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REVIEW ARTICLE

Enhancing resistance to finger millet blast using traditional and molecular approaches and outlook for future possibilities

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Abstract

The biodiversity of agricultural pests and diseases has changed significantly due to climate change, posing an immense challenge to sustainable crop production. Finger millet, the third most important millet, is typically cultivated in arid, semi-arid, hilly and tribal provinces across Africa and Asia. However, its growth and yield are severely threatened by blast disease, a destructive condition caused by the filamentous ascomycete fungus *Magnaporthe grisea*. Because the pathogen produces rapidly evolving virulence genes, blast resistance frequently breaks down, leading to yield instability in all provinces where finger millet is cultivated. Blast disease is estimated to reduce yield by 28 %–36 % on average and in extreme cases, it can result in total crop loss. The disease affects the crop in three progressive stages: leaf blast, neck blast and finger blast. In comparison to leaf blast, the loss is higher in neck blast and finger blast, which drastically decrease grain size and number and in extreme cases, this results in total panicle sterility. In this current review, we emphasized the significance of finger millet and its susceptibility to blast disease, pathogen, field screening technique, genetic resources available at different research organizations involved in the advancement of finger millet in the world, genetic diversity of blast pathogen, conventional and molecular tools like transcriptome analysis and transgenesis that have been employed to increase finger millet's resistance to blast disease and explored prospective future paths for the creation of new blast-resistant finger millet cultivars.

Keywords: blast disease; finger millet; mutation; transcriptomics; transgenesis

Introduction

Finger millet (*Eleusine coracana* L.) Gaertn, is an annual herbaceous plant of the family *Poaceae*, sub-family *Chloridoideae*, tribe *Eragrostideae* and genus *Eleusine* (1). As noted by Goron and Raizada (2), finger millet possesses a genome of 1593 Mb and a basic chromosome number of x = 9 (AABB). This crop is allotetraploid with AABB genomic constitution and chromosome configuration of 2n = 4x = 36 (3). Of the nine species within the *Eleusine* genus, eight, including *Eleusine coracana* and *E. indica*, are indigenous to Africa (4). The wild progenitor of finger millet, *E. coracana* subsp. *africana* likely arose from the hybridisation of *E. indica* (AA genome) with an unidentified, potentially extinct, B-genome donor (5). Finger millet is believed to have originated in East Africa (Ethiopia and Uganda highlands), was domesticated in Africa (6). It was then later disseminated to the lowlands of Africa and then introduced into the Western Ghats of India around 3000 years ago (7). India is considered a secondary centre of origin of finger millet (8). It was hypothesised that *E. coracana* is the domesticated version of the wild grass *E. africana*. According to recent studies, the most likely source of *E. coracana* L. "A" genome is *E. indica*, a pantropical plant with (2n = 2x = 18) chromosomes (5). It is referred to as Tellebun in Sudan, Bulo in Uganda and Ragi in India. It has a 97 %–99 % self-pollination rate (9). Its spikelet features hermaphrodite florets that are either chasmogamous or cleistogamous and its panicle is made up of finger-like, bisexual spikes. Based on the shape of its inflorescence, finger millet is divided into 2 subspecies, i.e. *africana* and *coracana* (10).

Raised in economically poor and resource-limited areas of Africa and Asia with low soil fertility, finger millet stands out for its climate resilience and remarkable nutritional value. As a vital food security crop in arid and semi-arid zones, it holds the third position among millet crops globally (10–12). It is a crucial food crop for global nutrition and food security because of its remarkable nutraceutical properties and long duration of storage (13). Although historically finger millet was once regarded as a "poor man's crop", its nutritional content and ability to withstand climatic change have made it popular again in recent decades (7). Given the nutritional significance of finger millet, the Government of India has included it under nutri-cereals. Promoting the cultivation of finger millet alongside other underutilised millet crops not only brings attention to neglected millet crops but also supports the United Nations Sustainable Development Goals (SDGs). This effort aligns predominantly with SDG 2 (Zero Hunger), SDG 3 (Good Health and Well-being), SDG 12 (Responsible Consumption and Production) and SDG 13 (Climate Action) (14).

India, Kenya and Uganda are the leading finger millet-producing countries worldwide (15). Karnataka accounts for approximately 60 % of the total area dedicated to finger millet cultivation in India, with additional areas being grown in Maharashtra, Uttarakhand, Odisha, Tamil Nadu, Gujarat and Andhra Pradesh (16). Ragi is a C4 plant and it uses the C4 carbon fixation pathway to enhance photosynthetic ability by reducing photorespiration, which occurs under low atmospheric CO_2 concentrations (17, 18). By the year 2050, it is expected that the world will encounter a significant agricultural crisis stemming from a decrease in the availability of arable land caused by global population growth and industrialisation, which will result in food shortages for the world population (19). Thus, plant breeders and geneticists have enormous pressure to boost the productivity of major crops, as well as minor or underutilised crops that are grown under poor resource ecologies, like finger millet, to overcome the food shortage for the global population.

Several abiotic and biotic factors influence the production and yield of finger millet. The utmost detrimental disease impacting the growth and productivity of this crop across its cultivated areas is blast disease, caused by filamentous ascomycete fungus, *Magnaporthe grisea* (Herbert) Barr; the same parasite pathogen also infects rice (19-21). Blast disease has an impact on almost all development phases of finger millet, including leaf, neck and finger blast (Fig. 1), which causes the most harm by reducing biomass up to 100 % and affecting average yield annually (22). All finger millet-growing regions have unstable yields due to the frequent loss of blast resistance, which is driven by the rapid evolution of the pathogen's virulence genes (23). Future sustainable production of finger millet is ensured through the use of innovative and effective techniques that offer dynamic and long-lasting resistance against several pathogen biotypes across a wide variety of agroecological zones. Providing a thorough grasp of viable ideas for finger millet breeding, we analysed the breeding and molecular techniques presently being utilised to enhance disease resistance and suggest possible future pathways for developing new blast-resistant finger millet varieties. Previous studies have shown that various genetic groupings of pathogens have been identified within millet blast populations (24). These studies had limited success because the phenotypic features identified in blast were highly variable (genetic instability of the pathogen). The investigations' main focus was to screen and select finger millet cultivars or new advanced lines that are resistant to specific strains of the blast fungus. Furthermore, when these strategies are applied, breeders may find that developing new types with broad-spectrum resistance against the disease requires a significant investment of time and resources. These investigations are also prone to human error and environmental influences, often leading to inconsistent results (25).

