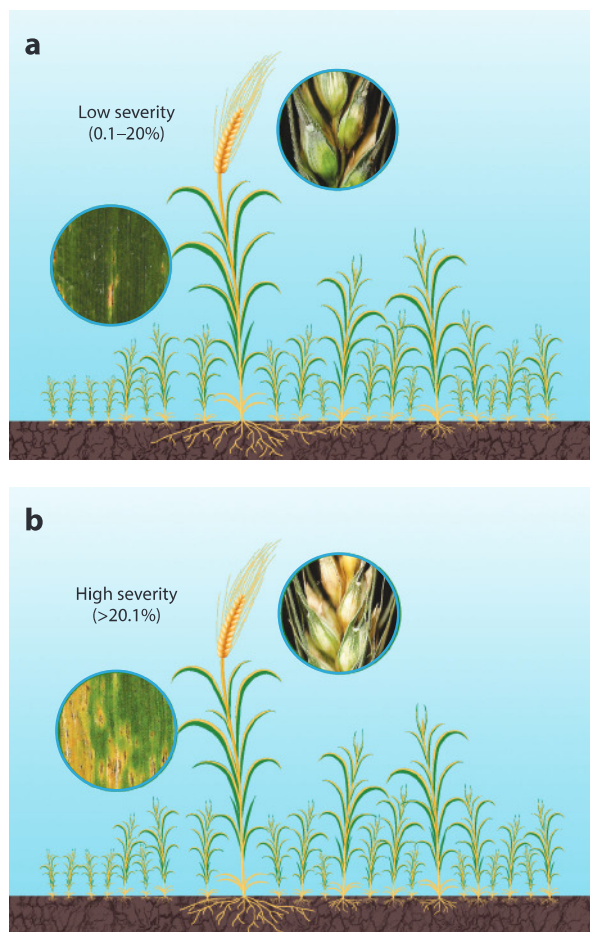
A decrease in ribulose-1,5-bisphosphate-carboxylase/oxygenase (RuBisCO) activity and on the RuBisCO activation state was detected on flag leaves of infected wheat plants (41). As leaf blast symptoms developed, CO_2 assimilation decreased (120). The reduction in CO_2 influx in the infected leaves caused stomatal closure (8, 41). A negative correlation was observed between net carbon assimilation (A) and CO_2 internal concentration (C_i) as well as between A and blast
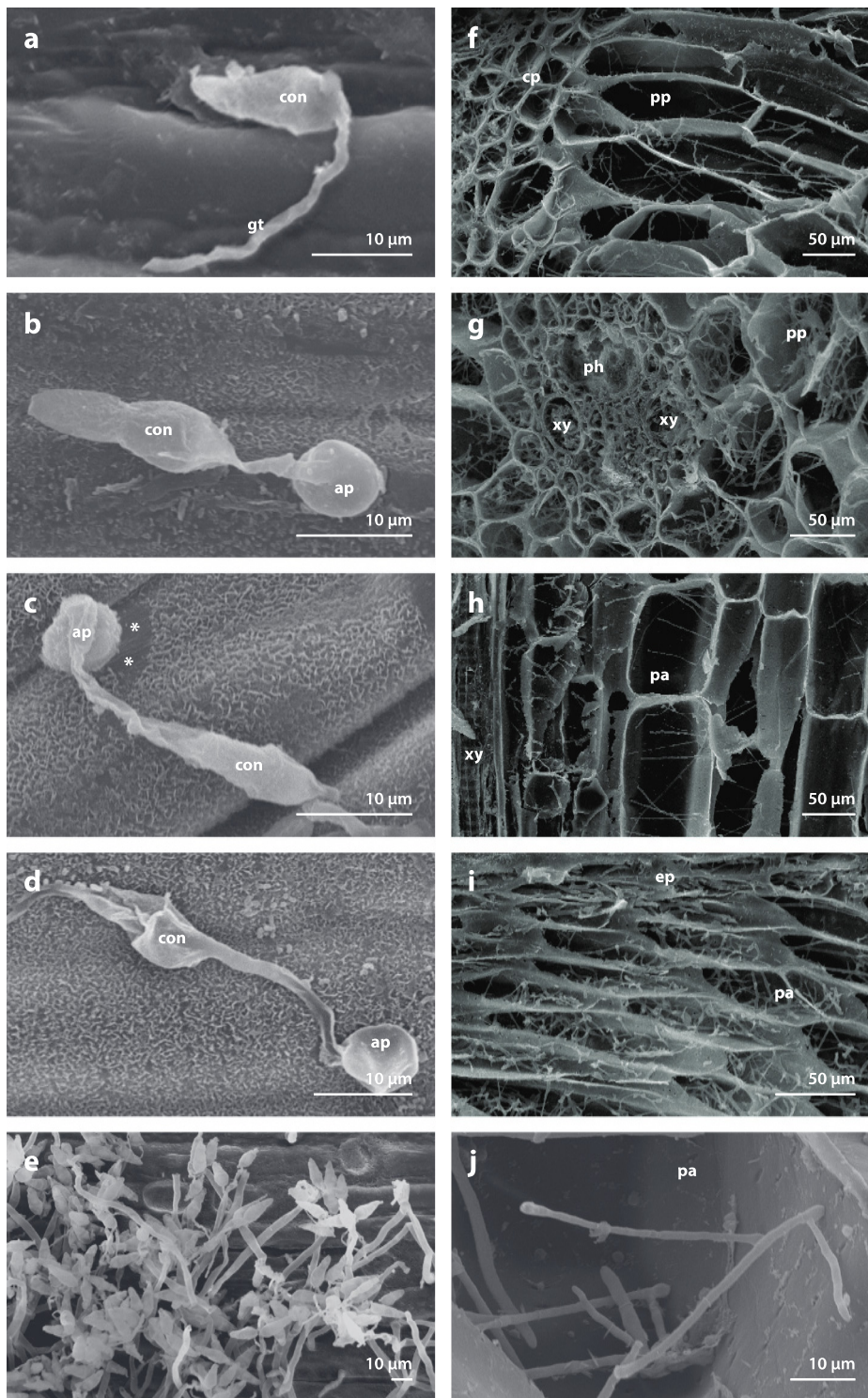
Figure 5

