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PLANT DISEASE FEATURE

Integrated Strategies for Durable Rice Blast Resistance in Sub-Saharan Africa

Samuel K. Mutiga,[1,2] Felix Rotich,[3] Vincent M. Were,[4] John M. Kimani,[5] David T. Mwongera,[5] Emmanuel Mgonja,[6] Geoffrey Onaga,[7] Kadougoudiou Konaté,[8] Claudine Razanaboahirana,[9] Joseph Bigirimana,[10] Alexis Ndayiragije,[10] Emily Gichuhi,[5] Mary J. Yanoria,[11] Miriam Otipa,[5] Lusike Wasilwa,[5] Ibrahima Ouedraogo,[8] Thomas Mitchell,[12] Guo-Liang Wang,[12] James C. Correll,[2,†] and Nicholas J. Talbot[4,†]

[1] Biosciences eastern and central Africa – International Livestock Research Institute (BecA-ILRI), Nairobi, Kenya
[2] Department of Entomology and Plant Pathology, University of Arkansas, Fayetteville, AR 72701, U.S.A.
[3] Department of Agricultural Resource Management, University of Embu, Embu, Kenya
[4] The Sainsbury Laboratory, University of East Anglia, Norwich NR4 7UH, U.K.
[5] Kenya Agricultural and Livestock Research Organization (KALRO), Nairobi, Kenya
[6] Tanzania Agricultural Research Institute, Arusha, Tanzania
[7] National Agricultural Research Organization, Kampala, Uganda
[8] Institute of Environment and Agricultural Research, Bobo-Dioulasso, Burkina Faso
[9] Institut Polytechnique Unilasalle, 60000 Beauvais, France
[10] International Rice Research Institute (IRRI), Bujumbura, Burundi
[11] IRRI, Los Baños, 4030 Laguna, Philippines
[12] Department of Plant Pathology, The Ohio State University, Columbus, OH 43210, U.S.A.

Abstract

Rice is a key food security crop in Africa. The importance of rice has led to increasing country-specific, regional, and multinational efforts to develop germplasm and policy initiatives to boost production for a more food-secure continent. Currently, this critically important cereal crop is predominantly cultivated by small-scale farmers under suboptimal conditions in most parts of sub-Saharan Africa (SSA). Rice blast disease, caused by the fungus *Magnaporthe oryzae*, represents one of the major biotic constraints to rice production under small-scale farming systems of Africa, and developing durable disease resistance is therefore of critical importance. In this review, we provide an overview of the major advances by a multinational collaborative research effort to enhance sustainable rice production across SSA and how it is affected by advances in regional policy. As part of the multinational effort, we highlight the importance of joint international partnerships in tackling multiple crop production constraints through integrated research and outreach programs. More specifically, we highlight recent progress in establishing international networks for rice blast disease surveillance, farmer engagement, monitoring pathogen virulence spectra, and the establishment of regionally based blast resistance breeding programs. To develop blast-resistant, high yielding rice varieties for Africa, we have established a breeding pipeline that utilizes real-time data of pathogen diversity and virulence spectra, to identify major and minor blast resistance genes for introgression into locally adapted rice cultivars. In addition, the project has developed a package to support sustainable rice production through regular stakeholder engagement, training of agricultural extension officers, and establishment of plant clinics.

Keywords: rice blast, breeding, resistance gene pyramiding, disease surveillance, sub-Saharan Africa, *Pyricularia*, *Magnaporthe*, low income countries, development, small holder farming, fungus

Rice is Important for Food Security in Africa.

The rapidly growing African population is facing critical large-scale food insecurity. To overcome this challenge, there is an urgent need to optimize crop production on the fixed arable land parcels of Africa, which are under threat from urbanization. Rice holds enormous potential as a food crop for Africa and is a key component of the African Union's Comprehensive African Agriculture Development Program (CAADP) strategy for achieving food and nutritional security across the whole continent. The increasing demand for rice in Africa could be a consequence of urbanization, which has brought with it the need for fuel-efficient cooking methods and hence a shift to fast cooking foods. Enhancing self-sufficiency in rice production can enable countries to create more jobs locally and to reallocate budgets into importation of commodities that cannot be locally produced in sub-Saharan Africa (SSA) (Séré et al. 2011). However, to meet the growing demand for rice (Fig. 1), there is a need to address constraints on rice production.

[†]Corresponding authors: J. C. Correll; Jcorrell@uark.edu, and N. J. Talbot; Nick.Talbot@tsl.ac.uk

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Cultivation of rice in SSA begun as early as the 12th century, but rice production has doubled in the last two decades, with an increase of 2% between 1992 and 2002 followed by a 4% increase between 2003 and 2013 (Linares 2002; Zenna et al. 2017). This increase in rice production can be attributed to favorable government policies and increased cultivation and intensification. Also, cultivar improvements for farmer-preferred traits, such as grain yield, resistance to shattering, tolerance to abiotic and biotic stresses, and synchrony in flowering, as well as consumer preferred traits, such as aroma, color, cookability, and grain size, have contributed to increased cultivation (Asante et al. 2013; Rutsaert et al. 2011). Currently, rice production is dominated by small-holder farmers who own small paddies on large irrigation schemes and have progressed from semisubsistence to commercial farming (Dalton and Guei 2003; Onyango 2011).

Recent reports show that, with a total of 13.9 million tonnes in 2016, SSA contributed only about 3% of global rice production (Nigatu et al. 2017). More than 80% of the rice production in SSA comes from eight countries (Nigeria, Madagascar, Côte d'Ivoire, Tanzania, Mali, Guinea, Sierra Leone, and Senegal), with Nigeria and Madagascar accounting for one-third of rice production. It is expected that rice production will increase in Tanzania, Angola, Côte d'Ivoire, Guinea, Mali, Senegal, and several other countries. However, the overall growth in production is expected to be slower over the next decade, averaging 3% annually through 2026 (Nigatu et al. 2017).

Following the food crisis of 2007–08 and concerns over climate change, regional policy efforts to boost food security were established in Africa. Efforts to enhance food security included those by the Coalition for African Rice Development (CARD, https://riceforafrica.net/). This effort included initial membership from West African countries, but has more recently including members from East Africa (AfricaRice 2011). CARD included the Rice Offensive Program adopted in 2014 by the Economic Community of West African States (ECOWAS), with the objective of boosting rice production to 25 million tonnes per annum by 2025 (Fofana et al. 2014). The initiative identified some areas that individual member countries of CARD could improve in order to boost production within a decade (mainly between 2008 and 2018), which was set out in the National Rice Development Strategies program (Table 1). A recent (2020) review by the Alliance for a Green Revolution in Africa (AGRA), Japan International Cooperation Agency (JICA), and Pricewaterhouse Coopers showed that the CARD countries' projection goals have been successful in a few African countries, such as Senegal and Tanzania, but the overall goal of self-sufficiency has not yet been achieved (JICA and Pricewaterhouse Coopers 2018).

The demand for rice in Africa is growing at a rate of 6%, faster than anywhere else in the world and the continent was ranked second with 25% ($6 billion) of global net imports in 2018. Most rice (~34%) is imported from Asian countries, such as Vietnam, Thailand, Pakistan, and India (Dalton and Guei 2003; Gulati and Sudha 2003; Nigatu et al. 2017). More regional and country-based efforts are therefore required to avert food security crises that could be caused by the rapid urbanization and population increases across SSA.

The focus of this review is to highlight efforts toward enhancing food security in SSA through better management of rice blast disease. Blast has been identified as a major constraint because of its devastating damage at multiple stages of rice growth (Séré et al. 2011). We review current constraints on rice production, potential technologies and innovations for overcoming these challenges, including genetic and genomic resources, with a focus on managing rice blast disease. Breeding to achieving durable blast resistance is likely to be critical in enabling sustainable rice production in SSA. Here, we define durable disease resistance as resistance that remains effective during prolonged and widespread use in environments favorable to the pathogen or disease spread (Johnson 1981) and we recognize that this is likely controlled by multiple factors. We have therefore aimed at integrating the most promising approaches to achieve rice blast resistance. Here, we present a review of how we are integrating pathogen genetics and the evaluation of virulence spectra in the prevailing rice blast population, with marker assisted backcrossing of corresponding rice blast resistance genes and multilocational testing of rice breeding populations in a collaborative international effort. Our overarching aim is to develop resilient, high-yielding, locally adapted, blast-resistant rice cultivars for Africa.

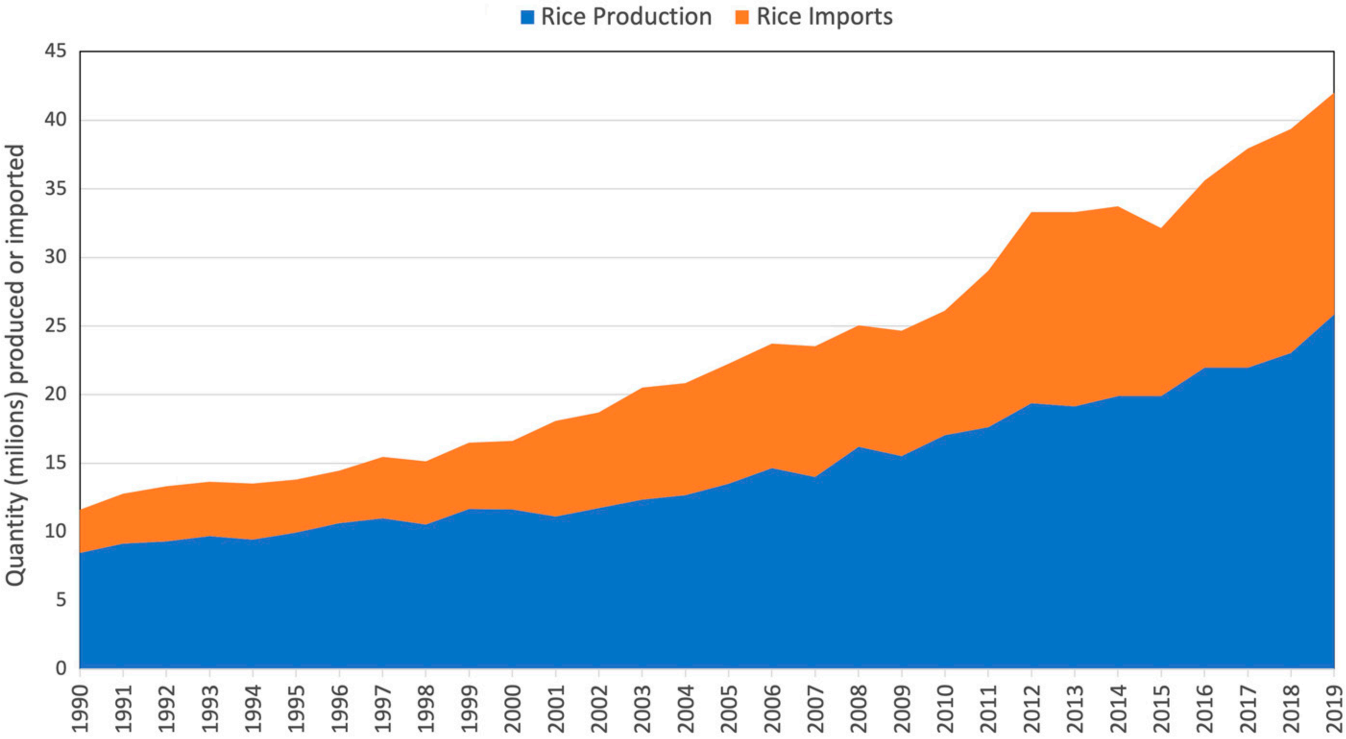

Fig. 1. Quantities of paddy rice (milled equivalent) produced and imported in sub-Saharan Africa within the last three decades, 1990–2019. Source: FAOSTAT. http://www.fao.org/faostat/en/#data. Accessed 11 March 2021.

Rice Production Constraints in SSA.

Production of rice in SSA is constrained by both abiotic and biotic factors, and the limited adoption of appropriate technologies (Mujawamariya et al. 2017). Abiotic stresses include extreme temperatures, drought, low and high nutrient content in the soil, and an interaction of nutrients and water that leads to suboptimal pH. Biotic factors include many diseases and pests that cause significant losses at different stages of growth and development of the crop (Mujawamariya et al. 2017). Key management challenges also include lack of capital and awareness of appropriate technologies for application across the rice value chain. Furthermore, policies and incentives are inadequate for both production and marketing (Elbehri 2013).

The effects of abiotic stresses vary greatly across rice agroecologies. For example, rice cultivars adapted to rainfed conditions may not perform optimally under stagnant water ecologies, and a shortage of water can lead to a decline in yield of cultivars adapted to continuously flooded conditions (Korres et al. 2016). Similarly, extremely low temperatures can delay vegetative and reproductive stages and cause sterility in rice. Conversely, extremely high temperatures (above 35°C) can cause wilting, reduced flowering, and low grain weight and quality (Krishnan et al. 2011). Furthermore, a deficiency of essential nutrients (nitrogen, phosphorus, and potassium) and other microelements in most regions of SSA can result in physiological disorders (Njinju et al. 2018; Tsujimoto et al. 2019). Nutrient depletion in the soil is a common problem and leads to a huge demand for synthetic fertilizers (Stewart et al. 2019). The majority of the farmers, for example, do not have sufficient knowledge of fertilizer application, and may apply fertilizer at inappropriate rates that cause physiological disorders (Tsujimoto et al. 2019).

Biotic stresses of rice include weeds, pests, and diseases (Abebrese et al. 2019; Aliou et al. 2013; Wubneh and Bayu 2016). Among the weeds of economic importance in rice production are the parasitic witchweeds (*Striga asiatica*, *S. aspera*, and *S. hermonthica*) (Rodenburg et al. 2016). Pests of rice include arthropods, birds, and mammals (e.g., rodents, squirrels, monkeys, etc.). These pests cause grain yield losses of 20 to 90% (Aliou et al. 2013). Damage by birds occurs mainly at grain filling and can cause up to 100% yield loss (De Mey and Demont 2013). For example, in 2018, many farmers in Kenya (Ahero, Kisumu County; and Mwea, Kirinyaga County) lost their entire crop to the red-billed quelea (*Quelea quelea*) (Ignatius Odanga, Kenya online standard digital media, 25 April 2018). The effects of rodents have been experienced in our rice research activities in East Africa, where rats cause significant damage to aromatic cultivars of rice, e.g., Basmati 370 and Komboka. Rice diseases include those that are caused by pathogenic fungi, bacteria, viruses, and nematodes in SSA leading to diseases that cause varying levels of yield and quality reduction leading to economic losses (Abebrese et al. 2019; Wubneh and Bayu 2016). The most common bacterial diseases are leaf blight (*Xanthomonas oryzae* pv. *oryzae*) and brown sheath rot (*Pseudomonas fuscovaginae*), which cause up to 41% yield reduction (Awoderv et al. 1991; Wubneh and Bayu 2016). The most prevalent fungal diseases are blast (*Magnaporthe oryzae*), brown spot (*Cochliobolus miyabeanus*), root rot complex, seedling blight complex, and sheath rot (*Sarocladium oryzae*) (Godfray et al. 2016). Viral diseases include rice yellow mottle virus and tungro disease complex (Abo and Sy 1997; Kouassi et al. 2005). The parasitic nematodes include stem (*Ditylenchus angustus*), foliar (*Aphelenchoides besseyi*), root (*Hirschmanniella oryzae*), cyst (*Heterodera oryzicola*), and root knot (*Meloidogyne graminicola*) nematodes. Root knot nematode is the most economically important and can cause up to 10% of rice yield loss (Jain et al. 2012).

