Received: 21 July 2021 | Accepted: 8 October 2021

DOI: 10.1002/tpg2.20175

The Plant Genome

ORIGINAL RESEARCH

A high-density linkage map of finger millet provides QTL for blast resistance and other agronomic traits

Thomas H. Pendergast, IV[1,2,3] | **Peng Qi**[1,2,3] | **Damaris Achieng Odeny**[4] | **Mathews M. Dida**[5] | **Katrien M. Devos**[1,2,3]

[1] Dep. of Plant Biology, Univ. of Georgia, Athens, GA 30602, USA

[2] Institute of Plant Breeding, Genetics and Genomics, Univ. of Georgia, Athens, GA 30602, USA

[3] Dep. of Crop and Soil Sciences, Univ. of Georgia, Athens, GA 30602, USA

[4] The International Crops Research Institute for the Semi-Arid Tropics–Eastern and Southern Africa, Nairobi, Kenya

[5] Dep. of Applied Sciences, Maseno Univ., Private Bag-40105, Maseno, Kenya

Correspondence
Katrien M. Devos, Dep. of Crop and Soil Sciences, Univ. of Georgia, 3111 Miller Plant Sciences, Athens, GA 30602, USA.
Email: kdevos@uga.edu

Assigned to Associate Editor Emma Mace.

Abstract

Finger millet [*Eleusine coracana* (L.) Gaertn.] is a critical subsistence crop in eastern Africa and southern Asia but has few genomic resources and modern breeding programs. To aid in the understanding of finger millet genomic organization and genes underlying disease resistance and agronomically important traits, we generated a $F_{2:3}$ population from a cross between *E. coracana* (L.) Gaertn. subsp. *coracana* accession ACC 100007 and *E. coracana* (L.) Gaertn. subsp. *africana* , accession GBK 030647. Phenotypic data on morphology, yield, and blast (*Magnaporthe oryzae*) resistance traits were taken on a subset of the $F_{2:3}$ population in a Kenyan field trial. The $F_{2:3}$ population was genotyped via genotyping-by-sequencing (GBS) and the UGbS-Flex pipeline was used for sequence alignment, nucleotide polymorphism calling, and genetic map construction. An 18-linkage-group genetic map consisting of 5,422 markers was generated that enabled comparative genomic analyses with rice (*Oryza sativa* L.), foxtail millet [*Setaria italica* (L.) P. Beauv.], and sorghum [*Sorghum bicolor* (L.) Moench]. Notably, we identified conserved acrocentric homoeologous chromosomes (4A and 4B in finger millet) across all species. Significant quantitative trait loci (QTL) were discovered for flowering date, plant height, panicle number, and blast incidence and severity. Sixteen putative candidate genes that may underlie trait variation were identified. Seven LEUCINE-RICH REPEAT-CONTAINING PROTEIN genes, with homology to nucleotide-binding site leucine-rich repeat (NBS-LRR) disease resistance proteins, were found on three chromosomes under blast resistance QTL. This high-marker-density genetic map provides an important tool for plant breeding programs and identifies genomic regions and genes of critical interest for agronomic traits and blast resistance.

1 | INTRODUCTION

Finger millet [*Eleusine coracana* (L.) Gaertn.] is an inbreeding C4 allotetraploid ($2n = 4x = 36$, AABB) that is an important cereal crop in eastern Africa and southern Asia

Abbreviations: CC, coiled coil; GBS, genotyping-by-sequencing; NBS-LRR, nucleotide-binding site leucine-rich repeat; NP, nucleotide polymorphism; QTL, quantitative trait loci; SNP, single-nucleotide polymorphism; TPS, trehalose-phosphate synthase

(Puranik et al., 2017). Its grain has excellent nutritional qualities with a higher concentration of calcium than any other cereal and is enriched with other minerals, vitamins, and amino acids (Devi et al., 2014; Kumar et al., 2016). Finger millet is a staple food in semi-arid, poorer areas with marginal lands, as it has wide environmental tolerances (Kumar et al., 2016; Opole et al., 2018; Talwar et al., 2020). Although currently considered mainly of regional importance, the role of finger millet in global food security is expected to increase because of the growing impacts of climate change, which will likely result in increased drought risk and more erratic weather patterns (Bandyopadhyay et al., 2017; Sultan & Gaetani, 2016; Wambi et al., 2021). Increased health awareness and promotion of finger millet as a 'smart food' is also expected to lead to its enhanced consumption (Wangari et al., 2020).

Despite its potential as a climate and nutrition smart crop, the production of finger millet suffers from low historical investment and is further challenged by several biotic and abiotic factors. Current yield in farmers' fields is typically very low (400–2,000 kg ha^{-1}) because of the frequent reliance on landraces, cultivation under low inputs, low genetic variability within breeding pools, and breeding approaches that have lagged behind those of other cereal crops (National Research Council, 1996; Dida et al., 2007). Among the diseases that affect finger millet production, blast disease caused by *Magnaporthe oryzae* is the most important. *Magnaporthe* is a complex of ascomycete fungi that cause blast disease across a broad range of Poaceae hosts and are the most destructive pathogens of human food crops (Choi et al., 2013; Gladieux et al., 2018; Qi et al., 2019). In finger millet, *M. oryzae* can cause yield reductions of up to 50% (Takan et al., 2004) and can persist in native grass reservoirs, allowing outbreaks throughout the year (Manyasa et al., 2019). As most finger millet production is undertaken by resource poor farmers on small parcels of land, disease management through host resistance is the most sustainable and environmentally conscious method of control as opposed to repeated fungicide applications (Babu et al., 2015; Dida et al., 2021; Manyasa et al., 2019). Genetically informed breeding programs that focus on blast resistance, maturation rate, and other crucial traits may be the most efficient mechanism for increasing finger millet yields across eastern Africa and southern Asia (Sood et al., 2016). As such, it is imperative to identify the genetic factors that underlie these traits.

Although there have been a number of recent advancements in transcriptome (Akbar et al., 2018; Hittalmani et al., 2017; Zhang et al., 2019) and whole-genome studies of finger millet (Hatakeyama et al., 2018; Hittalmani et al., 2017), modern breeding efforts in finger millet have generally been hampered by the lack of genomic resources and genetic tools (Wambi et al., 2021). Indeed, the majority of finger millet trait studies have been conducted with low numbers of molecular markers and population sizes, yielding poor genomic resolution (e.g., Babu et al., 2014; Ramakrishnan et al., 2016; Ramakrishnan et al., 2017). However, a few recent studies have used genotyping-by-sequencing (GBS) to develop genetic markers (Puranik et al., 2020; Sharma et al., 2018; Tiwari et al., 2020). Because of the difficulty of generating crosses in finger millet, all trait mapping has thus far been done using association mapping (Wambi et al., 2021). We have previously demonstrated the use of GBS to generate a high-density genetic map of finger millet in a cross between the wild finger millet [*E. coracana* (L.) Gaertn. subsp. *africana*] acc. MD-20 and the cultivated [*E. coracana* (L.) Gaertn. subsp. *coracana*] line Okhale-1 (Qi et al., 2018). Here, we harness GBS to generate an accurate, high-density genetic map in another wild × cultivated biparental mapping population and use the map to identify genomic regions underlying crucial blast resistance and other agronomic traits determined in a replicated field trial conducted in Kenya.

Core Ideas

- We generated a high-density genetic map for the genomic- and resource-poor finger millet.
- We identified QTL and candidate genes for agronomic and blast resistance traits.
- We conducted genomic comparisons across finger millet, rice, sorghum, and foxtail millet.

2 | MATERIALS AND METHODS

2.1 | Genetic mapping

2.1.1 | Mapping population

The F_2 mapping population was generated in the mid-1990s from a cross between the putatively (it may be an introduction) Ethiopian *E. coracana* subsp. *coracana* accession ACC 100007 [obtained from the International Crops Research Institute for the Semi-arid Tropics (ICRISAT), Nairobi, Kenya] and the Kenyan wild finger millet accession GBK 030647 (collected from Makueni, Kenya, and obtained from the gene bank of Kenya, Muguga, Kenya). Individual F_2 plants were selfed to produce F_2–derived F_3 families. For 151 $F_{2:3}$ families and parental lines, 16–24 seeds were planted into 20-cm diam. pots in a greenhouse at the University of Georgia. Eight weeks after germination, healthy leaves were collected from at least 12 individuals per line for bulk DNA extraction to reconstitute the F_2 genotype.

2.1.2 | DNA extraction and GBS library preparation

Collected leaf tissue was flash frozen in liquid nitrogen and stored at −80 °C until DNA extraction. The bulked leaf tissue was ground with a TissueLyzerII bead mill (Qiagen). Genomic DNA was extracted using Wizard® Genomic DNA Purification Kits (Promega) and DNA quantity and quality were determined by Nanodrop spectrophotometer and 1% agarose gel electrophoresis.

We largely followed the GBS restriction digest and library construction protocol described in Qi et al. (2018). Briefly, extracted DNA was diluted to 50 ng μl^{-1} with TE buffer, and digested with the restriction enzymes *Pst*I, *Msp*I and *Ape*KI. A common Y-adaptor and individual barcoded adaptors were then ligated to the *Msp*I and *Pst*I sites, respectively. We note that the use of a third restriction enzyme (*Ape*KI), as was used here, is no longer recommended (Qi et al., 2018). Library quality was verified by agarose gel electrophoresis and quantity determined with a Qubit 2.0 fluorometer. Fragments smaller than 300 bp were removed using Sera-Mag SpeedBeads (GE Healthcare Life Sciences). DNA samples with a concentration higher than 5 ng μl^{-1} were pooled in equal amounts (30 ng) and the library pools were sequenced on an Illumina NextSeq platform using paired-end 150-bp reads to obtain, on average, two million reads per sample.

2.1.3 | Bioinformatics and genome alignment

We used the UGbS-Flex pipeline described in Qi et al. (2018) (see http://research.franklin.uga.edu/devoslab/software-and-scripts-overview for in-house scripts and descriptions) for read processing, read alignment to a draft KNE 796 finger millet genome assembly solely based on Illumina reads, and single-nucleotide polymorphism (SNP) calling. Briefly, reads were split by barcode and then processed to remove barcodes, adaptor sequences, restriction sites, and low-quality sequences. Processed reads were aligned to the scaffolds of the draft finger millet KNE 796 assembly using Bowtie2 (Langmead & Salzberg, 2012). The SNPs were called using the Genome Analysis Toolkit (GATK) version 3.4 (McKenna et al., 2010) UnifiedGenotyper function. The SNPs with three or more alleles, a quality depth value <10, and allele frequencies <10% or >90% were removed. Mapping scores were generated from SNP read counts as A (homozygous cultivated parent), B (homozygous wild parent), H (heterozygous), D (A or H), and C (B or H) using the script SNP_Genotyper.py (Qi et al., 2018). We treated SNPs with a read depth of <8× as missing data. We consolidated SNPs within 1 kb into a single representative marker using the SNP_Genotyper.py script (Qi et al., 2018). The SNPs and progeny lines with 30% or more missing data were removed, and marker cosegregation was tested via the SNP_cosegegration.py script (Qi et al., 2018). The marker with the highest information content in a set of cosegregating markers was used to generate the framework map. Markers with segregation ratios that differed significantly from expected Mendelian ratios ($p \leq 1 \times 10^{-10}$ via chi-squared tests) were removed. Because the genotypic information showed that our accession GBK 030647 was not the true parent of the cross, no SNP filtering was conducted based on the parental genotypes.

2.1.4 | Genetic map construction

We used an iterative genetic mapping procedure that combines functions of MSTMap (Wu et al., 2008) and MAPMAKER [modified from Lander et al. (1987) with a Python interface (Qi et al., 2018)] to generate a framework map. The mapping function was set as a 'F2 intercross'. Cosegregating markers were returned to the framework map at their representative marker location. Linkage maps were drawn with MapChart (Voorrips, 2002).