Scanning electron micrographs of the *Pyricularia graminis-tritici* (*Pygt*) infection process on wheat leaves (*a–e*) and the spike rachis (*f–j*). Adaxial leaf surfaces of wheat seedlings at (*a*) 6, (*b*) 12, (*c*) 24, (*d*) 72, and (*e*) 120 hours after inoculation with *Pygt*. Conidium germination (*a*) developing a germ tube and (*b*) forming an appressorium on the leaf surface; (*c*) leaf wax removal near appressoria sites (*asterisks*). (*d*) Withered conidium and appressorium. (*e*) Abundant colonization and conidia production at the leaf surface. (*f, g*) Transverse and (*h–j*) longitudinal sections of the wheat spike's rachis at (*f, g*) 120 and (*h–j*) 168 hours after inoculation with *Pygt* showing extensive intra- and intercellular hyphae colonization within tissues. Abbreviations: ap, appressorium; con, conidium; cp, cortical parenchyma; ep, epidermis; gt, germ tube; pa, parenchyma; ph, phloem vessels; pp, pith parenchyma; xy, xylem vessels.

severity (8, 41). Blast-infected leaves also exhibited a decrease in the light-saturated A (A_{max}) and the light saturating point, coupled with an increase in dark respiration (R_d), indicating plant photoinactivation (7). Indeed, leaf infection by *Pygt* damaged the photosynthetic machinery, as evidenced by a significant reduction in the maximum photosystem II (PSII) quantum efficiency (F_v/F_m), the capture efficiency of excitation energy by the open PSII reaction centers (F_v'/F_m'), the photochemical quenching coefficient (q_P), and the electron transport rate. There was also a decrease in the concentration of photosynthetic pigments due to intense leaf chlorosis (8, 123).

a Low severity (0.1–20%)

b High severity (>20.1%)

Legend:
- Increase (>50%)
- Increase (20–50%)
- Decrease (>50%)
- Decrease (20–50%)
- Not altered
- Unknown/undetermined

Physiological and biochemical events	Variables/parameters	Leaves			Spikes		
		ND	HS	LS	ND	HS	LS
Oxidative stress	H_2O_2						
	O_2^-						
	EL						
Lipid peroxidation	MDA						
Antioxidative system (enzymes)	APX						
	CAT						
	GPX						
	GST						
	GR						
	POX						
	SOD						
	PPO						
Defense enzymes and metabolites	GLU						
	CHI						
	PAL						
	Lignins						
	Phenolics						
Carbon metabolism	RuBisCO						
	SPS						
	SuSy						
	AGPase						
	Acid invertase						
	Alkaline invertase						
	FBPase						
	Sucrose						
	Starch						
	Fructose						
	Glucose						
	Malate						
	Fumarate						
Nitrogen metabolism	Protein						
	Amino acids						
Leaf gas exchange	A						
	g_s						
	C_i						
	E						
	LCP						
	LSP						
	A_{max}						
	R_d						
	V_{max}						
	J_{max}						
Photosynthetic pigments	Chlorophylls						
	Carotenoids						
Chlorophyll a fluorescence	F_v/F_m						
	F_v'/F_m', Φ_{PSII}, YII						
	NPQ; q_p; YNPQ						
	YNO						
	ETR						

(*Caption appears on following page*)

Figure 6 (*Figure appears on preceding page*)

Biochemical and physiological changes occurring on leaves and spikes of wheat plants noninfected with *Pyricularia graminis-tritici* and with low or high blast severity. Data shown were compiled from several articles (6, 7, 8, 10, 36, 41, 42, 92, 120, 123, 133, 162). Abbreviations: A, net CO_2 assimilation rate; AGPase, ADP-glucose pyrophosphorylase; A_{max}, maximal net carbon assimilation rate; APX, ascorbate peroxidase; CAT, catalase; CHI, chitinase; C_i, internal CO_2 concentration; E, transpiration rate; EL, electrolyte leakage; ETR, electron transport rate; FBPase, fructose bisphosphatase; F_v/F_m, variable-to-maximum chlorophyll a fluorescence ratio; GLU, β-1,3-glucanase; GPX, glutathione peroxidase; GR, glutathione reductase; g_s, stomatal conductance to water vapor; GST, glutathione-S-transferase; H_2O_2, hydrogen peroxide; HS, high severity; J_{max}, maximum rate of electron transport used on ribulose-1,5-bisphosphate regeneration; LCP, light compensation point; LS, low severity; LSP, light saturation point; MDA, malondialdehyde; ND, no disease; NPQ, quenching nonphotochemical; $O_2{}^-$, anion superoxide; PAL, phenylalanine ammonia-lyase; POX, peroxidase; PPO, polyphenoloxidase; q_P, quenching coefficient; R_d, respiration; SOD, superoxide dismutase; SPS, sucrose-phosphate synthase fructose bisphosphatase; SuSy, sucrose synthase; V_{max}, maximum rate of carboxylation; YII, photochemical yield; YNO, quantum yield of nonregulated energy dissipation; YNPQ, yield for dissipation by downregulation; Φ_{PSII}, photochemical yield of photosystem II.