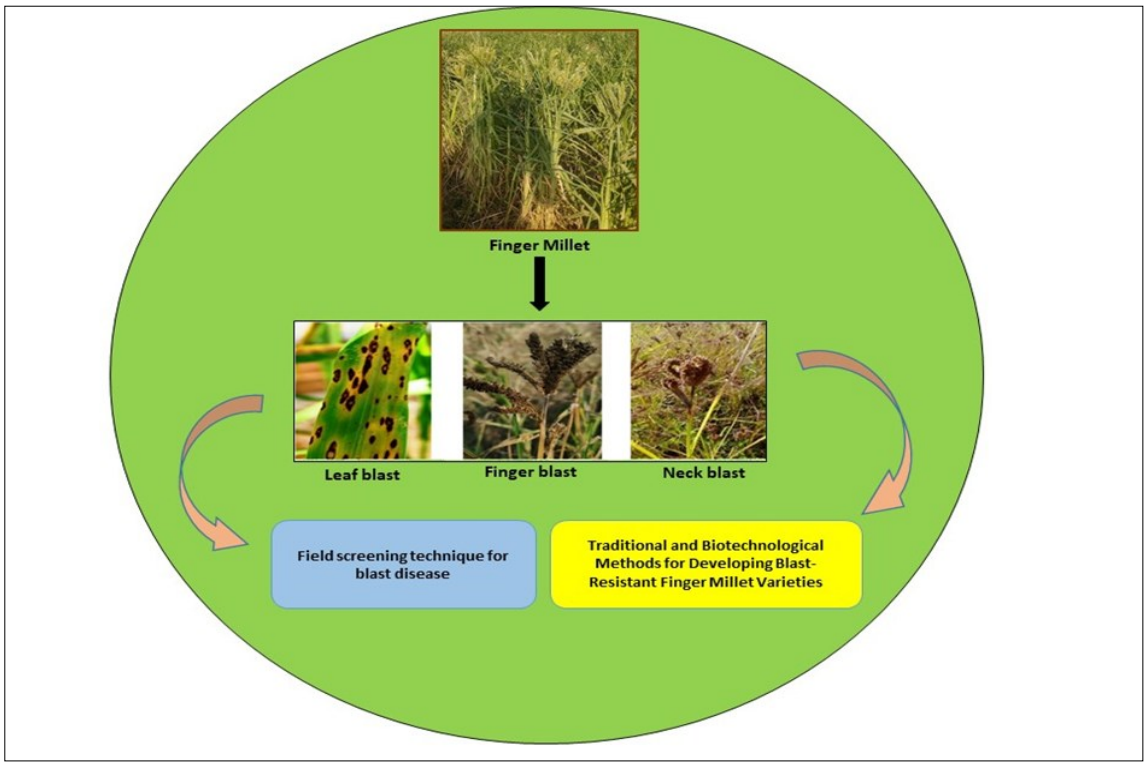

Fig 1. Three types of blast in finger millet.

A growing array of contemporary genomic tools has emerged alongside the development of high-throughput sequencing technologies. These tools encompass molecular markers, expressed sequence tags (ESTs), gene expression analysis, genome-wide association studies (GWAS), genetic engineering techniques and more recently, advancements in next-generation sequencing (NGS). Recent studies have focused on understanding biotic stresses in finger millet, particularly by advancing molecular genetics related to blast disease. This research seeks to establish an integrated management system for developing resistance to blast disease in finger millet (23). The current review critically highlights the significance of finger millet and blast disease, pathogen, field screening technique, genetic resources of finger millet conserved in India and abroad, genetic diversity of blast pathogen, conventional and molecular techniques used to develop resistance varieties and future direction in breeding of resistant varieties. To plan and carry out a breeding program for resistance in finger millet against blast, researchers, breeders and students would undoubtedly benefit from the comprehensive and up-to-date information provided in this review.

Occurrence and symptoms of Blast disease

The cultivation of finger millet is significantly impacted by both abiotic and biotic stresses. The blast disease, being one of the most critical biotic factors caused by *Magnaporthe grisea*, greatly reduces its productivity and overall yield (26). The disease was first identified in Uganda in 1933, while farmers recognised it as one of the main production barriers in 1997 (27). The fungus *Magnaporthe grisea* (Herbert) Barr causes one of the most devastating diseases that occurs throughout the rainy and winter seasons every year. It is the top production constraint in East Africa, where the majority of landraces are susceptible (28). Cloudy sky, frequent rain and drizzles enhance the infection by allowing dew to accumulate on leaves for a longer period. The sporulation rate intensifies as humidity rises up to or above 90 % and at a temperature of 25 °C–28 °C (29). Due to infection, the plant's neck-infected tissue has an excess of β-glucosidase released by both plants and pathogens can break down the fungal cell wall. These fragments can trigger the plant's defence system, both locally and throughout the plant. This often results in resistance. Finger millet is prone to infection throughout its development phases, but in severe conditions, the infection spreads to the plant's leaves, stem, node, collar, neck, roots and fingers, leading to substantial crop losses in all regions of finger millet cultivation (30).