2.1.5 | Comparative genomic analyses

We used 1-kb regions, centered on mapped SNPs, from the finger millet KNE 796 scaffold-level assembly as BLASTN queries against the high-quality KNE 796 reference assembly v.1.1, rice (*Oryza sativa* L.) (v7.0; Ouyang et al., 2007), sorghum [*Sorghum bicolor* (L.) Moench] (v3.1.1; McCormick et al., 2018), and foxtail millet [*Setaria italica* (L.) P. Beauv.] (v2.2; Bennetzen et al., 2012) genome assemblies. Assemblies were downloaded from the Joint Genome Institute Phytozome website (https://phytozome-next.jgi.doe.gov). Each linkage map marker was matched to the corresponding top hit in each assembly with an *e*-value $\leq 1 \times 10^{-5}$.

2.2 | Trait mapping

2.2.1 | Kenyan field trial and trait measurement

On 28 Feb. 1997, 148 $F_{2:3}$ families from the cross ACC 100007 × GBK 030647 were planted in a randomized complete design in three blocks in an experimental nursery in Alupe, Busia county, in western Kenya (0.502295° N, 34.125344° E) to evaluate the lines for blast (*M. oryzae*) resistance. Two 2-m rows were sown for each $F_{2:3}$ family and parental line with 40 cm between rows, which were thinned to 20 plants per row after emergence. A total of 12 life-history and agronomic trait measurements were recorded: emergence date, flowering date, plant height, panicle maturity date, number of panicles, panicle weight, grain yield, leaf blast severity,

and panicle blast incidence and severity at milk and mature stages (See Supplemental File S1 for detailed trait measurements). Pairwise Pearson correlations were performed using PROC CORR in SAS v9.4.

2.2.2 | Quantitative trait locus mapping

We conducted quantitative trait locus (QTL) analyses on the 12 traits, averaged over three replicates using the composite interval mapping function in QTL Cartographer 2.5 (Wang et al., 2012). Although 148 $F_{2:3}$ families were phenotyped and 151 families were genotyped, only 84 families were common to both experiments because of insufficient seed availability for some of the phenotyped lines. We used population type SF2 with a walk speed of 0.5 cM. We established logarithm of the odds significance thresholds ($p \leq .05$) by running 1,000 permutations of each trait.

2.2.3 | Candidate gene analysis

The significant portion of each QTL peak was mapped against the *E. coracana* v1.1 genome assembly as well as the *O. sativa* v7.0, *S. bicolor* v3.1.1 and *S. italica* v2.2 genome assemblies (see "Comparative genomic analyses" section above) to identify genomic regions of interest. These regions, plus 2 Mb on either side, were searched for candidate genes by examining all genes annotated in the finger millet genome assembly (https://phytozome-next.jgi.doe.gov) within these extended QTL regions. Genes with annotations matching known trait pathways were identified. Additionally, we searched the literature for QTL and their underlying candidate genes that were mapped for the same traits to the syntenic regions of rice, sorghum, and foxtail millet. Finally, we conducted BLASTP analyses with proteins encoded by trait-associated, causal Poaceae genes known from the primary literature against the *E. coracana* v1.1 genome assembly.

3 | RESULTS

3.1 | Genetic map construction

We obtained 71,824 SNP and insertion–deletion markers in the $F_{2:3}$ population. As both SNP and insertion–deletion markers were used for mapping, these marker variants will be referred to as nucleotide polymorphisms (NPs). Filtering and consolidation were performed on NP markers with Mendelian and distorted segregation ratios (chi-square p values $> 1 \times 10^{-10}$), yielding a total of 5,422 markers that were incorporated into the genetic map. The genetic map comprises 18 linkage groups, corresponding to the 18 chromosomes of finger millet and has a total length of 2,938 cM. Using 500 bp of flanking sequence on either side of the mapped markers as BLASTN queries against the high-quality KNE 796 v1.1. genome assembly (https://phytozome-next.jgi.doe.gov) showed that the markers were distributed across the finger millet genome (Figure 1) with an average of 301 markers per linkage group (Table 1, Figure 2) and an average of 0.54 cM between markers. Full linkage map data are presented in Supplemental Table S1. The NP variants for the mapped markers together with 500 bp of flanking sequence on either side are given in Supplemental Table S2.

Overall, the genetic map is highly colinear with the *E. coracana* v1.1. assembly (Figure 3; Supplemental Figure S1). Additionally, the linkage map corresponds to 99% of the *E. coracana* v1.1 genome assembly, indicating no loss of distal chromosome arms, with an average of 200,000 bp between markers. A notable gap in the linkage map occurs between 7.1 and 25.6 cM on chromosome 9A and between 6.6 and 21.2 cM on chromosome 9B (Figures 2 and 3).

3.2 | QTL mapping

We identified eight significant QTL for five traits: days to 50% flowering, plant height, panicle number, leaf blast severity, and panicle blast incidence at maturity. The QTL information is presented in Table 2 and Figure 4. All QTL were located on the B subgenome. A forked QTL for days to 50% flowering was found on chromosome 1B, explaining 16% of the observed variation. Of particular interest is the plant height QTL on chromosome 3B with a r^2 of 0.546. We found three QTL related to *M. oryzae* infection: peaks on chromosomes 1B and 8B for leaf blast severity and on 6B for blast incidence on panicles at the mature stage. Enhanced resistance was provided by the cultivated parent at the 1B locus, and by the wild parent at the 6B and 8B loci. The *M. oryzae* resistance QTL on chromosomes 6B and 8B may be of particular interest, as they explain 29.3 and 24.1% of phenotypic variation, respectively, and could provide a novel source of resistance not present in cultivated germplasm. Phenotypic data, trait histograms, and correlations are provided in Supplemental Tables S3 and S4, and Supplemental Figure S2. In general, blast incidence and severity traits were highly correlated and negatively correlated with grain yield and panicle weight (Supplemental Table S4). Interestingly, while most trait correlations were predictable, plant height was positively correlated with leaf blast severity ($r^2 = 0.3205$, $p = .003$). Plant height was not correlated with panicle blast severity or incidence at maturity or milk stage (Supplemental Table S4).

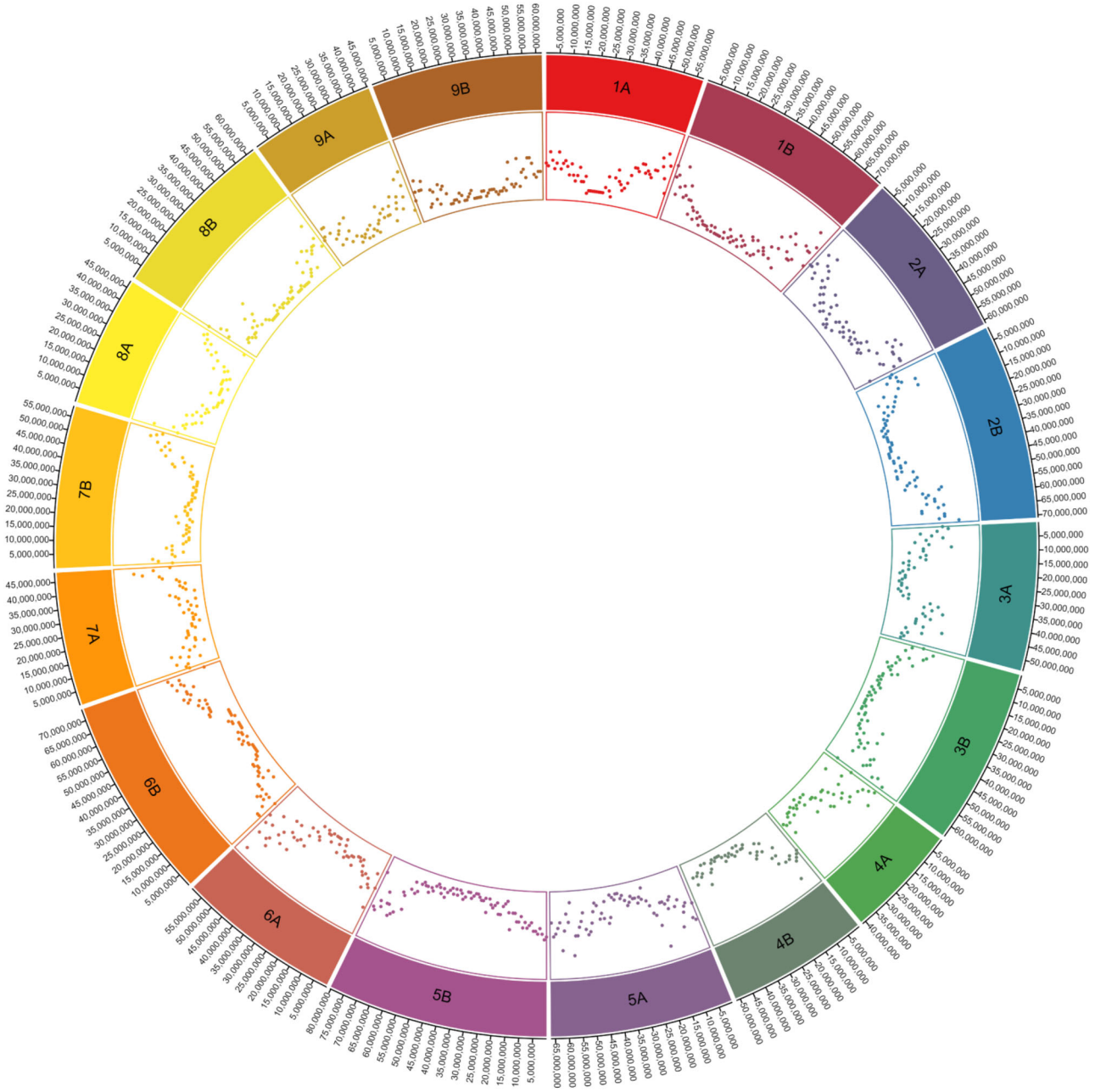

FIGURE 1 The distribution of markers (per Mb) in the ACC 100007 × GBK 030457 linkage maps relative to the *Eleusine coracana* v1.1 reference genome. Inner ring height min = 0, max = 25

3.3 | Comparative analyses

Finger millet chromosomes have been named largely based on their synteny with rice chromosomes (Dida et al., 2007; Srinivasachary et al., 2007). We find the same global pattern of colinear relationships as determined by Srinivasachary et al. (2007), albeit breakpoints of evolutionary rearrangements are better defined in the current analysis because of the larger number of common markers used. Eight finger millet linkage groups align with their namesake numerical *Oryza sativa* v7.0 chromosome (Table 3; Supplemental Table S1). However, finger millet chromosomes 9A and 9B are most homologous with rice chromosome 11. The other exceptions to this one-to-one syntenic pattern are the centromeric insertions of rice chromosomes 10 in 2, 12 in 5, and 9 in 6 to form finger millet chromosomes 2A and 2B, 5A and 5B, and 6A and 6B, respectively (Table 3; Supplemental Figure S3). This pattern is somewhat conserved across other grasses, with similar insertions with foxtail millet (chromosomes 2A and 2B and 6A and 6B, Supplemental Figure S4) and sorghum

TABLE 1 Marker number and map length for $F_{2:3}$ population linkage groups

Finger millet chromosome	No. of markers	Length
		cM
Chrom_1A	370	187.2
Chrom_1B	347	192.5
Chrom_2A	420	213.6
Chrom_2B	378	216.7
Chrom_3A	314	174.5
Chrom_3B	266	166.6
Chrom_4A	243	132.3
Chrom_4B	229	97.6
Chrom_5A	431	185.5
Chrom_5B	344	186.8
Chrom_6A	377	203.5
Chrom_6B	350	211.5
Chrom_7A	240	143.4
Chrom_7B	247	163.4
Chrom_8A	252	117.2
Chrom_8B	196	134.6
Chrom_9A	207	108.8
Chrom_9B	211	102.1
Average	301	163.2
Total	5,422	2,937.8

(chromosomes 2A and 2B, 5A and 5B, and 6A and 6B; Supplemental Figure S5).

3.3.1 | Candidate gene analysis

Eleusine coracana v1.1 genomic regions within significant QTL peaks plus 2 Mb of flanking sequence and the syntenic regions in rice, sorghum, and foxtail millet were delimited and examined for candidate genes. We found probable gene candidates for plant height, panicle number, and blast resistance traits (Table 4). Because of the width of the QTL peak, we did not examine the region spanned by the flowering time QTL for candidate genes.