Supplying wheat plants with silicon decreased the impact of wheat blast on A, stomatal conductance (g_s), and transpiration rate (E) (8). Silicon supply also improved the concentration of chlorophylls and some components of the xanthophyll cycle (e.g., α- and β-carotene, violaxanthin, antheraxanthin, zeaxanthin, and lutein) in infected plants, but no significant changes on photosynthesis were detected (7).

Reductions in carbohydrate (fructose, glucose, and sucrose) concentration and in sucrose phosphate synthase activity were observed on wheat flag leaves and grains infected by *Pygt*. The supply of triosephosphate was lower because of the reduced CO_2 fixation, and the breakdown of sucrose increased because of higher invertase activity (120). Surprisingly, starch concentration increased in the flag leaves, which was associated with the downregulation of genes encoding both α- and β-amylases in the flag leaves (120). In contrast, the starch quantities decreased in the infected grains, which was associated with lower sucrose transport from the photosynthetic organs coupled with lower ADP-glucose pyrophosphorylase (AGPase) expression and lower AGPase activity. Because the expression of α- and β-amylase genes was induced at the early stages of fungal infection, there was an increase in the breakdown of starch in the infected grains (120). Taken together, these changes in both production and partitioning of carbohydrates substantially diminished the synthesis of endosperm, resulting in smaller and shrunken grains, explaining at least in part the decrease in grain yields when wheat plants are infected by *Pygt*.

Supplying silicon to infected plants significantly increased the starch and sucrose concentrations and decreased the concentrations of fructose and glucose in the flag leaves and spikes. By lowering blast severity, silicon preserved the production of plant photoassimilates and reduced the hexose-to-sucrose/starch ratios (92).

Concurrent with changes in the carbon balance, a large reduction in the metabolism of organic acids and amino acids occurred on infected wheat plants at the reproductive stage (120). At the earliest stages of *Pygt* infection, the concentrations of amino acids derived from glycolytic intermediates (e.g., alanine, cysteine, phenylalanine, and valine) as well as arginine, cysteine, histidine, methionine, proline, and tryptophan were higher in the leaves of infected plants. This suggests that *Pygt*, during its postulated biotrophic phase, is capable of manipulating the wheat plants to obtain the necessary amino acids to favor its successful infection (6) (**Figure 6**).

Antioxidative Systems and Host Defense Mechanisms Are Pivotal for Wheat Basal Resistance to Blast

Leaf and spike resistance to wheat blast were associated with high concentrations of superoxide anion radical ($O_2{}^-$) and hydrogen peroxide (H_2O_2) and also with reduced lipid peroxidation,

especially on cultivars exhibiting partial resistance (42, 133). Compared to susceptible cultivars, wheat cultivars with high levels of basal resistance to blast usually showed higher activities of ascorbate peroxidases (APXs), catalases, glutathione-*S*-transferases (GSTs), glutathione reductases, peroxidases (POXs), and superoxide dismutases (SODs) (42). Hence, the antioxidative system plays a key role in wheat plants' defenses against *Pygt* infection (6). Spraying wheat leaves with picolinic acid, a nonhost-selective toxin produced by *Pygt*, decreased blast symptoms and stimulated a rapid response of the antioxidant metabolism because of higher APX, GST, POX, and SOD activities that are involved in removal of reactive oxygen species (6). On wheat flag leaves infected by *Pygt*, polyphenoloxidase activity remained high regardless of the basal level of blast resistance of the cultivar. In contrast, phenylalanine ammonia-lyase activity and concentrations of phenolics and lignin were higher in cultivars with the highest level of partial resistance (133). The activity of chitinase (CHI) and β-1,3-glucanase (GLU) increased in response to *Pygt* infection in leaves and spikes of the cultivars with high partial resistance (133). On wheat plants supplied with silicon, higher CHI and peroxidase activities, lignin concentration, and the expression levels of the defense-related genes *PR-1*, *CHI*, *PAL*, and *POX* were linked with resistance to blast (36, 92, 162) (**Figure 6**).

Foliar amendment with magnesium to attain a high leaf concentration of this macronutrient increased wheat susceptibility to blast, whereas amendment with calcium reduced blast severity because of a high expression of the defense-related genes *allene oxide cyclase 1* (*AOS*), *CHI*, *GLU*, *PAL*, *polyphenol oxidase* (*PPO*), *POX*, and *PR-1* (38, 40) (**Figure 6**).

Biochemical Changes on Wheat Spikes and Grains Caused by Blast

The colonization of the rachis vascular vessels by *Pygt* hyphae resulted in their disintegration, interrupted the translocation of nutrients to the grains, and caused the spikes' death (36). Soluble sugars (e.g., fructose, glucose, and sucrose) and starch were reduced up to 25% and 45%, respectively, on grains obtained from infected spikelets (120). Moreover, an increase in the relative expression of the genes encoding α- and β-amylases, AGPase, and sucrose synthase (*SuSy*) was detected on infected spikes (120). The decrease in sucrose concentration in the grains was associated with lower sucrose supply. Silicon improved the source-sink relationship on infected wheat flag leaves and spikes, reducing any changes in the production and partitioning of assimilates during grains filling (92).

