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Disease Control and Integrated Management

e-Xtra*

A Probabilistic Bio-Economic Assessment of the Global Consequences of Wheat Leaf Rust

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ABSTRACT

This study provides a bio-economic assessment of the global climate suitability and probabilistic crop-loss estimates attributable to wheat leaf rust. We draw on a purpose-built, spatially explicit, ecoclimatic suitability model for wheat leaf rust to estimate that 94.4% of global wheat production is vulnerable to the disease. To reflect the spatiotemporal variation in leaf rust losses, we used a probabilistic approach to estimate a representative rust loss distribution based on long-term, state-level annual U.S. loss estimates. Applying variants of this representative loss distribution to selected wheat production areas in 15 epidemiological zones throughout the world, we project global annual *average* losses of 8.6 million metric tons of grain for the period 2000 to 2050 based on a conservative, baseline scenario, and 18.3 million metric tons based on a high-loss scenario; equivalent to economic losses ranging from \$1.5 to \$3.3 billion per year (2016 U.S. prices). Even the more conservative baseline estimate implies that a sustained, worldwide investment of \$50.5 million per year in leaf rust research is economically justified.

Keywords: climate suitability, disease control and pest management, *Puccinia triticina*, R&D investment, wheat leaf rust, yield loss

Wheat is a major staple food source, supplying about one-fifth of the calories consumed globally and occupying more of the world's cropland than any other crop (FAO 2019a). Cropping agriculture is inherently risky. Farmers must deal with the vagaries of weather, pests, diseases, and markets in securing global food supplies, and wheat producers are no exception. Among the significant risks affecting wheat farmers worldwide are the crop losses caused by the cereal rusts (i.e., stem, stripe, and leaf rust). Probabilistic estimates of the mean annual global losses attributable to stem rust (caused by *Puccinia graminis* f. sp. *tritici*) and stripe rust (*P. striiformis* f. sp. *tritici*) on wheat were valued at \$1.12 billion and \$979 million (2010 prices), respectively (Beddow et al. 2015; Pardey et al. 2013). Wheat leaf rust (caused by *P. triticina*) is well-adapted to wheat growing climates and is more widely distributed than either stem or stripe rust (Chester 1946, p. 13; Huerta-Espino et al. 2011; Kolmer et al. 2009, p. 90; Roelfs et al. 1992, p. 2). Although wheat leaf rust does not generally cause extremely severe damage, early onset of infection from this pathogen can still result in yield losses that exceed 50% of disease-free yields in certain locations and years (Huerta-Espino et al. 2011).

Leaf rust occurs regularly throughout the United States, Canada, and Mexico, causing notable losses in wheat output (Huerta-Espino et al. 2011; Roelfs 1989; Singh et al. 2002). In the United States, severe leaf rust epidemics resulted in 25 to 30% yield loss in hard red winter wheat in Oklahoma in 1938 (Chester 1939) and 50% losses in Georgia in 1972 (Roelfs 1978). In the eastern prairies of Canada, yield losses ranging from 5 to 15% are common on susceptible wheat cultivars (Samborski 1985). In Mexico, leaf rust is one of the most important wheat diseases, resulting in severe epidemics on durum wheat during the 1976 to 1977 (Dubin and Torres 1981) and 2001 to 2009 crop seasons (Huerta-Espino et al. 2011; Singh et al. 2004a). In South America, wheat leaf rust has resulted in major yield losses in Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay (Germán et al. 2004). In East and South Asia, wheat grown throughout China, India, Pakistan, Bangladesh, and Nepal during the early 2000s was deemed especially vulnerable, while the wheat growing areas of Central Asia were also particularly hospitable to the pathogen (Singh et al. 2004b). For example, leaf rust occurs on more than half of the wheat growing area in China, with losses in the range of 10 to 30% being common in commercial wheat fields (Huerta-Espino et al. 2011). In India and Pakistan, severe losses occurred during the 1971 to 1973 seasons (Joshi et al. 1975; Saari and Prescott 1985; Saari and Wilcoxson 1974). A nationwide 10% yield loss was reported in Pakistan during the 1978 leaf rust epidemic (Hussain et al. 1980) and an estimated loss of 1 million metric tons was reported in India during the 1980 leaf rust epidemics (Joshi et al. 1986). In Russia, leaf rust occurs every year and has resulted in yield losses up to 30 to 40% (Mikhailova 2018). In Eastern Europe, leaf rust was (and likely still) is a persistent problem causing 3 to 5% yield losses on average (Samborski 1985). In North Africa, leaf rust has caused severe yield losses in Morocco, Egypt, and Tunisia (Huerta-Espino et al. 2011). In Ethiopia, severe leaf rust disease is also common (Hailu and Woldeab 2015; Samborski 1985) while in South Africa, leaf rust epidemics have frequently occurred on spring wheat grown in the Western Cape, winter wheat in the Orange Free State and irrigated wheat in other provinces (Pretorius et al. 1987). In Australia, leaf rust is also widely dispersed, occurring in all wheat growing regions (Murray and Brennan 2009a, b).

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Although leaf rust occurs to some extent wherever wheat is grown, a long held view is that leaf rust was a less significant (economic) problem than stem rust because the pathogen typically does not cause catastrophic crop losses in infected fields (see, for example, studies by Carleton 1896, p. 497; Carleton 1899, pp. 40-42; Farrer 1898, pp. 163-164). Nevertheless, around the middle of the 20th century, Chester (1946) published a qualitative assessment of the global impact of leaf rust based on expert estimates, and concluded that "…leaf rust leads the list of rusts in its toll of wheat (p. 16)." The high frequency of occurrence and the wide geographic distribution of the disease led later authors (Huerta-Espino et al. 2011; Samborski 1985) to also conclude that leaf rust is responsible for more crop damage worldwide than either of the other wheat rusts.

To control leaf rust, farmers can use pathogen resistant cultivars or improve disease management practices, including the application of fungicides. Although data on fungicide use for wheat production is limited, the general pattern is that the overall use of pesticides are increasing rapidly worldwide (FAO 2019b). Among the major pesticides (i.e., herbicides, insecticides, and fungicides), fungicides are the least widely used, with developing countries typically applying less than industrialized countries (Heisey and Norton 2007). In the United States, fungicides are commonly used to control foliar fungal diseases (including the rusts) on wheat, although the economic returns vary greatly depending on disease pressure, wheat varieties, input costs, and grain prices (Puppala et al. 1998; Sylvester et al. 2018; Wegulo et al. 2011; Weisz et al. 2011).

As an alternative to fungicide use, host-plant resistance has long been an integral part of breeding strategies in the development of new crop varieties. Using resistant cultivars is often the most economical method, particularly considering the cost of chemical treatment relative to the value of losses typically avoided at the farm level (Obert et al. 2005). Many of the rust resistance genes are race-specific, with only a small group of "slow rusting genes" providing more durable and nonspecific resistance (Herrera-Foessel et al. 2012; Kolmer et al. 2008; Martinez et al. 2001; Singh and Huerta-Espino 2003; Singh et al. 1998). Wheat breeders typically pyramid multiple leaf rust resistance genes to extend the effective period and slow the breakdown of resistance (Boskovic et al. 2001; Chhuneja et al. 2011; Cox et al. 1994). As Nobel Laureate Norman Borlaug famously noted, "rust never sleeps" (Borlaug 2008): new races of rust pathogens constantly evolve and eventually overcome the resistance that has been bred into current wheat varieties, thereby exposing global wheat production to ever-recurring threats. Thus the control of wheat rust diseases by way of resistance breeding is a seemingly never-ending task. By implication, sustained worldwide investments in research and development (R&D) are required to maintain resistance against the ever-evolving pathogen.