Most notably, several LEUCINE-RICH REPEAT-CONTAINING PROTEIN, or LRR, genes were present under the 1B, 6B, and 8B QTL for blast severity and incidence. A cluster of three LRR genes on 6B comprising *ELECO.r07.6BG0498680*, *ELECO.r07.6BG0498670*, and *ELECO.r07.6BG0498660*, has high homology to a single LRR gene on chromosome 6A (*ELECO.r07.6AG0545170*). Further analysis showed that these three adjacent 6B LRR are simply sequential fragments of a single gene and are annotated as separate genes because of the presence of two stop codons. In addition to the stop codons, portions of exons are also missing in the 6B copy, indicating that this gene is nonfunctional in the reference accession KNE 796. The 6A homoeolog, *ELECO.r07.6AG0545170*, may also be nonfunctional, as it appears to be truncated at the 3′ end. A BLASTP analysis with the 6A copy showed that rice (v7.0 assembly) carries a cluster of three homologous NBS-LRR genes (*LOC_Os06g41640*, *LOC_Os06g41660*, and *LOC_Os06g41670*) in the syntenic chromosome region. A second LRR within the QTL on 6B, *ELECO.r07.6BG0498840*, lacks the coiled-coil (CC) domain. *ELECO.r07.6BG0498840* lacks both a 6A homoeolog and orthologs in rice, sorghum, and foxtail millet. It has weak homology at the protein level (37% identity) to the rice Pik-2 protein encoded by *LOC_Os07g09900*. Finally, an LRR/RPM1 encoding gene, *ELECO.r07.6BG0503170*, is located in the 2 Mb flanking the QTL significance region. *ELECO.r07.6BG0503170* lacks a functional protein homoeolog on chromosome 6A in finger millet because of the presence of a stop codon in the 6A gene but is conserved in rice (*LOC_Os06g48520*), sorghum (*Sobic.010G248400*), and foxtail millet (*Seita.4G244000*).

Underlying the expanded blast resistance QTL region on chromosome 8B, we find *ELECO.r07.8BG0643550*, which likely encodes a RGA-2-like disease resistance protein. A full-length homoeolog is present on chromosome 8A but is incorrectly annotated in the KNE 796 assembly (v.1.1 annotation). No orthologs were observed in the three grasses analyzed. In addition, two neighboring LRR genes (*ELECO.r07.8BG0647230* and *ELECO.r07.8G0647240*) were annotated in this region. However, both are part of a single LRR/RMP1 protein and were split during the annotation because of the presence of a stop codon. The 8A homoeolog lacks the CC domain. Again, no orthologs were identified in rice, sorghum, and foxtail millet. *ELECO.r07.8BG0644280*, similarly to the other candidates described here, was annotated as a LEUCINE-RICH REPEAT-CONTAINING PROTEIN. However, we did not consider it a likely disease resistance gene, as it has LRRs but no nucleotide binding site or CC domain, and homologous proteins in sorghum, switchgrass, and other grasses have been annotated as 'uncharacterized proteins.'

Three LRR genes were identified in the QTL region on chromosome 1B. *ELECO.r07.1BG0094990* encodes a likely RPP13-like protein and is present in homoeologous–orthologous positions on finger millet chromosome 1A (*ELECO.r07.1AG0044970*), rice chromosome 1 (*LOC_Os01g70080*), sorghum chromosome 3 (*Sobic.003G409300*), and foxtail millet chromosome V (*Seita.5G435000*). Some 20 kb downstream is a second RPP13-like encoding gene, *ELECO.r07.1BG0095030*. Although no 1A homoeolog was annotated, a BLASTN analysis of *ELECO.r07.1BG0095030* to the KNE 796 genome assembly showed that a full-length homoeolog was present on chromosome 1A. No orthologs were identified

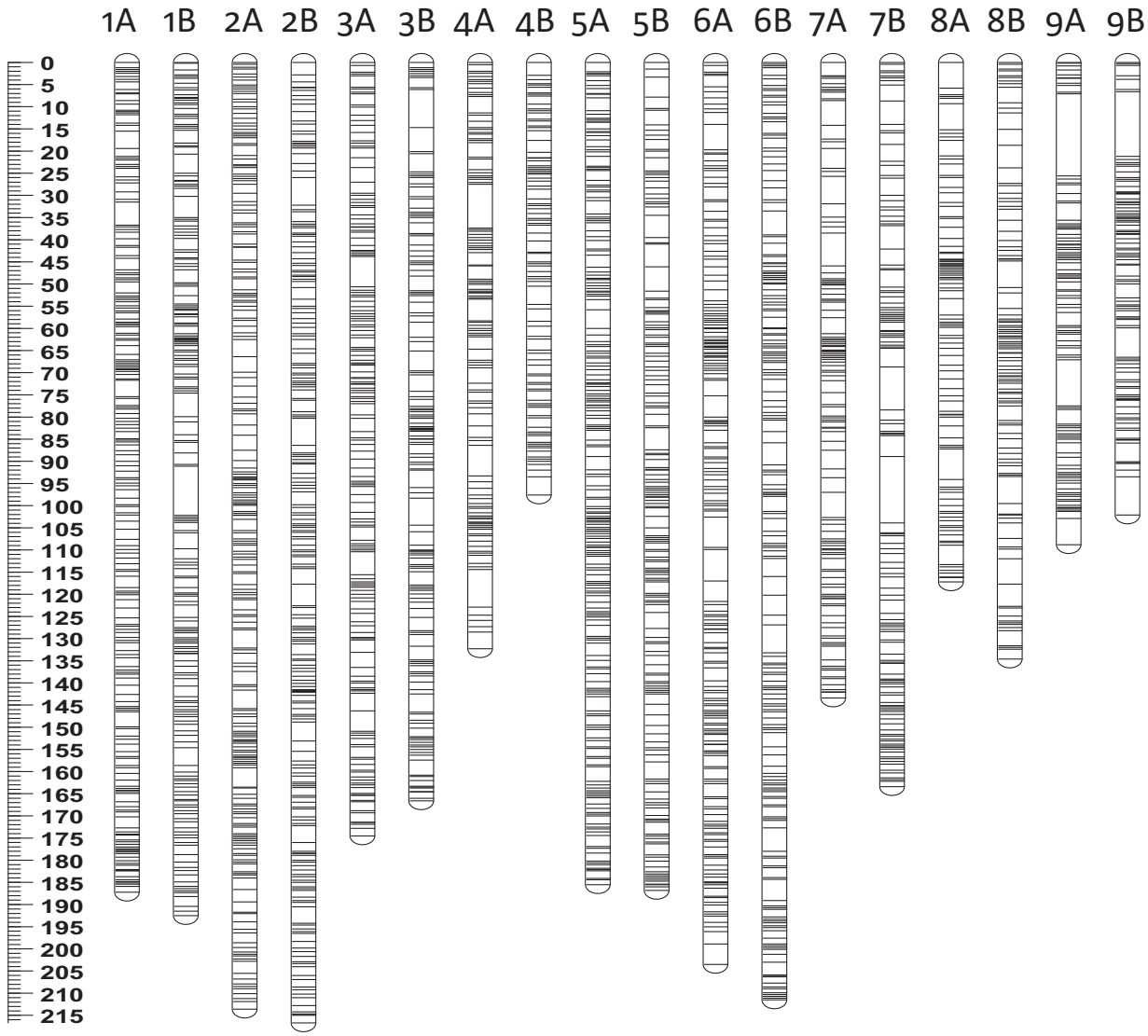

FIGURE 2 Linkage map of ACC 100007 × GBK 030457, with 5,424 markers across the 18 chromosomes. Marker names and locations are found in Supplemental Table S1

in any of the three grasses analyzed. The third LLR gene, *ELECO.r07.1BG0096930*, was annotated as encoding 'disease resistance protein RPS2' (Axtell & Staskawicz, 2003; Li et al., 2019). Although no CC domain was present, homology-based analyses indicated that the protein is full length. No homoeolog was annotated on 1A because of the presence of three frameshift mutations in the corresponding region. An ortholog was identified in rice (*LOC_Os01g72680*) but not in sorghum or foxtail millet.

For plant height, we found five candidate genes under the chromosome 3B QTL (Table 4). *Teosinte branched1* (*Tb1*) and *KNOTTED1* (*KN1*) are transcription factors that regulate bud outgrowth and meristem maintenance that ultimately affect plant height and architecture (Bolduc et al., 2012; Dixon et al., 2020; Doebley et al., 1997; Dong et al., 2019; Kebrom et al., 2006). Similarly, *GROWTH-REGULATING FACTOR 1* (*GRF1*) is an important transcription activator during gibberellic acid (GA)-induced stem elongation (Kim & Tsukaya, 2015; van der Knaap et al., 2000). *GAI* (*Rht1*, *Dwarf-8*) encodes a DELLA protein that represses GA-responsive growth (Ikeda et al., 2001; Wu et al., 2011). Finally, phytochromes, including phytochrome A, are universal sensory photoreceptors critical to resource allocation and plant architecture (Garg et al., 2006; Kebrom et al., 2006; Krahmer et al., 2018; Legris et al., 2019; Wies et al., 2019).

In addition to searching for genes linked to panicle development and number, we also examined genes regulating tillering because the number of panicles per plant is, de facto, the number of fertile tillers. We found three candidate genes, with one also identified by Alam et al. (2014) within a tillering QTL in the orthologous genomic region in sorghum, *DWARF88/DWARF14*. The other two candidate

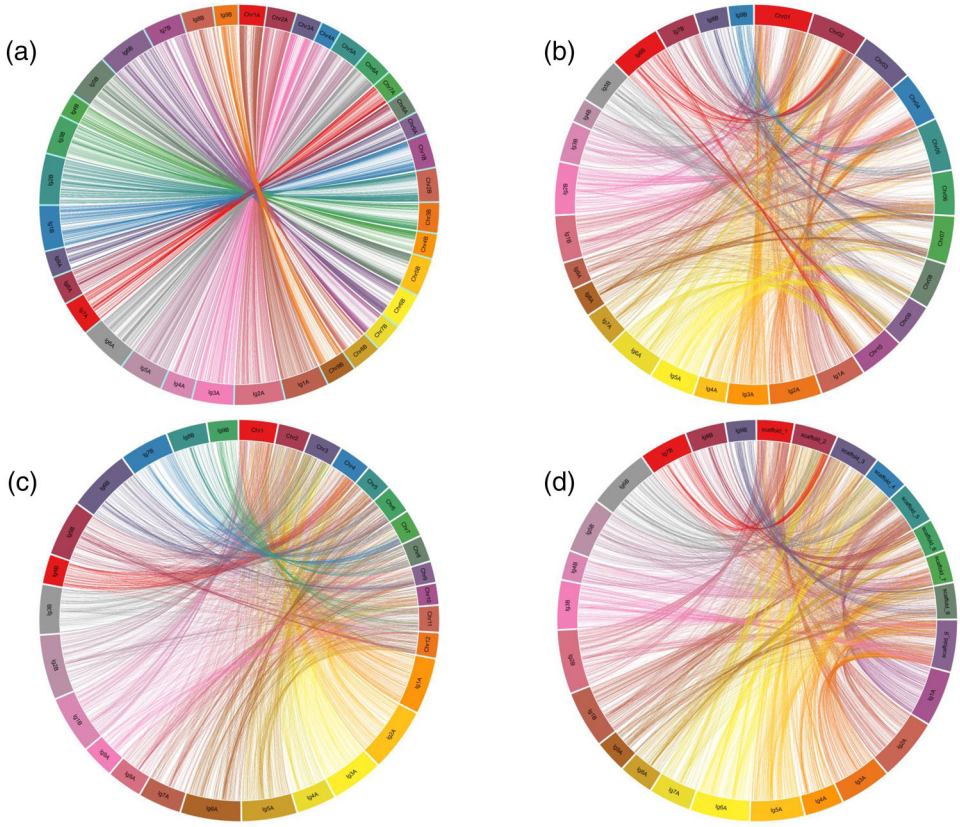

FIGURE 3 Circos diagrams showing relationships between the ACC 100007 × GBK 030457 linkage map and (a) *Eleusine coracana*, (b) *Sorghum bicolor*, (c) *Oryza sativa*, and (d) *Setaria italica* genome assemblies

genes found under this QTL are *grassy tillers1* (*gt1*; Whipple et al., 2011), responsible for regulating tillering and lateral bud dormancy in maize (*Zea mays* L.), and *CYP90B2*, a cytochrome P450 involved in brassinosteroid biosynthesis (Sakamoto et al., 2006). Alam et al. (2014) also identified *REDUCED CULM NUMBER* (*RCN1*) as a potential gene candidate for the sorghum tillering QTL, but this gene was located some 500 kb outside the 2-Mb lower boundary of the significance interval for the tillering QTL in finger millet that we considered for candidate gene mining.