STRATEGIES TO MANAGE WHEAT BLAST

Strengthening Quarantine and Biosafety Regulations in Disease-Free Countries

Since wheat blast has now escaped from South America and is causing epidemics in Southeast Asia, the first major global concern is to avoid additional spread of the pathogen to disease-free countries to prevent future outbreaks in new regions. Because the pathogen can be spread long distances on infected seeds (31, 51, 132, 148), improving and/or reinforcing quarantine and seed-trading laws provides the best path toward preventing further spread of wheat blast to blast-free regions and countries (95, 126, 134, 154). We believe that trade in wheat seeds (including germplasm exchange) from the wheat blast endemic areas in Latin America and Southeast Asia (Bangladesh) should be strictly regulated or totally prohibited. A globally coordinated awareness program should advise quarantine officers from around the world to pass and implement new quarantine regulations that consider the threat represented by the introduction of *Pygt* into their territories via trade in wheat seeds and grain. As important as regulating the international seed trade, local authorities should

reinforce strict laws prohibiting the diversion of wheat grain imported to meet the demands of the flour milling industry into the local wheat seed industry, which appears to have happened in Bangladesh (74, 126) (**Figure 1***a,b*; **Supplemental Material 3**).

Wheat Blast Management Strategies in Endemic Areas

Strategies for wheat blast management must be based on knowledge of *Pygt* biology and wheat blast epidemiology, including the pathogen's disease cycle, survival strategy, means of spread, host range, and reproductive mode(s) as well as the most conducive weather conditions for disease development. We believe that integrated disease management (IDM) strategies will be needed to minimize crop losses without impacting environmental sustainability (93). The adoption of IDM strategies should be coordinated locally, taking into account the particular circumstances of each country or region (93).

Cultural and sanitary practices. *Pygt* can survive and produce perithecia on crop residues between wheat-cropping seasons. Invasive grasses may also play an important role as bridges between wheat-cropping seasons and as sources of secondary inoculum (18, 151). If minimum tillage or no-tillage is not required for soil conservation in the region, deep plowing of crop stubble can be used, and thus contributes to a decrease in the amount of initial *Pygt* inoculum (23, 70). Decreasing the population of known grass hosts of *Pygt* within and surrounding wheat fields may not be easy to implement, but it would contribute to reducing the initial inoculum pressure for the subsequent season (93). Following the introduction of wheat blast in Bangladesh, officials in India recommended the destruction of crop residues (especially the debris of barley, oats, millets, and wheat) and eradication of invasive grasses such as *E. indica*, *Echinochloa* spp., *Brachiaria* spp., *Digitaria* spp., *Lolium* spp., *Cenchrus* spp., and *Chloris* spp. (62, 111, 126). Nevertheless, this control measure might not be cost-effective for small farmers or advisable for regions practicing soil conservation agriculture (23). Because of the wide host range of *Pygt* (18, 19, 149), crop rotation is a viable option for blast management only if nongrass crops, for example, soybean and common vetch (129), are available, which are commonly used for managing other wheat diseases. In Southeast Asia, jute (*Corchorus olitorius*) cultivation might be an option for crop rotation (62).

Adjusting the sowing date to avoid the occurrence of flowering or grain filling during blast-conducive periods of high temperature, rain, and high relative humidity has been one of the most effective cultural practices to manage wheat blast in Bolivia, Brazil, and Paraguay, significantly reducing disease incidence and increasing grain yield and weight (24, 93, 94).

Improved detection methods of seedborne inoculum for certified healthy seeds. The wheat blast pathogen is seedborne and seed transmitted (51, 89). Seeds are considered the primary sources for long-distance dispersal of *Pygt* (31, 51, 132, 147, 148). *Pygt* conidia can survive and remain infectious for almost two years on or inside seeds, and even healthy-looking seeds from infested fields might carry fungal spores (117). Therefore, the use of seeds that are certified to be pathogen-free or of fungicide-treated wheat seeds should be mandatory either for exports or for internal seed market trading within countries where the seedborne wheat blast pathogen is endemic (141). In Brazil, wheat seed treatments were compulsory by law (93). However, since the 1970s, the legislation has been relaxed, so the importance of adequate seed health testing has been neglected (93). As a consequence of the relaxation in regulations affecting wheat seed health, the wheat blast pathogen has been efficiently dispersed on seed throughout Brazil and has reached Bolivia and Paraguay via frequent imports of Brazilian wheat seed used for sowing (**Figure 1***a,b*; **Supplemental Material 3**).

Accurate methods for detection of seedborne inoculum are extremely important for limiting the spread of *Pygt* into new areas where it has not been previously reported. Clean seed will also reduce the amount of initial inoculum in endemic areas (1, 95). Ideal detection methods would combine specific molecular markers (110) as targets and use template DNA extracted directly from potentially infested seed lots. The ability to specifically detect *Pygt* at very low levels of seed infection, for example, by using loop-mediated isothermal amplification (20), would increase the likelihood of successful detection at very low concentrations [$\leq 6 \times 10^{-6}$ ng/μL] of genomic DNA without the need to purchase expensive instruments for detection.

Seed treatment. *Pygt* sporulation on infected seeds was reduced by 52–100% after treatment with benomyl compared to nontreated seeds (11). A significant reduction in wheat blast incidence under field conditions was observed in Bolivia after treating seeds with a mixture of benomyl and carbendazim (155). However, because these benzimidazoles are high-risk fungicides for developing resistance (73, 83), their efficacy might diminish if they have already been extensively deployed to manage other wheat diseases. The only seed treatment labeled for managing *Pygt* in Brazil is the triazole difenoconazole. The eradicant dimethyldithiocarbamate thiram, labeled for other seedborne pathogens, was found effective against *Pygt* (11, 52).

