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Novel sources of resistance to blast disease in finger millet

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Abstract

Finger millet (*Eleusine coracana* (L.) Gaertn. subsp. *coracana*) is the most important millet in eastern Africa and perhaps the oldest domesticated cereal grain in Africa. One of the major factors limiting finger millet production is blast disease caused by the fungus *Magnaporthe grisea*. Crop wild relatives and landraces present a potential source of novel genes. This study investigated the response of cultivated and wild relatives of finger millet to an isolate of blast disease from western Kenya. Previous germplasm collections were purified through two generations of single-seed descent before screening alongside improved and farmer-preferred varieties (FPVs) under a screen house across three seasons. Farmer-preferred varieties were identified through participatory varietal selection (PVS). The plants were inoculated twice during each growth period using hand-spraying method and data on disease incidence recorded at grain-filling stage. Genotypic data was generated using diversity arrays technology (DArT) sequencing and data analysis done using Genstat 18.2 and TASSEL 5.2.58. We observed high heritability (81%), indicating that the variation observed was predominantly genetic. Wild accessions were generally more resistant to the disease in comparison to the cultivated accessions. Preliminary genome-wide association study (GWAS) using general linear model with principal component analysis led to the identification of 19 markers associated with blast disease that will be be developed into assays for genotype quality control and trait introgression. Wild accessions and landraces of finger millet present a good reservoir for novel genes that can be incorporated into crop improvement programs.

1 | INTRODUCTION

Finger millet (*Eleusine coracana* (L.) Gaertn. subsp. *coracana*) is a nutrient-dense tetraploid ($2n = 4x = 36$) cereal crop grown mainly in the marginal and medium agricultural zones of the developing world (Dida, Srinivasachary, Ramakrishna, Bennetzen, Gale, & Devos, 2007; Odeny et al., 2020). It belongs to the family Poaceae, genus *Eleusine* in the tribe Eragrostideae and is believed to have been domesticated in the east-African region from wild finger millet (*Eleusine coracana* (L.) Gaertn. subsp. *africana* (Kenn.-O'Byrne) Hilu & de Wet) (Dida et al., 2007). Finger millet is currently grown predominantly in eastern Africa

Abbreviations: DArT, diversity arrays technology; FPV, farmer-preferred variety; GeRRI, Genetic Resources Research Institute; GWAS, genome-wide association study; KALRO, Kenya Agricultural and Livestock Research Organisation; PVS, participatory varietal selection; SNP, single nucleotide polymorphism.

and India. It is adapted to a wide range of environments and can withstand harsh environmental conditions including high temperature (Yogeesh, Naryanareddy, Nanjareddy, & Gowda, 2016), moisture deficit, and water stagnation (Lenné et al., 2007). The grains are superior to major staple cereals in terms of nutrition, as they are a good source of quality protein and various minerals (Gupta et al., 2017). Finger millet straws are greatly valued and used as feed for animals (Wolie & Dessalegn, 2011).

Finger millet production is challenged by a number of biotic and abiotic factors that affect the ultimate yields. Among the biotic factors is finger millet blast disease caused by *Magnaporthe grisea* (teleomorph: *Pyricularia grisea*) (Ramakrishnan et al., 2016). The same pathogen parasitizes rice (*Oryza sativa* L.) and is arguably the most devastating disease in rice (Gupta et al., 2017). The disease affects finger millet at all growth stages but neck and finger blast are the most destructive forms (Takan et al., 2012) capable of causing up to 100% reduction of biomass and average yield per year (Lenné et al., 2007; Nagaraja et al., 2007). Pathogen genetic groups have been reported within finger millet blast populations (Shanmugapackiam, Ragupathi, & Raguchander, 2015; Takan et al., 2004), making management of the pathogen complex. The most effective and practical solution to finger millet farmers, the majority of whom are women, is to develop blast resistant finger millet varieties.

Several blast-disease-resistant lines have been developed in rice through the introgression of genes from landraces (Yadav et al., 2019) and wild relatives (Amante et al., 1992; Devi et al., 2015; Jeung et al., 2007). Wild finger millet relatives, as well as landraces that are abundant in eastern Africa, can be used to improve blast-disease resistance in finger millet, as they are generally more diverse and have coevolved with the pathogen over time under nonintensive cultivation conditions. The genus *Eleusine* is comprised of 10 annual or perennial grasses, some of which are commonly found in Africa. The species *E. coracana* (AABB) (with two subspecies: *coracana* and *africana*) and *E. kigeziensis* S. M. Phillips (AADD) are mainly tetraploids while *E. floccifolia* (Forssk.) Spreng. (BB), crabgrass [*E. indica* (L.) Gaertn.] (AA), American yard grass [*E. tristachya* (Lam.) Lam.] (AA), *E. jaegeri* Pilg. (DD), and *E. intermedia* (Chiov.) S. M. Phillips (AB) are diploids, although some autotetraploids of the known diploids have also been reported. With the exception of subsp. *coracana*, all other taxa are considered wild. All the cross-compatible wild species, which consist mainly of subsp. *africana* (Agrawal & Maheshwari, 2016) are a major resource for prebreeding in finger millet.

One of the major concerns in prebreeding is the potential linkage drag (Zamir, 2001), which defines the nondesirable traits from wild relatives that cosegregate with the traits of interest during trait introgression. The use of genomics-assisted breeding provides an opportunity for overcoming linkage drag (Dempewolf et al., 2017). Until recently, genomic resources have been limited in finger millet and breeding has been undertaken mainly using conventional methods. Two draft reference genomes have been published recently (Hatakeyama et al., 2017; Hittalmani et al., 2017), and an improved chromosomal-level genome is underway (unpublished data, 2020). These resources provide an excellent opportunity for genomics-assisted breeding that would enhance the success of trait introgression from wild relatives. Recent genomic studies in finger millet include the characterization of germplasm (Gimode et al., 2016; Manyasa, Tongoona, Shanahan, Mgonja, & De Villiers, 2015; Lule et al., 2018), association mapping (Kalyana, Agrawal, Pandey, Jaiswal, & Kumar, 2014; Lule et al., 2018; Sharma et al., 2018), as well as linkage mapping (Qi et al., 2018). Breeding for blast resistance in finger millet remains traditional, especially in eastern Africa, and there are no markers developed so far for more efficient crop improvement.