There is a need to develop technologies and policies that can mitigate challenges to rice production and postharvest losses. Breeding is an approach through which most of these challenges could be tackled. Additionally, better peri- and postharvest handling technologies could reduce the documented losses of 15 to 50% of the market value of rice production (Somado et al. 2008). There is also a need for comprehensive policies across the entire rice value chain (Somado et al. 2008).

Blast Disease in an Era of Increasing Rice Demand in SSA

The importance of rice blast disease. Rice blast originated in Asia and spread to the rest of the world with the expansion of rice production (Saleh et al. 2014). The disease was first named "rice fever disease" in China, as early as 1637 (Yingxing 1637). It was first reported in SSA in 1922 and has since become the most devastating and widespread disease of rice (Bidaux 1978; Séré et al. 2011). Blast occurs at all growth stages, infecting leaves (foliar blast), collar (collar blast), panicle (panicle blast), and neck (neck blast) (Fig. 2) and contaminating rice seed. Neck blast causes the highest economic losses because the pathogen destroys vascular tissue in the panicle and prevents grains from filling (Ghatak et al. 2013). The disease is well-known to be most severe under water stress and/or high nitrogen levels. In the past two decades, blast disease has caused yield losses of up to 100% across the continent. Country-specific reports show the following percent grain yield losses: Ghana and some parts of Gambia, up to 100%; Nigeria, 35 to 65%; Burkina Faso, rainfed lowland 1 to 22% and irrigated systems 4 to 45%; Sierra Leone, more than 80%; Kenya, 48%; other east African countries, 30 to 40% (Chuwa 2016; Fomba and Taylor 1994; Kihoro et al. 2013; Nutsugah et al. 2005; Onaga and Asea 2016; Séré et al. 2011).

The spread of *M. oryzae* across SSA has been facilitated by human activities, such as trade and sharing contaminated rice seed. Due to increasing demand for rice, African rice growers are always looking for improved seed from multiple sources, but often without adherence to biosafety regulations (Ministry of Agriculture – Kenya 2008). Ineffective regulations for movement of seed and lack of access to seed testing facilities are therefore major drivers for the

Table 1. Regional goals for rice production in sub-Saharan Africa[a]

Country/region	Policy date	Production by date of policy (1,000 tons per annum)	Projected year of the goal	Projected production (1,000 tons per annum)
West Africa				
Benin	2008	110	2018	700
Burkina Faso	2008	195	2018	537
Nigeria	2008	3,316	2018	12,470
Senegal	2008	968	2017	1,601
East Africa				
Kenya	2008	52	2018	179
Rwanda	2008	66		374
Tanzania	2008	899	2018	1,963
Uganda	2008	178	2018	689

[a] Source: Coalition for African Rice Development (CARD) Final Review Assessment Report, March 2018. https://riceforafrica.net/images/stories/PDF/FinalReviewAssessment_mar2018.pdf

spread of the rice blast pathogen across different countries within the continent. Because the major source of primary inoculum for rice blast is rice seed, rice growers must be informed about proper phytosanitary measures. Furthermore, there is a need to establish effective regional blast surveillance programs, monitoring, and joint mitigation strategies, including regional research and gene deployment efforts (Figs. 3, 4, and 5).

Cultivation practices and the prevailing environment affect occurrence and severity of rice blast (Defoer et al. 2004; Tsujimoto et al. 2019). As intensification and expansion of rice production continues, the crop is now being cultivated in environments such as rainfed upland agro-ecologies that are more prone to rice blast (Ahmadi et al. 2004). The area under rainfed upland ecologies is greater in western (44%) compared with eastern (15%) African countries (Defoer et al. 2004). Another potential driver of rice blast could be the high frequency and rate of nitrogenous fertilizer application, particularly in West Africa (Long et al. 2000; Tsujimoto et al. 2019). There is a need to establish holistic strategies that integrate environmental, pathogen, and human capacity development aspects in management of blast disease (Fukuta et al. 2019; Odjo et al. 2014).

Current blast management strategies and implications to rice growers. To enhance rice production, it is essential to manage rice blast effectively using economically and environmentally sustainable approaches. Although there are some widespread common rice blast management practices, specific approaches are unique to some production ecologies, seasons, and regions. In most cases, there is a need to manage more than one disease. Because rice is mainly cultivated by resource-poor farmers, there are obvious farm-to-farm differences observed in the frequency of blast disease, even when similar cultivars are grown within a small geographical region. Such differences occur due to variation in crop management practices. The effect of crop management is more pronounced in farms without support of trained staff. Based on our own experiences in rice

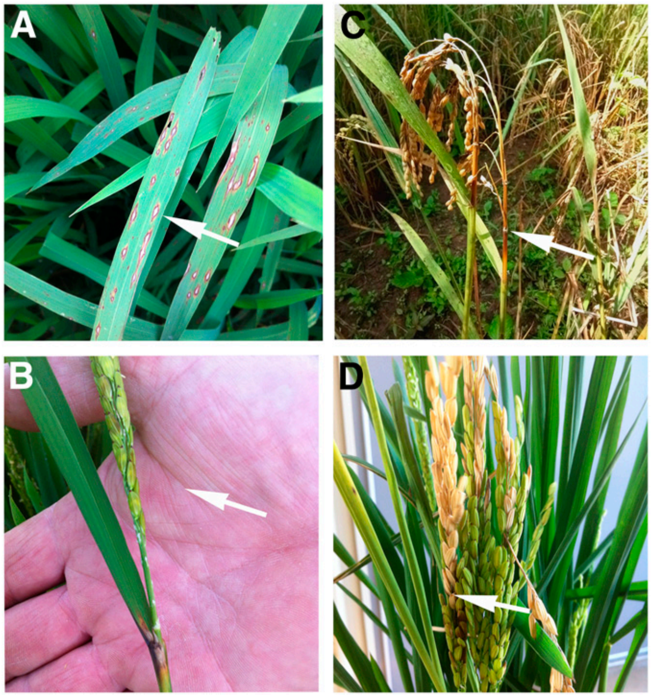

Fig. 2. Rice blast disease symptoms at different stages of development in the plant, from field sites across sub-Saharan Africa. **A,** foliar blast; **B,** collar blast; **C,** neck blast; and **D,** panicle blast. A and B were kindly provided by Dr. Yeshi Wamishe (associate professor, extension plant pathologist, University of Arkansas, Division of Agriculture, Rice Research and Extension Center, Stuttgart, AR); C and D were provided by project partners in Burkina Faso.

Fig. 3. Illustrations of an 8-year effort building a multinational team to tackle rice blast disease in sub-Saharan Africa. Drs. Correll (University of Arkansas, U.S.A., left) and Ouedraogo (INERA, Burkina Faso, right) at INERA offices (**A**) and thereafter visiting a rice breeding site (**B**) (Burkina Faso); **C,** Dr. Drissa Silué, a plant pathologist at AfricaRice Center, Cotonou, Benin, now relocated to Abidjan, Côte d'Ivoire (left), Dr. Correll (center), Dr. Moussa Sie (a rice breeder at AfricaRice Center, right). Drs. Sie and Drissa participated in development of the New Rice for Africa, NERICA cultivars; **D,** Drs. Correll, Ouedraogo, and Thomas Mitchell (Ohio State University, U.S.A.) and colleagues at the Kenya Agricultural and Livestock Research Organization (KALRO; formerly KARI), Nairobi, Kenya; **E,** team visit to the Biosciences eastern and central Africa Hub, a regional laboratory facility that builds partnerships to facilitate application of molecular biology tools in African research systems; The team has established blast screening at multiple hotspots in East and West Africa; **F,** Drs. Kimani (KALRO) and Mutiga (University of Arkansas/BecA-ILRI Hub) at a hotspot where adapted rice cultivars, breeding populations, and blast differential lines were evaluated in Kenya, 2017–2020.

farming systems in Africa, blast disease is more likely to be a serious problem in small-holder farms compared with large-scale production facilities. Below, we highlight chemical, cultural, and host resistance methods for rice blast management and their implications for rice farming systems in SSA.

Chemicals have been used for direct control of rice blast with some success in African countries, such as Burkina Faso and Kenya (Gianessi 2014). Fungicides recommended for control of blast disease include carbendazim, edifenphos, triadimefon, and tricyclazole (Seebold et al. 2004; Tuli et al. 2017). A soil amendment with silicon, or a foliar spray with or without tricyclazole or edifenphos, have also significantly reduced blast disease severity and incidence (Seebold et al. 2004). Although fungicides show potential for management of blast disease, there are many challenges that hinder their use in SSA. First of all, their cost is often prohibitive such that they are mainly used in a limited number of African countries (e.g., Nigeria and Malawi) due to government subsidies (Sheahan and Barrett 2017). Second, there are environmental concerns due to inappropriate application of pesticides and potential health hazards. There has been a new trend to use natural plant extracts to protect rice against pests and diseases and this approach has been suggested to mitigate some of the negative environmental impacts of synthetic pesticides (Kassankogno et al. 2015; Mohammed et al. 2019).

Cultural control of blast involves practices to alter the crop ecosystem, accompanied by a choice of improved rice cultivars to reduce the impact of *M. oryzae*. Among the frequently applied cultural practices for blast management are: i) optimal application of water, because drought stress, or even suboptimal flood depth, leads to increased susceptibility of rice to *M. oryzae* (Carrijo et al. 2018; Wamishe et al. 2018); and ii) optimal application of soil fertilizers, because suboptimal rates have been associated with increased blast severity (Long et al. 2000). Application of silicon-containing fertilizers on rice has been shown to reduce severity of blast in rice (Seebold et al. 2000). Finally, iii) choice of adapted and improved rice cultivars can enhance resilience of the crop and could reduce vulnerability to diseases such as blast (Acevedo et al. 2020).

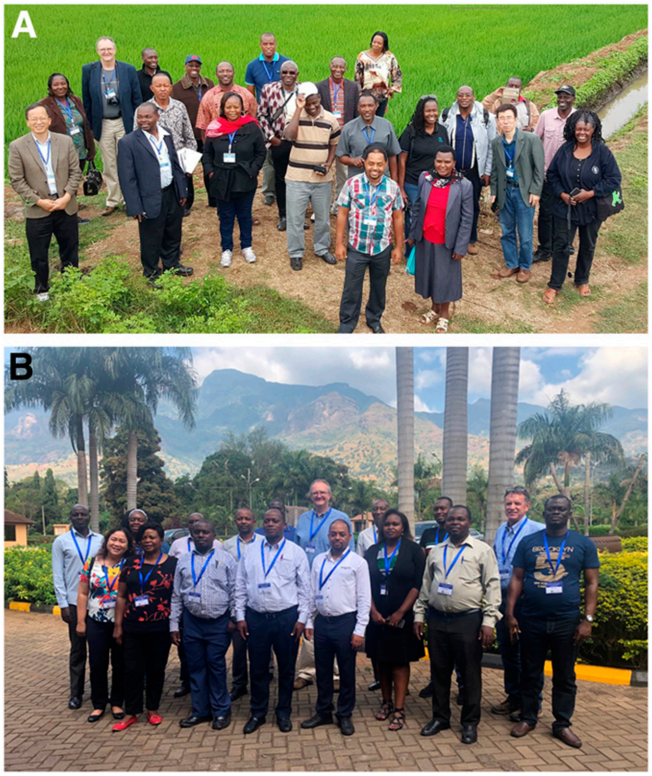

Fig. 4. Participants at Durable Rice Blast Resistance for sub-Saharan Africa meetings. **A,** Annual meeting held at Palace Hotel, Arusha, Tanzania, 22-24 July 2017; **B,** inception meeting held 11-15 August 2019 at Nashera Hotel in Morogoro, Tanzania.

Breeding for blast resistant cultivars is likely to be critical for future management of blast. Host resistance to rice blast attained through plant breeding is likely to be more sustainable than other approaches. However, because blast resistance can be overcome through genetic changes in the pathogen population, there is a need to adopt integrated strategies that would enable durability of disease control. More importantly, there is a need to consider additional farmer-preferred traits to ensure that developed cultivars are acceptable to both farmers and consumers (Table 2). In our current research effort, we therefore focus on pooling resources to generate blast resistant rice cultivars to reduce the impact of the disease in SSA.

Blast Resistance Mechanisms and Utility of Resistant Rice Cultivars in SSA

The use of host resistance to safeguard rice against blast is the preferred, most effective, and most economic option for rice growers worldwide (Li et al. 2019). In SSA, breeding for durably resistant rice cultivars will be of particular economic importance to small-scale rice growers, because they cannot afford the costs of other recommended disease management methods. If blast resistance can be provided in improved rice cultivars, farmers will require less application of fungicides. Reduced use of fungicides will have a significant positive impact on the wider environment and to the carbon footprint of rice cultivation. Reduced use of pesticides will also lead to lower costs of rice production, and hence more profits for farmers and increased access of food to consumers across SSA.

Breeding for blast resistance in SSA is the best sustainable solution for three main reasons. First, known blast disease resistance genes have been identified in several international rice germplasm collections, in addition to other forms of resistance. Second, we and others have observed phenotypic differences in blast resistance among currently cultivated rice cultivars in various African countries. Thirdly, previous research based on large-scale pathotyping has shown that some monogenic rice lines carrying known blast resistance genes have not been overcome by common isolates of *M. oryzae* found in SSA.