Little grey or brownish spots first appear on the leaves and after two to three days of infection, the spots develop into greyish-white, diamond-shaped lesions with a brown border (Fig. 2) and sooty black lesions develop on the inflorescence (23). It was reported that the finger blast considerably lowers overall grain production, finger length, seed weight and seed number per finger. Blast disease reduces protein, starch and ash content in the seed of finger millet and as a result, its grain quality is reduced (31). It is assessed that the average loss is caused by blast disease in the yield of around 28 %–36 % and in severe cases, it can reduce yield by 100 % (29). Neck and finger blast cause greater yield losses than leaf blast, reducing both grain size and quantity and in severe cases, leading to total panicle sterility (16).

Mode of infection of Blast pathogen

During infection, conidia contact the host leaf using sticky secretions from the spore's apical tip during hydration. To facilitate germination, the spore firmly attaches to the hydrophobic (non-stick) surface. Subsequently, the conidia generate germ tubes that ultimately lead to the formation of melanised appressoria. The mature appressorium penetrates the leaf cuticle to reach the epidermal cells after producing enzymes that break down cell walls and accumulate appropriate solutes, such as glycerol (32). Without appreciably changing the host's cell walls, *Magnaporthe grisea* penetrates host tissues and uses the plasmodesmata to disseminate to nearby cells (33). The fungus produces abundant spores from diseased lesions. These enable rapid spread to nearby finger millet plants and their relatives through wind and water under humid conditions (34). The host is infected by *M. grisea* in 2 stages, viz. biotrophic stage, in which the fungus feeds on living cells and the necrotrophic stage, in which it feeds on dead cells (35).

Field screening technique for blast disease

An efficient field-screening method for the identification of susceptible and resistant plants was reported in the previous studies (26). Using this method, susceptible checks are sown every four test entry rows, spray *Magnaporthe grisea* strain which is treated with an aqueous conidial suspension (1 x 10^5 spores/mL) that has been cultured on oatmeal agar medium at a temperature of 27 ± 1 °C for ten days during the pre-flowering stage. To ensure high humidity and wetness on the leaf, sprinkler irrigation is conducted twice daily. The severity of leaf and finger blast diseases is assessed by calculating the proportion of all the tillers from ten randomly chosen plants in a row at physiological maturity. Leaf blast is rated on a 1 to 9 scale (Fig. 3), neck blast and finger blast are rated on a scale of 1 to 5 (Fig. 4A and 4B).

Fig. 2. Symptoms of blast disease in finger millet (A) Leaf blast; (B) Finger blast; (C) Neck blast.

Fig 3. Scoring of leaf blast on a 1–9 scale: (1 indicates highly resistant; 2–3 indicates resistant; 4–5 indicates moderately resistant; 6-7 indicates susceptible; 8–9 indicates highly susceptible) (26).

Fig. 4. (A) The neck blast is rated on a scale of 1 to 5; (B) The neck blast on a scale at 5 (36).

Genetic resources of finger millets conserved in India and abroad

The key to genetically improving any crop involves having access to and availability of an array of genetic resources. Genetic resources must be characterised for efficient use in any breeding programme. Finger millet germplasm, which was collected and conserved by different organisations in India and abroad, is given in Fig. 5.1. About 6804 finger millet germplasm were collected and conserved at the gene bank of ICRISAT, India. A composite collection having 1000 accessions was also developed at the same institute (37). Similarly, 2875 accessions at KARI, Muguga, Kenya, 2156 accessions at IBC Addis Ababa, Ethiopia, 1452 accessions at USDA-ARS, Griffin, USA, 1231 accessions at SAARI, Soroti, Uganda. Other countries that conserved and characterised finger millet for different traits are also given in (Fig. 5). The other status of germplasm of finger millet kept in African gene banks, both cultivated and wild 6700, Asia 28663, United States of America 1456, Europe 36, Oceania 18 and a total of 36873 (38). Plant breeders can obtain germplasm from these sources and can initiate a finger millet improvement programme sustainably.

Traditional and biotechnological methods for developing Blast-resistant finger millet varieties

New finger millet cultivars that possess resistance against blast disease are desired. Traditional breeding techniques aimed at introducing robust and enduring resistance to *M. grisea* have led many breeding programs to explore various finger millet germplasm (40, 41) like IC0474832, IC0473539, IC0473580, IC0473822, IC0473823, IC0473864, IC0473880, IC0331685 and IC0331687 (42). The NGS is a rapid progress approach, which along with high-performance computation and falling related costs, have led to widespread discovery of plethora of genetic resources in plants and other creatures, the amount of data generated by post-genomic research in the modern period has allowed us a greater grasp of the molecular, biochemical and physiological processes at work in genotype and it is like to phenotype, particularly for complex traits, promoted systematic crop breeding improvement and facilitated the optimal utilization of genetic resources, marker-assisted selection, for example, is a novel DNA-driven breeding strategy, marker-assisted backcross breeding, gene pyramiding and speed breeding technology (13, 43-46). An organised breeding programme is currently underway in India to create enhanced high-yielding cultivars that also possess blast resistance. The development of high-yielding cultivars of finger millet with blast-resistance has benefited greatly from the identification of many sources of stable blast disease resistance and their use in breeding programmes. Several improved cultivars/breeding lines have included blast resistance and some varieties/genotypes, including OEB 259, GPU 45, HR 374, GPU 48, VL 315, GPU 28, VL 340, VL 149 and PRM 9809, are claimed to be blast resistant. In the core growing region of finger millet in India, the blast-resistant cultivar GPU 28 dominated the farmers' fields (47). Varieties VL 149 and PRM 1 demonstrated 0.84 % and 10.42 % of neck blast and finger blast, respectively. They also observed a 36.56 % and a 19.51 % increase in yield across both types. Genotypes that are resistant to peroxidase activity, total phenolics, chlorophyll and polyphenol