But what is the nature, geographical extent, and magnitude of leaf rust losses worldwide, and what do they imply about the economically justifiable investment in R&D to mitigate the effects of this disease? In a recent global study on the impact of pathogens and pests on major food crops, Savary et al. (2019) conducted an online survey of expert opinion and report an average annual global loss attributable to leaf rust of around 3.3%. Others have summarized leaf rust losses for specific regions or countries during various epidemic years (Chester 1946; Dubin and Brennan 2009; Huerta-Espino et al. 2011; Kolmer et al. 2007; McCallum et al. 2012; Saari and Prescott 1985). However, production losses are typically reported anecdotally and there is a dearth of quantitative evidence on the losses attributable to leaf rust at a global scale.

Most if not all the prior loss assessment studies have largely ignored the epidemiological nature of the losses whereby (extreme) losses for a given locale in a given year are not necessarily indicative of the losses occurring over longer periods of time or more encompassing geographical areas, or both. For example, in a regional study on the economic benefits of leaf rust resistance breeding for the Yaqui Valley, Mexico, Smale et al. (1998) applied a constant yield loss of 9% per year to derive their internal rate of return estimates. In Australia, Brennan and Murray (1988) and Murray and Brennan (2009a, b) published estimates of the wheat losses associated with rusts and other plant diseases that were derived by combining elicited averaged state-level disease severity estimates and adjusted by the frequency of disease occurrence. A study by Marasas et al. (2004) on the economic returns to the use of CIMMYT-related spring wheats in developing countries also used average annual yield losses (ranging from 1 to 6%) for each of the seven wheat growing environments they identified. Loss evaluation methodologies based on upscaling (in time and space) estimated (local) average annual yield losses are questionable for assessing the production losses attributable to leaf rust at a global scale over the longer run. It is highly unlikely that local (perhaps maximal) losses in any particular locale or particular year are representative of the losses occurring at that same locale in any other year or at any other locales.

As a practical matter, the complex interactions among pests, hosts, and environmental conditions involved in the development of disease epidemiology, combined with the limited relevant data, make it difficult to estimate with much precision the when, where, and severity of leaf rust disease outbreaks at scale. To predict disease epidemics and estimate potential losses for a given location in a given season, one approach would be to develop a process-based pest model coupled with a relevant crop growth model to simulate yield with and without diseases to derive an estimate of yield losses at various spatial and temporal resolutions. Process-based crop-pest simulation models have been used to model yield losses attributable to one or more diseases under controlled experimental field or representative farm conditions in crops like potato (Johnson 1992), groundnut (Savary and Zadoks 1992; Savary et al. 1990), rice (Pinnschmidt et al. 1995; Willocquet et al. 2000, 2002, 2004), barley (Teng et al. 1977), and wheat (Willocquet et al. 2008, 2018).

Crop-pest system models have been used to inform different types of decisions, ranging from within-season tactical disease control methods at a field scale to long-term strategic research and development prioritization decisions (Savary et al. 2006). For example, the approach presented by Teng et al. (1977) to simulate cereal rust epidemics relied on daily weather data, crop growing conditions (growth stage, crop density, etc.), and pathogen infection parameters. Building on a "production situation-injury profile" paradigm, Willocquet et al. (2008) developed the WHEATPEST model to simulate multiple pest damages to wheat yield based on farmers' field surveys in the United Kingdom and the Netherlands. The WHEATPEST model combines simulated attainable crop growth and yield for three production systems (conventional, integrated, and organic) with three groups of injury profiles to provide a basis for ranking the damages attributable to various wheat pests and diseases.

Depending on the complexity of these mechanistic yield loss models, their development and calibration typically require substantive spatial and temporal data on climate, weather, soil, host-plant characteristics, pathogen physiology, and production practices, along with parameterization of the damage functions linking pest and diseases stresses to potential crop losses (Aubertot and Robin 2013; Donatelli et al. 2017; Savary et al. 2006). As Willocquet et al. (2008, p. 26) emphasized, a paucity of relevant, accurate and comprehensive data represent significant impediments to applying such models to scale. Cunniffe et al. (2015) outlined the major challenges in modeling plant diseases, wherein capturing the temporal and spatial variation of both pathogen and host populations and the dynamic link between them remain among the top challenges faced by plant disease modelers.

Recognizing that the spatiotemporal dynamics of crops, pathogens and their interactions constitute some of the main drivers of crop yield losses, this study aims to assess the impact of wheat leaf rust disease on global wheat production by using a fit-for-purpose, probabilistic evaluation approach developed by Pardey et al. (2013). Rather than attempt to explicitly model the detailed processes linking wheat plant growth and leaf rust disease epidemics, here we estimate crop losses at scale by combining a global ecoclimatic suitability model of wheat leaf rust with a wheat production allocation model and associated loss distribution evidence at an epidemiological zone scale to characterize the spatiotemporal variation (distribution) of wheat leaf rust disease losses at a global (and multidecadal) scale. Our approach takes explicit account of the spatial heterogeneity in wheat leaf rust suitability based on long-run climate data, while also factoring in the temporal variation in yield losses based on a century of observational loss data for the United States and with due allowance for the representativeness of the probabilistic loss distributions derived from long-run U.S. data for wheat growing regions elsewhere in the world. Having a spatially explicit sense of where wheat production occurs worldwide, the climate-related risk of leaf rust occurrence where wheat is produced, and the likely yield loss consequences across vulnerable areas makes it possible to tractably conduct a probabilistic, bio-economic assessment of the global damages attributable to wheat leaf rust over multiple decades as a basis for making economically informed decisions about investments in wheat rust research worldwide.

MATERIALS AND METHODS

Ecoclimatic model of global leaf rust suitability. Spatially and temporarily explicit evidence on the occurrence of leaf rust is important for understanding the climate suitability of the disease. To this end we compiled and collated leaf rust survey data from multiple countries and multiple sources to develop, calibrate and validate our geo-referenced, ecoclimatic model of wheat rust. For the United States, we compiled county-level occurrence data reported in the USDA, CDL (Cereal Disease Laboratory) cereal rust bulletins for the period 2007 to 2012 (USDA-CDL 2015). For Australia, Robert Park, University of Sydney, provided unpublished leaf rust survey data for the period 1987 to 2014 with town or city-level resolution. For the Africa, western Asia, and south America regions, we obtained geo-coded leaf rust survey data for the period 2007 to 2014 from David Hodson, CIMMYT, by way of the database maintained by the Global Wheat Rust Monitoring System (BGRI-Borlaug Global Rust Initiative 2015). Although the occurrence of leaf rust is reportedly wide-spread throughout wheat growing areas of the world, many regions (e.g., Europe, central Asia, or China) lack accessible rust occurrence data for model development and validation purposes. Our compilation of 4,849 observations spanning the period 1987 to 2014 are mapped in Supplementary Figure S1.

The climate suitability of *P. triticina* worldwide was modeled using a CLIMEX Compare Locations model (Beddow et al. 2010; Sutherst and Maywald 1985; Sutherst et al. 2007), which was run with the CliMond 1975H climatology dataset consisting of temporal averages of 10' resolution gridded historical temperature and rainfall data for the period 1950 to 2000 (Kriticos et al. 2012). The CLIMEX parameters were based on a compilation and informed assessment of the published evidence on the biology of the leaf rust pathogen (specifically, the temperature and moisture responsiveness of the pathogen). The final variant of the model used for this study was geo-spatially calibrated using a natural rainfall scenario to align with the reported spatial occurrence of rust in Australia, Brazil, Pakistan, and the United States. Subsequently, an irrigated scenario (2.5 mm day^{-1} applied as top-up) was run, and the results compared with xeric areas where cropping is conducted under irrigated conditions. The complete set of CLIMEX model parameters are reported in the Supplementary Material along with a detailed description of the parameterization of the model we developed and used provided in Chai et al. (2016).