Host resistance can be achieved through breeding for resistance using either conventional, marker-assisted selection, and/or genetic engineering methods (Ashkani et al. 2015). Due to lack of access to affordable high throughput technologies, breeders in most developing countries have predominantly relied on conventional selection to improve cultivars over several decades (Lenaerts et al. 2019). Recent advances in DNA technologies have, however, led to improvements in their affordability. In addition, establishment of centers of excellence, such as the Biosciences eastern and central Africa – International Livestock Research Institute (BecA-ILRI Hub) that can support molecular breeding in developing countries has provided new hope toward accelerating gains of selection in SSA (Fig. 3). Thus, it is now possible to apply molecular breeding approaches involving DNA markers, such as QTL mapping, marker-aided selection, gene pyramiding, allele mining, and genetic transformation in SSA. Given their low cost, these high-throughput methods can make breeding programs more efficient to facilitate rapid introgression of resistance genes into susceptible varieties (Ashkani et al. 2015).

To facilitate molecular breeding, blast resistance must first be identified in existing germplasm, and genomic regions or genes associated with blast resistance determined. Globally, many genes conferring blast resistance have been mapped and cloned (Table 3) (Li et al. 2019). Most known blast resistance genes, or *Pi* genes, encode nucleotide binding site-leucine-rich repeat (NBS-LRR) proteins and are able to recognize pathogen-derived effectors encoded by avirulence genes to activate effector-triggered immunity (ETI) (Jones and Dangl 2006). The relationship in which a plant disease resistance gene recognizes a corresponding pathogen effector gene is well known and follows the gene-for-gene model (Flor 1971). Due to differences in virulence spectra of isolates of *M. oryzae* from different regions, effective *R*-genes inevitably vary among cultivated rice lines in SSA. Thus, the best model for breeding for durable disease resistance must also include an understanding of pathogen population biology, because selection pressure on the pathogen population is based on deployed rice cultivars (Depotter and Doehlemann 2020; Sánchez-Vallet et al. 2018).

Some *Pi* genes have been introgressed into rice cultivars in various breeding programs in different parts of the world, but similar efforts have been lacking in SSA (Miah et al. 2013). To utilize the knowledge of known resistance genes in African rice breeding programs, several approaches can be applied individually or in combination (Fig. 6). First, the utility of resistance genes must be tested against collections of *M. oryzae* isolates from SSA through inoculation of plants carrying individual *Pi* genes (monogenic lines) under controlled conditions, or at blast hotspots. Second, given that a lack of adaptation of tested rice germplasm may make a cultivar susceptible to multiple stresses during hotspot evaluation, prior introgression into an adapted rice background may also be needed. Third, a breeding strategy that involves gene pyramiding needs to be developed to combine *Pi* genes with other resistance specificities that can safeguard the cultivar against a diverse set of tested pathogen populations (Tables 3 and 4). The newly developed breeding populations must then be tested at blast hotspots. Finally, new resistance genes can also be identified in adapted rice cultivars, and associated markers could then be utilized in marker-assisted or genome-wide selection breeding programs to improve cultivated rice germplasm. Cultivars should then undergo multilocational trials and registration through established national procedures.

To the best of our knowledge, very few research programs have attempted to identify *Pi* genes or associated loci in African rice germplasm (Mgonja et al. 2016, 2017). Through studies conducted within our consortium, several major and many minor quantitative trait loci (QTLs) for blast resistance were identified in a diverse panel of rice of African rice cultivars. These QTLs are good candidates for new resistance loci and can therefore be used in marker-assisted breeding programs. Similarly, analyses of disease reactions using the international rice blast differential lines (IRBLs), based on inoculations with over 100 isolates of *M. oryzae* originating from nine African countries, have identified *Pi9* as the most effective individual *R* gene in SSA (Mutiga et al. 2017). This screening information has then been used to establish the breeding strategy described later in this review.

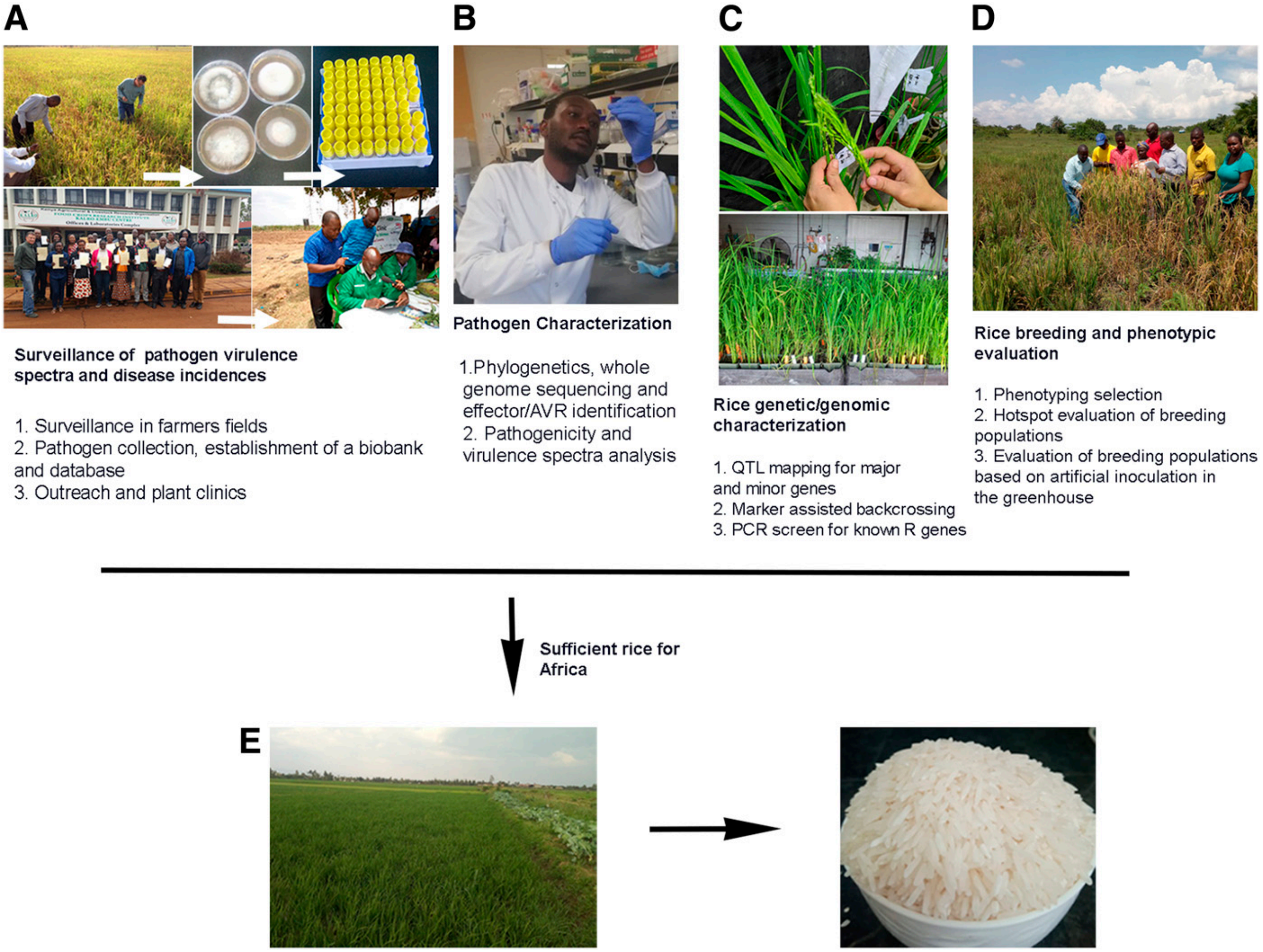

Fig. 5. Collaborating research institutions and their roles in enhancing durable rice blast resistance in sub-Saharan Africa. **A,** Dr. Correll (University of Arkansas) and colleagues collect symptomatic leaves in Mwea, Kenya, from which isolates of *Magnaporthe oryzae* are cultured and stored in cryo-tubes; training and award of certificates to Kenyan agricultural extension officers on diagnosis of rice diseases; trained officers apply skills in field-based Plant Clinics and relay data through a web-based tool to a shared national repository. **B,** Dr. Vincent Were (The Sainsbury Laboratory, UK) preparing genomic DNA for sequencing. **C,** Dr. Mary-Jeanie Yanoria (International Rice Research Institute, IRRI, Los Baños, Philippines) prepares rice plants to introgress *Pi9* R gene into Basmati 370 (top). Blast symptoms in an artificially inoculated diverse panel of rice used in genome-wise association studies (GWAS) in Wang Lab, The Ohio State University (bottom). **D,** Scientists from the Kenya Agricultural and Livestock Research Organization (KALRO) and Biosciences eastern and central Africa-International Livestock Research Institute, BecA-ILRI Hub observe high vigor and grain yield of one of the promising cultivars in August 2019 at Alupe, a blast hotspot evaluation site in Busia County, Kenya. **E,** A rice field with no symptoms of disease or any pest damage at West Kano, Kisumu, Kenya (left) and a bowl full of milled rice grain symbolizing sufficient food for the people of Africa (right). All photographs were taken during different activities of members of this blast research team.

Resources for Development of Durably Resistant Rice Cultivars for SSA

Resource 1: Rice germplasm developed through past breeding efforts. Native African rice, *Oryza glaberrima*, has been cultivated for the past 2,000 to 3,000 years in several West African countries (Linares 2002). Owing to the excellent adaptative traits of native African rice, breeders have evaluated and released a series of these cultivars for cultivation in different agro-ecologies of SSA (Linares 2002; Rutsaert et al. 2011). Further efforts have since focused on improvement of adapted rice germplasm to acquire traits of Asian rice (*Oryza sativa*), because these are preferred by urban consumers (Gridley et al. 2002; Tollens et al. 2013; Wopereis 2013). Below, we provide a brief history of past efforts and resultant cultivars, as these affect the current and future rice genetic improvement activities in SSA. More importantly, a knowledge of these cultivars and their performance in associated agro-ecologies is important to practical breeders who want to utilize the germplasm in regional efforts.

The West Africa Rice Development Association (WARDA; later renamed AfricaRice) is responsible for important efforts to improve the native African rice germplasm (Tollens et al. 2013). Early breeding initiatives in the 1970s and 1980s by WARDA involved attempts to introduce improved rice cultivars from other parts of the world, particularly from Asia through collaborative efforts of the International Rice Research Institute (IRRI), International Institute of Tropical Agriculture (IITA), and Institut de Recherche Agronomique Tropicale (IRAT). WARDA conducted multilocational trials of introduced germplasm to identify the best performing cultivars in different environments, as described in the rest of this section (Tollens et al. 2013).

Between 1988 and 1990, WARDA gave specific subcenters the responsibility of developing lines that performed best in the corresponding agro-ecologies (upland at M'bé, Côte d'Ivoire; lowland at IITA, Ibadan, Nigeria; irrigated systems at Saint-Louis, Senegal; and the mangrove-swamp environment based at the Rokupr research station, Sierra Leone). Rice lines were designated based on breeding

Table 2. Agronomic traits and field-based blast reactions in popular rice cultivars of sub-Saharan Africa

Cultivar name	Pedigree	Maturity (days)	Aroma	Panicle color	Ecology[a]	Blast reaction[b]	Yield (t ha^{-1})	Country where cultivated[c]
Basmati 217	NIBAM 10	140	Strong	Straw	LI	S	3	KE
Basmati 370	NIBAM 11	110	Strong	Straw	LI	S	3.5	KE
IR 2793-80-1	NIBAM 108	160	None	Straw	LI	S	4	KE
BW 196	NIBAM 109	170	None	Straw	LI	R	6	KE
ITA 310	NIBAM 110	105	None	Straw	LI	S	5	KE
NERICA 1	WAB 450-I-B-P-38-HB	93–120	Yes	Pale Purple	UI	S	2–4.0	KE; TZ
NERCA 2	WAB 450-11-1-P31-1-HB	95–100	None	Golden	UR	S	4.0–5.0	TZ
NERICA 4	WAB 450-I-B-P-91-HB	95–125	None	Golden	UI	S	3.0–6.0	KE; TZ; UG
NERICA 7	WAB 450-1-B-P-20-HB	90–100	None	Golden	UR	S	6.0–6.5	TZ
NERICA 10	WAB 450-11-1-1-P41-HB	90–100	None	Black/purple	UI	S	2.5–3.0	KE
NERICA 11	WAB 450-16-2-BL2-DV1	85–95	None	Golden	UI	S	1.8–2.0	KE
Komboka (IR 05N221)	IR 74052-297-2-1/IR 71700-247-1-1-2	100–140	Yes	Golden	LR/LI/UI	S	5–6.5	KE; TZ; UG
MWIR 2	Unknown	120	None	Golden	LI/LR	MR	4.5	KE
MWUR 4	Unknown	125	None	Golden	UR	MR	4	KE
Dourado precoce	Brazil	120	None	Golden	UR	MR	4.2	KE
SARO 5 (TXD 306)	Supa/Pyongyang 8//Subarimati/Supa	120–135	Mild	Golden	LR/LI	S	5–8.5	KE; TZ; UG
TXD 88	Supa/KM 67//Subarimati	120–125	none	Golden	LR/LI	S	7.0–8.8	TZ
TXD 85	SUPA/KM 67	110–120	None	Golden	LR/LI	S	6.0–6.5	TZ
SUPA Kilombero	Unknown	120–135	Strong	Golden	LR	S	2.0–3.0	TZ
WAB 450	CG 14 × WAB 56-104	93–100	None	Golden	UR	S	5.5–6.0	TZ
SATO 1	Unknown	110–120	None	Golden	LR/LI	S	6.5–7.0	TZ
SATO 9	Unknown	110–120	None	Golden	LR/LI	S	7.0–8.4	TZ
Wita 9	IR 2042-178-1/CT 19	130	Mild	Golden	LI	S	6.0–7.5	UG
Kaiso (K5)	Unknown	130	None	Golden	LR	S	4.0–5.0	UG
Supa (Surinam V-880)	Unknown	160	Strong	Golden	LR	S	3.0–3.5	KE; UG
NamChe-5 (NM7-27-1-B-P-77-6)	CT 16317-CA-4-M/WAB 365-B-1H1-HB	125	No	Golden	LR/UR	R	5.0–6.0	UG
NamChe-1 (WAB 95-B-B-40-HB)	TA 257/(IDSA 6/ROK 16)	125	No	Golden	LR/UR	R	5.0–6.0	UG
NamChe-3 (NM 7-29-4-B-P-80-8)	CT 16342-CA-25-M/CK 73	120	No	Golden	LR/UR	R	5.0–6.0	UG
Kaiso (K85)	Unknown	130	No	Golden	LR/LI	S	4–5	UG
Kaiso (K98)	Unknown	135	No	Golden	LR	S	4–5	UG
Abenego (Landrace)	Unknown	125	No	Golden	LR	S	5–6	KE; UG
Musesekara (IR 13A256)	IR 68897B/IR 73013-95-1-3-2 R	131	No	Golden	LI	R	6–7	BI
Gwizumwimbu (IR 79511-47-2-6-5)	IR 72158-11-5-2-3 (IRRI)/Janaki (Nepal)	138	No	Golden	LI	R	6–7	BI
Kazosi (IR 87546-84-3-3-2)	IR 05N173/BR 29	131	No	Golden	LI	R	5.6–7.26	BI
Mugwiza (IR 91028-115-2-2-2-1)	IR 01A111/MTU 1010	135	Yes	Golden	LI	R	4.0–6.0	BI
WAB 2099 (WAB 2099-WAC 1-TGR5-B)	Unknown	149	No	Golden	LI	U	4.5–5.6	BI