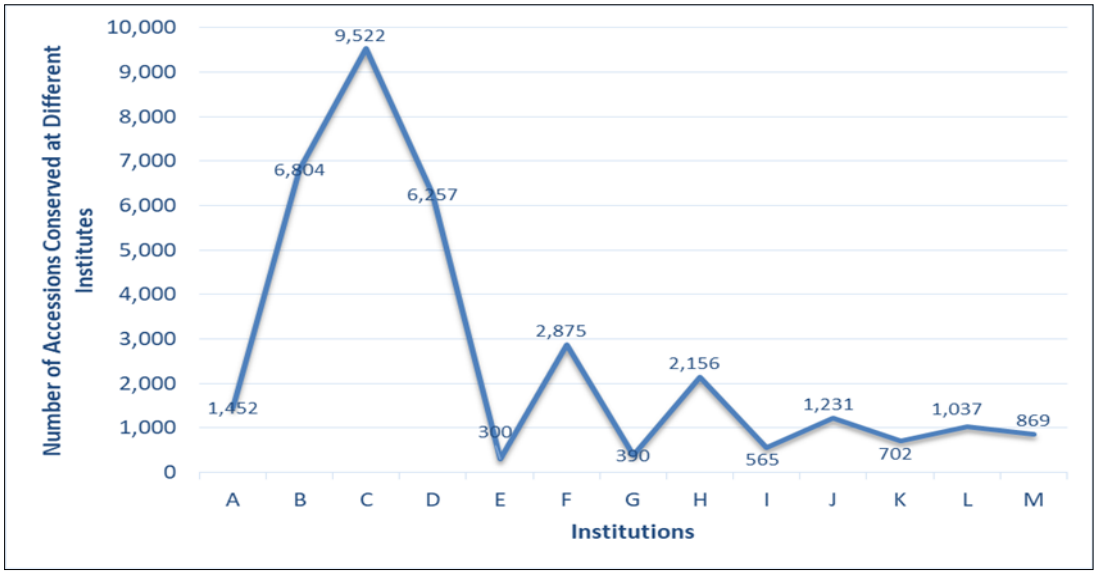

Fig. 5. Genetic resources of finger millet available at different organisations in India and abroad (39). Here, A- USDA ARS, B- ICRISAT, India, C- NBPGR, India, D- AICRP on Minor Millet Project, India, E- ICGR, Chinese Academy of Agricultural Sciences, China, F- KARI, Muguga, Kenya, G- Mt. Makulu Central Research Station, Zambia, H- IBC, Addis Ababa, Ethiopia, I- National Institute of Agro-biological Sciences, Kannondai, Japan, J- SAARI, Soroti, Uganda, K- National Centre for Genetic Resources Preservation, USA, L- SADC Plant Genetic Resource Centre, Zambia, M- CPBBD, Nepal Agricultural Research Council, Nepal.

oxidase activity were found to be higher in GPU 26 and GPU 28, while ascorbic acid and IAA oxidase activity were found to be lower in these two groups. In resistant genotypes, the low molecular weight protein fractions of 14 KD, 29 KD and 43 KD were successfully expressed. GPU 26 improved the biochemical and physiological indices among the genotypes (48).

Mutation breeding

In finger millet, mutation breeding was employed to create early-maturing types, generate polygenic diversity and create fully or partially male-sterile lines (49). It facilitates cross-pollination by preventing self-pollination and allowing for the production of hybrids with desirable traits from two parent lines. Mutagens, both physical and chemical, as well as in combination, were employed for this. Gamma irradiation was used to develop the early finger millet mutant known as Hamsa, which has more fingers and a larger grain-yielding region. Subsequently, key finger-millet-producing states made extensive attempts to create region-specific cultivars by fusing high production, blast resistance and tolerance to drought. In 1996, the medium-duration variety GPU 28 was introduced, which takes 110–115 days to reach maturity. This type is suitable for delayed sowing during a severe drought. Additionally, it also displayed resistance to neck and finger blast, a significant disease in the cultivation of finger millet (47). Six finger millet cultivars (Indaf-9, Co10, PR 202, GN1, IE 744 and HR 24) were treated with chemicals ethyl methane sulfonate (EMS), methyl methane sulfonate (MMS) and diethyl sulphate (DES) and with physical (gamma rays) mutagens to isolate a variety of early-maturing and dwarf mutants Tikka (50). Low doses of EMS and NG were used to develop the high-yielding mutants of white finger millet variety Co9, Devkota; while NG was used to generate the bold-grain mutants of MS2698 and short-duration mutants of Cv. Sarada (51, 52). Devkota added that a second phase of mutagenic treatment might provide potential improvement (51). Mutants of early types, high tillering type, numerous dwarfs and TNAU-294, Indaf-8 and HR-911were derived by gamma radiation. Mutation breeding could be a potential tool to augment blast resistance in finger millet in the future.

Molecular marker and mapping for Blast resistance

Despite being an expensive and time-consuming procedure, restriction fragment length polymorphism (RFLP) has been the main technique used to assess genetic variation among various isolates of *M. grisea* based on *M. grisea* repeats (MGR sequences). Randomly amplified polymorphic markers are among the most often used DNA-based markers (53, 54). Reproducibility issues plague RAPDs and these molecular markers are not locus-specific. In comparison, microsatellites, also known as SSR markers, address locus-explicit, highly polymorphic, multi-allelic and codominant marker frameworks which have become the markers preferred in plant hereditary qualities and reproducing applications. These markers are an arbitrary rehashing of DNA groupings found throughout the eukaryotic genome (55). AFLP analysis revealed that finger millet isolates causing leaf, neck and panicle blasts were similar genetically, suggesting that the same strains could produce distinct blast expressions under the right conditions (27). SSR marker generation is a laborious, expensive and time-consuming process. A few SSRs and markers using minisatellites for *M. grisea* have already been developed (56, 57). MGR-DNA fingerprinting was used to identify finger millet *M. grisea* isolates gathered from southern India and they also reported that the blast fungus that was gathered from the 2 hosts didn't spread cross-infect either host and that its fingerprint patterns were distinct (58). There is a good chance of gene flow between these two host-limited populations of *M. grisea* because of the finger millet variants' high level of sexual compatibility (59).