A participatory varietal selection (PVS) enables skilled farmers to select, both on-farm and on-station, the best performing varieties from a group of pre-evaluated seed selected by breeders (Witcombe, Gyawali, Sunwar, Sthapit, & Joshi, 2006). A PVS study done in Uganda revealed that finger millet farmers preferred high yielding, brown seed color, and medium height as the top most important attributes in an ideal variety, which should also harbor some resistance to major biotic and abiotic stresses (Owere, Tongoona, Derera, & Wanyera, 2014). Similar preferences have been observed among finger millet farmers in western Kenya, but would need to be confirmed in order to ensure farmers' needs are addressed during crop improvement. Involving farmers in the selection of preferred genetic material has been reported as a promising method for increasing adoption of improved varieties (Ojulong et al., 2017) and refining elite landraces (Roy et al., 2017).

The present study was conducted using 101 finger millet genotypes that included wild relatives, landraces, and improved genotypes popularly grown in Kenya. An initial PVS was done using 26 cultivated genotypes that had been preselected by breeders to establish farmer preferences and engage them in the varietal development process. All the 101 diverse genotypes were screened across three seasons under controlled environment for their response to finger millet blast disease following artificial inoculation. Genotypic information from the germplasm was used to correctly identify germplasm collections, assess the extent of genetic diversity, and develop a promising set of functional molecular markers for blast resistance in finger millet.

2 | MATERIALS AND METHODS

2.1 | Assembling germplasm

Seeds of 52 finger millet accessions (Supplemental Table S1) that were landraces, wild, or hybrids between wild and

TABLE 1 A set of 26 popular genotypes in Kenya that were assembled for participatory varietal selection and their unique attributes

Genotype	Unique attributes
1. KACIMMI72	*Striga* and lodging resistant; blast and drought tolerant; high yielding; brown grain color
2. KACIMMI22	Blast tolerant; high yielding
3. GBK043065	Blast tolerant; high yielding
4. KACIMMI42	Blast, *Striga*, and lodging resistant; drought tolerant; brown grain color; high yield; large open panicles
5. P-224	High yielding; easy to thresh; tolerant drought, *Striga* and blast; brown grain color; medium maturing
6. GBK011044	Blast tolerant; high yielding
7. KACIMMI21	Resistant to crown rot; high yielding; tolerant to blast
8. OKHALE-1	Tolerant to *Striga* and blast; good malting quality; lodging resistant; brown grain color; high yielding
9. KACIMMI49	*Striga* and lodging resistant; blast and drought tolerant; high yielding; brown grain color
10. GBK043145	High yielding; resistant to blast
11. KAL-ATARI	High yielding; good malting quality; tolerant to blast; brown colored grains preferred by farmers
12. EKAMA-WHITE	High yielding, good malting quality; tolerant to blast; brown colored grains preferred by farmers; easy to thresh; lodging resistant
13. KAC65	*Striga* and lodging resistant; blast tolerant and drought tolerant; high yielding; brown grain color
14. IE4115	Blast, *Striga*, and lodging resistant; drought tolerant; brown grain color; released variety
15. GBK043254	High yielding; resistant to blast
16. GBK043258	High yielding; tolerant to *Striga*
17. GBK008301A	High yielding
18. IKHULULE	Resistant to blast, *Striga* and lodging; drought tolerant; dark brown grain color; high yielding
19. GBK000494	High yielding; tolerant to blast
20. KNE1034	High yielding; early maturing; drought tolerant; tolerant to blast; resistant to lodging
21. GBK000451	High yielding
22. KAL (Millet)	High yielding; resistant to blast and *Striga*; brown grain color; early maturing; resistant to lodging
23. GBK036800	High yielding; tolerant to blast
24. IE2872	High yielding; highly susceptible to blast
25. U15	Early maturity; resistant to blast, *Striga* and lodging; drought tolerant; released variety
26. Maseno60D	Extra early flowering and maturity; drought tolerant; released variety

cultivated genotypes were obtained from previously collected germplasm that had been maintained at ICRISAT–Nairobi, Maseno University, or at the Kenya Agricultural and Livestock Research Organisation (KALRO)–Genetic Resources Research Institute (GeRRI) (http://www.kalro.org/Genetic_Resources_Research_Institute) located in Muguga, Nairobi (Supplemental Table S1). The collections from ICRISAT and Maseno University were mainly from a previous Bioinnovate (www.bioinnovate-africa.org)-funded project. The seeds of the 52 accessions were multiplied in Kiboko (ICRISAT Field Station, Kenya) under a polyhouse to ensure no escape of weedy material into the farmers' fields. Plants were bagged at flowering and seeds harvested per plant. Two rounds of single-seed descent were done to ensure seed purity and uniformity per genotype. In addition, finger millet breeders assembled 49 improved varieties, inbred lines, and popular landraces in Kenya, making the total number of all accessions used in the study as 101 (Supplemental Table S1). More details on the genotypes used in the current study can be found in the Germinate3 website (https://ics.hutton.ac.uk/cwr/fingermillet) (Raubach et al., 2020).

2.2 | Participatory varietal selection

Twenty-six out of the 49 genotypes assembled by breeders (Table 1) were used for PVS. The 26 varieties for PVS were planted in a triple five-by-five lattice design on farm at Nyancheki (Kisii) and on KALRO stations at Kakamega, Alupe, and Kisii. Each plot consisted of three rows, each measuring 4 m with spacing of 0.5 m between rows and a 1-m path between replications. The trials were planted following recommended cultural practices. To collect data on farmer preferences, 20 farmers (13 male and seven female) from Nyancheki village were invited to rank the performance of the genotypes at grain-filling stage. The farmers' participation was purely based on their availability. The farmers, segregated by gender, rated the genotypes and selected top

preferred 10 based on yield, effect of blast disease, grain color, and earliness (days to maturity). The top 10 farmer-preferred varieties (FPVs) were selected for use as potential recurrent parents in blast disease introgression.