4 | DISCUSSION

4.1 | Finger millet genetic maps and genomic structure

Here we present a new high-density marker linkage map for finger millet from an *E. coracana* subsp. *coracana* × *E. coracana* subsp. *africana* cross. The first high-density map for finger millet was generated in a cross between the wild accession MD-20 and cultivated accession Okhale-1 (Qi et al., 2018). This map was not aligned to the KNE 796 v1.1 genome assembly. The current ACC 100007 (cultivated) × GBK 030647 (wild) genetic map contains 5,422 markers evenly distributed across 18 linkage groups, corresponding to and covering all A and B subgenome chromosomes in the KNE 796 v1.1 assembly. The A genome map spans 1,466 cM; the B genome map has a length of 1,472 cM. Most chromosomes display an S-shaped marker distribution across the physical map, with fewer markers and strongly reduced recombination in the putative pericentromeric regions (Supplemental Figure S1). The exceptions are chromosomes 4A and 4B, which appear abridged. Finger millet chromosomes 4A and 4B are syntenic to chromosome 4 in rice, chromosome VII in foxtail millet, and chromosome 6 in sorghum (Supplemental Figures S3–S5), which are acrocentric chromosomes (Bennetzen et al., 2012; Cheng et al., 2001; Kim et al., 2005). Chromosome 5 in *Brachypodium distachyon* (L.) Beauv., which is syntenic to rice chromosome 4 (The International Brachypodium Initiative, 2010) is also acrocentric (Filiz et al., 2009), suggesting that this is the ancestral chromosome structure. Given how dynamic plant and specifically Poaceae chromosome evolution is, it is surprising that an acrocentric chromosomal configuration has been maintained across the PACMAD and BOP clades, which diverged over 50 million yr ago (Hodkinson, 2018; Soreng et al., 2017).

Although our markers were distributed every 0.54 cM, on average, the proximal arm of chromosomes 9A and 9B contained 18.5 and 14.6 cM gaps, respectively (Supplemental

TABLE 2 Significant quantitative trait loci (QTL) for Alupe, Kenya, field trial for agronomic and disease resistance traits

Trait	Chromosome	Position	Position	Interval (cM)		LOD	Additive r^2	Additive and dominance r^2	ACC_100007 allele	GBK_030647 allele	Heterozygotic
		cM	bp	cM							
Flowering date	1B	143.11	67,193,196	–	–	4.243	0.160	0.144	55.28	53.27	52.8
	1B	174.31	70,857,353	–	–	4.111	0.052	0.139	54.63	53.53	51.8
Plant height	3B	40.11	6,996,166	40.11	41.21	4.778	0.546	0.214	100.76	91.29	94.7
Panicle number	3B	130.11	58,178,601	129.11	131.71	4.615	0.019	0.224	5.89	7.73	5.83
Leaf blast severity	1B	176.61	70,536,697	176.61	177.61	4.644	0.074	0.158	2.05	2.26	2.05
	1B	188.21	71,941,629	187.31	190.21	5.422	0.095	0.181	2.04	2.28	2.05
	8B	40.21	3,204,750	34.11	41.61	5.496	0.241	0.241	2.33	2.03	2.15
Panicle blast incidence at maturity	6B	195.9	69,513,189	191.11	198.91	4.696	0.293	0.201	70.75	69.39	71.2

Note. Additive and dominance contributions to variance explained and average trait values by allele are presented. LOD, logarithm of the odds.

Figure S1). Qi et al. (2018) encountered similarly large marker intervals on 9A and 9B in the *E. coracana* subsp. *africana* MD-20 × *E. coracana* subsp. *coracana* accession Okhale-1 linkage map and attributed this to the presence of a reciprocal 9A–9B translocation in one of the mapping parents. Support for the presence of the translocation was provided by comparisons with the A-genome donor progenitor goosegrass [*E. indica* (L.) Gaertn.] as well as evidence of cross-type pairing configurations that led to some progeny having four copies of the A-genome region involved in the translocation and none of the corresponding B-genome region or vice versa (Qi et al., 2018). Examination of the genotypic data in the ACC 100007 × GBK 030647 population (Supplemental Table S1) also showed several progeny that either lacked 9A markers (progeny 11) or lacked 9B markers (progeny 19, 112, 114, 130, 137, 154, 168, 169, and 221) in the entire region distal to the large 'gap' in the genetic map. Therefore, one parent of our ACC 100007 × GBK 030647 population likely carries the same 9A–9B translocation present in one parent of the MD-20 × Okhale-1 cross. Though it is currently unknown if the translocation occurred in the cultivated or the wild finger millet, the fact that the translocation is present in heterozygous condition in two wild × cultivated crosses leads us to hypothesize that it occurred during or shortly after the domestication of finger millet.

4.2 | QTL analysis and candidate gene identification

To our knowledge, this represents the first QTL analysis conducted in a biparental mapping population in finger millet. We identified eight significant QTL for five traits: flowering date, plant height, panicle number per plant (which equates to the number of fertile tillers), leaf blast severity, and panicle blast incidence at maturity (Table 2). The small number of QTL detected likely is due to the fact that both genotypic and phenotypic data were available for only 84 $F_{2:3}$ families. Small population sizes may also overestimate the effect of a QTL (Vales et al., 2005). While these QTL will need to be validated, they likely represent highly penetrant QTL as several of them correspond to syntenic QTL mapped in other grass species for the same trait (Table 4).

We identified several genes underlying the QTL that are worth further consideration. For all genes, except for the LRR genes, orthologs were present in syntenic positions in all three species analyzed (rice, sorghum, and foxtail millet). Disease resistance genes tend to not be evolutionary conserved (Leister et al., 1998), so the lack of orthology for LRR genes across species was not unexpected. More surprising was the fact that for only three of the eight NBS-LRR genes analyzed, both homoeologous gene copies were structurally intact. This is in contrast to the candidate genes for plant height and

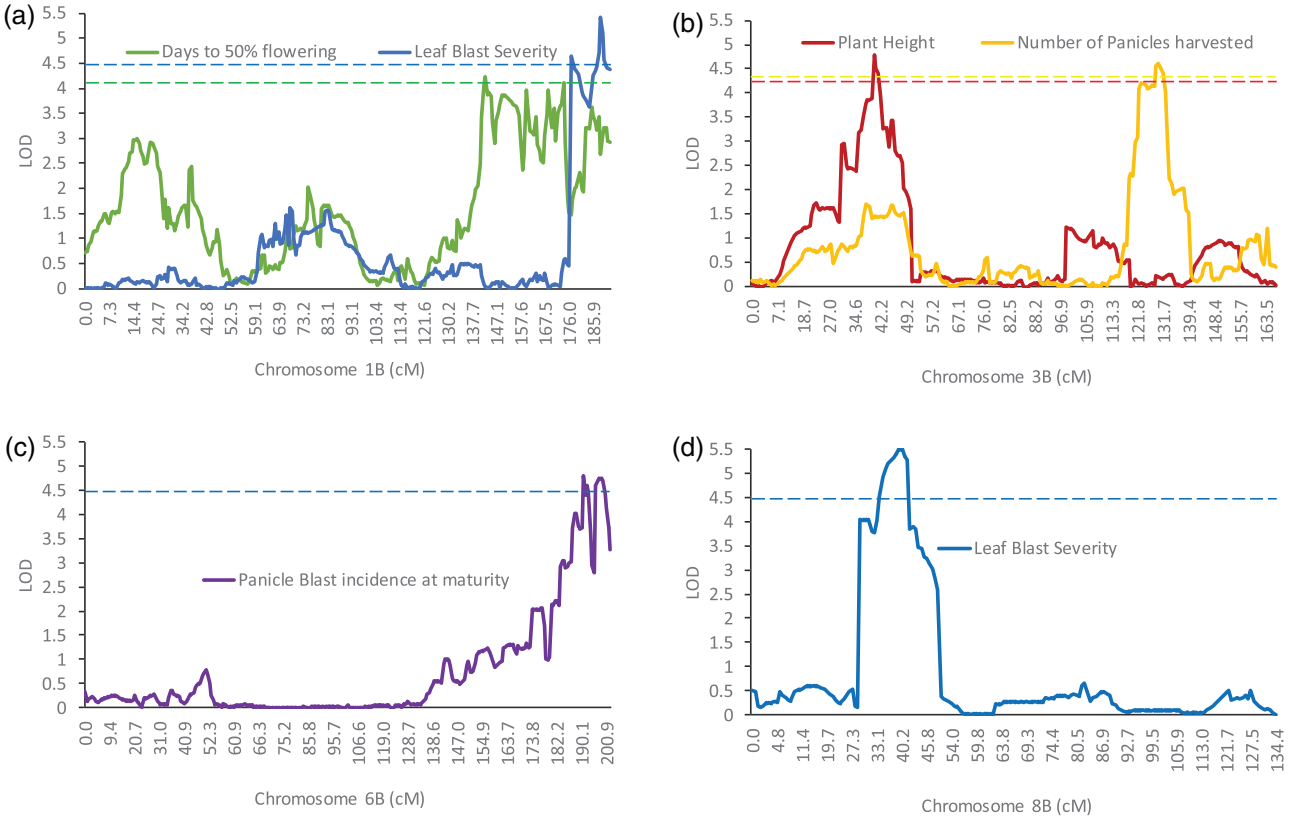

FIGURE 4 Quantitative trait loci for days to 50% flowering, leaf blast severity, plant height, number of panicles harvested, and panicle blast incidence on chromosomes (a) 1B, (b) 3B, (c) 6B, and (d) 8B. LOD, logarithm of the odds

tillering, which all had homoeologs on both the A and B genomes. For one LRR gene (*ELECO.r07.6BG0498840*), the homoeolog was completely absent. For the others, however, high sequence identity was identified on the homoeologous chromosome, but the corresponding proteins were truncated because of the presence of nonsense or frameshift mutations. This suggests a relatively recent inactivation of those genes and could indicate that having one NBS-LRR gene copy might be more advantageous because of the fitness cost associated with resistance gene expression in the absence of a pathogen (Tian et al., 2003).

The leucine-rich repeat containing protein genes (Table 4) hold promise as candidate genes for blast resistance. In rice, NBS-LRR genes encode the most prolific type of disease resistance proteins (McHale et al., 2006); Zhou et al. (2004) identified almost 500 NBS-LRR genes in the Nipponbare cultivar of rice. In a meta-analysis of the response of 430 NBS-LRR genes to infection with *Xanthomonas oryae* pv. *oryzae* and *Magnaporthe oryzae*, Ding et al. (2020) identified 38 genes that were responsive to both pathogens in multiple experiments. This includes *LOC_Os01g70080* and *LOC_Os01g72680*, which are orthologous to *ELECO.r07.1BG0094990* and *ELECO.r07.1BG0096930*, respectively, two genes underlying the blast resistance QTL on chromosome 1B. A BLASTP query to NCBI's refseq protein database with the protein encoded by *ELECO.r07.6BG0498840*, which colocalized with the blast resistance QTL on chromosome 6B, yielded *Pik-2* as the top hit with the homology starting at amino acid (AA) 67 in the finger millet protein and AA 302 in *Pik-2*. The highest homology in the rice genome was to *LOC_Os07g09900*, which has 100% identity to *Pik-2* but lacks the CC domain and part of the NB-ARC domain (homology starts at AA 39 in *LOC_Os07g09900* and AA 295 in *Pik-2*). Further investigation is needed into the structural integrity of *ELECO.r07.6BG0498840* and the other identified candidate genes in the parents of the mapping population, and to determine whether these genes indeed play a role in blast resistance.