The population structure of *M. grisea* infecting isolates of finger millet, goosegrass and crabgrass from the northwest Himalayas of India was investigated using native protein and isozymes. It showed a significant amount of genetic variability among different populations of host-limited pathogens, including infected ones that were grouped based on host specificity. The pathogen did not exhibit gene flow between isolates and the pathogen subpopulations that were attacking weeds and rice were genetically different despite sharing a field (60). Polymorphic SSR markers were created using *M. grisea*'s newly released complete

genome sequence data and 176 SSR markers were compiled into a genetic map (61). 58 SSRs representing different genes controlling blast resistance in finger millet and rice were generated from 82 GenBank accessions utilising the sequences' CDS, 5′UTR, 3′UTR and intron regions (61). An extensive degree of genetic diversity was observed, with isolates from the same region being categorised together, irrespective of the crop from which the infected samples were collected. This was determined through a PCR-based RAPD analysis of *M. grisea* isolates from various hosts (62). Earlier studies, they isolated 136 isolates of the blast pathogen from different areas in India and demonstrated that Avr-Pizt was present in the highest frequency, followed by Avr-Pia (63). They also divided these isolates into four groups, showing a high degree of variation using molecular markers.

Marker-assisted selection

This breeding scheme is organised such that the main genes are combined and eliminate known lineage in a target region and it should be backed by a high degree of generic blast resistance provided by QTLs (64). By combining genetically varied main resistance genes, resistance durability has been improved in several crops. MAS is especially powerful for gene pyramiding when multiple resistance genes need to be combined (65). It would now be practical to speed up the transmission of advantageous genes between varieties using molecular methods. One approach that is particularly promising for assisting the selection of desirable traits is the use of molecular markers like RFLP, RAPD, AFLP and microsatellites, Sequence Tagged Sites (STS), SCAR and Cleaved Amplicon Polymorphisms (CAPs). There are thorough evaluations of the use of these methods to improve plant accessibility (66). With the development of comprehensive genetic maps and marker-assisted selection, in many crops, however, desired traits are now being introduced through the use of wild accessions as donor lines (67). Since finger millet is a crop that is highly neglected and underutilised, there is little information on its EST sequences. By comparing finger millet's blast resistance to rice's completely sequenced genome, for example, a comparative genomic method may be used to find the genetic markers linked to essential agronomic features (68). The study outlines the planned EST-SSRs, detailing their source, repeat motif, predicted product size and the function of homologous genes. Previously reported that the information about blast resistance is available in the NBS-LRR region associated with rice and finger millet, as well as in rice genes related to *M. grisea* and blast resistance genes (Piz, Pi-ta, Pi1, Pi2, Pi3, Pi4, Pi5, Pi14, Pi16, Pi21 and Pi25) (69). The finger millet NBS-LRR region was utilised to create five genic SSR markers, while the rice NBS-LRR region, which also includes sequences for blast-resistant genes, was used to develop 12 primer pairs (68). Finger millet blast resistance may be increased in the future through the use of marker-assisted selection.

Comparative genomics and SSR

Comparative genomics assisted in finding blast resistance genes using SSR markers because there was a lack of knowledge available about the finger millet genome (68). Mbinda and Masaki first reported the development of 58 functional markers, based on comparative genomics analysis of blast genes (Pi ta, Piz, Pi 15, Pi 21, Pi 25, Pi 14 and Pi 16) from 82 Genbank accessions, that is, sequences of different blast genes (23). The 2nd and 6th chromosomes of finger millet include resistance genes, according to an association mapping investigation employing 104 SSRs by the GLM (general linear model) technique resulted in the identification of 5 QTLs for blast resistance, amongst which 4 were for finger blast and 1 for neck blast. On the other hand, the MLM (mixed linear model) technique identified 7 markers associated with leaf, neck and finger blast. Both GLM and MLM methods connected the three markers FMBLEST32, UGEP18 and RM262 to blast disease. Rice Pi genes and blast R genes were syntonically mapped using the NBS-LRR EST sequences by association mapping. To identify useful QTLs, genetic mapping of blast resistance genes and other QTLs was done, along with association mapping. After conducting an *in silico* comparative genomics analysis with the genomes of monocot model plants, including maize, rice, sorghum, foxtail millet, wheat, switchgrass and Brachypodium, the data on the identified QTLs were utilised to pinpoint candidate genes linked to these QTLs. Seven QTLs were identified that were linked to leaf blast resistance and other agronomical traits. Blast resistance was significantly correlated with the UGEP101 and UGEP95 markers (26). The SSR and Sequence-related amplified polymorphism (SRAP) are two indicators that utilised to analyse variation among genotypes of finger millet that were resistant or susceptible to blast (4). Development of EST-SSR markers was done by genomic data of blast resistance of the gene. IE 4709 (blast resistant) and INDAF 7 (sensitive) were identified as the parents with the most varied genotypes; these genotypes have potential for further mapping population for resistance genes. The average band polymorphism was found to be high for both SSR primers (> 93 %) and SRAP (> 95 %). The maximum genetic diversity of Indian germplasm GE-4449 and GE-4440 was reported to be 98 %. The pairwise genetic similarity index created by SSR markers was able to differentiate between resistant and susceptible genotypes more effectively than the SRAP genotyping data. Using the massive rice sequencing data from comparative genomics, highlighted several methodologies suitable for resistance gene analogues (RGAs) allele mining in finger millet (70). This creates the opportunity to introduce blast-resistant alleles into high-yielding, blast-sensitive and regionally adapted germplasm using molecular breeding and genetic engineering methods.