2.3 | Blast inoculum preparation

A field isolate of *M. grisea* was collected from Maseno University Field Station from finger millet plant tissues (neck tissue) showing typical symptoms of blast. The collected diseased sample was refrigerated upon arrival in the lab at 4 ˚C for subsequent pathogen isolation. Blast-infected samples obtained from the neck were cut into small pieces (~2 by 2 cm), surface sterilized using 10% sodium hypochlorite (NaOCl) for 30 s, and rinsed in autoclaved double distilled water twice. The sterilized infected plant tissues were then suspended on toothpicks and placed on wet Whatman paper in petri dishes to induce sporulation for 24–48 h at room temperature under artificial light. Single conidia were identified under the microscope from sporulating lesions and aseptically transferred into petri dishes with malt extract agar and incubated at room temperature for 10 d to get pure monoconidial isolates. Inoculum was prepared by flooding 10-d-old monoconidial isolate cultures with 20 ml of autoclaved double distilled water, followed by filtering the conidial suspension through a two-layer cheesecloth. The concentration of spore suspension was adjusted using distilled water to 1×10^6 spores ml^{-1} before inoculation. Pathogenicity of the isolated culture was confirmed by Koch's postulate.

2.4 | Screening *Eleusine* spp. against blast disease

We used 101 accessions (Supplemental Table S1) comprising of FPVs, wild genotypes, landraces, inbred lines, improved varieties, and some interspecific crosses (*coracana* × *africana*) to screen against the blast isolate at Maseno University (0˚01′00.0″ S, 34˚36′00.0″E) in 2016, 2017, and 2018. The genotypes were planted in 20-L pots in a screenhouse, with each pot containing five plants and arranged in a completely randomized design. Inoculation was done using the hand-sprayer method (Hayashi, Kobayashi, Vera Cruz, & Fukuta, 2009) at 3 wk after emergence (leaf blast) and at maturity (neck blast). The percentage disease incidence (PDI) was scored for every genotype at grain filling stage using the following formula:

$$PDI = (No.\ of\ diseased\ plants) / (Total\ no.\ of\ plants\ screened) \times 100$$

2.5 | Correct identification of wild accessions and landraces, genotyping, and genetic diversity

We used both morphological and molecular analysis to correctly classify the new germplasm collections obtained from KALRO–GeRRI, ICRISAT, and Maseno University. Morphological identification was done using seed size, seed color, and inflorescence. To undertake molecular analysis of the landraces and wild accessions, seeds of previously single-seed advanced genotypes were planted at the World Agroforestry Centre (Nairobi, Kenya) for the purpose of DNA extraction alongside known genotypes classified as *E. coracana* subsp. *coracana*, *E. coracana* subsp. *africana*, and *E. kigeziensis*. Leaf tissues were collected at seedling stage and genomic DNA extracted using ISOLATE II Genomic DNA extraction kit (Bioline Pty Ltd.) according to manufacturer's instructions. Purity and quantity of the extracted DNA was determined using gel electrophoresis and a Qubit 2.0 Fluorometer (Life Technologies), respectively, with final dilution to 50 ng μl^{-1}. The DNA was sent to the Integrated Genotyping Service and Support at the Bioscience eastern and central Africa–International Livestock Research Institute hub for library construction and DArT sequencing (https://www.diversityarrays.com/products-and-services/applications/) as previously described (Wójcik-Jagła, Fiust, Kościelniak, & Rapacz, 2018). The resulting raw reads were mapped to a previously assembled finger millet genome (https://phytozome-next.jgi.doe.gov/info/Ecoracana_v1_1) and raw SNP markers called for minimum depth coverage of five and maximum mismatch of three. Raw SNPs were filtered for a minor allele frequency of ≥.05 and maximum missing data of 30% for GWAS and 10% for genetic diversity analysis using the genotyping-by-sequencing pipeline of the TASSEL 5.2.58 (Bradbury et al., 2007) program. We generated a neighbor-joining cladogram of the 52 accessions (Supplemental Table S1) alongside six genotypes of known classification as reference using TASSEL 5.2.58.

2.6 | Developing a set of functional markers for blast resistance

To develop a putative set of functional markers for marker-assisted selection of blast resistance, we undertook a preliminary association analysis using all the 101 genotypes phenotyped for resistance to blast. The DNA extraction and genotyping was done as already described. Association mapping based on general linear model with principal component analysis was conducted in TASSEL 5.2.58 software. We selected the top SNP markers located within genes with a maximum *P*-value cut-off of $\leq 9.08 \times 10^{-4}$ and distributed across the 18 chromosomes.

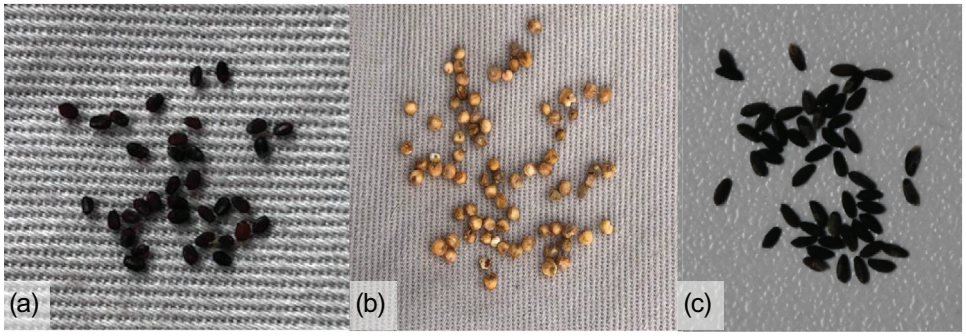

FIGURE 1 Pictures showing the difference in color between (a) the cultivated *Eleusine coracana* subsp. *africana* seed, (b) the cultivated *Eleusine coracana* subsp. *coracana* and (c) *Eleusine kigeziensis*. The seeds of wild accessions are generally black (a and c) while those of cultivated species range from light brown to dark brown

2.7 | Data analysis

Analyses of variance across seasons was determined using Genstat 18.2. Variance components were estimated by following linear model $Y_{ijk} = \mu + G_i + S_j + \varepsilon_{ijk}$, where Y_{ijk} was the phenotypic performance of the *i*th genotype at the *j*th season, μ was the mean, G_i was the genetic effect of the *i*th genotype, S_j was the effect of the *j*th season, and ε_{ijk} was the residual. Genotypes were treated as fixed effects and the other effects as random. Broad-sense heritability was estimated from the variance components as the ratio of genotypic to phenotypic variance.