[a] LI = lowland irrigated; LR = lowland rainfed; UR = upland rainfed; UI = upland irrigated.
[b] MR = moderate resistance; R = resistant; S = susceptible
[c] BI = Burundi; KE = Kenya; TZ = Tanzania; UG = Uganda.

subcenters of origin as follows: WAB in Côte d'Ivoire, WAT in Nigeria, WAS in Senegal, and WAR in Sierra Leone. The nomenclature was, however, changed in 2010 to ARS in Senegal, ART in Nigeria, ARB in Côte d'Ivoire, and ARC for Cotonou, Benin, reflecting the name change from WARDA to AfricaRice. The most promising rice lines bred or introduced for rainfed lowland and irrigated ecosystems, south of the Sahel zone, were included in the WITA series, the most well-known being WITA 4 (from line TOX 3100-44-1-2-3-3) (Tollens et al. 2013). The Sahel zone refers to an ecoclimatic and biogeographic zone of transition in Africa between the Sahara to the north and the Sudanian savanna to the south, including a 1,000-km belt cutting through Mauritania, Senegal, Burkina Faso, Mali, Niger, Nigeria, Chad, South Sudan, Sudan, and Ethiopia. A task force oversaw development of high-yielding, irrigated rice cultivars tolerant to the prevalent abiotic stress factors of heat, low rainfall, and salinity in the Sahel region. Thus, the initial set of Sahel cultivars included short duration Sahel 108 (IR 13240-108-2-2-3, an IRRI line), and medium-duration cultivars Sahel 201 (BW 293-2) and Sahel 202 (ITA 306). These lines were first introduced in 1994 and widely adopted by rice farmers within 5 years (Kohl 2016). By 2012, new aromatic Sahel cultivars (Sahel 177, Sahel 328, and Sahel 329) had been widely adopted in Senegal. For the upland environment, the most popular cultivars were WAB 56-50, WAB 56-104, and WAB 56-125 (Tollens et al. 2013).

Table 3. Contemporary list of characterized rice genes associated with partial and complete resistance to blast disease

Chromosome	Gene	Marker[a]	Donor rice	Resistance type	Reference
1	*Pit*	SNP	Tjahaja	Complete	Hayashi et al. 2010
	Pi27(*t*)	SSR	Q 14	Complete	Zhu et al. 2004
	Pitp(*t*)	SSR	Tetep	Partial	Barman et al. 2004
	Pi35(*t*)	SSR	Hokkai 188	Partial	Nguyen et al. 2006
	Pi37	SSR	St. No.1	Complete	Lin et al. 2007b
	Pi64	SSR	Yangmaogu	Complete	Ma et al. 2015
	Pish	RFLP	Shin 2	Complete	Takahashi et al. 2010
2	*Pi-d*(*t*)*1*	SSR	Digu	Complete	Chen et al. 2004
	Pig(*t*)	SSR	Guangchangzhan	Complete	Zhou et al. 2004
	Pitq5	RFLP	Teqing	Complete	Tabien et al. 2000
	Pib	SNP	Tohoku, IL 9, Koshiihikari	Complete	Hayashi et al. 2006
	Pi14(*t*)	Isozyme	Maowang	Complete	Tabien et al. 2000
	Pi16(*t*)	Isozyme	AUS 373, Maowamg	Complete	Pan et al. 1996
3	*Pi66*(*t*)	SSR	AS 201	Partial	Liang et al. 2016
4	*pi21*	STS	Owarihatamochi	Partial	Angeles-Shim et al. 2020
	Pi63	SSR	Kahei	Partial	Xu et al. 2014
	Pi5(*t*)	RFLP	RIL 29 (Morobere kan)	Complete	Lee et al. 2009; Wang et al. 1994
5	*Pi10*	InDel	Tongil	Complete	Wu et al. 2005
6	*Pi26*	RFLP	Gumei 2	Complete	Ahn et al. 1996; Wu et al. 2005
	Piz-5	STS	Tadukan	Complete	Hittalmani et al. 2000
	Piz	InDel	Zenith	Complete	Hayashi et al. 2006
	Piz-t	InDel	Toride 1	Complete	Zhou et al. 2006
	Pi9	STS	75-1-127 (101141)	Complete	Qu et al. 2006; Zhou et al. 2020
	Pid2	CAPS	Digu	Complete	Chen et al. 2006
	Pitq1	RFLP	Teqing	Complete	Zhou et al. 2004
	Pi8	Isozyme	Kasalath	Complete	Pan et al. 1996
	Pi13(*t*)	Isozyme	Kasalath	Complete	Ebitani et al. 2011
	Pi2(*t*)	RFLP	Cultivar 5173	Complete	Liu et al. 2002; Yu et al. 1991
	Pi50(*t*)	SSR	Jefferson	Complete	Su et al. 2015; Zhu et al. 2012
8	*Pi33*	SSR	IR 64, Bala	Complete	Berruyer et al. 2003
	Pizh/*Pi11*(*t*)	RFLP	Zhaiyeqing	Complete	Zhu et al. 1993
	Pi36	SSR/InDel	Q 61	Partial	Jiang et al. 2019; Liu et al. 2007
9	*Pi5*(*t*)	CAPS	RIL 125, RIL 249, RIL 260 (Moroberekan)	Complete	Lee et al. 2009; Wang et al. 1994
	Pi-15	SSR	GA 25	Partial	Lin et al. 2007a
11	*Pia*	CAPS	Aichi Asahi	Complete	Zeng et al. 2011
	PiCO39(*t*)	CAPS	CO 39	Complete	Chauhan et al. 2002
	Pilm2	RFLP	Lemont	Complete	Tabien et al. 2000
	Pi7(*t*)	RFLP	RIL 29 (Moroberekan)	Complete	Campbell et al. 2004
	Pikm	InDel SSR	Tsuyake	Complete	Ashikawa et al. 2008
	Pik	InDel	Kusabue	Complete	Zhai et al. 2011
	Pik-p	SNP	HR 22	Complete	Yuan et al. 2011
	Pik-s	SSR	Shin 2	Complete	Fjellstrom et al. 2004
	Pi47	SSR	XZ 3150 × CO 39	Complete	Huang et al. 2011
	Pi60(*t*)	InDel	93-11	Complete	Lei et al. 2013
	Pi-jnw1	SSR; InDel	Jiangnanwan	Complete	Wang et al. 2016b
12	*Pi24*	RGA	Zhong 156	Complete	Zhuang et al. 2002
	Pitq6	RFLP	Teqing	Complete	Tabien et al. 2000
	Pita	SNP;RAPD	Taducan; Yashiro-mochi	Complete	Bryan et al. 2000; Kiyosawa 1966
	Pi20(*t*)	SSR	IR 24	Complete	Li et al. 2008
	Pita-2	SNP	Shimokita	Complete	Hayashi et al. 2006
	Ptr	SSR	Katy		Bryan et al. 2000
	Pi48	SSR	XZ 3150 × CO 39	Complete	Huang et al. 2011
	Pi61(*t*)	InDel	93-11	Complete	Ma et al. 2014

[a] CAPS = cleaved amplified polymorphic sequence; InDel = insertions or deletions; SSR = single sequence repeat; SNP = single nucleotide polymorphism; RAPD = random amplified polymorphic DNA; RGA = resistance gene analogs; RFLP = restriction fragment length polymorphism; STS = sequence-tagged sites.

A considerable effort was made to import and improve Asian rice cultivars that perform well under African conditions, particularly where water control was problematic, but success proved elusive. A concerted effort was therefore launched to incorporate desirable local traits from *O. glaberrima* into high-yielding *O. sativa*. WARDA scientists crossed the two species and following embryo rescue and other wide-hybridization techniques, made backcrosses with reasonably productive *O. sativa* varieties to obtain "the new rice for Africa" (NERICA) cultivars between 1994 and 1996 (Gridley et al. 2002; Somado et al. 2008). NERICA lines were improved compared with earlier cultivars from other individual programs within the respective countries and have now been adopted by farmers in over 320,000 hectares across Africa (Wopereis 2013).

Efforts to improve earlier rice cultivars to boost commercial production and resilience (superior performance under prevalent abiotic and biotic stresses) across SSA led to a series of multilocational testing and selection of diverse germplasm between 2010 and 2013. The outcome of the effort was identification of cultivars that suit different ecologies in different countries. These were named the Advanced Rice for Africa (ARICA) cultivars (Saito et al. 2018; Somado et al. 2008; Wopereis 2013). To date, 18 cultivars have been named to form the ARICA panel (Wopereis 2013). The desirable traits for a rice cultivar to be included in the ARICA group include superior grain yield and resilience over other cultivated genotypes in tested countries (Wopereis 2013). ARICA cultivars can be considered the next generation of rice cultivars for Africa, after the initial success of NERICAs and earlier improved cultivars (Tollens et al. 2013).

Additional efforts to boost rice grain yield were focused on development of hybrid rice cultivars, because those imported directly from China showed disappointing performance under multilocation trials in SSA (El-Namaky and Demont 2014). Hybrids adapted to African conditions have been developed using tropical materials and cytoplasmic male sterility from IRRI and AfricaRice breeding programs (El-Namaky and Demont 2014). In parallel, Egypt led in African efforts to develop and commercialize hybrid rice (El-Namaky and Demont 2014). Due to grain yield potential, hybrid rice is now being adopted by commercial growers in the rest of SSA (El-Namaky and Demont 2014).

Relevance of environmental adaptation of rice germplasm in breeding for resistance to blast. Studies have shown significant differences in variation of virulence of *M. oryzae* across environments, countries, and regions in SSA (Table 4). These findings imply that rice breeders should introgress blast resistance genes into adapted backgrounds to enhance phenotypic stability of resultant cultivars (Dixit et al. 2014; Mutiga et al. 2017). Rice breeding efforts

Table 4. A biobank of *Magnaporthe oryzae* in which isolates varying virulence spectra from rice growing countries in Africa are stored at the International Livestock Research Institute Research Facility with backups at The Kenya Agricultural Livestock and Research Organization, The University of Arkansas-Fayetteville, AR, U.S.A., and The Sainsbury Laboratory, UK.

Country of origin	Number of isolates[a]	Rank of virulence[b]
Benin	19	4
Burkina Faso	150	9
Ghana	3	1
Kenya	232	7
Mali	3	5
Nigeria	45	6
Tanzania	25	3
Togo	8	2
Uganda	5	8
Total	490	

[a] Represents the collections made from individual countries through the current research effort.

[b] Ranking is based on frequency of virulent strains of *M. oryzae* with 1 = highest frequency; 9 = least frequency; based on pathotype analysis previously reported in Mutiga et al. (2017).

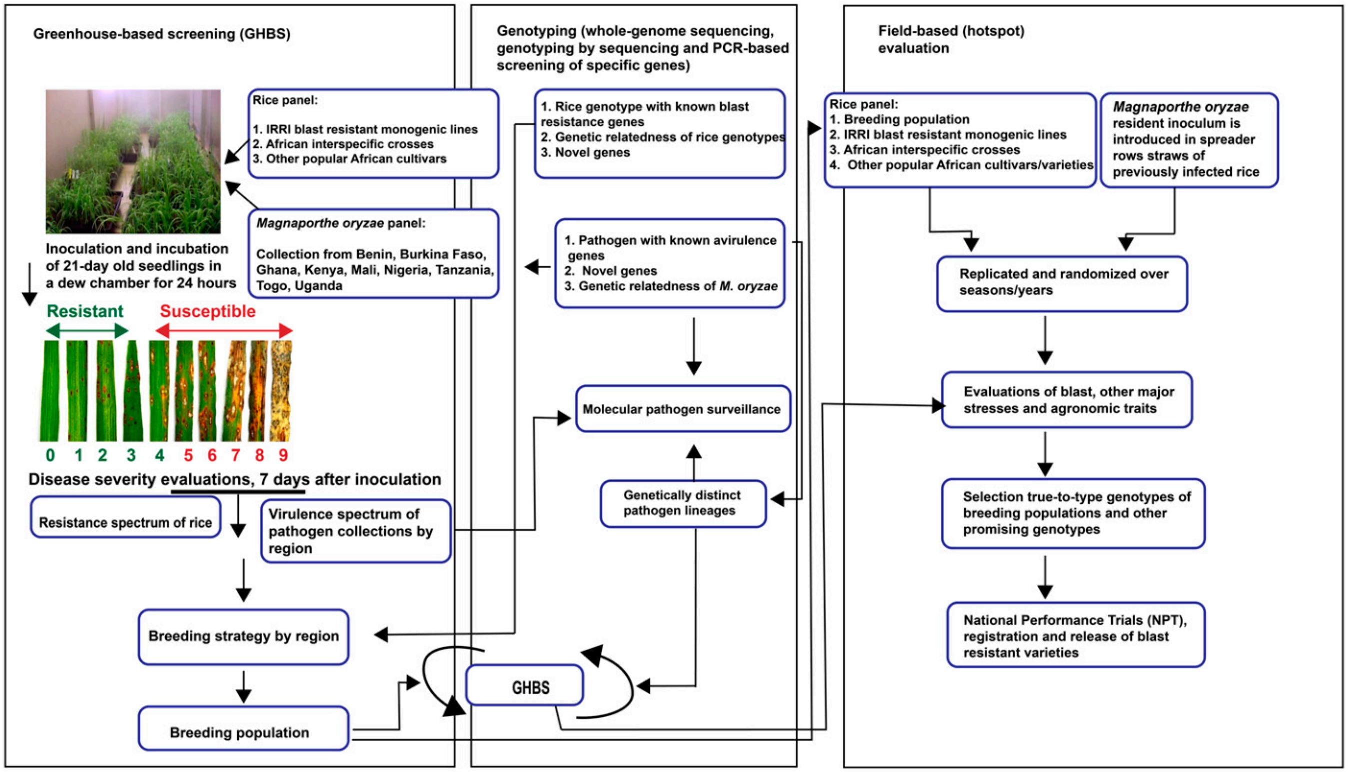

Fig. 6. Rice blast disease screening pipeline developed in the current effort for sub-Saharan Africa. The pipeline facilitates pathogen surveillance, rapid greenhouse testing, and predictive breeding based on the prevailing pathogen population, coupled with field tests at disease hotspots to evaluate new cultivars for development to proceed to national performance trials and variety registration.

can then, for example, be anchored on germplasm derived from *O. glaberrima*, which is native and therefore has valuable agronomic traits (Mokuwa et al. 2013; Wambugu et al. 2013). However, the popularity of *O. glaberrima* has declined by 20% compared with Asian cultivars in West Africa and most parts of SSA (Bezançon and Diallo 2006; Wambugu et al. 2013). Blast breeding efforts therefore need to consider relative benefits of rice germplasm with both *O. sativa* and *O. glaberrima* genetic backgrounds (Veltman et al. 2019). NERICA and ARICA varieties were released in programs that aimed at bringing adaptive traits into genotypes that fit modern rice demands (Saito et al. 2018; Somado et al. 2008).