Previously, it used single-copy orthologous genes from closely related grasses; this phylogenetic study demonstrated that finger millet genotype ML365's entire genome was sequenced (8). There is an agreement in genome size 1196 mb, covering 82 % of the genome size and the GC content of the genome was 44.76 %. To arrive at a consensus number, the numbers they reported for genes will need to be re-examined. Based on a preliminary analysis, the genomic sequences of finger millet and other cereals revealed that there were ninety-five per cent, ninety per cent and sixty-five per cent collinear blocks with maize, rice and sorghum, respectively. Using these R-gene sequences, mapping of resistance genes and allele mining in finger millet accessions could be achieved. Hiremath and Gowda assessed the molecular diversity of finger millet accessions that were resistant and susceptible to blast disease using SSR markers (71). Among 32 accessions, 62 alleles were identified by 25 markers; the highest number of alleles was detected by the marker UGEP8 (five), followed by UGEP12 and UGEP60 (four). Earlier studies conducted a trial on 134 finger millet accessions for blast resistance using 20 SSR markers (72). One accession (Acc. BKFM0031) was the resistant one, eight were moderately resistant and the rest 125 accessions varied from moderately to severely susceptible. The accessions were collected either from the same origin or those having similar types of infection

and then were grouped into 3, using the SSR weighted neighbour-joining method starting from the main node. Only a few accessions that were from different locations exhibited genetic similarities, while accessions from the same region were also not nearly grouped. This required more analysis and molecular study regarding blast-resistant genes. The markers/QTLs identified by many workers that were associated with blast resistance in finger millet are presented in Table 1.

Single-nucleotide polymorphism (SNP)

This study investigated how finger millet's wild and cultivated species responded to a blast disease isolated from western Kenya. Improved, farmer-preferred varieties (FPVs) and some new selections were used for screening. Diversity arrays technology (DArT) sequencing was used to generate the genotypic data and Genstat 18.2 and TASSEL 5.2.58 were used to analyse the data. A total of 19 functional SNPs were found to be associated with the disease. It was discovered that wild relatives were more resistant than cultivated ones; this may be because a major gene is involved in the observed resistance. The strong genetic influence on blast resistance is evident in the consistently high heritability observed throughout all seasons (75).

Genome-wide association study (GWAS)

Due to their comprehensive genome coverage, co-dominant inheritance, high repeatability, multiallelic characteristics and specific chromosomal locations, SNP markers, often referred to as next-generation markers, are preferred in GWAS studies (12, 76). To determine marker-trait connections, 186 genotypes were assessed and quantified using GWAS and genotyping-by-sequencing (GBS). Three subpopulations with different admixture levels were detected by GBS and 2977 SNP markers of high quality were generated. Four MTAs were identified for neck blast resistance and orthologues of *O. sativa* candidate genes were found to be associated with the linked SNPs. These QTL-associated markers will be useful in future for marker-assisted breeding approaches aimed at producing high-yielding finger millet cultivars and fungal resistance.

Biotechnology for resistance to Blast disease

Conventional plant breeding is labour-intensive, time-consuming and influenced by environmental variability (77). However, novel methods for crop genetic modification and accelerating agricultural development are provided through molecular or biotechnological techniques like genome editing and genetic engineering. Establishment of effective *in vitro* regeneration systems for transformation and following regeneration of cereal crops is considered a crucial prerequisite for the application of these methods. The research started on the transformation of finger millet by utilising the biolistic technique to compare the effects of 5 different gene promoters on the expression of β-glucuronidase reporter gene (78). Transgenic plants were generated that exhibited resistance to leaf blast disease by using the biolistic technique (79). Further modifications in finger millet mediated by the *Agrobacterium tumefaciens* method of genetic transformation of finger millet were introduced in previous reports (80).

Transgenesis for Blast Resistance in Finger Blast

A variety of techniques were used employing genetic engineering of finger millet for blast resistance was done by various workers. Two species of finger millet, namely Eleusine coracana L. and Echinochloa crusgalli, were used and high transgene expression was found to result from the suitability of the Ubiquitin 1 gene promoter when biolistic and callus regeneration techniques were employed (78). Using this knowledge, a particle inflow gun–mediated method was employed for genetic transformation and gene delivery (79). For this, they extracted a gene from prawns that codes for antifungal protein (PIN), which was chemically unified and further cloned into expression vectors for bacteria and plants. This was the first successful production of pin gene expressing transgenics using the bombardment technique in finger millet, which showed significant levels of resistance to leaf blast fungus. Ignacimuthu and Ceasar inserted the rice chitinase gene (*chi11*) into finger millet through Agrobacterium-mediated transformation to impart resistance to leaf blast (81). The introduction of chitinase arrests the growth and early development of the fungus. These two discoveries were for leaf blasts; no such discoveries have yet been made for the other two major types of blasts, i.e. neck blasts and finger blasts. By investigating several physical and chemical factors that have been demonstrated to affect gene transfer using the Agrobacterium method, transgenic lines were developed from the callus of the PR-202 variety with a transformation efficiency of 44.4 % (82). Several reports of *in vitro* regeneration in finger millet were

Table 1. QTLs/markers linked to finger millet blast disease

Trait	Gene	QTLs/SSR /EST marker	Phenotypic variance (%)	Probability	Distance and location of the chromosomes	References
Finger blast	Rice *Pi-d(t)* blast gene	RM262	0.01, 5.0–10.0	0.007	2A (72 cM)	(73)
		FMBLEST32	0.01, 4.5–8.0	0.007	6B (20 cM)	
	Rice *Pi5* blast gene	UGEP24	8.0	0.003	3B (115.3 cM)	
		UGEP81	7.5	0.009	6B	
Neck Blast		UGEP53	10.5	0.008		
		UGEP18	11.0–13.0	0.01,0.009	1B (70 cM)	
Leaf blast	*Pi21*	FMBLEST35	10.0	0.009	4B (7.0 cM)	(68)
		RM23842	11.0	0.009	6B (3.5 cM)	
		FMBLEST15	8.0	0.006	4B (6.0 cM)	
Leaf blast		UGEP101	21.05			(26)
		UGEP95	8.95			
		TP979411	15.1			(12)
		TP229691	15.0			
Finger Blast		EU075234			6^{Th}	(68)
		EU075225			11^{Th} end, 8^{th} above Centromere	
	Pi21	GU301915			4^{Th}	
	IgA-specific serine endopeptidase	UGEP16			1^{th} (10.7 kb)	(74)
	1,4-β-Glucanase	UGEP101			3^{Th}	