3 | RESULTS

3.1 | Correct identification of wild and landrace germplasm

We used both morphological (Figure 1) and molecular methods (Figure 2) to correctly identify the 52 wild and landrace accessions that were collections from previous projects or from GeRRI. Wild accessions bore smaller, dark-colored seeds as opposed to larger brown to light-colored seeds of cultivated accessions (Figure 1). The cultivated accessions also had more compact heads than the wild accessions. For molecular identification, we used 63,010 SNPs after filtering for a minor allele frequency of ≥.05 and maximum missing data of 10%. Neighbor-joining clustering of the 52 accessions revealed three major clusters comprising of *E. coracana* subsp. *coracana*, *E. coracana* subsp. *africana*, and *E. kigeziensis* (Figure 2). The dendrogram also revealed that some of the genotypes were hybrids between cultivated and wild accessions (Figure 2).

3.2 | Participatory Varietal Selection

Twelve out of the 26 improved varieties (~46%) were selected by men and women farmers (Table 2). Eight (GBK043254, IE4115, KACIMMI72, KACIMMI42, KACIMMI49, KNE1034, U15, and Okhale1) of the 12 genotypes were selected by both men and women. KACIMMI72 was the top preferred variety by both men and women (Table 2). Most of the top 10 ranked varieties were also among the top yielding varieties (Figure 3). Despite being the highest yielder, GBK043145 was not ranked by either gender group among the top 10 preferred varieties. Given the low numbers of farmers that participated in this PVS, the results provided here were exclusively used in the current study to choose a subset of recurrent parents for the blast introgression program.

3.3 | Genetic variation for response to blast disease and new sources of resistance

The ANOVA across seasons revealed significant variations among the 101 genotypes in their reaction to blast disease (Table 3). The estimate of broad-sense heritability was 81% (Table 3), indicating that the variability observed was predominantly genetic. Twelve of the 101 genotypes (Figure 4) screened across the 3 yr consistently showed high resistance to blast disease with no (0%) disease incidence. The 12 most resistant genotypes were either wild relatives (*E. floccifolia*, *E. kigeziensis*, or *E. coracana* subsp. *africana*) or landraces, with only one improved variety (KACIMMI22) (Figure 4) appearing among the top 12. Only one out of the 10 most susceptible genotypes was a wild relative (Figure 4). None of the top-ranked FPVs made it to the top 12 most resistant genotypes. Box plots drawn also showed that the wild accessions were, on average, more resistant than their cultivated counterparts (Figure 5).

3.4 | Development of putative functional SNP markers for blast resistance

Because of the low number of 101 genotypes used in the current study, which limits the power for a full GWAS,