Domestication of cereals has typically been accompanied by a reduction in tiller number. At the single QTL locus mapped for fertile tiller number, the cultivated allele is dominant and, as expected, associated with a reduction in tiller number. No likely candidate genes were identified if only the region significantly associated with tillering was considered. *ELECO.r07.3BG0288630*, a trehalose-6-phosphate synthase 6 (TPS6), was located in this region, and while trehalose-6-phosphate synthase (TPS) converts glucose-6-phosphate and UDP-glucose to trehalose-6-phosphate (Tre6*P*), a metabolite that signals the availability of sucrose (Lunn et al., 2006)

TABLE 3 Percentage of *Eleusine coracana* linkage map markers aligned to individual chromosomes (Chr.) in the *Oryza sativa* v7.0, *Setaria italica* v2.2, and *Sorghum bicolor* v3.1.1 genome assemblies by BLASTN analyses

		***Eleusine coracana* linkage groups**																	
Genome	**Chr.**	**1A**	**1B**	**2A**	**2B**	**3A**	**3B**	**4A**	**4B**	**5A**	**5B**	**6A**	**6B**	**7A**	**7B**	**8A**	**8B**	**9A**	**9B**
Oryza sativa 7.0 Genome	1	0.59	0.66	0.03	0.01	0.03	0.04	0.08	0.07	0.08	0.06	0.06	0.03	0.07	0.02	0.07	0.05	0.04	0.04
	2	0.03	0.02	0.45	0.52	0.04	0.03	0.06	0.03	0.03	0.06	0.02	0.06	0.08	0.07	0.04	0.02	0.07	0.03
	3	0.05	0.04	0.06	0.04	0.65	0.72	0.06	0.06	0.10	0.03	0.04	0.05	0.05	0.08	0.02	0.04	0.01	0.09
	4	0.03	0.05	0.04	0.06	0.02	0.01	0.58	0.64	0.04	0.02	0.00	0.04	0.04	0.02	0.04	0.06	0.08	0.06
	5	0.06	0.04	0.04	0.02	0.03	0.01	0.04	0.03	0.25	0.37	0.06	0.03	0.04	0.02	0.02	0.03	0.07	0.04
	6	0.02	0.03	0.04	0.03	0.01	0.02	0.02	0.01	0.04	0.03	0.38	0.38	0.05	0.05	0.08	0.05	0.02	0.04
	7	0.03	0.02	0.05	0.03	0.04	0.04	0.02	0.02	0.06	0.03	0.03	0.02	0.47	0.61	0.01	0.04	0.04	0.03
	8	0.03	0.01	0.03	0.04	0.05	0.01	0.05	0.03	0.06	0.02	0.06	0.04	0.02	0.04	0.50	0.55	0.02	0.08
	9	0.02	0.03	0.04	0.03	0.04	0.03	0.00	0.03	0.02	0.03	0.22	0.25	0.03	0.03	0.07	0.02	0.05	0.01
	10	0.05	0.04	0.18	0.17	0.04	0.03	0.02	0.03	0.02	0.04	0.03	0.03	0.04	0.02	0.03	0.05	0.04	0.04
	11	0.04	0.03	0.02	0.03	0.03	0.04	0.04	0.01	0.09	0.05	0.05	0.03	0.06	0.02	0.04	0.07	0.40	0.41
	12	0.03	0.02	0.04	0.03	0.02	0.02	0.05	0.04	0.24	0.24	0.03	0.05	0.04	0.03	0.07	0.02	0.15	0.13
Setaria italica v2.2 Genome	1	0.03	0.03	0.54	0.59	0.02	0.02	0.05	0.04	0.04	0.03	0.04	0.05	0.05	0.03	0.05	0.03	0.06	0.07
	2	0.05	0.03	0.06	0.04	0.05	0.02	0.08	0.04	0.06	0.04	0.30	0.32	0.57	0.61	0.05	0.05	0.09	0.02
	3	0.04	0.04	0.03	0.04	0.03	0.03	0.14	0.11	0.48	0.57	0.05	0.04	0.06	0.07	0.06	0.05	0.10	0.09
	4	0.03	0.02	0.04	0.02	0.03	0.03	0.03	0.03	0.05	0.03	0.39	0.39	0.03	0.03	0.08	0.04	0.09	0.04
	5	0.70	0.76	0.03	0.04	0.04	0.02	0.03	0.07	0.05	0.07	0.06	0.07	0.08	0.03	0.04	0.03	0.05	0.10
	6	0.03	0.02	0.03	0.03	0.01	0.02	0.02	0.04	0.04	0.03	0.03	0.01	0.02	0.01	0.61	0.66	0.05	0.04
	7	0.04	0.04	0.04	0.03	0.03	0.00	0.52	0.61	0.10	0.11	0.03	0.04	0.03	0.05	0.02	0.05	0.06	0.10
	8	0.04	0.02	0.04	0.02	0.03	0.02	0.04	0.01	0.10	0.05	0.04	0.01	0.04	0.05	0.02	0.03	0.41	0.45
	9	0.05	0.05	0.20	0.19	0.74	0.82	0.10	0.04	0.08	0.06	0.05	0.08	0.12	0.11	0.06	0.05	0.07	0.10
Sorghum bicolor 3.1.1 Genome	1	0.06	0.05	0.20	0.20	0.68	0.75	0.06	0.06	0.04	0.04	0.04	0.02	0.10	0.09	0.09	0.08	0.07	0.13
	2	0.04	0.02	0.05	0.05	0.07	0.03	0.03	0.03	0.07	0.04	0.26	0.31	0.50	0.61	0.11	0.05	0.09	0.04
	3	0.66	0.73	0.04	0.02	0.04	0.03	0.04	0.04	0.06	0.06	0.08	0.07	0.05	0.01	0.06	0.05	0.04	0.03
	4	0.02	0.03	0.52	0.55	0.05	0.02	0.06	0.06	0.04	0.02	0.04	0.06	0.04	0.03	0.05	0.04	0.07	0.03
	5	0.04	0.03	0.02	0.03	0.04	0.04	0.05	0.05	0.08	0.08	0.05	0.07	0.07	0.04	0.02	0.03	0.46	0.44
	6	0.04	0.03	0.04	0.02	0.03	0.05	0.60	0.60	0.03	0.03	0.03	0.05	0.05	0.04	0.04	0.04	0.03	0.03
	7	0.04	0.04	0.05	0.02	0.01	0.02	0.03	0.03	0.05	0.04	0.06	0.02	0.04	0.06	0.52	0.57	0.05	0.06
	8	0.04	0.02	0.02	0.04	0.00	0.02	0.02	0.02	0.24	0.23	0.02	0.01	0.05	0.05	0.04	0.05	0.09	0.11
	9	0.03	0.03	0.02	0.04	0.05	0.03	0.03	0.03	0.33	0.39	0.04	0.04	0.05	0.04	0.02	0.06	0.04	0.04
	10	0.03	0.02	0.04	0.02	0.03	0.01	0.07	0.07	0.05	0.08	0.38	0.36	0.05	0.02	0.06	0.02	0.06	0.07

leading to the release of axillary bud dormancy, TPS6 is a class II TPS and likely does not encode an active TPS (Lunn, 2007). In *Arabidopsis thaliana* (L.) Heynh. and rice, only class I *TPS1* genes encode active TPS enzymes involved in trehalose-6-phosphate synthesis. Extending the region for candidate gene mining by 4 Mb (2 Mb on either side of the QTL) identified two genes with antagonistic effects on bud outgrowth. *ELECO.r07.3BG0288160* is a cytochrome P450 90B2, which catalyzes C22 hydroxylation, a rate-limiting step in the brassinosteroid biosynthesis pathway (Sakamoto et al., 2006). Brassinosteroids have been shown to enhance bud outgrowth in rice (Zhongming et al., 2020). On the other hand, strigolactones repress bud outgrowth, and the extended QTL interval also carries *ELECO.r07.3BG0290150* which encodes the strigolactone receptor D14 (Arite et al., 2009). Both strigolactones and brassinosteroids have been shown to act on TB1 (TEOSINTE BRANCHED 1; synonym FC1 = FINE CULM 1) to control tillering in rice (Zhongming et al., 2020). One other gene of interest is *ELECO.r07.3BG0290610*, which is orthologous to rice *HOX12*, a homeodomain-leucine zipper transcription factor. *HOX12* physically interacts with the promoter of *ELONGATED UPPERMOST INTERNODE* (*EUI1*), which encodes a gibberellic acid (GA) deactivating enzyme (Gao et al., 2016). Reduced expression of *HOX12* and, consequently, *EUI1*, both of which are predominantly expressed in panicles in rice, leads to an accumulation of active GA and

TABLE 4 Candidate and putative orthologous genes for significant quantitative trait loci for plant height, panicle number, and blast traits

Trait	*Eleusine* candidate gene	Location	*Eleusine* annotation	Citation	Top NCBI refseq ortholog annotation
Plant height	*ELECO.r07.3BG0288160*	3B:57652863..57658368	steroid 22-alpha-hydroxylase (CYP90B1, DWF4)	Sakamoto et al., 2006	cytochrome P450 90B2 isoform X3 [*Setaria italica*]
	ELECO.r07.3BG0263000	3B:6489471..6492795	GROWTH-REGULATING FACTOR 1-RELATED	van der Knaap et al., 2000	growth-regulating factor 6 [*Setaria italica*]
	ELECO.r07.3BG0263200	3B:6638456..6644930	HOMEOBOX PROTEIN KNOTTED-1-LIKE 1	Bolduc et al., 2012	homeotic protein knotted-1 [*Setaria italica*]
	ELECO.r07.3BG0263770	3B:7137439..7141344	PHYTOCHROME A	Garg et al., 2006	phytochrome a [*Sorghum bicolor*]
	ELECO.r07.3BG0264730	3B:8220833..8222672	DELLA protein	Ikeda et al., 2001	DELLA protein DWARF8 [*Sorghum bicolor*]
	ELECO.r07.3BG0264770	3B:8269067..8270141	TRANSCRIPTION FACTOR TCP18	Kebrom et al., 2006	transcription factor TEOSINTE BRANCHED 1 [*Setaria italica*]
Panicle number	*ELECO.r07.3BG0290150*	3B:59106455..59107477	STRIGOLACTONE ESTERASE D14 HOMOLOG-RELATED	Gao et al., 2009	strigolactone esterase D14 [*Setaria italica*]
	ELECO.r07.3BG0290610	3B:59611419..59612360	Homeobox domain (Homeobox)	Whipple et al., 2011	homeobox-leucine zipper protein HOX12 [*Setaria italica*]
Leaf blast severity	*ELECO.r07.1BG0094990*	1B:70693463..70696489	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	disease resistance protein RPP13 [*Setaria italica*]
	ELECO.r07.1BG0095030	1B:70715176..70718968	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	putative disease resistance RPP13-like protein 3 [*Sorghum bicolor*]
	ELECO.r07.1BG0096930	1B:71772194..71775080	Disease resistance protein RPS2	Li et al., 2019	disease resistance protein SUMM2 [*Oryza sativa* Japonica Group]
	ELECO.r07.8BG0644280	8B:1983964..1986934	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	uncharacterized protein LOC8068551 [*Sorghum bicolor*]
Panicle blast incidence at maturity	*ELECO.r07.6BG0498660*	6B:69751619..69753631	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	putative disease resistance protein RGA3 [*Setaria italica*]
	ELECO.r07.6BG0498670	6B:69753799..69754243	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	putative disease resistance RPP13-like protein 1 [*Setaria viridis*]
	ELECO.r07.6BG0498680	6B:69754298..69755513	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	putative disease resistance protein RGA3 [*Setaria italica*]
	ELECO.r07.6BG0498840	6B:69902293..69905460	LEUCINE-RICH REPEAT-CONTAINING PROTEIN	Ding et al., 2020	disease resistance protein Pik-2 [*Oryza sativa* Japonica Group]

Note. Annotations presented are from the *Eleusine coracana* v1.1 genome assembly and the top hit from the NCBI refseq protein ortholog search

elongated panicle exsertion. In maize, however, the ortholog to *HOX12*, *grassy tillers1* (*gt1*), depends on *tb1* activity and negatively regulates axillary bud outgrowth in response to shade signals (Whipple et al., 2011).