Disease forecasting and risk monitoring of infection periods based on weather conditions. Systematic monitoring of weather-based parameters across distinct wheat-growing regions to forecast *Pygt* infection periods provides a valuable tool to predict the occurrence and magnitude of wheat blast epidemics (101). Optimum weather conditions for the development of wheat blast include the simultaneous occurrence of high temperatures (25–30°C) and long and frequent leaf wetness periods (24–40 h) (16). Brazilian scientists developed a predictive model for wheat blast outbreaks based on daily climatic data called Sisalert (Plant Disease Epidemic Risk Prediction System) that simulates the risks of disease epidemics (**http://dev.sisalert.com. br/monitoramento/?page_id=14**) (47, 101). An American-adapted climate model based on the Brazilian predictive model indicated that the weather parameters were favorable to wheat blast in 25% of the US winter wheat-cropping regions, including suitable conditions for outbreaks 70% of the year in Louisiana, Mississippi, and Florida (29). Similar wheat blast predictive models should be developed for other countries confronted with wheat blast, including Bolivia and Paraguay in South America and Bangladesh in Southeast Asia. Automated collection of weather data coupled with constantly updated infection models, such as Sisalert, could provide a warning of the imminent risk of wheat blast infection periods (160, 161), enabling real-time decision making for fungicide applications to be most effective in reducing yield losses while reducing the environmental impact.

Effectiveness of fungicide sprays on leaves and ears. Fungicides are regularly used to manage wheat blast and other ear-associated diseases in Brazil. However, the field efficacy of fungicides is considered low, resulting in only small decreases in blast severity on symptomatic spikes (85, 104). Disease control and reduced crop losses were detected only when mixtures of triazole and quinone outside inhibitor (QoI) fungicides were applied early on moderately resistant wheat cultivars under low or moderate disease pressure (104, 121, 122, 124). In such cases, the effectiveness of applications at early heading and early grain-filling stages seemed to be associated with a reduction in *Pygt* inoculum produced on the lower leaves, leading to a reduction in ear infections (28).

Recent recommendations to manage the disease in Asia included spraying of triazoles combined with strobilurins (e.g., tebuconazole and trifloxystrobin) (62). In Brazil, these fungicides provided only partial control under high disease pressure (85, 86), reducing disease incidence by only 50%

in comparison to nontreated plots (85). The limited efficacy of fungicide treatments in Brazil is likely due to many factors, including the difficulty of reaching the infection sites on spikelets (105), the high diversity of *Pygt* strains (152), highly favorable weather conditions coupled with high levels of varietal susceptibility (33), and the intrinsic inefficacy of some active ingredients (59, 85, 104, 150). Another facet of wheat blast that compromises the efficacy of chemical management is that *Pygt* has a broad host range, including several invasive grass species, growing in or near wheat fields, on which fungicides are not sprayed (17, 118) and thus provide a continuous external source of new inoculum (18). These factors should be considered when applying fungicides to control wheat blast in Asia.

A total of 28 fungicides have been labeled for wheat blast in Brazil, including 11 triazoles and 7 mixtures of triazoles and QoIs (96). These two fungicide groups have been used intensively for management of rusts and other wheat foliar diseases for one to three decades (39, 100, 119, 142). Although these fungicides were used intensively over many years to manage wheat diseases, it was never suggested that the low efficacy of fungicides against wheat blast may result from fungicide resistance.

In fact, resistance to both triazole (tebuconazole and epoxiconazole) and QoI fungicides (azoxystrobin and pyraclostrobin) was found to be pervasive in *Pygt* populations across the major wheat-growing areas of central and southern Brazil (43, 17, 112) (**Figure 7**). All six Brazilian populations of *Pygt* tested exhibited high resistance to azoxystrobin, pyraclostrobin, and both tebuconazole and epoxiconazole, with half maximal effective concentration (EC_{50}) values that were at least 30 to 200 times higher than the wild-type isolates (**Figure 7**). These findings suggest that these strobilurin and triazole fungicides are not likely to provide long-term control of wheat blast in Asia.

Five new fungicide formulations labeled for managing wheat diseases in Brazil combine the second-generation carboxamide fluxapyroxad [a succinate dehydrogenase inhibitor (SDHI)] with the QoI pyraclostrobin and the demethylation inhibitor epoxiconazole (96), two of the molecules for which the *Pygt* populations have already been found to be resistant (112). Since none of these formulations were labeled for wheat blast, their effectiveness against *Pygt* has yet to be determined. The second-generation SDHIs are also high-risk fungicides (73), and resistance could arise from single point mutations in any of the four genes in the *Pygt* genome encoding the targeted components of the SDH complex (SDH-A, B, C, and D) (3). To decrease the risk of selecting for resistance to SDHI fungicides in populations of *Pygt*, only mixtures or coformulations with low-risk fungicides (such as the dithiocarbamate mancozeb and the isophthalonitrile chlorothalonil) should be deployed to manage wheat blast (156).

Biofortification and biocontrol alternatives for managing wheat blast. Many nonfungicidal chemicals and biological products have been assessed for their ability to control wheat blast. Potassium phosphate reduced blast severity on three wheat cultivars and potassium silicate inhibited fungal growth in vitro (33). Application of silicon to wheat leaves limited *Pygt* colonization through the potentiation of the flavonoid biosynthetic pathway and the deposition of phenolic compounds. Silicon applications also increased the expression of defense-related genes (32, 33, 36, 37). In a field experiment, treatments with silicon increased yields by 26–92%, while treatments with phosphite increased yields by 9–80%. For comparison, treatments with synthetic fungicides (mixtures of epoxiconazole + pyraclostrobin, or tebuconazole + trifloxystrobin) increased yields by 90–121% (104).