The CLIMEX model generates two climate-suitability indexes; specifically, an ecoclimatic index (EI) and an annual growth index (GI_A). With a scale between 0 and 100, GI_A takes into account the effects of temperature and moisture to describe the suitability of the climate for the growth of a species. EI integrates the GI_A to provide an overall measure of the potential of a given location to support a permanent population, where EI close to 0 indicates a location not favorable for long-term survival and EI values of 100 represents the constant and ideal growth conditions achievable only in incubators (Sutherst et al. 2007). For our leaf rust CLIMEX model, we use EI to identify geo-coded areas that are climatically suitable for wheat leaf rust to persist year round (with a cut off of $EI \geq 5$), and GI_A to identify geo-coded areas that are climatically suitable for growth and infections to occur during the favorable growing season (with a cut off of $GI_A \geq 5$). For the purposes of our bio-economic evaluation, a composite climate suitability map was created by (i) using geo-coded data on global irrigation patterns taken from Siebert et al. (2005) to combine the modeled results from the natural rainfall and irrigation climate-suitability scenarios, (ii) including both the EI (annual persistence) and GI_A (seasonal growth) values, and (iii) spatially masking out the climate-suitability areas that lay outside the geo-coded areas of wheat production worldwide based on data taken from You et al. (2015).

To validate the model, we spatially intersected the surveyed occurrence data with our modeled suitability layer to assess the spatial concordance between the model results and the observed data on the distribution of the disease (Supplementary Fig. S1 for sources of leaf rust occurrence data). Overall, 95% of the reported historical occurrences of the disease are encompassed by our modeled results (Supplementary Table S1). The distribution of *P. triticina* is strongly influenced by land use, particularly host plant availability (wheat cropping) and irrigation. The reported range also includes a large area of ephemeral habitat, where, due to the mobility of its spores, *P. triticina* infects crops during clement seasons. The map of reported occurrences therefore includes areas where it cannot persist year round because the climate is too cold (e.g., Canada) or too dry (e.g., Egypt, except the dry delta region where irrigation on wheat production provides moisture for rust infections [Saari and Wilcoxson 1974]). The reported distribution may also be affected by misidentified or under-reported *P. triticina* occurrences, which is minimized by careful consideration of the biology of sporulation and infection.

Probabilistic Monte Carlo simulations. Given the spatio-temporal dynamics in leaf rust damages, scattered reports for any given location on yield losses attributed to leaf rust are unlikely to be representative of leaf rust damages on a global scale over the long run. Instead of relying on local average yield loss estimates, we conducted a probabilistic assessment of global losses attributable to leaf rust by first estimating a distribution of leaf rust losses and then applying a Monte Carlo simulation method to evaluate the future threat to wheat production posed by the pathogen. This probabilistic approach allows us to explicitly account for both the spatial variation in the climate suitability of leaf rust and the temporal dynamics of the yield losses attributed to leaf rust.

Note: The USDA-CDL has maintained a record of U.S. historical leaf rust crop loss data reported on an annual, state-by-state basis since 1918 (USDA-CDL 2018). The USDA-CDL's state-level rust losses constitute informed estimates made by local experts (plant pathologists, extension personnel, researchers, and others). Although loss estimates derived from controlled experiments and formal state-wide surveys would have considerable value, the state-wide, seasonal-specific assessments provided by local experts nonetheless constitute valuable data, not least because they are intended to reflect the loss consequences of wheat rust averaged across the state-wide area under commercial wheat production.

The stochastic structure of leaf rust losses reflected in these data allowed us to estimate a probabilistic distribution of leaf rust losses in the United States over the period 1918 to 2016 by fitting conditional beta functions (Supplementary Materials provide detailed description of the distribution fitting methods). First, a baseline distribution of leaf rust losses was estimated using data over the entire period of 1918 to 2016. Since the advent of systemic fungicides in the late 1960s, use of fungicides for crop protection has increased and is now commonly applied to control foliar fungal diseases of the U.S. wheat crop (Guy et al. 1989; Hewitt 1998; Wegulo et al. 2011). In the United States, many different leaf rust resistance genes are present in the wheat cultivars released to farmers (Kolmer et al. 1991, 2007). Thus, the reported losses in the United States (at least for more recent decades) are likely to represent a conservative estimate of the prospective losses in other high-input areas of the world where the use of resistant varieties and fungicides may not be as prevalent as they are in the United States.

TABLE 1. Conditional beta parameter estimates for reported U.S. leaf rust losses[a]

Parameter	Baseline scenario	Reference high-loss scenario
A	1.427 (0.185)	6.704 (1.749)
B	86.848 (13.392)	189.647 (51.306)
Maximized log-likelihood	304.297	83.330
Number of observations	99	28

[a] Authors' estimates. The baseline scenario is estimated using the observed annual, state-specific, U.S. wheat leaf rust losses for the period 1918 to 2016; the reference high-loss scenario is estimated using only those years where reported leaf rust losses exceed 2% in the U.S. Standard errors are in parentheses. Parameters *a* and *b* are statistically significant with P values ≤ 0.01.

Notably, based on the long-term pattern of leaf rust losses in the United States, there are no obvious shifts in the frequency and magnitude of leaf rust losses before and after the 1960s when the use of fungicides and resistant varieties became more prevalent. Thus, we used the entire period of 1918 to 2016 to estimate a baseline distribution of wheat leaf rust losses.

Absent effective leaf rust control measures, one would expect more frequent occurrence of higher leaf rust losses than is reported in the United States. Consequently, in addition to our baseline crop loss distribution, we also constructed several counterfactual high-loss scenarios. We first choose three thresholds (i.e., 1, 2, or 3%, respectively) to identify different samples of high-loss years in the U.S. series where the reported yield losses exceed each of the threshold levels. We then modeled a counterfactual probabilistic distributions of leaf rust losses by pooling years when the reported annual losses exceeded each of the chosen thresholds. In other words, each of the high-loss scenarios are built on the assumption that, without effective leaf rust control, higher-than-threshold (albeit still variable) leaf rust losses are expected to occur every year in the sample. For each of the baseline (i.e., lower) loss and three high-loss scenarios, the corresponding beta distribution parameters were estimated using the maximum likelihood routine in STATA, and are reported in Table 1 (baseline scenario and high-loss scenario with a threshold of 2%) and Supplementary Table S3 (alternative high-loss scenarios with thresholds of 1 and 3% for sensitivity testing, Supplementary Material).

Coupling our probabilistic leaf rust loss structure with the historical and prospective regional and global wheat production data from FAO (2017) and Pardey et al. (2014), we undertook Monte