Domestication tends to have resulted, in general, in an increase in plant height in herbaceous crops (Milla & Matesanz, 2017). However, this trend has been reversed over the past 50 yr or so in cereal crops with the introduction of dwarfing genes, several of which have been cloned, including *Rht-1* in wheat (*Triticum aestivum* L.) (Peng et al., 1999), *sd1* in rice (Monna et al., 2002; Spielmeyer et al., 2002), *d2* in pearl millet [*Cenchrus americanus* (L.) Morrone] (Parvathaneni et al., 2019), and *dw1, dw2* and *dw3* in sorghum (Hilley et al., 2016, 2017; Multani et al., 2003). As far as we know, no dwarfing genes have been characterized in finger millet, nor have any conscious efforts been made to breed cultivars with reduced stature. At the plant height QTL identified on chromosome 3B, the cultivated allele increased plant height. Interestingly, one of the genes underlying the height QTL is *ELECO.r07.3BG0264730*, an ortholog of the wheat *Rht-1* (*GAI)* gene and central repressor of GA signaling. It is conceivable that reduced expression of *GAI* or reduced functionality of the GAI protein in the cultivated parent compared with the wild parent could be causal to the variation in plant height. However, several other, potentially interacting genes that affect plant height are also located in the QTL interval (Table 4). *GRF1* can repress expression of *KN1* (Kuijt et al., 2014; Omidbakhshfard et al., 2015) and *KN1* directly regulates gibberellin levels through its binding with the GA catabolism gene *ga2ox1* (Bolduc & Hake, 2009). PhyA can also control GA levels, at least in pea (*Pisum sativum* L.), under both red and blue light by acting on *GA3ox1* and *GA2ox2* to decrease the synthesis and increase the catabolism, respectively, of active GA (Reid et al., 2002). *Teosinte branched1* (*Tb1*) is best known for its effect on branching but has recently been shown to also restrict stem internode elongation in bread wheat in a dosage-dependent manner (Dixon et al., 2020). In a study to identify the genetic pathways regulated by TB1, Dong et al. (2019) found that TB1 appears to function as a transcriptional activator, including of genes involved in biosynthesis, inactivation and signaling of GA, suggesting that *tb1/gt1* may inhibit GA production. All five genes thus affect either directly or indirectly GA levels and hence are likely candidates for the plant height QTL.

5 | CONCLUSIONS

Historically, the self-pollinating nature and challenging emasculation of *Eleusine* has made the generation of hybrids and hence the generation of biparental mapping populations difficult (Dida et al., 2007; Hiremath & Salimath, 1992; Host et al., 2021). Here, a GBS approach to linkage and trait mapping in an *E. coracana* subsp. *coracana* × *E. coracana* subsp. *africana* $F_{2:3}$ population has yielded a highly accurate, high-density genetic map that offers highly significant QTL for critical agronomic traits, especially blast resistance. *Magnaporthe oryzae* is the most destructive pathogen of finger millet and poses severe threats to subsistence farming as well as development of high-yielding cultivars (Mbinda & Masaki, 2021; Takan et al., 2004; Takan et al., 2012). Our study shows that wild finger millet accessions could provide blast resistance variation for application in finger millet breeding programs and provides information on several NBS-LRR genes that have homology to or are orthologs of genes that are known to be responsive to infection by *M. oryzae* in rice. The majority of the candidate LRR genes, however, lacked orthologs in rice, sorghum, foxtail millet and, surprisingly, also tended to lack functional homoeologs. The genomic resources, QTL, and candidate genes presented here provide important tools for emerging breeding programs in finger millet.

ACKNOWLEDGMENTS

The authors thank Stan King (formerly of the International Crops Research Institute for the Semi-Arid Tropics) for orchestrating the Kenyan field trial, Emma Bennetzen for phenotype data verification and correction, and Trudi Thomas for UGA greenhouse and harvest assistance. This study was in part funded by NSF-BREAD award IOS-1543901.

AUTHOR CONTRIBUTIONS

Thomas H. Pendergast IV: Formal analysis; Methodology; Writing-original draft; Writing-review & editing. Peng Qi: Formal analysis; Writing-review & editing. Damaris Achieng Odeny: Investigation; Writing-review & editing. Mathews M. Dida: Investigation; Writing-review & editing. Katrien M. Devos: Conceptualization; Formal analysis; Funding acquisition; Project administration; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ORCID

Thomas H. Pendergast, IV https://orcid.org/0000-0001-5681-9662

REFERENCES

Akbar, N., Gupta, S., Tiwari, A., Singh, K. P., & Kumar, A. (2018). Characterization of metabolic network of oxalic acid biosynthesis through RNA seq data analysis of developing spikes of finger millet (*Eleusine coracana*): Deciphering the role of key genes involved in oxalate formation in relation to grain calcium accumulation. *Gene*, *649*, 40–49. https://doi.org/10.1016/j.gene.2018.01.071

Alam, M. M., Mace, E. S., van Oosterom, E. J., Cruickshank, A., Hunt, C. H., Hammer, G. L., & Jordan, D. R. (2014). QTL analysis in multiple sorghum populations facilitates the dissection of the genetic and physiological control of tillering. *Theoretical and Applied Genetics*, *127*, 2253–2266. https://doi.org/10.1007/s00122-014-2377-9

Arite, T., Umehara, M., Ishikawa, S., Hanada, A., Maekawa, M., Yamaguchi, S., & Kyozuka, J. (2009). *d14*, a strigolactone-insensitive mutant of rice, shows an accelerated outgrowth of tillers. *Plant & Cell Physiology*, *50*, 1416–1424. https://doi.org/10.1093/pcp/pcp091

Axtell, M. J., & Staskawicz, B. J. (2003). Initiation of *RPS2*-specified disease resistance in *Arabidopsis* is coupled to the AvrRpt2-directed elimination of RIN4. *Cell*, *112*, 369–377. https://doi.org/10.1016/S0092-8674(03)00036-9

Babu, B. K., Dinesh, P., Agrawal, P. K., Sood, S., Chandrashekara, C., Bhatt, J. C., & Kumar, A. (2014). Comparative genomics and association mapping approaches for blast resistant genes in finger millet using SSRs. *PLoS ONE*, *9*, e99182. https://doi.org/10.1371/journal.pone.0099182

Babu, T. K., Sharma, R., Thakur, R. P., Upadhyaya, H. D., Reddy, P. N., & Girish, A. G. (2015). Selection of host differentials for elucidating pathogenic variation in *Magnaporthe grisea* populations adapted to finger millet (*Eleusine coracana*). *Plant Disease*, *99*, 1784–1789. https://doi.org/10.1094/pdis-10-14-1089-re

Bandyopadhyay, T., Muthamilarasan, M., & Prasad, M. (2017). Millets for next generation climate-smart agriculture. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.01266

Bennetzen, J. L., Schmutz, J., Wang, H., Percifield, R., Hawkins, J., Pontaroli, A. C., Estep, M., Feng, L., Vaughn, J. N., Grimwood, J., Jenkins, J., Barry, K., Lindquist, E., Hellsten, U., Deshpande, S., Wang, X., Wu, X., Mitros, T., Triplett, J., … Devos, K. M. (2012). Reference genome sequence of the model plant Setaria. *Nature Biotechnology*, *30*, 555–561. https://doi.org/10.1038/nbt.2196

Bolduc, N., & Hake, S. (2009). The maize transcription factor KNOTTED1 directly regulates the gibberellin catabolism gene *ga2ox1*. *The Plant Cell*, *21*, 1647–1658. https://doi.org/10.1105/tpc.109.068221

Bolduc, N., Yilmaz, A., Mejia-Guerra, M. K., Morohashi, K., O'Connor, D., Grotewold, E., & Hake, S. (2012). Unraveling the KNOTTED1 regulatory network in maize meristems. *Genes & Development*, *26*, 1685–1690. http://genesdev.cshlp.org/content/26/15/1685.abstract

Cheng, Z., Buell, C. R., Wing, R. A., Gu, M., & Jiang, J. (2001). Toward a cytological characterization of the rice genome. *Genome research*, *11*, 2133–2141. https://doi.org/10.1101/gr.194601

Choi, J., Park, S.-Y., Kim, B.-R., Roh, J.-H., Oh, I.-S., Han, S.-S., & Lee, Y.-H. (2013). Comparative analysis of pathogenicity and phylogenetic relationship in *Magnaporthe grisea* species complex. *PLoS ONE*, *8*, e57196. https://doi.org/10.1371/journal.pone.0057196

National Research Council (1996). *Lost crops of Africa: Grains* (Vol. 1). The National Academies Press.

Devi, P. B., Vijayabharathi, R., Sathyabama, S., Malleshi, N. G., & Priyadarisini, V. B. (2014). Health benefits of finger millet (*Eleusine coracana* L.) polyphenols and dietary fiber: A review. *Journal of Food Science and Technology*, *51*, 1021–1040. https://doi.org/10.1007/s13197-011-0584-9

Dida, M. M., Oduori, C. A., Manthi, S. J., Avosa, M. O., Mikwa, E. O., Ojulong, H. F., & Odeny, D. A. (2021). Novel sources of resistance to blast disease in finger millet. *Crop Science*, *61*, 250–262. https://doi.org/10.1002/csc2.20378

Dida, M. M., Srinivasachary, S. R., Bennetzen, J. L., Gale, M. D., & Devos, K. M. (2007). The genetic map of finger millet, *Eleusine coracana*. *Theoretical and Applied Genetics*, *114*, 321–332. https://doi.org/10.1007/s00122-006-0435-7

Ding, L., Xu, X., Kong, W., Xia, X., Zhang, S., Liu, L.-W., Liu, A., & Zou, L. (2020). Genome-wide identification and expression analysis of rice *NLR* genes responsive to the infections of *Xanthomonas oryzae* pv. *oryzae* and *Magnaporthe oryzae*. *Physiological and Molecular Plant Pathology*, *111*, 101488. https://doi.org/10.1016/j.pmpp.2020.101488

Dixon, L. E., Pasquariello, M., & Boden, S. A. (2020). TEOSINTE BRANCHED1 regulates height and stem internode length in bread wheat. *Journal of Experimental Botany*, *71*, 4742–4750. https://doi.org/10.1093/jxb/eraa252

Doebley, J., Stec, A., & Hubbard, L. (1997). The evolution of apical dominance in maize. *Nature*, *386*, 485–488. https://doi.org/10.1038/386485a0

Dong, Z., Xiao, Y., Govindarajulu, R., Feil, R., Siddoway, M. L., Nielsen, T., Lunn, J. E., Hawkins, J., Whipple, C., & Chuck, G. (2019). The regulatory landscape of a core maize domestication module controlling bud dormancy and growth repression. *Nature Communications*, *10*, 3810. https://doi.org/10.1038/s41467-019-11774-w

Filiz, E., Ozdemir, B. S., Budak, F., Vogel, J. P., Tuna, M., & Budak, H. (2009). Molecular, morphological, and cytological analysis of diverse *Brachypodium distachyon* inbred lines. *Genome*, *52*, 876–890. https://doi.org/10.1139/g09-062/m19935911

Gao, S., Fang, J., Xu, F., Wang, W., & Chu, C. (2016). Rice HOX12 regulates panicle exsertion by directly modulating the expression of *ELONGATED UPPERMOST INTERNODE1*. *The Plant Cell*, *28*, 680–695. https://doi.org/10.1105/tpc.15.01021

Gao, Z., Qian, Q., Liu, X., Yan, M., Feng, Q., Dong, G., Liu, J., & Han, B. (2009). Dwarf 88, a novel putative esterase gene affecting architecture of rice plant. *Plant Molecular Biology*, *71*(3), 265–276. https://doi.org/10.1007/s11103-009-9522-x

Garg, A. K., Sawers, R. J. H., Wang, H., Kim, J.-K., Walker, J. M., Brutnell, T. P., Parthasarathy, M. V., Vierstra, R. D., & Wu, R. J. (2006). Light-regulated overexpression of an *Arabidopsis* phytochrome A gene in rice alters plant architecture and increases grain yield. *Planta*, *223*, 627–636. https://doi.org/10.1007/s00425-005-0101-3