Different countries may also have preferred cultivars, based on their own traits of interest. Our collaborative team has gathered information on popular cultivars across several rice growing countries of SSA; the general response to blast disease and other preferred traits are shown in Table 2. Among preferred traits are aroma, time to maturity, panicle color, and grain yield (Table 2). While resistance to biotic stresses is a key factor in choice of cultivars, breeders have reported that farmers place a higher preference on other traits such as aroma, because this is associated with higher grain value at market. In commercial rice farming, consumer preferences tend to supersede farmer preference for grower traits. Thus, aromatic rice cultivars are generally susceptible to blast disease, yet they fetch higher market prices and are widely adopted in SSA (Singh et al. 2000). For example, Basmati 217, Basmati 370, Komboka, Supa Kilombero, and Supa Surinam V are very popular in East Africa despite being highly susceptible to blast disease (Table 2). A similar preference of cultivars Sahel 177, Sahel 328, and Sahel 329 is observed in West Africa, for example in Burkina Faso.

Rice breeding programs must therefore aim to develop high quality cultivars for both farmers and consumers. Farmers would like to produce rice at lower cost, by overcoming abiotic and biotic stresses through cultivation of a cultivar that carries most alleles for resilience. By contrast, consumers require the best characteristics in rice grain and straw. An effective breeding program must therefore evaluate the needs of both parties and combine traits preferred at both ends of the value chain. During the prebreeding stage, breeders assess these preferences and whether traits are influenced by environment (quantitative) or not (qualitative), because these affect the design of a breeding program.

Resource 2: Genomic Tools to Enhance Rice Blast Resistance in SSA

Genomic tools in biology of *M. oryzae* from SSA. Genomic tools can be used to study the effector gene repertoire of the *M. oryzae* population in order to gain insights into the most effective deployment of cultivars containing *R* genes. It is well known that rice *R* genes have corresponding pathogen effectors encoded by avirulence genes, many of which have been mapped to loci and identified (Dioh et al. 2000), as shown in Table 5. Known avirulence genes can thus be tested for their presence or absence in the prevailing pathogen population (Lopez et al. 2019). Knowledge of prevalent avirulence genes in each geographical area can thereby guide identification of corresponding *R* genes within rice cultivars (Tables 3 and 4), which can then be deployed most effectively to combat blast disease (Chuma et al. 2011; Wu et al. 2015; Zhang et al. 2015; Zhou et al. 2007). To gain insight into the genetic variability of blast pathogen populations, avirulence determinants can also be used to monitor frequencies of resistance gene breakdown and the possibility of host jumps by *M. oryzae*.

Table 5. Cloned avirulence genes of *Magnaporthe oryzae*

Avirulence gene	Matching *R*-gene	References
AvrPiz-t	*Piz-t*	Li et al. 2009
AVR Pi-ta	*Pi-ta*	Orbach et al. 2000
Avr1-CO39	*Pi-CO39*	Farman and Leong 1998
ACE1	*Pi33*	Böhnert et al. 2004
AvrPii	*Pii/Pi5*	Vo et al. 2019; Yoshida et al. 2009
AvrPia	*Pia*	Miki et al. 2009; Yoshida et al. 2009
AvrPik/km/kp	*Pik/km/kp*	Yoshida et al. 2009
PWL1	Not available	Kang et al. 2016
PWL2	Not available	Sweigard et al. 1995
AVR-Pi9	*Pi9*	Wu et al. 2005
AVR-Pib	*Pib*	Zhang et al. 2017
AVR-Pi54	*Pi54*	Ray et al. 2016
AVR-Rmg8	*Rmg8*	Anh et al. 2015

In addition to avirulence genes, a PCR-based screening of mating type loci of *M. oryzae* can shed light on potential shifts in pathogen population genetics and how this correlates with virulence (Table 5 and Fig. 6). Assessment of the presence of both mating type genes can, for example, be used to infer whether there is a risk of sexual recombination, particularly if there are also fertile female strains that can produce perithecia within the prevailing rice blast pathogen population (Odjo et al. 2021; Onaga et al. 2015; Saleh et al. 2012). Additionally, genotypic diversity analysis, based on genetic markers and vegetative compatibility groups, can also be used to investigate regional clustering, kinship, and associations between the pathogen virulence and the geographical region. Such information is important in development of pathogen surveillance programs, virulence monitoring, and the establishment of rice breeding strategies across SSA (Mutiga et al. 2017)

Surveillance and monitoring of genetic shifts in pathogen populations is important for a cultivar deployment strategy aimed at durable disease control (Xiao et al. 2020). A recent genomic strategy has, for instance, been developed to rapidly screen for shifts in a given pathogen population through a process named field pathogenomics (Hubbard et al. 2015). This technique uses advanced genomic tools to provide a high throughput reproducible approach for capturing the dynamics and diversity of a pathogen population in the field (Bueno-Sancho et al. 2017; Hubbard et al. 2015). Infected leaf samples are directly tested for pathogen genomic signatures and their characteristics, without isolation of the causal organism (Hubbard et al. 2015; Islam et al. 2016). To implement field pathogenomics in rice blast populations in SSA, a novel pipeline has been proposed for field use, named the mobile and real-time plant disease (MARPLE) system (Radhakrishnan et al. 2019), which involves use of a portable PCR machine to amplify target genes of interest and a portable Oxford nanopore sequencer for targeted genome sequencing (Fig. 7). Cloned and predicted putative effectors/avirulence genes can be enriched from DNA isolated from infected leaf tissue before sequencing (Fig. 7 and Table 5). Furthermore, other important virulence-related genes can also be sequenced to determine the virulence profile of field isolates, to infer phylogenetic relationships, and the evolutionary history of strains.

Genomic tools in rice blast resistance breeding. Attaining durable blast resistance will require robust tools to develop and deploy new cultivars across the diverse agroecologies of SSA. Previously, African breeding efforts did not have sufficient support with modern tools to boost efficiency in genetic gains, and breeders have mainly been funded by national governments to conduct trials and selection, across seasons and locations, for germplasm improvement. However, there is an ongoing transformation and establishment of centers of excellence using molecular biology tools to enhance international scientific research (e.g., BecA-ILRI Hub, https://www.ilri.org/research/programs/beca-ilri-hub, and AfricaRice Center, https://www.africarice.org/) (Fig. 3). There is also a strong focus on capacity building to enhance breeders' and pathologists' access to facilities to boost the utility of modern genomic tools for rapid genetic analysis and genetic gains in breeding. The African national agricultural research organizations are also embedding modern tools and molecular biology in their programs to enhance efficiency and have established strong international collaborations to boost these efforts (Fig. 3).

Genomic tools can be applied directly for improvement of rice cultivars for blast resistance. The use of PCR-based tests for identification of genes of interest in rice, for example, is now a common practice (Hayashi et al. 2006; Imam et al. 2014). This approach has been used to screen known genes associated with blast resistance in diverse collections of rice germplasm. Knowledge of the spectrum of major blast resistance genes (Table 3) within germplasm collections can enable breeders and pathologists to further test for their effectiveness, and to plan for parental crosses and/or a deployment strategy (Fig. 3). In marker-assisted breeding programs, PCR is used routinely to tag different *R* genes and thereby effectively introgress them into target backgrounds over backcross generations. Similarly, such genetic markers (Table 3) can be used in efficient selections such as pedigree and recurrent methods and improvement of important agronomic traits in germplasm containing blast resistance.

Genome-wide genotyping involves analysis of multiple DNA loci to identify genomic regions of interest in a genome. Such information has been used to assess the diversity of African rice germplasm and association of genetic clusters/chromosomal regions with blast resistance (Ndjiondjop et al. 2015; Odjo et al. 2017). Single nucleotide polymorphism (SNP) genotyping has been used, for example, to reveal the population structure and kinships of African rice germplasm (Orjuela et al. 2014). For a diverse panel, association mapping has been used, for instance, to identify important loci that can be fine mapped to identify novel blast resistance genes (Mgonja et al. 2017). For rice mapping populations (e.g., F_2, recombinant inbred lines, introgression lines, highly inbred families, multiparent advanced generation intercross, and nested association mapping), genotyping has been used to dissect the genetic architecture of blast resistance and to map loci linked to blast resistance in the population, derived from diverse parents (Kang et al. 1995; Kanyange et al. 2019; Urso et al. 2016). Low genotyping costs provide an opportunity for African scientists to incorporate genome-wide marker data into rice breeding programs (Tryphone et al. 2013).

Mutation breeding refers to random DNA manipulation by chemicals, radiation, or specific DNA sequences, to obtain rice mutants that are further selected for desirable traits (Kharkwal et al. 2004). Mutation breeding is aimed at identifying crop plants superior in phenotype to currently cultivated genotypes. The method rapidly generates mutations within the plant genome, but is tedious in selection of individuals with superior alleles (Holme et al. 2019). Although T-DNA-based insertional mutagenesis could provide many novel traits, particularly for rice breeders, it can also lead to difficulties due to regulations imposed on genetically modified organisms in most countries in SSA (Adenle 2011).

Genome editing now provides a highly efficient method for targeted modification of genomic loci that can affect the phenotype of rice. The technology, which is efficient and precise, has been in use for the last 10 years (first generation methods included zinc finger nucleases and transcription activator-like effector nucleases) (Zhang et al. 2018), but recent genome editing involving CRISPR/Cas9 has generated a lot of excitement in the scientific community because it is faster, cheaper, more accurate, and more efficient than other methods (Pickar-Oliver and Gersbach 2019). Unlike first-generation genome editing tools, CRISPR/Cas9 genome editing involves simple design and cloning methods (Jaganathan et al. 2018). Furthermore, the same Cas9 can be used with different guide RNAs that target multiple sites in the genome (Jaganathan et al. 2018). In a recent report, targeted editing of the transcription factor-encoding gene OsERF922 using CRISPR/Cas9, followed by selection of mutants for blast resistance, enabled identification of new blast-resistant genotypes of rice (Wang et al. 2016a). Thus, genome editing is an important tool in the toolbox of approaches for SSA breeding programs.

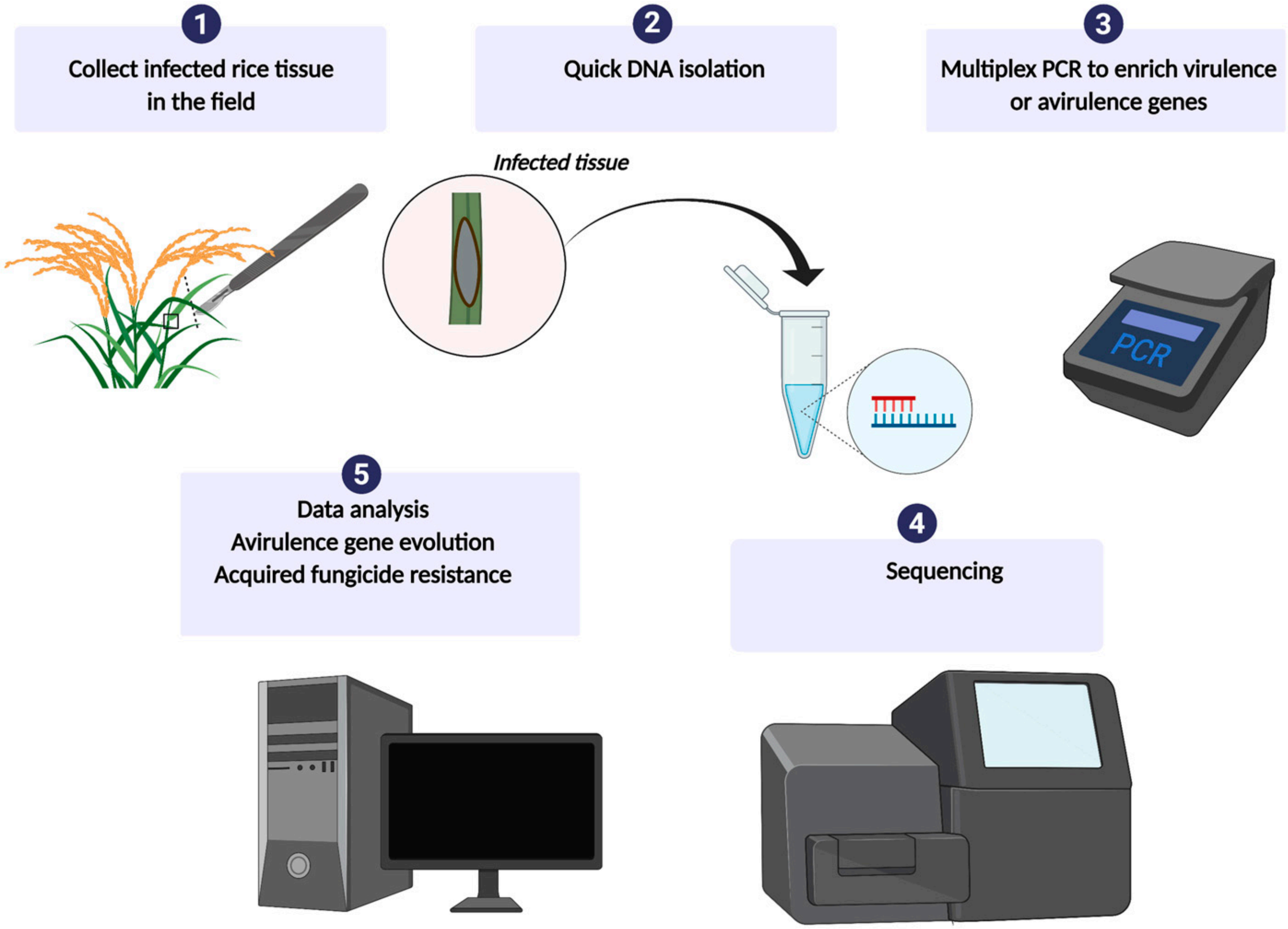

Fig. 7. Schematic illustration of a proposed field pathogenomics within rice blast surveillance pipeline. Rice leaf or neck infected tissue (1) is used for DNA isolation (2) and a portable multiplex PCR assay used to amplify and enrich selected *Magnaporthe oryzae* virulence and avirulence genes (3). Enriched genes of interest are sequenced (4) and used for data analysis (5).