Biological control agents that have been shown to work on rice blast should be tested for their efficacy against wheat blast. For example, *Bacillus methylotrophicus*, *Trichoderma harzianum*, and *Chaetomium globosum* may have potential for biological control of blast on wheat considering their ability to reduce blast symptoms on rice (43, 106, 135).
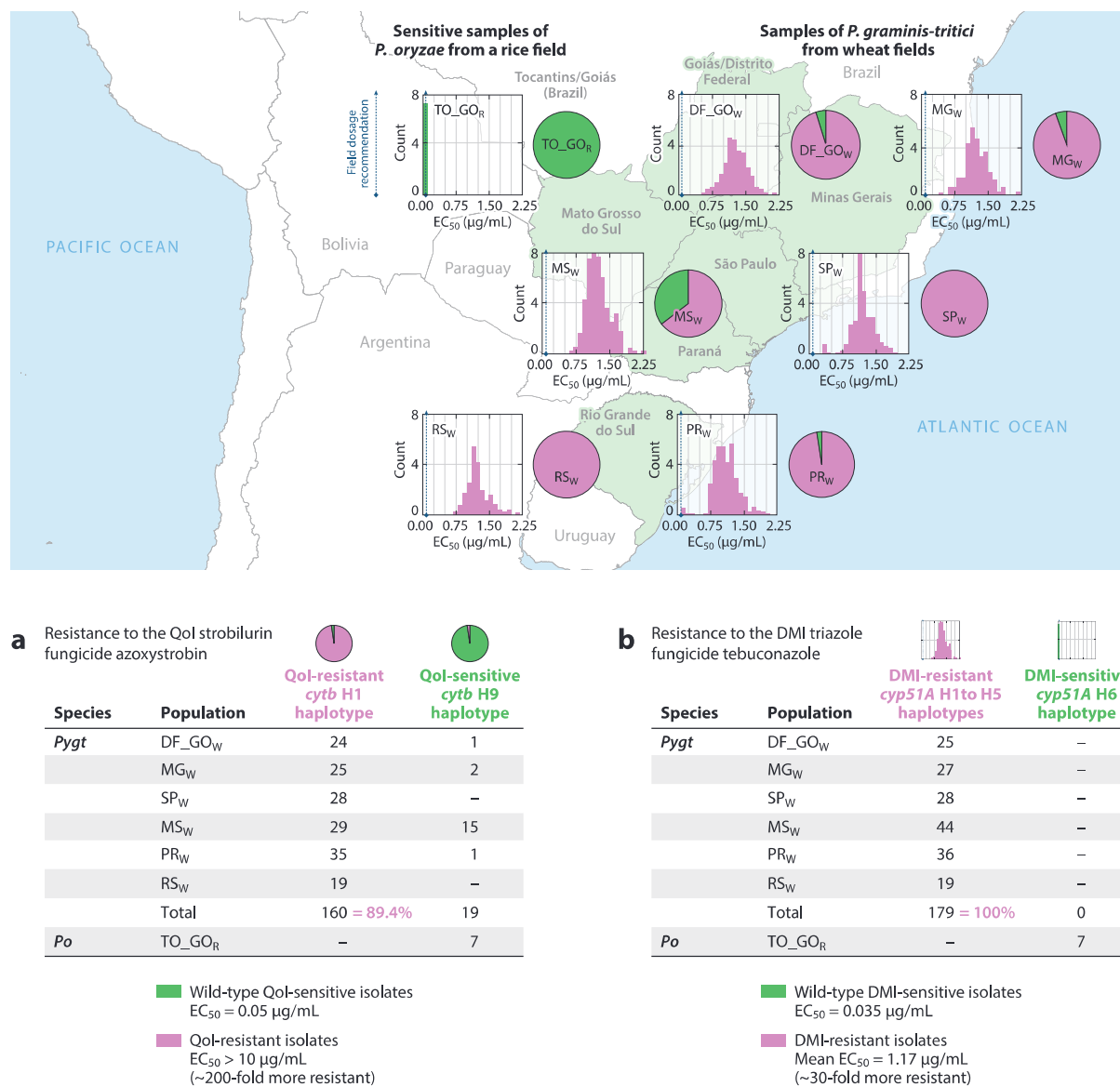
Figure 7

Resistance to quinone outside inhibitor (QoI) and demethylation inhibitor (DMI) fungicides is widespread in Brazilian populations of the wheat blast pathogen from 2012–2013. Data in panel *a* from Reference 17; data in panel *b* from Reference 112. Abbreviations: *cytb*, cytochrome b; *cyp51A*, lanosterol 14α-demethylase cytochrome P450 A; EC_{50}, half maximal effective concentration; *P. graminis-tritici*, *Pyricularia graminis-tritici*; *P. oryzae*, *Pyricularia oryzae*; *Po*, *P. oryzae*; *Pygt*, *P. graminis-tritici*; R, population from a rice field (TO_GO$_R$, Tocantins and Goiás); W, populations from wheat fields (including DF_GO$_W$, Distrito Federal and Goiás; MG$_W$, Minas Gerais; MS$_W$, Mato Grosso do Sul; PR$_W$, Paraná; SP$_W$, São Paulo; RS$_W$, Rio Grande do Sul).

***Pyricularia graminis-tritici* virulence groups, superrace A, and breeding for resistance to wheat blast.** Efforts to breed wheat cultivars with improved blast resistance have been constant in Brazil over the past 30 years but not very successful (34, 87, 115, 152). Resistance has not been stable as resistant cultivars proved to be susceptible when deployed across different geographical regions (152). At first, this was attributed to a combination of partial resistance and a cultivar-by-environment interaction reflecting the fact that wheat blast is distributed across broadly different Brazilian agroecosystems spanning a 2,800-km transect (19, 44, 86). However, it is now considered more plausible that the instability of resistance reflects a breakdown of resistance genes that may underlie a gene-for-gene interaction, with new races rendering the deployed resistance ineffective.