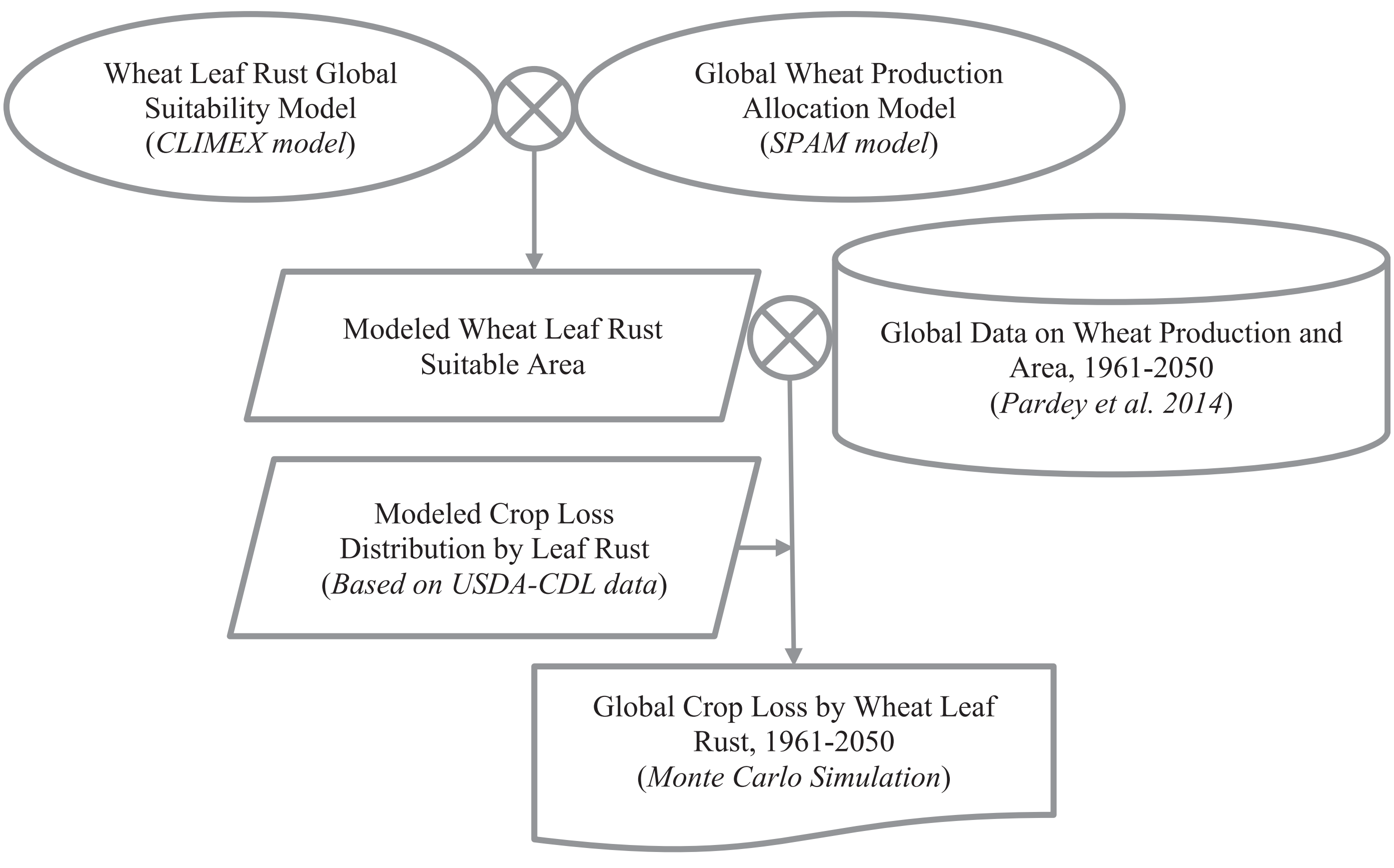

Fig. 1. Flowchart for the probabilistic global wheat rust loss estimation method. The CLIMEX model is developed based on the CliMond 1975H climatology dataset; SPAM 2005 version 2.0 is used for spatial wheat area and production allocation. Global data on wheat production and area were obtained from FAO (2017) for the period 1961 to 2010 and Pardey et al. (2014) for time period 2011 to 2050.

Carlo simulations to obtain probabilistic estimates of the prospective damages to the global wheat crop attributable to leaf rust. A schematic flowchart of our method is presented in Figure 1. Specifically, we first used the HarvestChoice spatial production allocation model (SPAM) 2005 estimates to identify wheat output, yield and area worldwide at a 5 arc minute pixel resolution for irrigated, high-input rainfed and low-input rainfed production systems (You et al. 2015). Following Pardey et al. (2013), to err on the conservative side when deriving the amount of research investment implied by our crop loss evidence, we consider only high-input growing areas. Based on the SPAM wheat allocation model, our high-input wheat areas include both "irrigated high inputs" and "rainfed high inputs", whereas low-input encompasses areas classified as either "rainfed low inputs" or "rainfed subsistence" (Supplementary Fig. S2 for the global wheat production map based on input uses). Here high-input refers to wheat production that uses a high level of inputs such as modern varieties, fertilizers, chemical pest, disease, or weed control, with most of the crop being marketed. In contrast, low-input wheat production uses traditional varieties, manual labor without (or with little) application of nutrients or chemicals for pest and disease control, and the production is mostly for own consumption. For our analysis we set aside low input wheat areas (constituting just 9.4% of 2005 worldwide wheat production) on the notion that crop production in these areas is likely constrained by a multitude of environmental and economic factors other than leaf rust, so that simply addressing losses stemming from this pathogen may not substantively improve counterfactual yields.

The modeled CLIMEX state variables (EI and GI_A) were spatially intersected with the spatial wheat information to derive estimates of the wheat area and production susceptible to leaf rust. Drawn directly on the epidemiological zone concept proposed by Saari and Prescott (1985) we applied our estimated probabilistic loss structures to each of 15 epidemiological zones worldwide. The epidemiological zones are defined in Table 1 of Beddow et al. (2013, pp. 20-22). The zones were deemed epidemiologically independent, such that an epidemic in a given zone was likely to occur independently of epidemics in other zones (Beddow et al. 2013).

Within each epidemiological zone, we first calculated the counterfactual potential yields (i.e., absent leaf rust) based on (i) national average yields reported by FAO (2017) for each of the years 1961 to 2010, (ii) projected yields reported by Pardey et al. (2014) for each of the years 2011 to 2050, and (iii) simulated leaf rust losses in the areas deemed suitable to leaf rust. We then calculated the counterfactual production losses based on the wheat production areas identified in each zone, which were then spatially aggregated to derive global leaf rust loss estimates. Our bio-economic probabilistic approach thus takes into account the spatial and temporal dynamics of pathogen suitability, the spatial location of the area and production of the host crop, and potential loss scenarios by linking "disease suitable" wheat areas to "potential" disease loss distributions. The simulation was implemented in R (R Core Team 2017) using 50,000 replicates with details for each of the steps described in the Supplementary Material.

Economically justified R&D investment in leaf rust control. For policy purposes, an important question is what is the economically justifiable investment in R&D targeted to incorporating leaf rust resistance traits into wheat varieties? Given the coevolving relationship between the R genes bred into new varieties and the virulence of the pathogen, we opted to estimate the annual average, long-run investment deemed necessary to avert production losses from a leaf rust pathogen that "never sleeps." To do so, we applied the modified internal rate of return (MIRR) concept described by Hurley et al. (2014) to estimate the maximum annual investment in R&D for the period 1990 to 2050 that could achieve at least a 10% MIRR per year with a probability of 95%. The optimization problem and specific parameters used are described in detail in the Supplementary Material.