Another promising technique is gene silencing, a molecular process by which expression of targeted genes is impaired or suppressed at the transcriptional or translational level (Souza et al. 2007). This method has been used to control papaya ringspot virus (Bau et al. 2003). Expression of *M. oryzae*-derived gene fragments in a BMV-mediated gene silencing system, a technique termed host-induced gene silencing, was also shown to block infection of rice by *M. oryzae* (Zhu et al. 2017).

Pooling Resources in "The Durable Rice Blast Resistance for Sub-Saharan Africa Project"

A brief highlight of an 8-year international collaborative effort in SSA. A collaborative research project was established in 2012 under the leadership of Drs. Nicholas J. Talbot and James Correll of the University of Exeter (now at The Sainsbury Laboratory, Norwich) UK, and the University of Arkansas, respectively. Partners include the national agricultural research systems (NARS) in East Africa (University of Embu, the Kenya Agricultural & Livestock Research Organization [KALRO], Tanzanian Agricultural Research Institute [TARI], and Ugandan National Agricultural Research Organization [NARO]) and West Africa (Burkina Faso's Environmental Institute for Agricultural Research [INERA]), international rice research centers based in SSA, including AfricaRice Center, BecA-ILRI Hub, and IRRI (the Philippines), and American universities (University of Arkansas – Fayetteville and The Ohio State University, U.S.A.) (Fig. 4). The Africa-based research institutions provide strategic environments for evaluation and registration of developed rice germplasm (Figs. 3, 4, and 5). The project has established strong research networks for improving African rice value chains through pathogen phenotypic and genotypic characterization, rice breeding, and training programs for agricultural extension agents and scientists to enhance research, disease surveillance, and farm advisory services (Figs. 3, 4, and 5). The effort has received grants from the UK's Department for International Development and the Bill & Melinda Gates Foundation through the United Kingdom's Biotechnology and Biological Sciences Research Council (BBSRC) under the Sustainable Crop Production Research for International Development (SCPRID, 2012–2018) and the Global Challenge Research Fund (GCRF) initiative on Sustainable Agriculture for sub-Saharan Africa (SASSA, 2018–2021).

The overall aim of the project was to use knowledge of pathogen diversity and novel host resistance genes to breed durably resistant rice cultivars for deployment in SSA. The project has brought together leading international scientists from the rice blast research community with complementary expertise in pathogen biology and genomics, rice genetics, and breeding, with extensive local expertise in outreach. The international team has proven to be well-equipped to carry out the fundamental science proposed, but also to translate these findings into durable resistance that can impact directly on farmers' ability to grow rice successfully in resource-poor regions of Africa. The project has had research activities in Benin, Burkina Faso, Burundi, Ghana, Kenya, Madagascar, Mali, Nigeria, Tanzania, Togo, and Uganda.

We recognized that pathogen and rice germplasm analysis would be a key starting point for the project that would provide insights into a breeding strategy for durable blast resistance (Figs. 3 and 8). The team considered that a resistant rice cultivar must possess several major resistance genes, in combination with different (polygenic) resistance specificities, that cannot be overcome by single gene mutations in the resident blast pathogen population, in order to have durability. Because understanding the rice-*M. oryzae* interaction in SSA would first require a good knowledge of pathogen diversity, the project team set out to collect isolates across rice growing regions of Africa. The pathogen collections have then been used in pathotype analysis; to test against rice cultivars of the international differential set carrying known *Pi* resistance genes, to identify novel blast resistance in African cultivars through genome wide association (GWAS), through greenhouse-based inoculations, and for pathogen characterization using genomic tools, such as pathogenomics, genome sequencing, and genotypic analysis (Table 3, Figs. 5, 6, 7, and 8). We set out to use this information to identify both existing and novel sources of rice blast resistance that could be deployed collectively through marker-assisted rice breeding programs.

For pathotype analysis, greenhouse-based inoculation with a representative collection of isolates of *M. oryzae* (n = 122) was initially

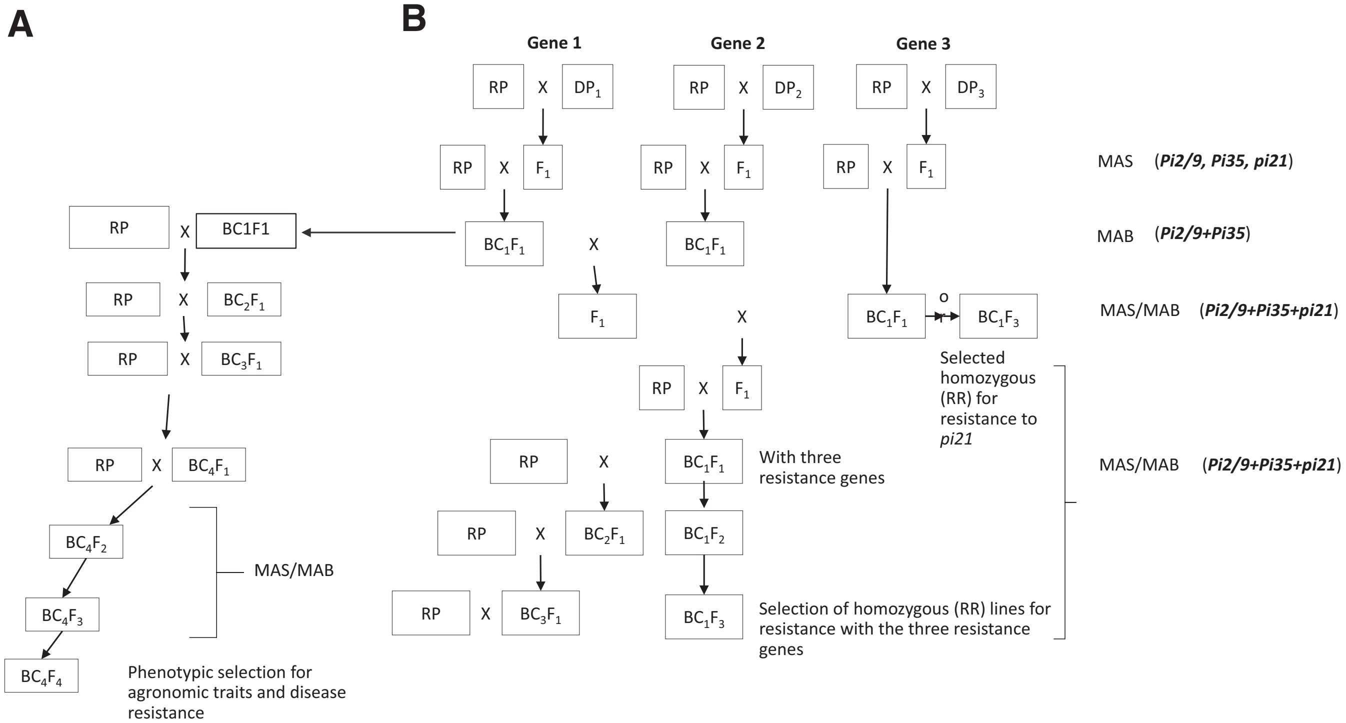

Fig. 8. An illustration of the breeding scheme for introgression of three distinct rice blast resistance specificities into locally adapted elite rice cultivars Basmati 370 or NERICA 2. The pipeline involves introgression of the major disease resistance gene *Pi9*/*Pi2*, the resistance QTL *Pi35*, and the recessive blast resistance locus *pi21*. **A,** Introgression of individual blast resistance genes with marker assisted backcrossing to attain homozygosity at BC3F4, followed by phenotyping. **B,** Pyramiding of the blast resistance gene specificities. Backcrosses carrying the three genes are selfed for several generations followed by phenotyping for blast resistance and other important agronomic traits. BC = backcross, DP = donor parent, RP = recipient parent, MAS/MAB = marker assisted selection/backcrossing.

conducted on a set of monogenic rice lines (IRBLs) carrying individual major genes for blast resistance. The IRBLs contain 24 *Pi* genes in the genetic background of Lijiangxntuanheigu (LTH) and were used along with some widely grown NERICA cultivars, including NERICA 2, 4, 5, 12, and 15 (Mutiga et al. 2017). The IRBLs contain the individual *Pi* genes (Table 3): *Pia*, *Pib*, *Pik*, *Pik-h*, *Pi-km*, *Pik-p*, *Pik-s*, *Pish*, *Pit*, *Pita*, *Pita-2*, *Piz*, *Piz-5*, *Piz-t*, *Pi1*, *Pii*, *Pi3*, and *Pi5* (*t*), *Pi7* (*t*), *Pi9*, *Pi11* (*t*), *Pi12* (*t*), *Pi19* (*t*), and *Pi20* (Kobayashi et al. 2007). LTH is a *japonica* rice variety from Yunnan Province of China that is highly susceptible to rice blast (Telebanco-Yanoria et al. 2010). This strategy was based on the following assumptions. First, that the interaction between the plant and the pathogen follows a gene-for-gene model (Flor 1971), which is well established for blast disease. Second, that the pathogen collection made at the outset of the project would be broadly representative of the virulence spectra in targeted rice growing regions of SSA. Third, that infection and disease development would be similar for artificial and field environments. Fourth, that test rice lines contain only single *Pi* genes. Fifth, that effective resistance genes would be reproducibly observed in both greenhouse and field conditions. Sixth, foliar blast symptoms would be positively correlated with resistance to other blast symptoms (such as neck and collar blast); and finally, that blast resistance in Africa would be conditioned by genes such as those previously identified in other parts of the world. Our findings initially showed, for example, that *Pi9* conferred broader resistance against the SSA blast population compared with other single *Pi* genes and that the genetic relatedness and virulence of isolates differed for isolates from East versus West Africa (Mutiga et al. 2017; Qu et al. 2006).

In a large-scale GWAS analysis of a rice diversity panel of African cultivars ($n = 162$) against eight isolates of *M. oryzae*, two from each of four African countries (Burkina Faso, Kenya, Tanzania, and Uganda), we identified genomic regions ($n = 31$) associated with blast resistance. Among the identified regions was one linked to the previously cloned *Pish* gene (Mgonja et al. 2017). A similar study based on a wider rice panel ($n = 190$) against another six *M. oryzae* isolates showed additional genomic regions ($n = 25$) out of which one was confirmed to be *Pi-ta*, a previously identified *R* gene (Mgonja et al. 2016). Together, these genomic regions have been valuable in marker-assisted selection breeding programs for SSA now underway (Mgonja et al. 2016, 2017).

Within this research effort, we have now collected over 1,000 isolates of *M. oryzae* from nine sub-Saharan countries. A subset of these isolates ($n = 300$) collected from Benin ($n = 18$), Burkina Faso ($n = 38$), Ghana ($n = 3$), Kenya ($n = 178$), Mali ($n = 3$), Nigeria ($n = 33$), Tanzania ($n = 26$), Togo ($n = 7$), and Uganda ($n = 10$) have been characterized using different techniques (Table 4). We have used sequencing of the internal transcribed spacer (ITS) region of the ribosomal RNA-encoding gene cluster, genotyping by sequencing (GBS), and vegetative compatibility testing, to define phylogenetic relationships and genotypic diversity of the collections (Mutiga et al. 2017). Additionally, genome sequencing of 29 isolates of *M. oryzae* that represent the full virulence spectrum in our African isolate collection has been completed in order to mine all corresponding avirulence genes. Also, Pac-Bio long read sequencing, in combination with RNA-sequencing analysis to improve the annotation of the genome of one Kenyan isolate (KE002) that produced incompatible reactions on rice lines with most resistance genes, has been completed and is a potential reservoir for many avirulence genes. This will make it possible to efficiently clone new avirulence genes and define their specificities.

The comprehensive screening of African isolates using the IRRI differentials provided further evidence that *Pi9* (a blast resistance gene that was first identified in *Oryza minuta*) could be introgressed into some African rice cultivars to protect rice against the prevailing rice blast population in SSA (Mutiga et al. 2017; Qu et al. 2006), in addition to highlighting potential utility of *Pi1*, *Pi2*, *Pish*, *Pi5*, and *Pib*. We also reasoned that pyramiding *Pi9* in different combinations with other loci that have been reported to confer broad and durable resistance in other parts of the world, such as *Pi2-A15*, *pi21*, and *Pi35*, would enhance resilience of the newly developed cultivars (Fukuoka et al. 2015; Yasuda et al. 2015). Thus, with a focus of attainable durable blast resistance for SSA, we developed an introgression strategy to stack major resistance genes, including *Pi9* and *Pi2-A15*, with the recessive resistance gene, *pi21*, and QTLs for blast resistance, such as *Pi-35*. These distinct specificities will ultimately be combined in four adapted African rice cultivars (NERICA 2, NERICA 12, Basmati 217, and Basmati 370). At the time of writing, four individual genes have successfully been introgressed into the four cultivars, with homozygosity having been achieved for *Pi9* and *Pi2-A15* in the backgrounds of Basmati 370 and NERICA 2. Although the breeding program has been affected by the Covid-19 pandemic of 2019–21, plans are underway to have at least three of these genes pyramided (*Pi9* + *pi21* + *Pi35* and *Pi2-A15* + *pi21* + *Pi35*) in Basmati 370 and NERICA 2 backgrounds by early 2023 (Fig. 8). Advancement of breeding lines is currently underway and takes advantage of the three seasons a year at IRRI in The Philippines, to accelerate our breeding efforts. The line development strategy is a classical marker-assisted backcrossing that targets blast resistance genes and other important agronomic and consumer-preferred traits that are identical to those of the adapted recurrent rice cultivars (Fig. 8). The strategy will provide cultivars for testing and registration through our partners in KALRO, INERA, and AfricaRice. The final selected lines will then be tested in 19 blast hotspot screening sites across SSA.