Gladieux, P., Condon, B., Ravel, S., Soanes, D., Maciel, J. L. N., Nhani, A., Chen, L., Terauchi, R., Lebrun, M.-H., Tharreau, D., Mitchell, T., Pedley, K. F., Valent, B., Talbot, N. J., Farman, M., & Fournier, E. (2018). Gene flow between divergent cereal- and grass-specific lineages of the rice blast fungus *Magnaporthe oryzae*. *mBio*, *9*, e01219-17. https://doi.org/10.1128/mBio.01219-17

Hatakeyama, M., Aluri, S., Balachadran, M. T., Sivarajan, S. R., Patrignani, A., Grüter, S., Poveda, L., Shimizu-Inatsugi, R., Baeten, J., Francoijs, K.-J., Nataraja, K. N., Reddy, Y. A. N., Phadnis, S., Ravikumar, R. L., Schlapbach, R., Sreeman, S. M., & Shimizu, K. K. (2018). Multiple hybrid de novo genome assembly of finger millet, an orphan allotetraploid crop. *DNA Research*, *25*, 39–47. https://doi.org/10.1093/dnares/dsx036

Hilley, J., Truong, S., Olson, S., Morishige, D., & Mullet, J. (2016). Identification of *Dw1*, a regulator of sorghum stem internode length. *PLoS ONE*, *11*, e0151271-e0151271. https://doi.org/10.1371/journal.pone.0151271

Hilley, J. L., Weers, B. D., Truong, S. K., McCormick, R. F., Mattison, A. J., McKinley, B. A., Morishige, D. T., & Mullet, J. E. (2017). Sorghum *Dw2* encodes a protein kinase regulator of stem internode length. *Scientific Reports*, *7*, 4616. https://doi.org/10.1038/s41598-017-04609-5

Hiremath, S. C., & Salimath, S. S. (1992). The 'A' genome donor of *Eleusine coracana* (L.) Gaertn. (Gramineae). *Theoretical and Applied Genetics*, *84*, 747–754. https://doi.org/10.1007/bf00224180

Hittalmani, S., Mahesh, H. B., Shirke, M. D., Biradar, H., Uday, G., Aruna, Y. R., Lohithaswa, H. C., & Mohanrao, A. (2017). Genome and transcriptome sequence of finger millet (*Eleusine coracana* (L.) Gaertn.) provides insights into drought tolerance and nutraceutical properties. *BMC Genomics*, *18*, 465. https://doi.org/10.1186/s12864-017-3850-z

Hodkinson, T. R. (2018). Evolution and taxonomy of the grasses (Poaceae): A model family for the study of species-rich groups. In J. A. Roberts (Ed.), *Annual Plant Reviews online* (pp. 255–294). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781119312994.apr0622

Host, A. D. R., Ramakrishnan, M., Maharajan, T., BarathiKannan, K., Atul Babu, G., Daniel, M. A., Agastian, P., Antony Caesar, S., & Ignacimuthu, S. (2021). Mining QTL and genes for root traits and biochemical parameters under vegetative drought in South Indian genotypes of finger millet (*Eleusine coracana* (L.) Gaertn) by association mapping and in silico comparative genomics. *Biocatalysis and Agricultural Biotechnology*, *32*, 101935. https://doi.org/10.1016/j.bcab.2021.101935

Ikeda, A., Ueguchi-Tanaka, M., Sonoda, Y., Kitano, H., Koshioka, M., Futsuhara, Y., Matsuoka, M., & Yamaguchi, J. (2001). *slender* rice, a constitutive gibberellin response mutant, is caused by a null mutation of the *SLR1* gene, an ortholog of the height-regulating gene *GAI/RGA/RHT/D8*. *The Plant Cell*, *13*, 999–1010. https://doi.org/10.1105/tpc.13.5.999

Kebrom, T. H., Burson, B. L., & Finlayson, S. A. (2006). Phytochrome B represses *Teosinte Branched1* expression and induces sorghum axillary bud outgrowth in response to light signals. *Plant Physiology*, *140*, 1109–1117. https://doi.org/10.1104/pp.105.074856

Kim, J.-S., Klein, P. E., Klein, R. R., Price, H. J., Mullet, J. E., & Stelly, D. M. (2005). Chromosome identification and nomenclature of *Sorghum bicolor*. *Genetics*, *169*, 1169–1173. https://doi.org/10.1534/genetics.104.035980

Kim, J. H., & Tsukaya, H. (2015). Regulation of plant growth and development by the GROWTH-REGULATING FACTOR and GRF-INTERACTING FACTOR duo. *Journal of Experimental Botany*, *66*, 6093–6107. https://doi.org/10.1093/jxb/erv349

Krahmer, J., Ganpudi, A., abbas, a., romanowski, a., & halliday, k. j. (2018). phytochrome, carbon Sensing, Metabolism, and Plant Growth Plasticity. *Plant Physiology*, *176*, 1039–1048. https://doi.org/10.1104/pp.17.01437

Kuijt, S. J. H., Greco, R., Agalou, A., Shao, J., Hoen, C. C. J., Övernäs, E., Osnato, M., Curiale, S., Meynard, D., van Gulik, R., Maraschin, S. d. F., Atallah, M., de Kam, R. J., Lamers, G. E. M., Guiderdoni, E., Rossini, L., Meijer, A. H., & Ouwerkerk, P. B. F. (2014). Interaction between the *GROWTH-REGULATING FACTOR* and *KNOTTED1-LIKE HOMEOBOX* families of transcription factors. *Plant Physiology*, *164*, 1952–1966. https://doi.org/10.1104/pp.113.222836

Kumar, A., Metwal, M., Kaur, S., Gupta, A. K., Puranik, S., Singh, S., Singh, M., Gupta, S., Babu, B. K., Sood, S., & Yadav, R. (2016). Nutraceutical value of finger millet [*Eleusine coracana* (L.) Gaertn.], and their improvement using omics approaches. *Frontiers in Plant Science*, *7*, 934–934. https://doi.org/10.3389/fpls.2016.00934

Lander, E. S., Green, P., Abrahamson, J., Barlow, A., Daly, M. J., Lincoln, S. E., & Newburg, L. (1987). MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics*, *1*, 174–181. https://doi.org/10.1016/0888-7543(87)90010-3

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with bowtie 2. *Nature Methods*, *9*, 357–359. https://doi.org/10.1038/nmeth.1923

Legris, M., Ince, Y. Ç., & Fankhauser, C. (2019). Molecular mechanisms underlying phytochrome-controlled morphogenesis in plants. *Nature Communications*, *10*, 5219. https://doi.org/10.1038/s41467-019-13045-0

Leister, D., Kurth, J., Laurie, D. A., Yano, M., Sasaki, T., Devos, K., Graner, A., & Schulze-Lefert, P. (1998). Rapid reorganization of resistance gene homologues in cereal genomes. *Proceedings of the National Academy of Sciences*, *95*, 370–375. https://doi.org/10.1073/pnas.95.1.370

Li, Z., Huang, J., Wang, Z., Meng, F., Zhang, S., Wu, X., Zhang, Z., & Gao, Z. (2019). Overexpression of *Arabidopsis* nucleotide-binding and leucine-rich repeat genes *RPS2* and *RPM1*(*D505V*) confers broad-spectrum disease resistance in rice. *Frontiers in Plant Science*, *10*, 417. https://doi.org/10.3389/fpls.2019.00417

Lunn, J. E. (2007). Gene families and evolution of trehalose metabolism in plants. *Functional Plant Biology*, *34*, 550–563. https://doi.org/10.1071/fp06315

Lunn, J. E., Feil, R., Hendriks, J. H., Gibon, Y., Morcuende, R., Osuna, D., Scheible, W. R., Carillo, P., Hajirezaei, M. R., & Stitt, M. (2006). Sugar-induced increases in trehalose 6-phosphate are correlated with redox activation of ADP glucose pyrophosphorylase and higher rates of starch synthesis in *Arabidopsis thaliana*. *Biochemical Journal*, *397*, 139–148. https://doi.org/10.1042/bj20060083

Manyasa, E. O., Tongoona, P., Shanahan, P., Githiri, S., Ojulong, H., & Njoroge, S. M. C. (2019). Exploiting genetic diversity for blast disease resistance sources in finger millet (*Eleusine coracana*). *Plant Health Progress*, *20*, 180–186. https://doi.org/10.1094/php-11-18-0068-rs

Mbinda, W., & Masaki, H. (2021). Breeding strategies and challenges in the improvement of blast disease resistance in finger millet. *Frontiers in Plant Science*, *11*, 2151. https://www.frontiersin.org/article/10.3389/fpls.2020.602882

McCormick, R. F., Truong, S. K., Sreedasyam, A., Jenkins, J., Shu, S., Sims, D., Kennedy, M., Amirebrahimi, M., Weers, B. D., McKinley, B., Mattison, A., Morishige, D. T., Grimwood, J., Schmutz, J., & Mullet, J. E. (2018). The *Sorghum bicolor* reference genome: Improved assembly, gene annotations, a transcriptome atlas, and signatures of genome organization. *The Plant Journal*, *93*, 338–354. https://doi.org/10.1111/tpj.13781

McHale, L., Tan, X., Koehl, P., & Michelmore, R. W. (2006). Plant NBS-LRR proteins: Adaptable guards. *Genome Biology*, *7*, 212. https://doi.org/10.1186/gb-2006-7-4-212

McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., Garimella, K., Altshuler, D., Gabriel, S., & Daly, M. (2010). The genome analysis toolkit: A MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Research*, *20*. https://doi.org/10.1101/gr.107524.110

Milla, R., & Matesanz, S. (2017). Growing larger with domestication: A matter of physiology, morphology or allocation? *Plant Biology*, *19*, 475–483. https://doi.org/10.1111/plb.12545

Monna, L., Kitazawa, N., Yoshino, R., Suzuki, J., Masuda, H., Maehara, Y., Tanji, M., Sato, M., Nasu, S., & Minobe, Y. (2002). Positional cloning of rice semidwarfing gene, *sd-1*: Rice "green revolution gene" encodes a mutant enzyme involved in gibberellin synthesis. *DNA Research*, *9*, 11–17. https://doi.org/10.1093/dnares/9.1.11

Multani, D. S., Briggs, S. P., Chamberlin, M. A., Blakeslee, J. J., Murphy, A. S., & Johal, G. S. (2003). Loss of an MDR transporter in compact stalks of maize *br2* and sorghum *dw3* mutants. *Science*, *302*, 81–84. https://doi.org/10.1126/science.1086072

Omidbakhshfard, M. A., Proost, S., Fujikura, U., & Mueller-Roeber, B. (2015). Growth-regulating factors (GRFs): A small transcription factor family with important functions in plant biology. *Molecular Plant*, *8*, 998–1010. https://doi.org/10.1016/j.molp.2015.01.013

Opole, R. A., Prasad, P. V. V., Djanaguiraman, M., Vimala, K., Kirkham, M. B., & Upadhyaya, H. D. (2018). Thresholds, sensitive stages and genetic variability of finger millet to high temperature stress. *Journal of Agronomy and Crop Science*, *204*, 477–492. https://doi.org/10.1111/jac.12279

Ouyang, S., Zhu, W., Hamilton, J., Lin, H., Campbell, M., Childs, K., Thibaud-Nissen, F., Malek, R. L., Lee, Y., Zheng, L., Orvis, J., Haas, B., Wortman, J., & Buell, C. R. (2007). The TIGR rice genome annotation resource: Improvements and new features. *Nucleic Acids Research*, *35*, D883–D887. https://doi.org/10.1093/nar/gkl976

Parvathaneni, R. K., Spiekerman, J. J., Zhou, H., Wu, X., & Devos, K. M. (2019). Structural characterization of *ABCB1*, the gene underlying the *d2* dwarf phenotype in pearl millet, *Cenchrus americanus* (L.) Morrone. *G3 Genes|Genomes|Genetics*, *9*, 2497–2509. https://doi.org/10.1534/g3.118.200846

Peng, J., Richards, D. E., Hartley, N. M., Murphy, G. P., Devos, K. M., Flintham, J. E., Beales, J., Fish, L. J., Worland, A. J., Pelica, F., Sudhakar, D., Christou, P., Snape, J. W., Gale, M. D., & Harberd, N. P. (1999). 'Green revolution' genes encode mutant gibberellin response modulators. *Nature*, *400*, 256–261. https://doi.org/10.1038/22307