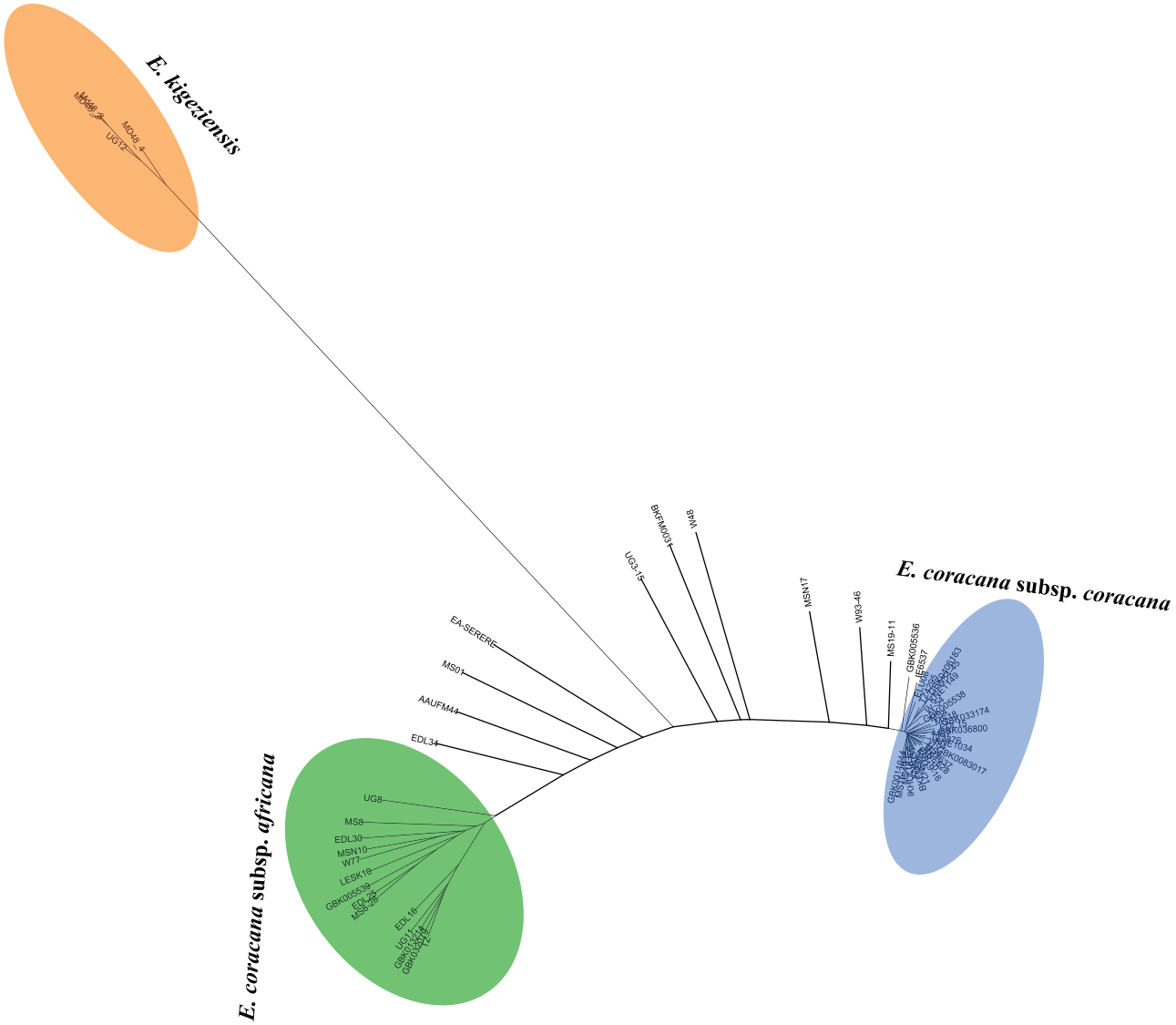

FIGURE 2 A dendrogram showing clustering of the 52 wild and landrace finger millet accessions. Three clusters are visible: the cultivated genotypes (Blue), *E. coracana* subsp. *africana* (Green), and *E. kigeziensis* (Orange). Admixtures can be seen stretching along the major clusters

TABLE 2 The ranking of most popular varieties by male and female farmers in western Kenya

Men		Women	
Variety	**Rank**	**Variety**	**Rank**
KACIMMI72	1	KACIMMI72	1
U15	2	KNE1034	2
KACIMMI49	3	Okhale1	3
KNE1034	4	KACIMMI42	4
Okhale1	5	GBK043254	5
KACIMMI42	6	U15	6
GBK000494	7	GBK043258	7
IE4115	8	IE4115	8
Maseno60D	9	KACIMMI65	9
GBK043254	10	KACIMMI49	10

the preliminary association analysis undertaken was purely to aid in the development of putative functional markers for future introgression activities. We filtered from a raw dataset containing 63,010 SNPs to a final number of 14,306 confident SNPs. A quantile–quantile plot was drawn (Figure 6) for the three seasons of data and the means revealed that the data generated was reliable. We selected 19 functional SNPs that were associated with blast resistance at a *P*-value threshold of $\leq 9.08 \times 10^{-4}$ and were located within genes, some of which are known to play important roles in disease resistance (Table 4). The candidate genes identified included a leucine-rich repeat receptor-like protein (Chr 1A), two receptor-like protein kinases (Chr 2A and 3A), two AP2-like ethylene responsive transcription factors (Chr 6B and 9B), and two F-box family proteins (Chr 9B) (Table 4).

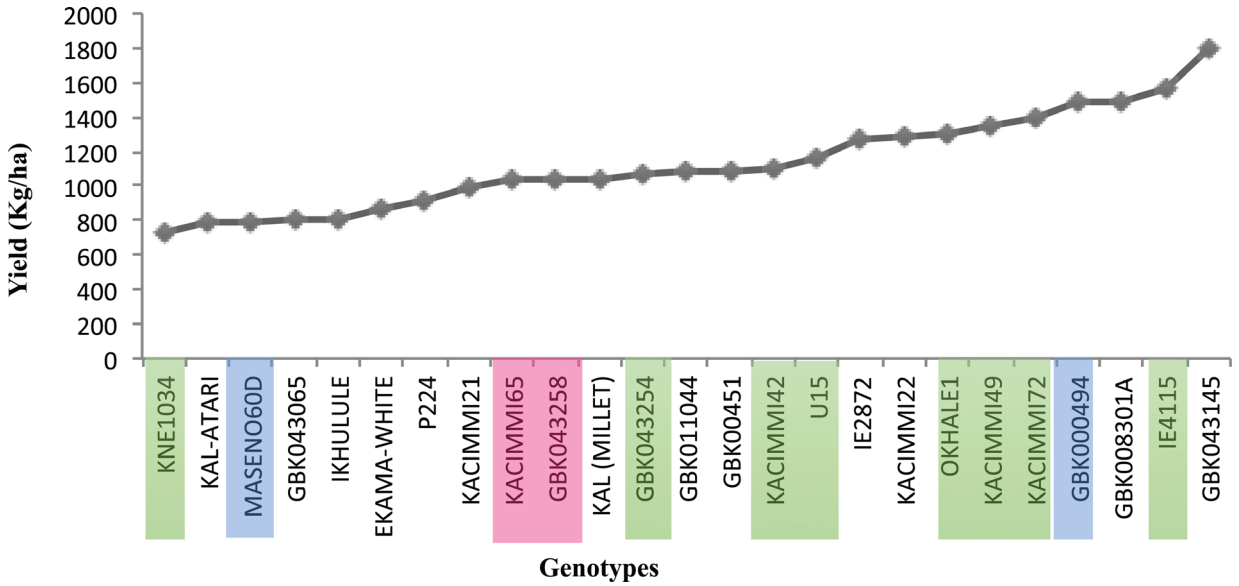

FIGURE 3 Yield of improved varieties used in participatory varietal selection highlighting the genotypes selected by both men and women (Brown), men only (blue), and women only (pink). Data shown is average yield across three environments

TABLE 3 Analysis of variance among the genotypes

Source of variation	Incidence
Season	549.58***
Accession	2314.9***
Season × accession	502.9***
σ^2_g	711.3
Broad sense heritability (H^2)	.81

***Significance at $p < .001$.

4 | DISCUSSION

This study has exploited the abundant finger millet germplasm present in eastern Africa, which is the center of domestication. As a result of frequent hybridization between wild and cultivated accessions, it was important to undertake proper identification of the recent collections before integrating them into prebreeding programs. Both morphological and molecular characterization was done to ensure purity and integrity of the germplasm. Although morphological characterization could have been sufficient to identify some of the accessions, we exploited the use of DArT sequencing (Kilian et al., 2012). This technology has been used successfully to characterize several crops with ranging ploidy levels including species from tribe Triticeae (Edet, Gorafi, Nasuda, & Tsujimoto, 2018), common bean (*Phaseolus vulgaris* L.) (Valdisser et al., 2017), snake melon [*Cucumis melo* L. subsp. *melo* var. *flexuosus* (L.) Naudin)] (Zaitoun et al., 2018), and tea [*Camellia sinensis* (L.) Kuntze] (Malebe, Mphangwe, Myburg, & Apostolides, 2019). In the current study, SNPs resulting from DArT sequencing distinctly clustered cultivated finger millet accessions from the wild subsp. *africana* and from *E. kigeziensis*. A number of genotypes that had hybridized between the different taxa were also distinguished. The clustering pattern was largely similar to a previous study (Gimode et al., 2016).