In parallel to these line advancement efforts, a blast hotspot evaluation and greenhouse-based inoculation testing of a panel of 66 rice lines is already underway. This hotspot test includes breeding populations at different stages of the advancement described above, the IRBL rice lines, and a collection of African cultivars previously showing some level of blast resistance, based on greenhouse-based inoculation tests. These blast disease hotspot tests are currently ongoing in Kenya, Burkina Faso, and Cote D'Ivoire. Growing these materials under conditions of high disease pressure will enable their durability to be evaluated across a broad geographic range in Africa. Greenhouse-based inoculation tests have also been conducted in various laboratories of our collaborating institutions.

Pathogen surveillance and establishment of a biobank of *M. oryzae*. We recognize that our strategy to control rice blast is dependent on an ongoing knowledge of the way the pathogen population will evolve against deployed rice genotypes carrying multiple blast resistance genes in SSA. This is consistent with the red queen hypothesis, which has been formulated in evolutionary biology to describe how species must adapt and evolve in order to survive when interacting with another ever-evolving opposing species (Strotz et al. 2018). Evaluation of the pathogen potential for new virulence emergence must therefore be achieved by continuous collection and testing against control methods or cultivated plant germplasm through country or regional phytosanitary schemes. Information generated from these tests can then be used to develop effective and sustainable strategies for managing the disease. Our team has therefore developed strategies to collect, characterize, compare, and archive isolates of *M. oryzae*. We have adopted a standard storage of *M. oryzae* cultures in dried filter paper at –20°C and in liquid N_2 as glycerol stocks, within our biobank in BecA-ILRI Hub (Table 4), with backups stored in KALRO, The University of Arkansas, and The Sainsbury Laboratory, UK. Information regarding virulence spectra of geographically diverse isolates is obtained through ongoing pathotyping efforts. To ease tracking and retrieval of the data, the project uses an online relational database (https://riceblast.ilri.org/) hosted by ILRI. The biobank is curated by project members in respective institutions, and the isolates are available to African and international researchers upon request and contingent on existing biosafety regulations.

The established regional repository of *M. oryzae* will be valuable for recording greenhouse-based screening (GHBS) of disease reactions for rice germplasm of interest and providing fungal isolates to regional rice breeders testing rice germplasm for resistance to blast and mapping disease resistance. The collections will also be useful for studying pathogen diversity and its association with rice blast incidence. Isolates are being genotyped through low coverage whole-genome sequencing technology, and this data will be used to monitor changes in pathogen genotype and virulence spectra. Knowledge of the virulence spectra across regions will then be used in ongoing marker-assisted breeding programs within SSA for *R*-gene deployment. The aim of the effort is to use isolates of *M. oryzae* collected in further studies to understand recent evolution of the blast pathosystem. Finally, we believe there will be an opportunity to learn about the relationship between the *M. oryzae* populations causing blast in rice and those causing blast disease in common wheat (*Triticum aestivum* L.) and finger millet (*Eleusine coracana* L.).

To strengthen regional rice disease surveillance systems and gain grower and consumer engagement, our project has trained agricultural extension personnel as "plant doctors" ($n = 35$) and established seven plant clinics across three counties (Busia, Kisumu, and Kwale) of Kenya. The effort is now being extended to other rice-growing counties in Kenya. There are also plans to establish similar clinics in Burkina Faso, Burundi, Tanzania, and Uganda. The concept of plant clinics is taken from previous efforts by the CABI Plantwise initiative, a global program that aims at increasing food security and improving rural livelihoods by reducing crop losses (Otieno et al. 2020). The model works with a goal of enhancing disease and pest diagnostics systems through building capacities within the NARS. Our outreach effort trains and empowers agricultural extension agents from rice growing areas by providing computer tablets to enable electronic capture of disease symptom data into a shared online repository (Fig. 4). Eligible agricultural extension personnel are from rice-growing regions of respective countries and trained centrally to graduate with uniform certification. Plant doctors establish weekly consultations with farmers and are provided with plant material to identify disease symptoms and prescribe appropriate effective control solutions (Fig. 5). Data collected from plant clinics is shared through the online repository/database for use in monitoring and risk mapping of blast disease in SSA. In Kenya, plant doctors have provided support through the plant clinics to about 3,000 farmers since the start of the program in 2017.

A pipeline for germplasm and pathogen characterization across SSA. The collaborative team effort has taken a comprehensive approach by combining multiple strategies to identify, characterize, and introgress resistance into adapted rice in SSA. In this section, we provide a description of the global long-term breeding strategy/design to durable blast resistance, results of which were partly highlighted in earlier sections. The approaches are building on the initial population level study of *M. oryzae* and breeding programs at IRRI (described earlier) in complementary phases, as follows. First, isolates of *M. oryzae* from target environments are characterized through artificial inoculation of rice cultivars carrying known *Pi* genes and other promising local genotypes (preferably those possessing traits preferred by farmers and consumers). Second, both the pathogen and rice cultivars are genetically characterized using robust genotyping methods (Fig. 6). Genetic characterization of rice genotypes provides information on diversity and relatedness, while SNPs can be further used in GWAS studies to identify genomic regions associated with blast resistance and other important agronomic traits of rice. Genomic characterization of isolates of *M. oryzae* enables the project to identify isolates representing diverse or emerging lineages for artificial inoculation on rice and further characterization of effector diversity. To conduct a GHBS, we use genotyped isolates of *M. oryzae* that represent diverse genetic clusters of varying mean disease reaction scores based on past pathotype characterization with IRBLs. Ongoing pathogen collection and genotypic analysis will also enrich the biobank and thereby boost its power in identifying emerging virulent genotypes of *M. oryzae*.

The third phase is a breeding strategy based on the outcome of the first two phases and utilizes the promising *Pi* genes in a multiparental crossing. Adapted cultivars are used as recipients while the source of *Pi* genes is used as donor. The initial cross involves development of F_1 progeny by crossing all the donor and recipient lines. The progeny are backcrossed to the recipient to obtain a BC_1F_1 generation, then crossed in pairs to bring at least two genes into the same background. Furthermore, backcrosses are confirmed using PCR methods and selected for an additional crossing with progeny carrying the other gene of interest (Figs. 5 and 8). Once these genes are in the same background, further backcrossing is conducted (five to six cycles) to recover most of the genome (and desirable agronomic traits) of the recipient parent before materials are fixed through selfing of the resultant genotype. Progeny are then tested by artificial inoculation with isolates of diverse virulence spectra/lineage and scored on a standard disease severity scale of 0 to 9 (Fig. 5).

The fourth phase involves phenotypic testing to confirm disease resistance in the developed genotypes. Phenotyping takes place under natural infection by hotspot evaluation or field-based screening (FBS), following standard methods for maximizing inoculum density within a trial, such as the use of spreader rows (Vasudevan et al. 2014). A complementary GHBS is then conducted using genetically diverse isolates of *M. oryzae*, which are available in our biobank. The two phenotyping levels are applied to avoid escapes and to ensure that the rice panel is challenged with *M. oryzae* of varying virulence spectra (Vasudevan et al. 2014).

Testing of breeding populations at different stages of cultivar development enhances tracking and confirmation of blast resistance and other important traits (Fig. 5 and 6). Screening for blast resistance will therefore be carried out as a continuous cycle in the future, with input from FBS, GHBS, and genotypic analysis of both rice and the blast pathogen. Genetic analysis of rice enables the program to detect known blast *R* genes in African rice cultivars, hence providing valuable information regarding which materials to include in FBS and GHBS programs. Rice germplasm found to harbor genes of interest can be included in the pathotype analysis panel (using isolates from the Biobank presented in Table 4), and then valuable information is obtained regarding environmental suitability of each rice line. Breeding populations can then be developed from rice genotypes that show a high likelihood of defeating the virulence spectrum of a test panel derived from *M. oryzae* collections from a specific rice-growing region. The populations are then advanced with parallel FBS and GHBS. Field selection ensures that the team can maintain good agronomic traits while eliminating undesirable traits (Fig. 5).

The project works with national rice breeding programs to ensure that materials are evaluated in the right disease hotspots, and to ease acceptance by future custodians of these new rice cultivars. To enhance purity of rice seed, crossing has been centralized at IRRI in the Philippines. Pathotyping or GHBS is also conducted in different laboratories (for independent quality checks), and FBS conducted in at least three locations within the respective countries of East and West Africa.

Prospects for durable rice blast resistance for SSA. A significant amount of effort has been applied to the development and testing of rice breeding populations. These materials are being advanced and evaluated alongside elite cultivars in several countries in SSA. We are learning a lot through the process regarding testing of materials across different blast hotspots. The project will test and advance fixed lines to the national performance trials of respective countries for further evaluation and potential variety registration.

An effort is also underway to apply modern tools for breeding to enhance efficiency and to develop markers for alleles involved in linkage drag during marker-assisted backcrossing. For example, SNPs generated during high density genotyping of diverse rice germplasm and the phenotypic data being obtained from hotspot evaluation of the same materials, could be included in a genomic selection (GS) program (Huang et al. 2019). This would boost throughput of germplasm evaluation, because any new rice lines could be genotyped, and performance predictions conducted using the GS model. Thus, the difficult process of testing materials over successive seasons could be minimized, based on genomic prediction (Huang et al. 2019). We are seeing an increasing hope in application of GS, as new technologies that are bringing down the cost of SNP genotyping have emerged and will eventually be affordable not only to donor-funded projects, but also to breeding programs funded by African governments (Happ et al. 2019; Poland and Rife 2012). We also envision the increasing use of gene editing to overcome linkage drag in breeding for blast resistance in SSA.

The project has built a strong network of trained African scientists and will continue to drive forward its overall aim of developing durable rice blast resistance to safeguard food security in SSA. To date, four PhDs have graduated from the project and are now contributing to research and training of other researchers and agricultural extension agents, particularly within the plant clinic system. Through this human capacity development, the project has so far trained 35 plant doctors, who are now involved in regular surveillance of blast and other constraints to rice production in some African countries (e.g., Kenya and Tanzania). There are ongoing efforts to further train more plant doctors and enhance their capacity to support farmers, and to collect and deliver samples to BecA-ILRI Hub for enrichment of the biobank with isolates of *M. oryzae*. Ultimately, the team will utilize climatic and fungal phenotypic/genotypic datasets in blast predictive models. The project is also mobilizing resources to conduct robust studies to enable the establishment of a stable virulence predictive model based on association between SNPs and disease reaction scores across rice growing regions in SSA.

Conclusions

A concerted endeavor has been established to engage in sustainable strategies to control rice blast disease in SSA and thereby contribute to ensuring food security in Africa. The project has built capacities for sustainable development through training 35 agricultural extension agents, four African rice scientists to PhD level, two early career postdoctoral scientists, and the establishment of a modern breeding pipeline and blast disease surveillance system. These established systems are working in tandem with those within local authorities to enhance efficiency and success in activities aimed at achieving durable blast resistance for SSA. By training scientists and developing a multinational team and a project model, the effort has invested in the future of not only rice production, but of tackling challenges in other food systems in Africa. Recently trained scientists are now at the forefront of enhancing food security in the region.

This research effort involves multiple countries that differ in biosafety requirements and food policy regulations. However, the countries share a common problem of an acute need to increase food production for their rapidly growing populations. It is imperative to always work with NARS to understand the challenges faced by individual countries. For example, our work with KALRO to strengthen plant clinic facilities in Kenya has been invaluable and the local authorities are now willing to give a further boost to future efforts through ongoing policies. Prior to the establishment of the plant clinics in this project, agricultural extension agents had difficulties in effective delivery of services to small-holder farmers, due to lack of adequate skills and technologies. The capacity building effort improves on the skills of the agricultural extension agents to not only work on rice blast, but also to enhance effective management of other diseases and pests under small-holder farm settings of Africa. Furthermore, an effective greenhouse-based facility for evaluation of blast resistance through artificial inoculation has been established at ILRI and has already gained use by regional scientists. While a screening facility may appear straightforward to establish, there needs to be a concerted effort to get things done and to have the facility adopted by the existing institutional systems. From an outside perspective, things often look fine, until you work closely with NARS and realize the actual challenges they face in delivery of services.

A great deal has been learned from the rice breeding strategy adopted. We are hopeful that the integrated approaches in this collaborative research for development will yield durable blast resistance in African rice cultivars. The project will generate further activities based on the findings of multilocation/seasonal testing of rice lines carrying pyramided blast resistance genes. We also envision using new technologies (such as gene editing) to overcome linkage drag during marker-assisted breeding.

We identify that there is still a need for more concerted regional efforts in breeding for blast resistance. Presently, there are multiple small rice breeding efforts within different countries of Africa. While these small research efforts may serve a purpose, there are similarities in agroecological zones, which experience similar abiotic and biotic stresses. Most of these problems could be tackled much more effectively in unified efforts at a regional level. For example, our research efforts have focused on pathogen collections and characterization from both East and West Africa, which has seldom occurred previously. There is a synergistic value in understanding the biology of the pathogen based on a broader collection across wider geographical regions across the continent. Such a combined effort may also mobilize more resources, including skills and finance, to achieve higher impact in the development of durable rice blast resistance for the whole of Africa, compared with fragmented national or subnational efforts.

Finally, in addition to breeding for blast resistant cultivars, government policies are also required to protect both farmers and consumers. Effective government regulations regarding the movement of infected plant materials and regular surveillance, for example, could prevent further introductions and spread of rice blast disease. With the support of our current effort, agricultural extension officers are now playing a key role in integrated management of crop stress factors by advising farmers and collecting data to enable real-time surveillance of threats to rice production. A regular surveillance and monitoring of the disease in farmers' fields, coupled with more efficient and better funded agricultural extension services, would undoubtedly enhance adoption of improved rice cultivars and prevent the severe economic damage associated with blast in Africa.

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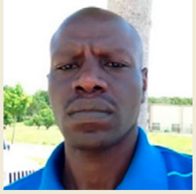
Samuel K. Mutiga

Dr. Mutiga is a research scientist working on the Durable Rice Blast Resistance for sub-Saharan Africa project with a joint appointment at the Department of Entomology and Plant Pathology, University of Arkansas, U.S.A., and Biosciences Eastern and Central Africa – International Livestock Research Institute (BecA-ILRI) Hub. He received a B.Sc. in horticulture (2004) and M.Sc. in plant protection (2008) from Moi University before joining Cornell University, U.S.A., where he obtained a Ph.D. in plant pathology with a focus on breeding for disease resistance in crop plants in 2014. He was a recipient or corecipient of: the Norman Borlaug Leadership in Agriculture Award 2012; The Global Hunger Award from The First Presbyterian Church of Ithaca in 2012; Capacity and Action for Aflatoxin Reduction in East Africa Grant through BecA-ILRI Hub by the Australian DFAT and CSIRO in 2011; and the current Global Challenge Research Fund – Sustainable Agriculture for sub-Saharan Africa grant in a subaward through Dr. Nicholas J. Talbot, The Sainsbury Laboratory, Norwich, UK. He has published 30 peer-reviewed articles with over 400 citations.