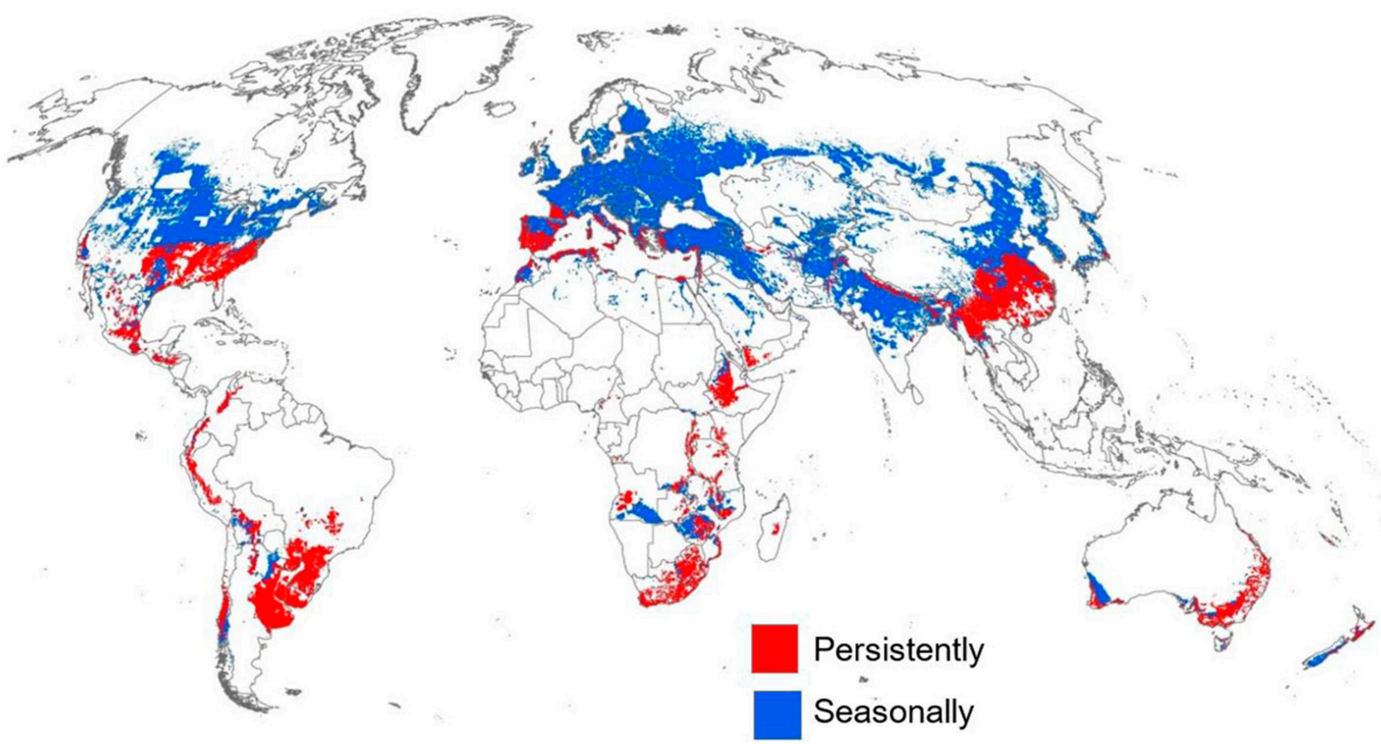

Fig. 2. Modeled global climate suitability for *Puccinia triticina*. (Reproduced, with permission, from Chai et al. [2016]). This map reports the annual growth index (indicating year-round or persistently suitable areas) and the ecoclimatic index (indicating seasonally suitable areas) within the global extent of wheat production reported by You et al. (2015). Note, areas that are persistently suitable are a subset of areas that are seasonally suitable. These potential survival estimates were modeled using a composite of natural rainfall and irrigation based on the irrigated areas reported by Siebert et al. (2005).

RESULTS

Global leaf rust suitability. Our modeled assessment of the geographic scope of the climate-suitable areas for wheat leaf rust accords well with the reported distribution of the disease: 95% of reported locations are encompassed by the mapped GI_A area. In the United States, leaf rust occurs throughout the wheat growing areas, including the south-eastern states, the Ohio Valley, the Southern Great Plains and the Northern Great Plains (Kolmer et al. 2007), and our modeled composite risk map closely matches the reported geo-coded occurrences of the disease from the U.S. field and experimental plot observations we compiled. It also agrees well with the geographical extent of the reported leaf rust occurrence within other wheat growing regions, including the eastern prairies of Canada, Mexico, Argentina and Uruguay in South America, southern China, Russia, South Africa, and Australia (Germán et al. 2004; Huerta-Espino et al. 2011; Murray and Brennan 2009a, b; Pretorius et al. 1987; Roelfs 1989; Singh et al. 2004a, b). The composite risk model also correctly identifies the xeric parts of Egypt, Pakistan, and India where wheat is grown under irrigation and where *P. triticina* has been recorded (BGRI-Borlaug Global Rust Initiative 2015; Soliman et al. 2012).

Overlaying our geo-coded leaf rust CLIMEX suitability estimates with a pixilated geography of global wheat production SPAM model (You et al. 2015) enables estimation of both the share of wheat area and production that are seasonally vulnerable to the disease (Fig. 2, Table 2). We estimate that 90.1% of the world's wheat growing area and 94.4% of the world's wheat production is climatically suitable for leaf rust infection. Notably, nearly 100% of the wheat output of the Asia and Pacific, Western Europe, and Latin America and Caribbean (LAC) regions could experience losses arising from leaf rust.

There is substantially more spatial variability in the zonal share of area and output for which the pathogen could persist year-round, as indicated by the mapped EI areas (Supplementary Fig. S1). For example, while the climate across most of the wheat growing areas in the Asia and Pacific and Western Europe regions is suitable for the disease during the growing season, the pathogen can survive year-round on less than a quarter of the wheat growing areas in both those regions. This is in stark contrast to the situation in Latin America and the Caribbean (LAC) and sub-Saharan Africa (SSA), where the pathogen can survive year-round on nearly all the area that is also intraseasonally suitable. This has substantial practical implications for LAC and SSA wheat growers as it means that, relative to other regions, farmers in these parts of the world are likely to face more sustained disease pressure rather than episodic outbreaks of the pathogen. These regional differences in the climate suitable versus persistence shares suggest that different strategies may be more or less cost-effective depending on whether the intent is to eliminate the source of the leaf rust inoculum, limit its geographical dispersal, or both.

Probabilistic estimation of global leaf rust losses. With leaf rust susceptible areas identified, we applied the estimated spatiotemporal rust loss structure to each of the epidemiological regions to estimate the worldwide yield loss consequences of leaf rust. The probabilistic patterns of leaf rust loss are obtained using several variants of the U.S. yield loss data from the USDA-Cereal Disease Laboratory. As shown in Figure 3, leaf rust loss patterns in the United States over the past 100 years reveal a good deal of spatiotemporal variability. States from the Great Plains (such as Texas, Oklahoma, and Kansas) experienced more frequent yield losses in general than Midwestern states (such as North Dakota, South Dakota, and Minnesota) or Pacific Northwest states (such as Washington, Oregon, and Idaho). Within any given state, losses can range anywhere from 0% to more than 30% depending on the state and year. These spatial-temporal variations in losses due to leaf rust are consistent with the findings of Kolmer et al. (2007) who revealed significant regional variation in the presence of virulence genes in *P. triticina* in response to the use of wheat cultivars with different resistance genes across different regions in the United States. Through mutation or new introduction from other areas, the frequency of different virulent leaf rust races can change rapidly, making the development of durable leaf rust resistance an ongoing challenge (Kolmer et al. 2007).

Since the quantity of wheat production differs markedly among U.S. states, the percent yield losses reported in each state have different consequences for the estimated national average yield loss. To derive a national average yield loss, state-level percent yield losses are weighted by each state's wheat production level. Over the past century, national average yield losses ranged from negligible levels (in the years 1924 to 1925, 1943 to 1944, and 2011) to more than 4% (in 1938, 1945, 1974, and 1985), and peaked with a national average loss of 10.0% in 1938 (Fig. 4, red/gray bar plot). The intertemporal variation in the aggregated national annual

TABLE 2. Regional and global persistence and suitable shares for wheat leaf rust[a]

	Production[c]			Area[c]		
	Wheat production global share	Within-region susceptible to leaf rust		Wheat area global share	Within-region susceptible to leaf rust	
Region[b]	Region/global (%)	Persistence share (%)	Suitability share (%)	Region/global (%)	Persistence share (%)	Suitability share (%)
Asia and Pacific	37.0	29.1	97.5	30.8	24.4	97.1
Western Europe	28.9	11.9	99.5	23.1	16.6	98.9
North America	13.7	13.6	87.0	13.7	12.5	84.7
FSU	12.3	0.2	82.6	21.6	0.2	71.5
Australasia	4.5	49.8	88.3	6.4	51.0	87.3
LAC	2.5	94.8	98.1	3.0	93.1	97.6
SSA	1.1	74.6	78.6	1.4	69.9	73.5
World	100.0	21.1	94.4	100.0	19.4	90.1

[a] Developed by authors based on data from Chai et al. (2016) and FAO (2017).