Screening of the new collections alongside improved material and FPVs revealed that the wild and landrace accessions were more resistant to the blast isolate used. Wild relatives have been used in several crops to introduce novel disease resistance alleles into cultivated material (Mammadov et al., 2018; Zhang, Mittal, Leamy, Barazani, & Song, 2017). Wild relatives have been reported as reservoirs of useful genes for rice improvement (Brar & Khush, 2018), and several blast resistance genes have been introduced from wild accessions (Das et al., 2012; Kumari et al., 2013; Rama Devi et al., 2015). Previous concerns on linkage drag (Zamir, 2001) when wild accessions were used as donor lines for introgression of traits, are now being overcome in many crops by the availability of dense genetic maps followed by marker-assisted selection (Dempewolf et al., 2017; Migicovsky & Myles, 2017). Despite finger millet not having much genomic resources currently, the progress in next-generation sequencing and the falling costs of genotyping globally will make it possible to utilize the identified wild sources of resistance in breeding programs. We also identified one improved variety (KACIMMI22) and four landraces (TZ1637, BKFM0031, ACC214988, ACC203544) with high resistance to the blast isolate that can be deployed immediately in breeding programs. The recently funded prebreeding programs in Uganda, Tanzania, and Ethiopia by the Templeton World Charity Foundation (https://www.croptrust.org/project/the-templeton-pre-breeding-project/) will especially benefit from deploying the resistant landraces and wild genotypes identified in this study.

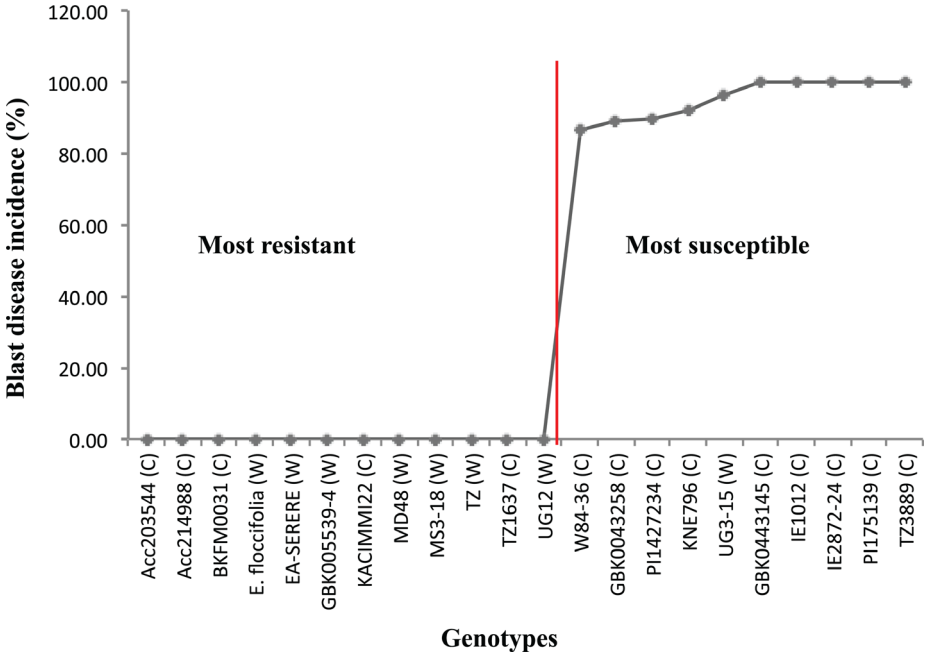

FIGURE 4 A contrast of the top 12 most resistant accessions with the 10 most susceptible accessions. There was only one wild accession among the most susceptible. The highly resistant genotypes were mostly wild accessions and landraces. The letters in brackets indicate whether a genotype is cultivated (C) or wild (W)