Felix Rotich

Dr. Rotich is a research scientist working on the Durable Rice Blast Resistance for sub-Saharan Africa project with an appointment as a lecturer at the University of Embu, Kenya. He received a B.Sc. in horticulture (2005) and M.Sc. in horticulture (2009) from Moi University, Kenya. He obtained a Ph.D. in plant science (plant pathology option) from the University of Arkansas, U.S.A., with Dr. J. C. Correll in 2015. He has authored or coauthored five peer-reviewed articles.

Vincent M. Were

Dr. Were is a postdoctoral researcher at The Sainsbury Laboratory Norwich, working toward understanding the population biology of rice blast in sub-Saharan Africa. He is also interested in understanding the biology of effector secretion and the involvement of effectors in the dialogue between plants and fungi at the plant-pathogen interface during infection. He holds a B.Sc. in biomedical sciences from the University of Nairobi (2009), an M.Sc. in biotechnology from the University of Queensland Australia (2012), and a Ph.D. in biological sciences at the University of Exeter, UK (2018) supervised by Dr. Nicholas J. Talbot. Vincent has coauthored three peer-reviewed articles and one book chapter.

David Mwongera Thuranira

Dr. Thuranira holds a B.Sc. degree in horticulture from Jomo Kenyatta University of Agriculture and Technology (JKUAT), an M.Sc. in microbiology, and a Ph.D. in biological sciences from the University of Exeter, UK, supervised by Dr. Nicholas J. Talbot. He is a research scientist at the Kenya Agricultural and Livestock Research Organization (KALRO) with over 18 years' experience working with small-holder farmers in Kenya. Dr. Mwongera has been involved in projects aimed at generating and disseminating integrated pest management practices in fruits and vegetables. He has coauthored/authored scientific papers in refereed journals and conference proceedings. Currently, Dr. Mwongera is working on understanding the population biology of the rice blast pathogen in Kenya and is working closely with rice breeders in developing durable rice blast resistance in rice varieties grown in SSA. He has been involved in developing the largest biobank of rice blast isolates in Kenya.

John M. Kimani

Dr. Kimani is the head of rice research program in Kenya Agricultural and Livestock Research Organization (KALRO). He holds a Ph.D. in plant breeding and genetics from University of KwaZulu Natal. He is a recognized and active plant breeder contributing to the development of rice varieties that have been released for commercialization and was instrumental in establishing the rice seed system in Kenya. He is currently working with Korea-Africa Food and Agriculture Cooperation Initiative (KAFACI) and the International Rice Research Institute (IRRI) to develop high yielding rice varieties and their seed system establishment. He was instrumental in modernizing rich research facilities at KALRO ICRC – Mwea, together with the Japan International Cooperation Agency (JICA) under the SATREPS Project and KR-2 project through Japanese Embassy in Kenya. Dr. Kimani has received many grants and has published approximately 55 peer-reviewed articles and book chapters.

Emmanuel Mgonja

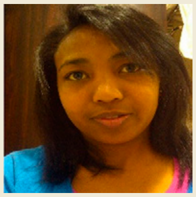
Dr. Mgonja is a crop protection research scientist working with Tanzania Agricultural Research Institute – Ifakara Center. He is the head of Crop Protection Section and has extensive experience in rice disease control and management. He received a B.Sc. in agronomy (2006) from Sokoine University of Agriculture, Tanzania, before joining Tokyo University of Agriculture, Japan, where he obtained an M.Sc. in international agricultural development (2011), majoring in plant pathology. He later joined The Ohio State University, U.S.A., where he obtained a Ph.D. in plant pathology in 2016 under the supervision of Dr. Guo-Liang Wang. He is the chief investigator for Rice Blast Disease Resistance for Better Adaptation to Climate Change, co-investigator for Plant Disease Surveillance Using Unmanned Aerial Vehicles (Drones), and a collaborator in the GCRF Durable Rice Blast Resistance for Sub-Saharan Africa projects.

Geoffrey Onaga

Dr. Onaga is a research scientist working with the National Agricultural Research Organization (NARO) of Uganda. He is developing rice pathogen surveillance systems and strategies to customize the deployment of resistance genes. He received a B.Sc. in agriculture (2004) and M.Sc. in plant breeding and seed systems (2010) from Makerere University, Uganda, before joining Georg-August University, Goettingen, Germany, where he obtained a Ph.D. in plant pathology in 2014. He has authored 18 peer-reviewed articles and four book chapters. He is a recipient of a recent grant for the development of a real-time field pathogen monitoring system for rice blast in Uganda and Ivory Coast, funded through the Science Granting Councils Initiative (SGCI); and VISID: a novel approach to improve rice resistance to emerging rice yellow mottle virus (RYMV) strains in East Africa, IRRI Seed Grant Award.

Kadougoudiou Konate

Dr. Konate is a research scientist working on rice breeding and varietal improvement network and on performant rice variety promotion and large dissemination project with a joint appointment by the National Center for Scientific Research and Technology through the National Research Institute of Burkina Faso (INERA) and as the focal point of the Breeding Task Force. Dr. Konate received his Ph.D. in plant genetics and improvement in 2017 from the Universite d'Abomey Calavi Bénin. He has authored four passport data outputs and participated actively in capacity building and regional research projects on drought tolerance and iron toxicity of rice, and on evaluation of genetic material.



Claudine Razanaboahirana

Ms. Razanaboahirana is an assistant engineer at CNRS (Centre National de Recherche Scientifique) in France, working on the Plastopol (plant storage polysaccharide) project. She works on starch synthase initiation enzymes on *Solanum tuberosum* and the use of CRISPR Cas9 to understand its function. She received an M.Sc. in agronomy (2011) from ASJA (Madagascar). She has worked as an assistant breeder for 5 years at FOFIFA Madagascar, where she conducts rice (*Oryza sativa*) phenotyping trials for blast disease, iron toxicity resistance, and cold tolerance. She received an ABCF scholarship for the molecular characterization of red rice at BecA-ILRI Hub Kenya in 2017. In 2019, she received another M.Sc. in plant breeding from Unilasalle University (France) and Ghent University (Belgium).

Joseph Bigirimana

Dr. Bigirimana is a senior scientist at the International Rice Research Institute (IRRI). He is currently the representative of IRRI in Burundi and coordinates research on rice pathology in the eastern and southern African region. He carries out research on rice diseases of regional importance including blast, rice yellow mottle virus, and sheath rot complex. In 2008–2010, he was appointed dean of the Faculty of Agronomy and Bioengineering at University of Burundi, teaching plant pathology in the same faculty. Dr. Joseph Bigirimana completed his Ph.D. at Ghent University (Belgium) Faculty of Agriculture and Applied Biological Sciences. After his Ph.D. studies, he did postdoctoral research at Ghent University and later at the International Center for Genetic Engineering and Biotechnology (ICGEB) in Italy. He has published several papers related to rice disease resistance and rice pathogen characterization.

Alexis Ndayiragije

Dr. Ndayiragije is a plant breeder and senior scientist at IRRI in charge of the eastern and southern Africa Plant Breeding program and IRRI representative in Mozambique. He did his Ph.D. research studies at the Faculty of Agricultural and Applied Biological Sciences at Catholic University of Louvain-La-Neuve in Belgium on rice salt stress resistance and polyamine metabolism. He has been working on rice research for more than 15 years.

Emily Gichuhi

Dr. Gichuhi is a research scientist working at Kenya Agricultural and Livestock Research Organization (KALRO) as a rice breeder. She received a B.Sc. in horticulture (2011) from Jomo Kenyatta University of Agriculture and Technology, Kenya, before joining Okayama University, Japan, where she obtained her M.Sc. in agriculture (2013) and later obtained a Ph.D. in agriculture with a focus on breeding for improved yields using wild rice germplasm (2017) from the same university. She has authored or coauthored five peer-reviewed articles and one book chapter.

Mary Jeanie Yanoria

Dr. Yanoria is a research scientist at the International Rice Research Institute (IRRI) working on rice fungal diseases. She developed the near isogenic and introgression lines with different blast resistance genes in several genetic backgrounds. She is also involved in the analysis of rice blast population structure and *AVR* gene analysis to monitor and predict effective blast resistance gene deployment. She received her B.Sc. in agriculture with a major in plant pathology at the University of the Philippines at Los Baños, Philippines. She was a recipient of a JSPS Ronpaku Fellowship in 2007 and was awarded a Ph.D. in agricultural science at Kyushu University in 2011. She was awarded a JSPS postdoctoral fellowship by JIRCAS, Tsukuba, Japan, between October 2011 to October 2013. She has authored 27 peer-reviewed articles. Jeanie is a coinvestigator in the GCRF Durable Rice Blast Resistance for Sub-Saharan Africa project.

Miriam Otipa

Ms. Otipa is a plant pathologist at Kenya Agricultural Livestock Research Organization. Within the GCRF Durable Rice Blast Resistance for sub-Saharan Africa project, she implements the plant clinics in Kenyan rice farming systems. She received a B.Sc. in botany from Moi University (1993) and an M.Sc. in plant pathology from the University of Nairobi (2004), and is currently pursuing a Ph.D. in horticulture in a sandwich program between Jomo Kenyatta University, Kenya, and The Ohio State University, U.S.A. She is a CABI global technical reviewer of pest management decision guidelines for Europe, Asia, and African countries; a recipient of the African Women in Agriculture Research and Development Fellowship 2008 and a mentor on the same program from 2010–2013; and principal investigator on several World Bank, USAID, AfDB, and European Union projects in pest and disease management. She has authored over 25 peer-reviewed articles, book chapters, and manuals.

Lusike Wasilwa

Dr. Wasilwa is a coinvestigator in the GCRF Durable Rice Blast Resistance for sub-Saharan Africa project. Dr. Wasilwa holds a B.Sc. degree in agriculture from the University of Eastern Africa, Baraton, Kenya, and an M.Sc. in horticulture and a Ph.D. in plant sciences from the University of Arkansas, Fayetteville, AR, U.S.A., with Dr. J. C. Correll. Upon completion of postdoctoral research at Rutgers University, NJ, U.S.A., she returned to Kenya, where she has held several leadership positions at the Kenya Agricultural & Livestock Research Organization and is the current director of Crop Systems. She serves on agricultural research, management, and development boards of Kenya. Dr. Wasilwa is a recipient of three medals from the International Society for Horticultural Science (ISHS) in recognition of service and a fellowship from the Gender and Diversity Rockefeller Fellowship Program to enhance the careers of women crop scientists in East Africa. She has authored many scientific and technical papers.

Ibrahima Ouedraogo

Dr. Ouedraogo is a senior plant pathologist at INERA, the National Agricultural Research Institute of Burkina Faso. He is a coinvestigator scientist working on the GCRF Durable Rice Blast Resistance for sub-Saharan Africa project. He has worked for many years with AfricaRice and has occupied several administrative responsibilities such as head of the National Rice Research Program and regional director of INERA for the western part of Burkina Faso. He has specialized in seed pathology in Denmark and as a Fulbright fellow in the U.S.A., where he was a visiting scientist at the Correll Laboratory, University of Arkansas. He has authored approximately 20 publications on rice pathology.

Thomas Mitchell

Dr. Mitchell is a professor and department chair at The Ohio State University, where he has been a faculty member since 2007. His research program focuses on using modern technologies to understand fungal biology and fungal-host plant interactions. He received his B.Sc. in plant sciences from The Pennsylvania State University and an M.Sc. in plant pathology from Clemson University. In 2000, he obtained his Ph.D. at North Carolina State University after which he stayed in North Carolina working as a research assistant professor until his move to Ohio. He has authored over 80 research articles and book chapters and has received several awards and honors.

Dr. Guo-Liang Wang

Dr. Wang is a professor in the Department of Plant Pathology, The Ohio State University. He received his B.Sc. degree in plant genetics from Hunan Agricultural University in China in 1982, his M.Sc. degree in plant genetics and breeding from Fujian Agricultural University in 1985, and his Ph.D. degree from the University of the Philippines in plant genetics and breeding in 1992. Dr. Wang's lab is currently using rice blast disease as a model pathosystem to understand the molecular basis of plant-microbe interactions. He received a total of $8.5 million for his research from various funding agencies including NSF, USDA-NIFA, DOE, USAID, and BSRRC/BM Gates Foundation. Dr. Wang published over 200 peer-reviewed papers with about 19,500 citations. He was elected as Fellow of the American Phytopathological Society (APS) in 2012, the American Advancement Association of Science (AAAS) in 2017, and was named an Ohio State University Distinguished Scholar in 2019.

James C. Correll

Dr. Correll is a distinguished professor of plant pathology at the University of Arkansas. He holds a Ph.D. from the University of California, Berkeley. He conducts research and has extensive experience in integrated pest management practices on a wide range of vegetable, fruit, and row crop diseases, particularly rice. Dr. Correll has been involved in a number of agriculture projects throughout Asia, Africa, and South America, funded through various entities including Winrock International, ACDI/VOCA, USAID, Land O'Lakes, Partners for the Americas, the Bill and Melinda Gates Foundation, and the BBSRC. He continues to strive to develop better working networks with international scientists on sustainable disease management practices, and breeding for disease resistance to reduce pesticide inputs. Dr. Correll has received several awards including being elected a Fellow of the American Phytopathological Society, The President's Volunteer Service Award from the President's Council on Service and Civic Participation, and the John White Outstanding Research Award. Most notably, he has professionally mentored several Ph.D. students and postdocs throughout the world.

Nicholas J. Talbot

Dr. Talbot coordinates the Durable Rice Blast Resistance for sub-Saharan Africa project, funded by BBSRC-GCRF. His research is focused on understanding plant infection by the rice blast fungus, and he is particularly interested in how *M. oryzae* uses appressoria to infect rice plants, how rice tissue is invaded, and how the fungus suppresses plant immunity. He received his Ph.D. in molecular genetics from the University of East Anglia. After postdoctoral research at Purdue University, U.S.A., he moved to the University of Exeter as a lecturer, later becoming professor of molecular genetics, head of the School of Biosciences, and deputy vice chancellor. He joined The Sainsbury Laboratory, Norwich, as executive director in 2018. He has authored more than 180 publications. He is a Fellow of the Royal Society of Biology, a member of EMBO, a member of Academia Europaea, and a Fellow of The Royal Society.

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