Recent extensive phenotyping of 173 *Pygt* strains encompassing 80 unique MLMGs (18) differentiated 25 seedling virulence groups (SVG) that were named SVG A to Y (**Supplemental Material 5**). SVG L was the predominant group, comprising 47% of the tested isolates. SVG A was the second most frequent group, found in 13% of tested isolates. Many of the wheat cultivars used as differentials lost their resistance to wheat blast during the adult stage, in agreement with earlier findings (151). The same pathogen isolates fell into nine different head virulence groups (HVGs) when virulence spectra were assessed on detached, mature wheat heads (**Figure 4**). HVG A was the predominant virulence group in Brazil, found in 138 isolates, followed by HVG B, found in 25 isolates. Both of these virulence groups were found in all *Pygt* geographical populations, including the grass-infecting populations from Mato Grosso do Sul and Paraná. The geographical distribution of *Pygt* virulence groups varied across regions. HVG A was capable of causing blast on the entire set of tested cultivars, forming a superrace that occurs at a relatively high frequency on Brazilian wheat. HVG A is also found on many invasive grass species, including *A. sativa*, *U. brizantha*, *C. distichophylla*, *E. crus-galli*, *R. repens*, *D. sanguinalis*, *E. indica*, *E. plana*, *C. echinatus*, *Cynodon* spp., *D. insularis*, *P. maximum*, and *S. sudanense*.

The identification of new sources of resistance to wheat blast is crucial. Among the few sources of resistance to wheat blast that have been identified in Brazil so far, the Brazilian wheat cultivars BR 18-Terena and BRS 229 have been frequently used in wheat-breeding programs due to their higher levels of resistance to head blast under field conditions (12, 54, 58, 137). However, these cultivars are now susceptible in some environments, probably due to the emergence of new *Pygt* races in these areas (145, 146).

In 1994, nine years after the first wheat blast epidemic in Brazil, a potential source of resistance genes was identified in *Aegilops tauschii* (syn. *Aegilops squarrosa*) (150), one of the ancestral grasses that contributed to the hexaploid genome of modern wheat (76, 109). Bread wheat cultivar Renan (66) and barley lineage CGN02857 (an East African barley accession obtained from the Centre for Genetic Resources germplasm collection at Wageningen University and Research Centre) were both derived from crosses with *A. tauschii* and considered promising sources of resistance to wheat blast. The association between the presence of the 2NS chromosomal translocation segment from *Aegilops ventricosa* in wheat and corresponding resistance to wheat blast was recently demonstrated (30). Near-isogenic lines of both spring and winter wheat carrying the 2NS/AS segment from *A. ventricosa* showed 64–81% less head blast in the field under natural epidemics in Bolivia compared to accessions lacking the segment. High levels of blast resistance under field conditions were detected in cultivars derived from the International Maize and Wheat Improvement Center (CIMMYT) line Milan, which possesses the 2NS translocation (30). Milan-derived cultivars such as Canindé I, CD 116, and Sausal ClAT have been released and widely deployed in South America, but the stability and durability of the resistance are unknown (81). However, Castroagudín et al. (17) provided evidence that the 2NS resistance (in cultivar Renan) may be overcome by three of the nine virulence groups of the wheat blast pathogen identified in Brazil, including the predominant

Supplemental Material >

HVG A superrace (**Figure 4**). Therefore, additional sources of resistance should also be identified and developed.

Four resistance genes (*Rmg2*, *Rmg3*, *Rmg7*, *Rmg8*) that function against the Br48 strain of *Pygt* (collected in 1991, not long after the first report of wheat blast in Brazil) have been identified in common wheat (*T. aestivum*) and in emmer wheat (*Triticum dicoccum*), a tetraploid species (4, 138, 165). The sources of these resistance genes included *T. aestivum* cv. Thatcher [carrier of *Rmg2* and *Rmg3* (165)]; *T. dicoccum* KU112 (St17), KU120 (St24), and KU122 (St25) [carriers of *Rmg7* (138)]; and *T. aestivum* 'S615' [carrier of *Rmg8* (4)]. It is not yet known whether the resistance genes identified by Tosa and collaborators (4, 138, 165) will be effective against contemporary populations of the wheat blast pathogen. In the 2017 screening of Embrapa's wheat genotypes for blast resistance in a disease hot spot in Uberaba, Minas Gerais (MG), the cultivar Lagoa Vermelha performed well during this epidemic year, showing high resistance to blast under high disease pressure (J.L.N. Maciel, personal communication). This cultivar has one of Thatcher's relatives (NewThatch) in its genealogy. However, because the *Rmg2* and *Rmg3* genes giving blast resistance in cultivar Thatcher are temperature sensitive (not useful at high temperatures) and do not work in ear infections (165), they were probably not associated with the levels of resistance found in Lagoa Vermelha. Instead, it is plausible that other wheat blast resistance genes may be present in the cultivar Lagoa Vermelha. In fact, in Patos de Minas, MG, the cultivar Thatcher showed high susceptibility to blast under Brazilian tropical conditions.

Based on the findings of diverse virulence spectra and race specificity in the wheat blast pathogen, we believe that the screening of wheat germplasm for blast resistance should be conducted under controlled conditions using a representative selection of the known pathogen virulence groups, including all of the contemporary virulence diversity now known to exist in populations of the wheat blast pathogen across Brazil. Field testing for blast resistance should be conducted at several locations across distinct agroecosystems, including Mato Grosso do Sul State, which is a hot spot for *Pygt* virulence diversity, with the highest number of SVGs (11) and HVGs (6) detected there. For countries where wheat blast has never been reported, a safer strategy than conducting trials in their own country would be to screen germplasm for blast resistance in Brazil, where the pathogen is endemic, virulent, genetically diverse, and distributed across a temperature cline from the warmer cerrado to the colder regions of Rio Grande do Sul. Three current examples of this strategy include (*a*) spring wheat cultivars with and without the 2NS translocation have been tested near Quirusillas in Bolivia (30); (*b*) Swiss wheat landraces introduced by Embrapa Cenargen, at the request of Swiss breeders, tested locally in Brazil against the most common seedling and head virulence groups characterized there (E. Alves, personal communication); and (*c*) a work plan between the Indian Council of Agricultural Research and CIMMYT to evaluate the reaction of 40 wheat varieties and advanced lines to wheat blast at hot spots in Brazil, Bolivia, Paraguay, and Argentina (62).