[b] For ease of exposition, we aggregated some of the Beddow et al. (2013) zones when reporting the results in this table. Specifically, the Latin America and the Caribbean (LAC) figures represent an aggregation of the estimates formed for the Central America and Caribbean, Andean, and Eastern South America zones. Sub-Saharan Africa (SSA) is an aggregation of the East Central Africa, West Central Africa, and Southern Africa zones. Asia groups together the Southeast Asia, Southwest Asia, and Northeast Asia zone estimates. Western Europe includes all countries on the European Continent from the North Africa and West Europe and Eurasian zones. FSU is the former Soviet Union countries.

[c] Wheat production share and wheat area share represent the share of wheat production and area within each region as a percentage of the 2005 global total wheat production and area, respectively. The within-region persistence share reflects the share of production and area that are susceptible to leaf rust infection year-round, while the suitability share indicates the respectable regional share of production and area that are susceptible to leaf rust infection only during wheat growing seasons.

(percentage) losses was generally more muted than the corresponding losses reported at the state level. Moreover, our results show that the pattern of variation in losses for any state are not especially representative of the year-on-year variation in losses for the country as a whole (and vice versa). In fact, the correlations of leaf rust yield losses between individual states and the national average are quite small for most states (typically less than 0.5), with the highest correlation being 0.8 for Kansas (Supplementary Table S2). These spatiotemporal characteristics of the U.S. data underscore the likelihood of sampling bias if more localized (e.g., state) losses—and particularly the extreme state-level losses—were taken to be representative of the losses over a larger (e.g., national scale) epidemiological zone.

The magnitude of the reported yield losses (in percentage terms) for the United States are likely to be a conservative representation of the losses pertaining to other wheat producing areas around the world, especially in lower-income countries where fungicide use is often limited. Thus, the high-loss scenarios included in our analysis were developed as a more likely reflection of the economic consequence of leaf rust disease in those areas of the world lacking in the effective use of control methods. In the main paper, we only report the high-loss scenario with a threshold of at least 2% yield loss and refer to it as the (reference) high-loss scenario. Results for alternative high-loss scenarios with 1 and 3% thresholds are reported in the Supplementary Material as a sensitivity check.

All the beta distribution coefficients fitted with these data are significant at the 0.01% level (Table 1 and Supplementary Table S3), and our calibrated beta distribution is a good characterization of the reported leaf rust loss data as evidenced by the cumulative (proportional loss) probability plot in Supplementary Figure S3. According to our fitted distributions, in the baseline scenario there is a 50% chance that the annual yield loss associated with leaf rust occurrence in an epidemiological zone exceeds 1.3%, and a 20% chance that the annual loss exceeds 2.5%. For our reference high-loss scenario, we estimate there is a 50% chance of losses exceeding 3.3%, and a 20% chance of losses exceeding 4.4%.

In the United States, if we assume the high-loss scenario was averted through deployment of resistant varieties and effective fungicides applications, the benefits of leaf rust control can then be measured as the difference between the counterfactual high-loss scenario and the observed baseline scenario. The white bar plots in Figure 4 illustrate a counterfactual high-loss scenario based on a random draw from our reference high-loss distribution for each of the years 1918 to 2016. In our simulation, avoidance of our reference high-loss scenario saved the United States an average of 0.81 million metric tons of wheat per year; equivalent to 1.96% of the annual U.S. harvest and worth $231.12 million (in 2016 U.S. dollars). Probabilistically, there is a 90% (i.e., high-odds) chance that the annual loss avoidance is at least 0.74 million metric tons, which translates to $212 million per year in U.S. benefits arising from effective leaf rust management.

Globally, we applied this probabilistic structure of losses to wheat production in each of our 15 epidemiological zones for the period of 2000 to 2050, and then reported the findings in Table 3 and Figure 5. In the conservative, baseline scenario, the average global loss attributable to wheat leaf rust was estimated at 8.6 million metric tons per year for the period 2000 to 2050, with a 90% chance of worldwide losses exceeding 5.1 million metric tons in any given year. In the reference high-loss scenario, the average annual loss worldwide was estimated at 18.3 million metric tons, with a 90% chance of exceeding 14.4 million metric tons. With global wheat production during this historical period averaging 699 million metric tons per year, our results imply that the average annual crop losses attributable to leaf rust accounted for 1.2% (in the baseline scenario) and 2.6% (in the reference high-loss scenario) of global production, valued at $1.5 billion and $3.3 billion of losses per year in 2016 U.S. prices, respectively. There is a 90% chance that the average annual crop loss will exceed $0.9 billion globally in the baseline scenario and $2.6 billion in the reference high-loss scenario.

Economically justified R&D investment in leaf rust control. Looking forward, if we assume that crop losses

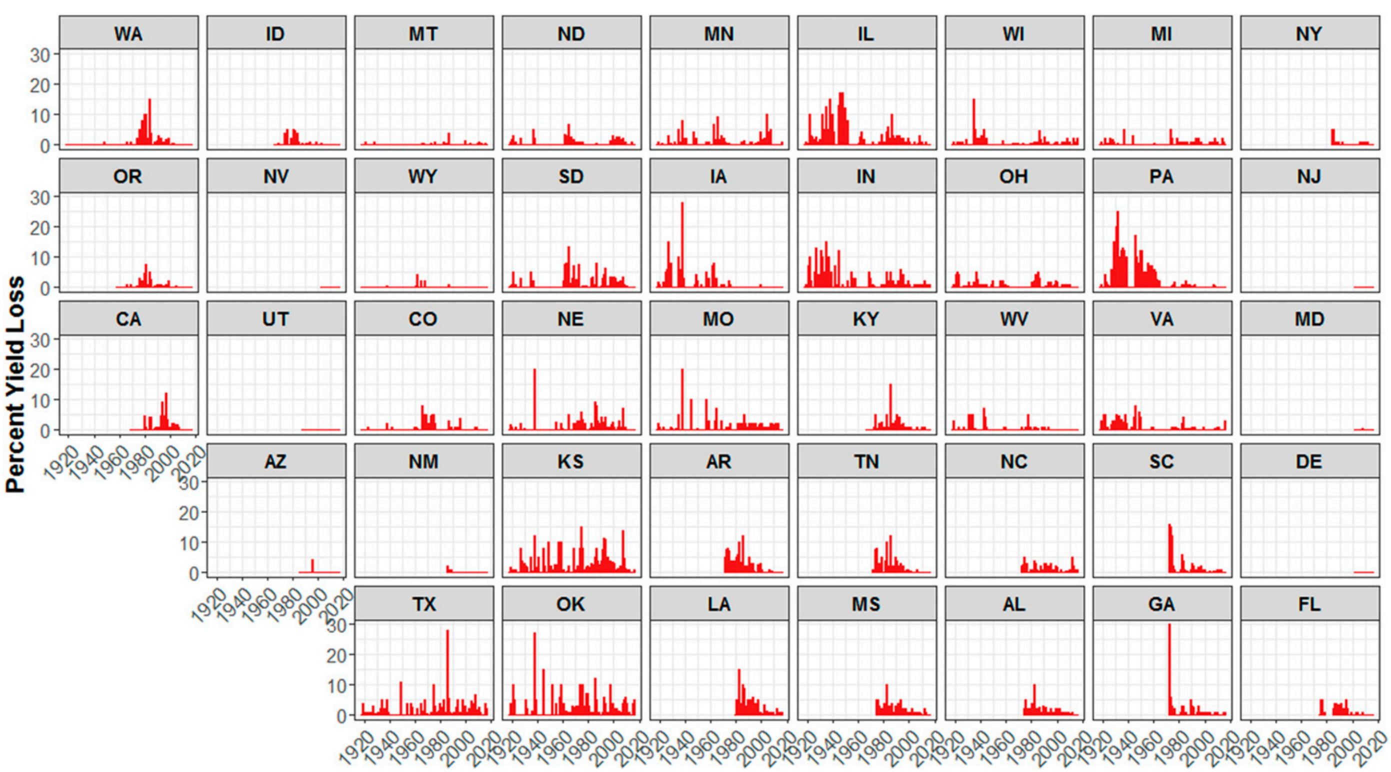

Fig. 3. Spatiotemporal variation in yield losses attributed to leaf rust in each U.S. state, 1918 to 2016 (developed by authors with data from USDA-CDL [2018]). States are arranged in a pattern that approximates their geo-spatial location.