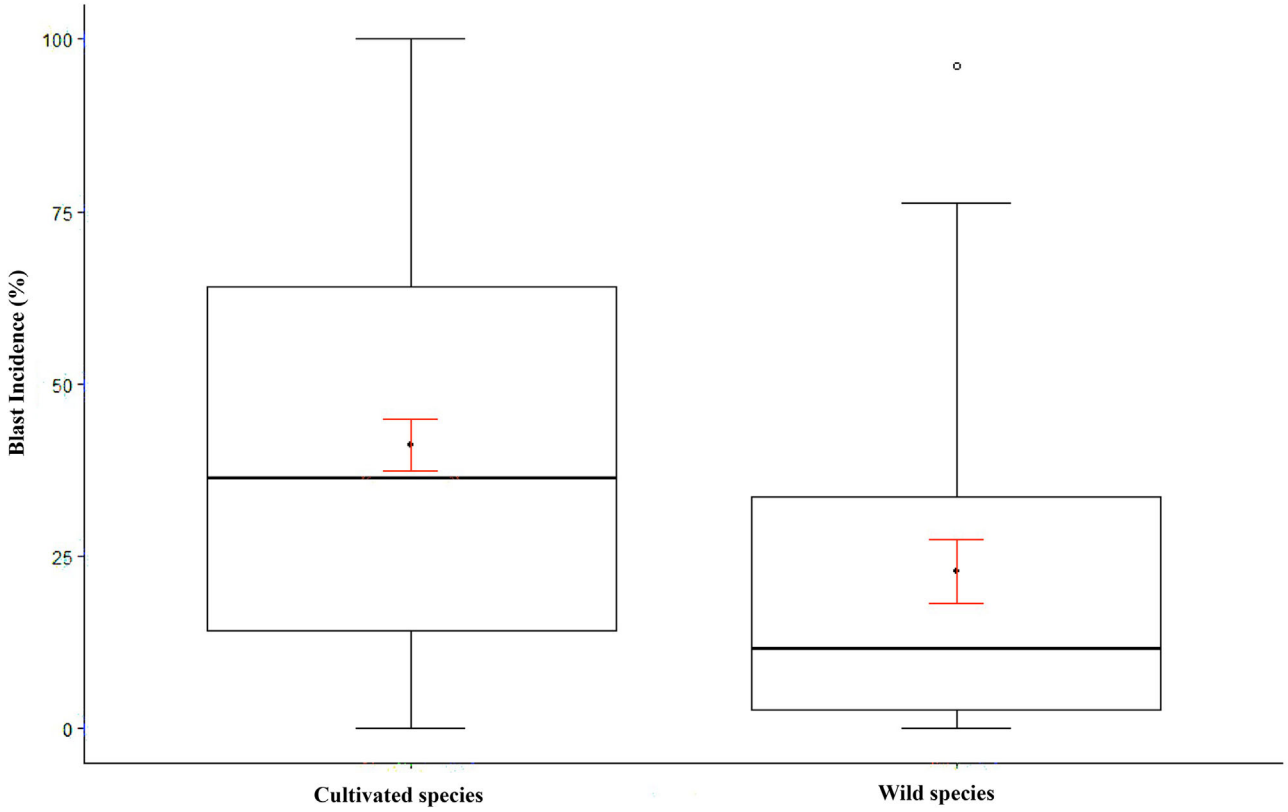

FIGURE 5 Box plots showing differences in the mean disease incidence between wild and cultivated accessions. All hybrids between *coracana* and *africana* were considered wild for the sake of making the comparisons. The box plots show an overall low disease incidence among the wild accessions in comparison to the cultivated accessions

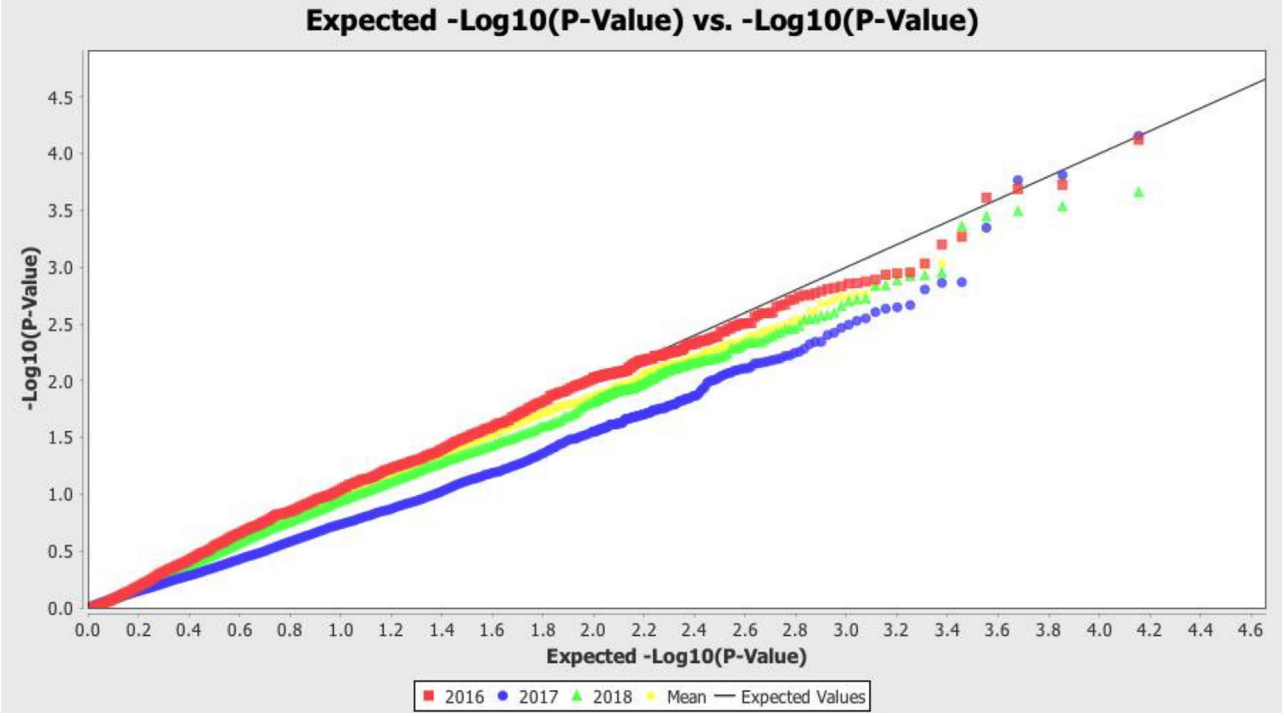

FIGURE 6 A quantile–quantile plot of general linear model plus principal component analysis genome-wide association study analysis for blast incidence in 2016 (red), 2017 (blue), 2018 (green), and means (yellow)

The resistant wild accessions and landraces will form a strong basis for future allele mining and full characterization of blast resistance in finger millet. Future studies will also need to characterize additional blast isolates in order to establish the rate of evolution of corresponding genes in the case of gene-for-gene interaction. Similar studies have been undertaken in rice for various geographical regions (Fukuta et al., 2019; Pagliaccia et al., 2018; Zhang et al., 2017) and will be important in finger millet to ensure relevant varieties are developed and deployed in strategic locations, which may have different blast pathotypes. In the current study, we used a blast isolate from the neck tissue but future studies will need to establish whether there are variations between blast isolates affecting various plant tissues. Differences in the aggressiveness of blast isolates from different tissues of the same plant have been reported (Ghatak, Willocquet, Savary, & Kumar, 2013) in rice, and there is evidence suggesting tissue-adapted fungal infection strategies (Marcel, Sawers, Oakeley, Angliker, & Paszkowski, 2010). Similar studies in finger millet will aid in understanding any tissue specialization strategies by the pathogen.

The observed high heritability across the three seasons reflects a high genetic control for resistance to blast in finger millet, which might suggest the involvement of a major gene in the resistance observed. Two major types of disease resistance, qualitative–horizontal–complete and quantitative–vertical–partial, have been exploited in plants. Qualitative resistance is modulated by a major disease resistance gene and an avirulence gene (Miah et al., 2013), while quantitative resistance involves several genes with minor effects (Corwin & Kliebenstein, 2017). In several studies, both major and minor disease resistance genes controlling a particular disease or multiple diseases have been reported to colocalize in the genome (Ali, Pan, Chen, Zahid, & Yan, 2013; Gebhardt & Valkonen, 2001). Although our study did not have the optimum genotype numbers to provide the needed power for a good association analysis, our preliminary GWAS results suggest the likely involvement of both major and minor genes but will need to be validated in the future.