SUMMARY POINTS

1. A series of shipments of mixtures of wheat and rye grain harvested from wheat blast epidemic areas in Brazil preceded the recent emergence of *Pygt* in Bangladesh in 2016. Strengthening quarantine and biosafety regulations to prevent further spread in Asia or introduction of wheat blast into other wheat-growing regions of the world, including Europe, Australia, and North America, should be of the highest priority.

2. *Pygt* is a genetically distinct, highly diverse species with a broad host range, falsifying the hypothesis of host-specific populations for the *P. oryzae* species complex. The recognition of *Pygt* as a genetically distinct species has important implications for quarantine regulators worldwide. A lack of awareness that the wheat blast pathogen *Pygt* is a different species than the rice blast pathogen *P. oryzae* may explain the quarantine breach that led to the introduction of *Pygt* into Bangladesh.

3. Contemporary populations of *Pygt* carry high genotypic and phenotypic (virulence) diversity, consistent with a mixed reproductive system and the potential for long-distance gene flow. These properties indicate that *Pygt* is a pathogen with a high evolutionary potential that should be managed carefully.

4. Wheat leaf infection by *Pygt* triggers a series of photochemical malfunctions that affect the ability of leaves to intercept light. Biochemical changes in wheat grains resulted in 25–45% reductions in soluble sugars (e.g., fructose, glucose, and sucrose) and starch content. The plant antioxidation systems play a key role in wheat defense against *Pygt* infection.

5. The two most common disease management strategies (i.e., deployment of resistant cultivars and fungicides) are prone to failure if deployed individually. Major gene resistance is likely to be broken rapidly due to the emergence of virulent races from the extremely variable *Pygt* population; no sources of durable resistance to *Pygt* have been identified to date, and fungicides have been shown to be only partially effective, mainly due to widespread resistance to QoIs and azoles.

6. A superrace called virulence group A occurs at a high frequency on Brazilian wheat and also on several grass species invading wheat fields. This superrace causes blast on the entire set of tested wheat cultivars, including the resistant cultivar Renan that carries the 2NS insertion.

7. Field testing for blast resistance in candidate germplasm should be conducted at several locations representing distinct agroecosystems in Brazil, including Mato Grosso do Sul State, which is a hot spot for *Pygt* virulence diversity.

FUTURE ISSUES

1. The development of wheat blast forecasting systems is warranted as an essential component for IDM. "We must explain the underlying causes of the sporadic nature of disease outbreaks [making it difficult to forecast]. Once the disease occurs, it is most often already associated with severe ear infections. The initial inoculum for ear infections is certainly coming from other grass hosts" (A. Urashima, personal communication). "We need to make better use of spore collectors for monitoring the fluctuation of [*Pyricularia*] spores in the air. Generally, the ear infection is more severe if the growth stage with first visible awns coincides with peaks of fungal spore release and favorable weather (high humidity)" (S. Igarashi, personal communication). "We should use the occurrence of rain (and leaf wetness periods) as an indicator for the proper timing for fungicide sprays (blast does not occur if there is no rain)" (E. Melo Reis, personal communication).

2. Following the introduction of *Pygt* into Southeast Asia, where is wheat blast likely to cause significant damage in the future, based on climate suitability models? Will *Pygt* be able to adapt to regions with colder temperatures? A detailed global wheat blast risk analysis map based on climatic suitability for the establishment of *Pygt* should be developed and publicized.

3. "Accelerating [international] breeding efforts to obtain wheat varieties with higher levels of resistance and more durable resistance is warranted" (A.C.P. Goulart, personal communication). "Will the 2NS [insertion] be effective against all virulence diversity?" (A. Urashima, personal communication). How should we choose germplasm for a completely new pathogen with which the host has had no coevolutionary history? Key to success will be choosing appropriate germplasm for screening (including wheat and its wild relatives), choosing appropriate *Pygt* strains, and using appropriate locations for screening wheat germplasm.

4. How can we improve the effectiveness of chemicals (fungicides) in controlling the disease? "We need to identify new, and more effective, fungicide molecules that control *Pygt* on wheat. Then we need to determine, based on a dose response curve, the most effective fungicide dose" (Dr. E. M. Reis, personal communication). How can we improve the strategies for fungicide applications? We need to test the "use of spray tips (3D technology) to ensure full coverage of the spikes (a cylindrical and upright target)" (Dr. E. M. Reis, personal communication).

5. What is the ancestral *Pygt* genotype that first infected wheat? Reconstructing the evolutionary history of *Pygt* using large genome-scale data sets will help address this question. This will require new *Pygt* collections that come from both wheat and other hosts that may be important disease reservoirs or places where the pathogen recombines. Larger collections would also enable more precise calculations of the frequencies and distribution of fungicide resistance mutations.

6. What is the genetic basis (if there is one) for the different host associations found among *Pygt* isolates? Association mapping coupled with functional analyses will be the key approaches to resolve this question.

7. Genomic monitoring is warranted to track the evolution of *Pygt* in Brazil and Bangladesh. The first steps were taken in 2017 with a high-throughput genotyping assay developed by the Open Wheat Blast community (**http://s620715531.websitehome.co.uk/owb/**).

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