attributable to leaf rust losses in the reference high-loss scenario are reduced to our baseline scenario through the development of resistant wheat varieties (along with the adoption of other disease management practices), we estimate that an on-going investment in R&D to control for leaf rust averaging $55.7 million per year (2016 U.S. prices) appears economically justified relative to alternative uses of scarce research funds. Furthermore, in a future where on-going investments in resistance breeding and other disease management practices eliminate all the losses attributable to leaf rust, a sustained annual investment of $50.5 million per year (2016 U.S. prices) is economically justifiable if our relatively conservative baseline scenario was deemed to prevail. These amounts can be interpreted as the recurring annual investment required for maintenance research to secure the world's wheat yield potential by improving the crop's resistance against the ever-changing leaf rust pathogen. With such a sustained investment, there is a 95% chance that the modified internal rate of return (MIRR) would exceed 10% per year, meaning this is an economically justifiable investment relative to other targets for the deployment of scarce R&D dollars.

The indications are that global public investments in wheat (rust) research are still quite limited (Pardey et al. 2013). In the United States, using data obtained from USDA-CRIS (2019), we estimate that public spending on all wheat pathology-related research averaged around $11.7 million (2016 U.S. price) per year for the period 1998 to 2015. Extrapolating from this figure, we estimate that total public spending on wheat pathology-related research worldwide was approximately $159 million (2016 PPP) per year during 2000 to 2011 (Supplementary Table S5). Notably these investment estimates encompass all aspects of wheat pathology research (including all three wheat rusts, Fusarium head blight, blotch, take all, leaf spot, Karnal bunt, etc.), of which research on leaf rust is but one component. Our baseline estimate of an economically justifiable investment of $50.5 million per year worldwide to mitigate the losses attributable to leaf rust is equivalent to approximately one third of the estimated global public spending on all wheat pathology research. By inference, it seems highly likely that there is a sizable and sustained underinvestment in research designed to avert the United States and global crop losses attributable to leaf rust.

DISCUSSION

Although leaf rust tends to cause smaller annual farm-level losses in any given locale than the other cereal rusts, those losses are persistent and widespread such that the global tally of losses attributable to the pathogen are substantial. Using the available data on the historical occurrences and losses attributable to leaf rust, our probabilistic evaluation of the global damage attributable to leaf rust projects the average losses worldwide during the period 2000 to 2050 to be 8.6 million metric tons per year for our conservative baseline scenario, and 18.3 million metric tons per year for our reference high-loss scenario: equivalent to $1.5 billion and $3.3 billion in losses per year in 2016 U.S. prices, respectively (Table 3). This justifies a sustained (i.e., in-perpetuity) annual investment of $55.7 million for averting losses worldwide with the reference high-loss scenario, versus $50.5 million of investment with a more conservative, baseline scenario.

The approach we used here uses a CLIMEX model in conjunction with geo-tagged historical average climatology data to derive the spatial suitability of wheat leaf rust pathogen at any given locale. Combining these spatial variations in the risk of leaf rust occurrence with the crop loss distributions that feature in our modeling approach capture spatiotemporal variations in the risk of leaf rust

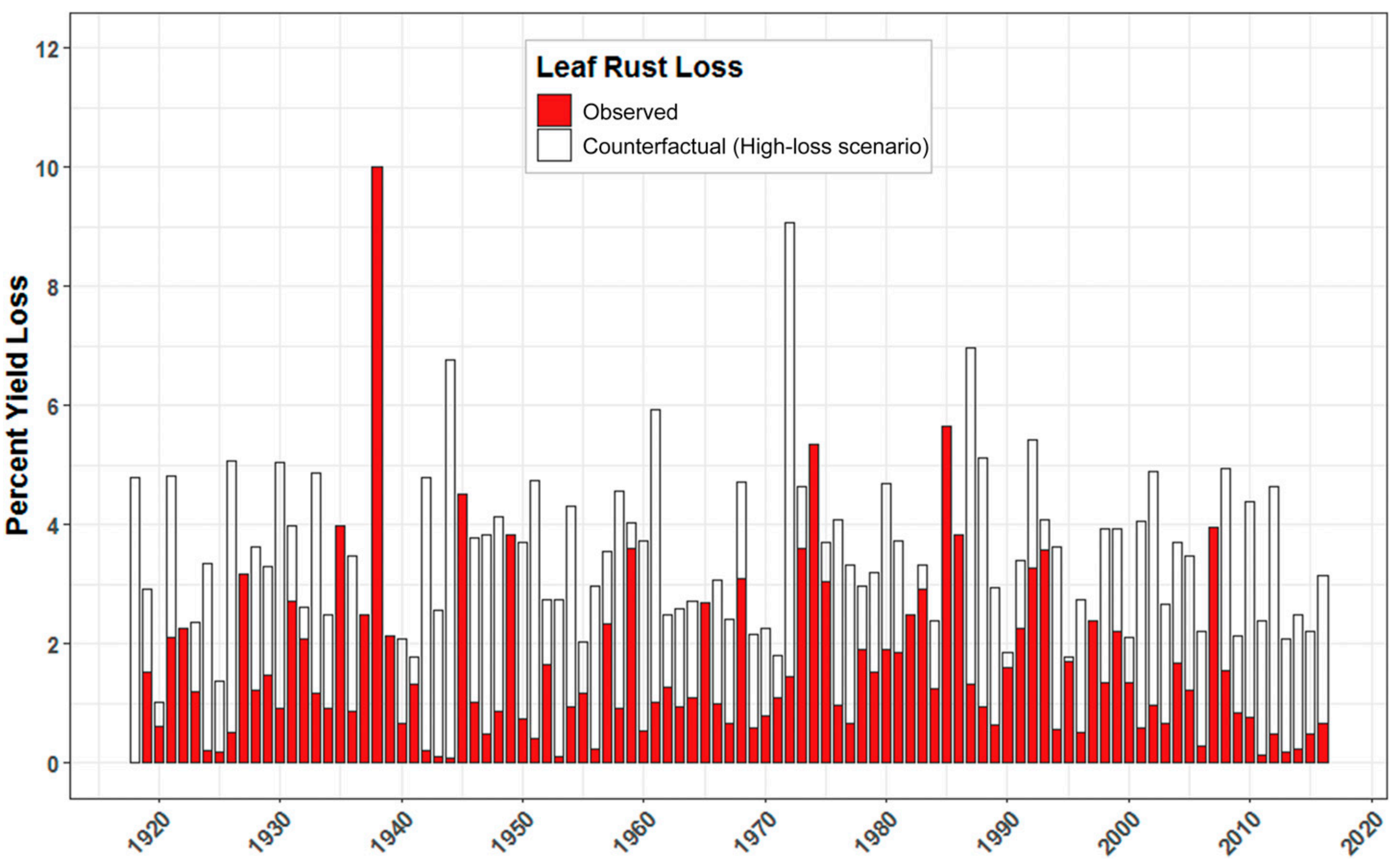

Fig. 4. Percentage of wheat yield losses attributed to leaf rust in the United States, 1918 to 2016 (developed by authors with data from USDA-CDL [2018]). The red/gray bars represent the U.S. national average percent wheat yield losses attributed to leaf rust. The white bars illustrate a simulated high-loss (i.e., exceeds 2% per year) counterfactual scenario absent effective leaf rust control.

losses in a probabilistic fashion. Our reduced-form method applies a probabilistic loss distribution at the scale of an epidemiological zone to sidestep the difficult and often data limited challenge of having to predict actual disease occurrence and the associated crop loss at each particular locale in any particular year. Nonetheless, we use the results from our CLIMEX model to differentiate the global wheat landscape according to the climate suitability for leaf rust occurrence.