Puranik, S., Kam, J., Sahu, P. P., Yadav, R., Srivastava, R. K., Ojulong, H., & Yadav, R. (2017). Harnessing finger millet to combat calcium deficiency in humans: challenges and prospects. *Frontiers in Plant Science*, *8*, 1311. https://doi.org/10.3389/fpls.2017.01311

Puranik, S., Sahu, P. P., Beynon, S., Srivastava, R. K., Sehgal, D., Ojulong, H., & Yadav, R. (2020). Genome-wide association mapping and comparative genomics identifies genomic regions governing grain nutritional traits in finger millet (*Eleusine coracana* L. Gaertn.). *Plants, People, Planet*, *2*, 649–662. https://doi.org/10.1002/ppp3.10120

Qi, H., Yang, J., Yin, C., Zhao, J., Ren, X., Jia, S., & Zhang, G. (2019). Analysis of *Pyricularia oryzae* and *P. grisea* from different hosts based on multilocus phylogeny and pathogenicity associated with host preference in China. *Phytopathology*, *109*, 1433–1440. https://doi.org/10.1094/phyto-10-18-0383-r

Qi, P., Gimode, D., Saha, D., Schröder, S., Chakraborty, D., Wang, X., Dida, M. M., Malmberg, R. L., & Devos, K. M. (2018). UGbS-Flex, a novel bioinformatics pipeline for imputation-free SNP discovery in polyploids without a reference genome: Finger millet as a case study. *BMC Plant Biology*, *18*, 117. https://doi.org/10.1186/s12870-018-1316-3

Ramakrishnan, M., Antony Ceasar, S., Duraipandiyan, V., Vinod, K. K., Kalpana, K., Al-Dhabi, N. A., & Ignacimuthu, S. (2016). Tracing QTLs for leaf blast resistance and agronomic performance of finger millet (*Eleusine coracana* (L.) Gaertn.) genotypes through association mapping and in silico comparative genomics analyses. *PLoS ONE*, *11*, e0159264. https://doi.org/10.1371/journal.pone.0159264

Ramakrishnan, M., Antony Ceasar, S., Vinod, K. K., Duraipandiyan, V., Ajeesh Krishna, T. P., Upadhyaya, H. D., Al-Dhabi, N. A., & Ignacimuthu, S. (2017). Identification of putative QTLs for seedling stage phosphorus starvation response in finger millet (*Eleusine coracana* L. Gaertn.) by association mapping and cross species synteny analysis. *PLoS ONE*, *12*, e0183261. https://doi.org/10.1371/journal.pone.0183261

Reid, J. B., Botwright, N. A., Smith, J. J., O'Neill, D. P., Huub, L., & Kerckhoffs, J. (2002). Control of gibberellin levels and gene expression during de-etiolation in pea. *Plant Physiology*, *128*(2), 734–741. https://doi.org/10.1104/pp.010607

Sakamoto, T., Morinaka, Y., Ohnishi, T., Sunohara, H., Fujioka, S., Ueguchi-Tanaka, M., Mizutani, M., Sakata, K., Takatsuto, S., Yoshida, S., Tanaka, H., Kitano, H., & Matsuoka, M. (2006). Erect leaves caused by brassinosteroid deficiency increase biomass production and grain yield in rice. *Nature Biotechnology*, *24*, 105–109. https://doi.org/10.1038/nbt1173

Sharma, D., Tiwari, A., Sood, S., Jamra, G., Singh, N. K., Meher, P. K., & Kumar, A. (2018). Genome wide association mapping of agro-morphological traits among a diverse collection of finger millet (*Eleusine coracana* L.) genotypes using SNP markers. *PLoS ONE*, *13*, e0199444. https://doi.org/10.1371/journal.pone.0199444

Sood, S., Kumar, A., Babu, B. K., Gaur, V. S., Pandey, D., Kant, L., & Pattnayak, A. (2016). Gene discovery and advances in finger millet [*Eleusine coracana* (L.) Gaertn.] genomics—An important nutricereal of future. *Frontiers in Plant Science*, *7*, 1634. https://doi.org/10.3389/fpls.2016.01634

Soreng, R. J., Peterson, P. M., Romaschenko, K., Davidse, G., Teisher, J. K., Clark, L. G., Barberá, P., Gillespie, L. J., & Zuloaga, F. O. (2017). A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. *Journal of Systematics and Evolution*, *55*, 259–290. https://doi.org/10.1111/jse.12262

Spielmeyer, W., Ellis, M. H., & Chandler, P. M. (2002). Semidwarf (*sd-1*), "green revolution" rice, contains a defective gibberellin 20-oxidase gene. *Proceedings of the National Academy of Sciences*, *99*, 9043–9048. https://doi.org/10.1073/pnas.132266399

Srinivasachary, Dida, M. M., Gale, M. D., & Devos, K. M. (2007). Comparative analyses reveal high levels of conserved colinearity between the finger millet and rice genomes. *Theoretical and Applied Genetics*, *115*, 489–499. https://doi.org/10.1007/s00122-007-0582-5

Sultan, B., & Gaetani, M. (2016). Agriculture in West Africa in the twenty-first century: Climate change and impacts scenarios, and potential for adaptation. *Frontiers in Plant Science*, *7*, 1262. https://doi.org/10.3389/fpls.2016.01262

Takan, J. P., Akello, B., Esele, P., Manyasa, E. O., Obilana, A. B., Audi, P. O., Kibuka, J., Odendo, M., Oduori, C. A., Ajanga, S., Bandyopadhyay, R., Muthumeenakshi, S., Coll, R., Brown, A. E., Talbot, N. J., & Sreenivasaprasad, S. (2004). Finger millet blast pathogen diversity and management in East Africa: A summary of project activities and outputs. *International Sorghum and Millets Newsletter*, *45*, 66–69.

Takan, J. P., Chipili, J., Muthumeenakshi, S., Talbot, N. J., Manyasa, E. O., Bandyopadhyay, R., Sere, Y., Nutsugah, S. K., Talhinhas, P., Hossain, M., Brown, A. E., & Sreenivasaprasad, S. (2012). *Magnaporthe oryzae* populations adapted to finger millet and rice exhibit distinctive patterns of genetic diversity, sexuality and host interaction. *Molecular Biotechnology*, *50*, 145–158. https://doi.org/10.1007/s12033-011-9429-z

Talwar, H. S., Kumar, S., Madhusudhana, R., Nanaiah, G. K., Ronanki, S., & Tonapi, V. A. (2020). Variations in drought tolerance components and their association with yield components in finger millet (*Eleusine coracana*). *Functional Plant Biology*, *47*, 659. https://doi.org/10.1071/fp19274

Tian, D., Traw, M. B., Chen, J. Q., Kreitman, M., & Bergelson, J. (2003). Fitness costs of R-gene-mediated resistance in *Arabidopsis thaliana*. *Nature*, *423*, 74–77. https://doi.org/10.1038/nature01588

Tiwari, A., Sharma, D., Sood, S., Jaiswal, J. P., Pachauri, S. P., Ramteke, P. W., & Kumar, A. (2020). Genome-wide association mapping for seed protein content in finger millet (*Eleusine coracana*) global collection through genotyping by sequencing. *Journal of Cereal Science*, *91*, 102888. https://doi.org/10.1016/j.jcs.2019.102888

Vales, M. I., Schön, C. C., Capettini, F., Chen, X. M., Corey, A. E., Mather, D. E., Mundt, C. C., Richardson, K. L., Sandoval-Islas, J. S., Utz, H. F., & Hayes, P. M. (2005). Effect of population size on the estimation of QTL: A test using resistance to barley stripe rust. *Theoretical and applied genetics*, *111*, 1260–1270. https://doi.org/10.1007/s00122-005-0043-y

van der Knaap, E., Kim, J. H., & Kende, H. (2000). A novel gibberellin-induced gene from rice and its potential regulatory role in stem growth. *Plant Physiology*, *122*, 695–704. https://doi.org/10.1104/pp.122.3.695

The International Brachypodium Initiative. (2010). Genome sequencing and analysis of the model grass *Brachypodium distachyon*. *Nature*, *463*(7282), 763–768. https://doi.org/10.1038/nature08747

Voorrips, R. E. (2002). MapChart: Software for the graphical presentation of linkage maps and QTLs. *Journal of Heredity*, *93*, 77–78. https://doi.org/10.1093/jhered/93.1.77

Wambi, W., Tumwesigye, W., Otienno, G., & Mulumba, J. (2021). Genetic and genomic resources for finger millet improvement: Opportunities for advancing climate-smart agriculture. *Journal of Crop Improvement*, *35*, 204–233. https://doi.org/10.1080/15427528.2020.1808133

Wang, S., Basten, C. J., & Zheng, Z.-B. (2012). *Windows QTL Cartographer 2.5*. Department of Statistics, North Carolina State University. http://statgen.ncsu.edu/qtlcart/WQTLCart.htm

Wangari, C., Mwema, C., Siambi, M., Silim, S., Ubwe, R., Malesi, K., Anitha, S., & Kane-Potaka, J. (2020). Changing perception through a participatory approach by involving adolescent school children in evaluating smart food dishes in school feeding programs—Real-time experience from central and northern Tanzania. *Ecology of Food and Nutrition*, *59*, 472–485. https://doi.org/10.1080/03670244.2020.1745788

Whipple, C. J., Kebrom, T. H., Weber, A. L., Yang, F., Hall, D., Meeley, R., Schmidt, R., Doebley, J., Brutnell, T. P., & Jackson, D. P. (2011). *grassy tillers1* promotes apical dominance in maize and responds to shade signals in the grasses. *Proceedings of the National Academy of Sciences*, *108*, E506–E512. https://doi.org/10.1073/pnas.1102819108

Wies, G., Mantese, A. I., Casal, J. J., & Maddonni, G. Á. (2019). Phytochrome B enhances plant growth, biomass and grain yield in field-grown maize. *Annals of Botany*, *123*, 1079–1088. https://doi.org/10.1093/aob/mcz015

Wu, J., Kong, X., Wan, J., Liu, X., Zhang, X., Guo, X., Zhou, R., Zhao, G., Jing, R., Fu, X., & Jia, J. (2011). Dominant and pleiotropic effects of a *GAI* gene in wheat results from a lack of interaction between DELLA and GID1. *Plant Physiology*, *157*, 2120–2130. https://doi.org/10.1104/pp.111.185272

Wu, Y., Bhat, P. R., Close, T. J., & Lonardi, S. (2008). Efficient and accurate construction of genetic linkage maps from the minimum spanning tree of a graph. *PLoS Genetics*, *4*, e1000212. https://doi.org/10.1371/journal.pgen.1000212

Zhang, H., Hall, N., Goertzen, L. R., Chen, C. Y., Peatman, E., Patel, J., & McElroy, J. S. (2019). Transcriptome analysis reveals unique relationships among *Eleusine* species and heritage of *Eleusine coracana*. *G3: Genes|Genomes|Genetics*, *9*, 2029–2036. https://doi.org/10.1534/g3.119.400214

Zhongming, F., Yuanyuan, J., Jie, H., Renkang, G., Shiyong, S., & Xuelu, W. (2020). Strigolactones and Brassinosteroids antagonistically regulate the stability of the D53–OsBZR1 complex to determine *FC1* expression in rice tillering. *Molecular Plant*, *13*, 586–597. https://doi.org/10.1016/j.molp.2019.12.005

Zhou, T., Wang, Y., Chen, J. Q., Araki, H., Jing, Z., Jiang, K., Shen, J., & Tian, D. (2004). Genome-wide identification of NBS genes in japonica rice reveals significant expansion of divergent non-TIR NBS-LRR genes. *Molecular Genetics and Genomics*, *271*, 402–415. https://doi.org/10.1007/s00438-004-0990-z

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Pendergast, T. H., Qi, P., Odeny, D. A., Dida, M. M., & Devos, K. M. A high-density linkage map of finger millet provides QTL for blast resistance and other agronomic traits. *Plant Genome*. 2022;*15:*e20175. https://doi.org/10.1002/tpg2.20175