The putative functional markers identified here were colocalized in majority of genes that have been reported to play significant roles in resistance to fungal pathogens in cereals. Receptor-like kinases have been reported to play a role in the resistance to fungal pathogens in cereals including barley (*Avena sativa* L.) (Karre, Kumar, Dhokane, & Kushalappa, 2017) and rice (Fan et al., 2018; Takahashi, Murano, & Ishikawa, 2018). There is evidence showing the involvement of ethylene responsive transcription factors in disease resistance in *Arabidopsis thaliana* (L.) Heynh. (Sun et al., 2018), soybean [*Glycine max* (L.) Merr.] (Zhao et al., 2017), and barley (Djemal, Mila, Bouzayen, Pirrello, & Khoudi, 2018). F-box family proteins, including Kelch repeat-containing family proteins, have been reported to be involved in disease resistance in Brassicaceae (Poveda, Hermosa, Monte, & Nicolás, 2019), wheat (*Triticum aestivum* L.) (Li et al., 2020), and maize (*Zea mays* L.) (Li et al., 2019). Despite the low

TABLE 4 Associated functional single nucleotide polymorphism markers after preliminary genome-wide association study analysis and their corresponding chromosomal locations and candidate genes

Linkage group	Variant	Position	*P*-value	R^2	Candidate gene	Position range
		bp				bp
1A	C/G	46,738,970	5.45×10^{-4}	.20	Leucine-rich repeat receptor-like protein kinase family protein	46,737,995–46,739,422
1A	T/C	46,069,153	4.58×10^{-4}	.17	Tryptophan aminotransferase	46,068,865–46,070,739
2A	A/G	1,629,966	8.00×10^{-4}	.16	Receptor-like protein kinase	1,628,200–1,631,642
2B	T/C	55,615,722	9.08×10^{-4}	.22	F-box domain containing protein	55,614,859–55,615,872
2B	C/T	59,973,963	8.97×10^{-4}	.15	Hexosyltransferase	59,969,697–59,974,158
3A	C/T	43,338,102	7.06×10^{-4}	.22	Receptor-like kinase	43,337,936–43,340,940
3B	G/C	1,190,087	6.25×10^{-4}	.15	Kelch repeat-containing family protein	1,184,856–1,190,100
4B	T/C	17,239,984	8.26×10^{-4}	.17	Short-chain dehydrogenase/reductase family protein	17,238,055–17,240,024
5A	C/A	19,465,261	8.51×10^{-4}	.16	Chaperone protein DnaJ	19,464,480–19,465,485
6A	A/G	18,000,182	1.91×10^{-4}	.18	Isoflavone reductase	17,999,945–18,002,150
6A	T/A	40,049,534	8.34×10^{-4}	.16	Bromodomain-containing protein	40,048,755–40,054,168
6A	G/T	50,715,487	4.45×10^{-4}	.25	Basic helix-loop-helix transcription factor	50,715,350–50,716,886
6B	G/A	70,331,237	1.86×10^{-4}	.25	AP2-like ethylene-responsive transcription factor	70,329,371–70,331,714
6B	T/C	66,546,058	5.22×10^{-4}	.16	Hydroxyproline-rich glycoprotein	66,546,087–66,551,222
6B	T/C	11,124,272	6.22×10^{-4}	.19	Protein kinase family protein	11,117,047–11,131,460
7B	C/G	53,831,328	5.86×10^{-4}	.16	Zinc finger protein Sdr4	53,830,526–53,831,497
9B	A/G	8,237,901	2.39×10^{-4}	.26	F-box family protein	8,236,911–8,237,819
9B	A/T	20,357,997	3.37×10^{-4}	.19	AP2-like ethylene-responsive transcription factor	20,355,486–20,360,563
9B	C/T	60,068,955	9.25×10^{-6}	.25	F-box family protein	60,067,953–60,069,524

numbers of germplasm used in the current study, the strong evidence of involvement of the putative candidate genes in disease resistance calls for further studies to confirm their role in blast resistance in finger millet. The markers identified can be immediately validated in diverse and biparental populations existing with breeders. Most finger millet breeders in eastern Africa use conventional breeding in their programs, which is slow and laborious. Once validated, the identified markers will form the first molecular toolkit for the blast resistance breeding in the region.

The preliminary PVS results will need to be repeated and validated using larger numbers of farmers. The gender differences revealed in the farmer-preferences calls for regular engagement of both male and female farmers during the varietal development process. The fact that none of the top 12 FPVs appeared resistant to the blast isolate used in the current study will require the immediate introgression of the identified resistance into the FPVs to reduce crop losses that the farmers regularly face resulting in food and nutrition insecurity. Such introgression programs will also need to take into account preferences of both male and female farmers to ensure that the varieties developed are relevant to both gender groups. More studies will be necessary to fully understand the trait preferences of each gender group.

Our investigation demonstrates the value of crop wild relatives as a major reservoir for favorable alleles for crop improvement. The use of molecular markers developed will speed up germplasm characterization and verification process and enhance the process of superior variety development. More studies will need to be done involving more germplasm alongside a larger collection of blast isolates to fully understand the nature of blast resistance. Multiparent populations will also need to be developed to ensure future genomic selection and characterization of major traits of interest.

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institutes around the world. For further information, see the project website: http://www.cwrdiversity.org/.

AUTHOR CONTRIBUTIONS

This project was conceived by DAO. DAO also analyzed the molecular data and drafted the manuscript. MMD undertook the morphological identification of finger millet and blast screening of the genotypes across the three seasons. CAO undertook PVS and provided improved germplasm. SJM prepared and characterized the blast isolate. MOA extracted DNA, analyzed the phenotypic data, and drafted part of the manuscript. EOM identified candidate genes associated with blast disease. HFO provided improved finger millet germplasm.

COMPETING INTERESTS

The authors declare that they have no competing interests

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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