Our probabilistic approach puts the longer run average annual crop loss attributable to leaf rust at 1.2% worldwide for our baseline scenario, with average annual yield loss of 2.6% for our reference high-loss scenario. These longer run global average loses are significantly lower than many local maximum yield losses reported during severe leaf rust epidemics, which can range between 5 to 50% (Chester 1939; Huerta-Espino et al. 2011; Hussain et al. 1980; Roelfs 1978; Samborski 1985). For comparison, our global leaf loss estimates of 1.2% (baseline scenario) to 2.6% (reference high-loss scenario) are lower, on average, than the 3.3% annual average global losses reported by Savary et al. (2019) on the basis of a survey of expert opinion. Nonetheless, our lower on-average global losses still admit the prospects of higher, sometimes substantially higher, losses at particular locales and points in time.

Lacking comprehensive, worldwide evidence on the frequency and severity of actual and potential leaf rust losses, our various high-loss scenarios (based on subsamples of relatively severe losses reported in the United States) at a minimum provide an indication of the potential magnitude of the global losses if resistance genes or fungicides are rendered ineffective due to pathogen mutation and/or climate change. The multiple scenarios we provide in this study help illustrate the sensitivity of the benefits associated with shifting the distribution of global wheat leaf rust losses from higher to lower levels of loss.

While the localized losses attributable to leaf rust are commonly considered less catastrophic than the losses ascribed to stem rust, this study reveals that the frequency and spatial extent of the losses associated with the disease add up over time (and space). Indeed, the bio-economic evidence presented here indicates that the economically justifiable investment for dealing with leaf and stem rust

TABLE 3. Global yearly leaf rust losses, 2000 to 2050[a]

	Baseline scenario		Reference high-loss scenario	
Probability of loss	(million metric tons)	(billion $U.S.)	(million metric tons)	(billion $U.S.)
90%	5.1	0.9	14.4	2.6
50%	8.2	1.5	18.2	3.3
20%	10.9	2.0	21.0	3.8
5%	14.1	2.5	23.8	4.3
Mean	8.6	1.5	18.3	3.3

[a] Authors' estimates. Baseline and reference high-loss scenarios are described in Table 1. Losses valued in 2016 dollars.

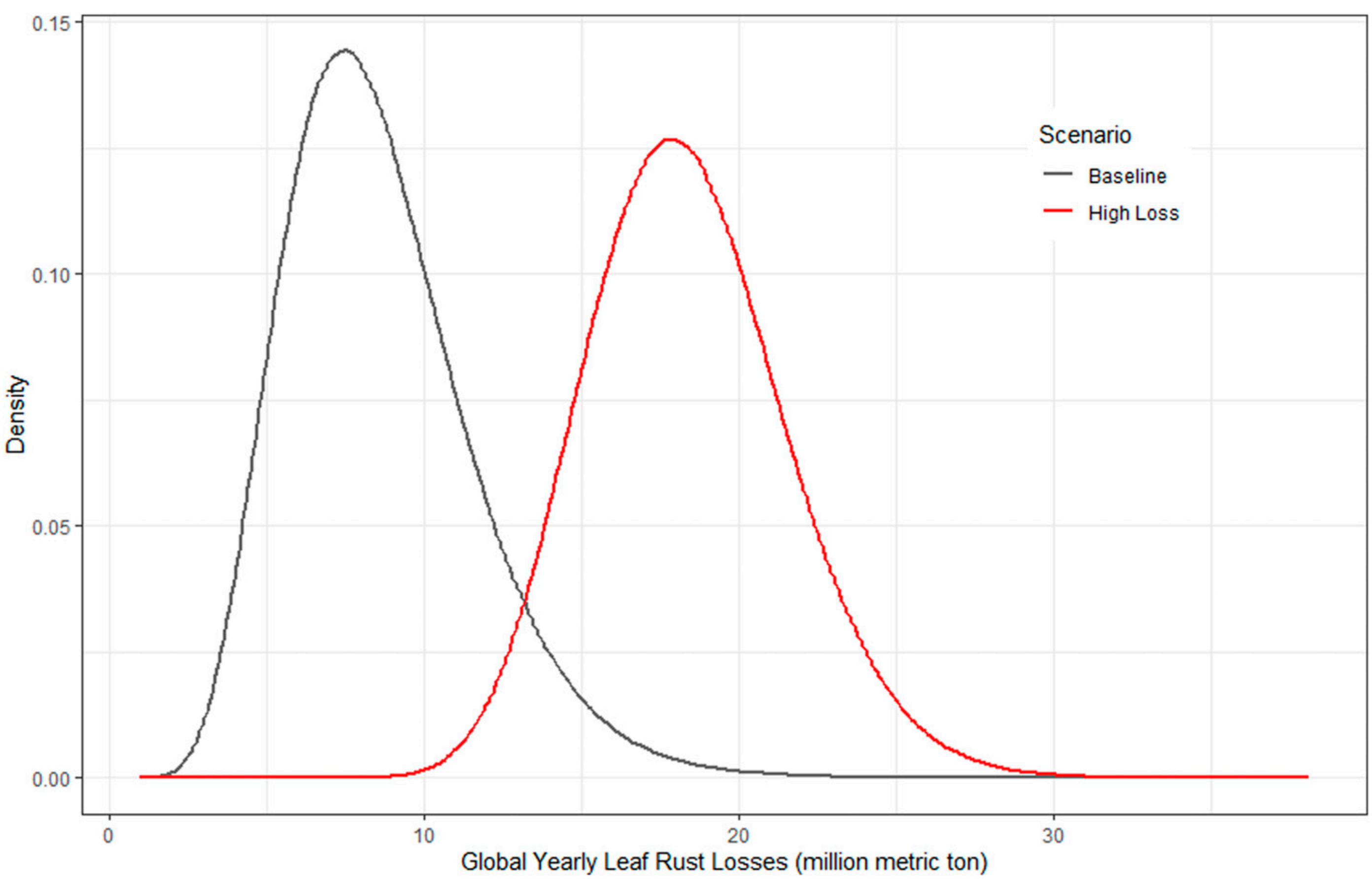

Fig. 5. Distribution of the global yearly leaf rust losses, 2000 to 2050. Baseline and high-loss scenarios are described as in Table 1.

worldwide are of similar orders of magnitude. However, viewed from another perspective our loss estimates for leaf rust are qualitatively different from those hitherto identified for stem rust. Setting aside recent losses in selected East African and Middle East countries in selected years associated with Ug99 susceptible varieties (see, for example Beddow et al. 2015), most of the losses attributable to stem rust worldwide are still largely prospective losses, thanks in part to the rather widespread and effective deployment of stem rust resistant varieties. In stark contrast, our projected losses through to 2050 attributed to leaf rust are in line with the losses presently being incurred by farmers the world over. In other words, these leaf rust losses will in all likelihood persist at this scale for decades to come, absent the amount of funding we have estimated are required to address them. Thus, investing in leaf rust control has the potential to yield high economic returns given the geographically widespread extent of losses attributable to the disease. This gives added impetus to securing and sustaining the economically justifiable funding for R&D that we determined are required to meet the substantial food security and economic livelihood challenges posed by this pathogen.

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