produced as a result of scientific attention. A regeneration method that uses shoot apical meristems produced *in vitro* has been developed recently (83). The highest rate of shoot induction was recorded in the MS medium enriched with 1.75 mg/L of benzylaminopurine (BAP). Previously reported that isolation of 57 kDa chitinase from finger millet plants infected with *P. grisea*, which exhibited antifungal properties against blast fungus *P. grisea in vitro* (84). They have also reported that finger millet showed a significant level of resistance to leaf blast, as indicated by expression of the rice chitinase gene (*chi11*). This finding could pave the way for the introduction of additional fungal-resistant genes, such as glucanase, into finger millet through Agrobacterium-mediated transformation. The transgenic plant's resistance against blast disease developed using different genes is given in Table 2.

Omics approaches in Finger Millet

Omics technologies have been widely employed in finger millet research to unravel its genetic and molecular characteristics and understand its response to various stresses and nutritional composition (66). Here are some key omics technologies utilised in finger millet research. These references demonstrate the application of various omics technologies, including genomics (87), transcriptomics (88), proteomics and metabolomics in finger millet crop research. They deliver important insights into the genetic diversity, stress tolerance mechanisms, nutritional value and improvement of finger millet crops.

Genomics in Finger Millet

To comprehend the evolutionary and functional characteristics of an organism, genomics involves extensive research of the structural and functional properties of the genome (89). Investigations into genome size and genetic and physical mapping were part of early genomics. A new era of omics has been brought about by NGS, which has made it possible for researchers to sequence, assemble and analyse genomes of several plant species (90). Whole genome sequencing for some important crops has made it possible to discover economically and agronomically significant genes and revolutionary breeding techniques for crop development. Developing a genetic linkage map in the initial stage of molecular breeding for crop improvement, genomic materials, including genome sequences and molecular markers, are crucial. A total of 83,875 SNPs were identified, of which about 23,000 were segregated across the complete set and thousands of SNPs were found to be segregated within each accession using the Illumina sequencing platform in finger millet (66, 91). Molecular markers have been broadly applied in research on the genetic diversity, taxonomy and population structure of various crops such as wheat, rice, maize, sorghum, soybean and barley. In finger millet genome studies, SSRs and SNPs have also been commonly utilised (92). The SNP markers are considered as most effective for genomic selection, high-density genetic mapping and genetic research due to their widespread presence across the genome. Genome-wide population genetic studies were conducted on three millet species, leading to the identification of 1,882 SNP markers (93). The original sequences from random genomic libraries, developed using Hind III, Sal I and Pst I digestion and hybridisation with probes from finger millet accession PI 321125, were used to design markers targeting QTLs associated with leaf blast resistance and agronomic characters (75). Despite the currently limited genetic resources for finger millet, advancements in next-generation sequencing and decreasing genotyping costs will facilitate the use of these naturally occurring resistance sources in breeding programs. Furthermore, Dida identified four landraces (ACC 214988, TZ 1637, BKFM 0031 and ACC 203544) and one improved variety (KACIMMI 22) with significant resistance to blast disease (75).

Other Omics approaches

The main tool for locating significant candidate genes involved in biological processes is gene expression profiling methods or transcriptomics (70). It entails extensive research and assessment of transcriptome-wide alterations. There are now studies that focus on these fundamental characteristics utilising cutting-edge technologies like high-throughput transcriptome sequencing (94). Ten years ago, the only methods for the expression of gene studies were serial assessments of gene expression (SAGE) and microarray. In recent years, advancements in NGS and sophisticated analytical tools have revolutionised scientific research (88). Several studies have explored the transcriptome of finger millet (8). Through a meta -analysis of publicly accessible gene expression data, researchers have proposed a theoretical model to explain the transport and distribution of calcium in cereal embryonic seeds, with a particular focus on finger millet. This comprehensive transcriptome analysis identified 82 distinct calcium sensor genes in developing inflorescences from genotypes exhibiting varying grain calcium levels (66). In finger millet accessions with high grain calcium content, it was discovered that the calmodulin and Cax1 transporter genes were strongly expressed throughout grain-filling phases (95). According to previous studies, proteomics is the thorough, comprehensive research study of all proteins, including their expression, structure and function (96). Between an organism's transcriptome and in-response its final responding metabolome, the proteome acts as a coupler. Mass spectrometry, on the other hand, offers a more specialised approach for identifying a wide range of proteins. During the grain-filling stage of developing seeds, enhanced calcium accumulation was associated with increased immunodetection of the protein calmodulin in both embryo and aleurone layer of a high-calcium finger millet genotype. Calreticulin, another calcium-binding protein, was identified in developing finger millet spikes using peptide mass fingerprinting (66, 97). Discovering a finger millet peptide or protein with nutraceutical potential through this approach could pave the way for the development of a groundbreaking dataset for research and therapeutic applications. While genomics, transcriptomics and proteomics have significantly advanced our understanding of genotypes and intricate biological processes, the lack of alignment between changes in transcriptome or proteome and the cellular metabolome highlights the critical role of metabolomics in the functional genomics era.

Table 2. Cloned functional Genes Linked to blast resistance in finger millet

Gene name	Promoter/reporter	Purpose	Reference
chi11	Maize ubiquitin promoter	Resistance against leaf blast	(81)
pPin 35S	*CaMVs35S*	Resistance against leaf blast	(79)
Pi21	*AB430853*, *DD461353*	Resistance against finger blast	(73)
Pb1, Pi25(t)	*IE 2183*	Resistance against neck blast	(85)
ELECO.r07.1BG0094990	-	Resistance against leaf blast	(86)
ELECO.r7.6BG498660	-	Resistance against panicle blast	(86)

The metabolic roles of several metabolites for climate resilience may potentially be revealed through millet metabolomic investigations. For instance, utilising data from the proteome, transcriptome and targeted metabolome, metabolic reconstruction and diverse omics mapping were carried out in millet (89). A large number of metabolites involved in C_4 metabolism were identified (98). Similar to this, integrated metabolomics research on the millet cultivars 04 and Yugu 2 under salt stress suggested that the lysphospholipid, phenylpropanoid, lignin and flavonoid production pathway is essential for seed germination. Three hundred thirty annotated metabolites were identified in 150 samples of millet germplasm through targeted metabolomics research (91). Additionally, the GWAS analysis of the data collected revealed genes for intricate physiological features. A comprehensive multi-omics study was conducted on 398 finger millet accessions, uncovering genomic regions linked with domestication, as well as common polymorphisms that influence metabolite characters and exhibit anti-inflammatory properties (17). Additional researchers have recognised the gene that determines grain colour in finger millet and confirmed it by genome editing (17). During the grain-filling stage, researchers identified a total of 2014 metabolites linked to millet (91). Research emphasised the essential role of metabolomics in examining stress-related phenotypes, as well as the associated genes and metabolites, in the quest to develop climate-smart crops for the future. The above-discussed omics approaches play a vital role in future for the improvement of blast disease. Whole-genome sequencing of the finger millet genotype ML-365, which is drought-tolerant and resistant to blast disease, was done using Illumina and SOLiD sequencing technologies (99).

Future prospectives

The world's increasing population establishes rising demands on food and nutritional security, which together make up agricultural sustainability. In addition, commercial crops such as wheat, maize, rice etc. have received greater attention because of their widespread use and acceptability as staple foods. Interest in millets has significantly increased in recent years, particularly small millets, mainly finger millet, due to rising health issues that their nutraceutical qualities address. Thus, systematic research on finger millet has to be prioritised and is still ongoing in several areas, such as the breeding of new varieties and genome sequencing. The development of scientific tools and NGS technology over the previous few years has significantly changed the situation (88). RNA sequencing has become a popular substitute for cDNA sequencing in gene expression research. With the advent of cutting-edge genomic technologies like genome editing and next-generation sequencing (NGS), cloning and transferring resistant (R) genes has become easier. Transgenics for drought and salinity tolerance have been created using the rice chitinase gene in finger millet to transfer resistance to leaf blast and the mannitol-1-phosphate dehydrogenase (*mtlD*) gene from bacteria (95). The CRISPR/Cas9 gene editing method depends on DNA or RNA sequence homology, as opposed to protein-guided ZFNs and TALENs (91). The use of such methods to finger millet contributes to a better knowledge of the crops and opens the door for potential crop genome modification to produce disease-resistant crops, which is environmentally beneficial. This will make finger millet an affordable, farmer-friendly and perhaps environmentally friendly substitute for nutraceutical supplements because they don't require pesticides. Achieving food and nutritional security also benefits from routine monitoring of newly discovered diseases as well as surveillance of the previously existing known ones (70).

Conclusion

A major challenge to sustainable agricultural production is the diversity of diseases and pests in agriculture, which has been greatly impacted by climate change. Consequently, plant breeders and geneticists face growing pressure to raise the production of key food crops to meet the anticipated food demand resulting from global population growth. Finger millet, a prominent millet crop cultivated in mountainous regions of tribal, semi-arid and arid areas of Africa and Asia, is particularly affected by a destructive disease known as blast disease, caused by the Filamentous ascomycetous fungus *Magnaporthe grisea*, which is a teleomorph of Magnaporthe grisea (Herbert) Barr. This review explores both traditional and molecular approaches to improve resistance to finger millet blast. Traditional methods involve the utilisation of genetic resources and conventional breeding techniques. Researchers have identified resistant varieties and wild relatives of finger millet that possess natural resistance to blast disease. Breeding efforts may utilise these genetic resources to create novel varieties with increased resistance. Blast disease poses a significant threat to finger millet, impacting its growth and yield across all cultivation areas. Due to the pathogen susceptibility to quickly growing virulence genes, blast resistance frequently breaks down, producing yield instability across all finger millet-growing regions. On average, blast disease is estimated to reduce yield by 28 %-36 %, with the potential to cause a complete loss of yield in extreme cases. The disease manifests in three stages: leaf blast, finger blast and neck blast. Neck blast and finger blast are particularly detrimental, significantly reducing grain size and quantity. In severe instances, this can result in complete sterility of the panicle. In conclusion, the development of finger millet varieties resistant to blast disease is essential to ensuring food security and sustainable production of crops. Traditional breeding, molecular approaches and emerging technologies offer promising avenues to enhance resistance. Continued research and collaboration among plant breeders, geneticists and pathologists will pave the way for future development of highly resistant finger millet genotypes, mitigating the impact of blast disease on this important cereal crop.

Authors' contributions

NK conceptualised and prepared the manuscript. K contributed to the conceptualisation, provided the resources and reviewed the manuscript. VS reviewed and edited the manuscript. IO prepared the initial draft of the manuscript. VKK reviews the literature. PJ contributed to the preparation of the manuscript. HSN conceived the idea and prepared the original draft of the manuscript. AK^1 reviewed the literature. SKS edited the manuscript. RK contributed to the preparation of the manuscript. VG edited the manuscript. AK^2 finalised the manuscript. MM contributed to the preparation of the initial draft. All authors agreed with the final version of the manuscript for publication. [AK^1 stands for Ankur Kumar, AK^2 stands for Arun Kumar]

Compliance with ethical standards

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