Breeding of Finger Millet for Agronomic and Nutritional Traits and Drought Tolerance in Ethiopia

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By

Adane Gebreyohannes

BSc, Applied Biology and MSc, Applied Genetics (Addis Ababa University, Ethiopia)

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African Centre for Crop Improvement

School of Agriculture and Science

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

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Thesis Summary

The changing climate, human population pressure, and lifestyle changes require new, improved, and adaptive plant genetic resources for value-added product development. Finger millet (*Eleusine coracana* (L.) Gaertn., 2n=4x=36, AABB) is a climate-resilient and highly nutritious small grain crop widely grown in the semi-arid tropics, including Ethiopia. It has multiple uses, including for food, feed, and the preparation of alcoholic and non-alcoholic beverages. However, finger millet is an under-utilized and under-researched crop with a mean yield of < 2.4 t/ha in Ethiopia despite a potential productivity of up to 6-8 t/ha. The yield gap is attributed to biotic and abiotic stresses, a lack of access to improved seeds and production inputs, and poor agronomic management practices. Recurrent and severe drought conditions are amongst the major production constraints of finger millet, limiting grain yield and quality. Therefore, the objectives of this study were: i) to systematically assess finger millet production systems in Ethiopia by identifying key production constraints, opportunities, and farmer-preferred traits and to inform ideotype and variety design for targeted breeding programs; ii) to evaluate and characterise genetically diverse Ethiopian finger millet accessions for agronomic performance, drought response, and grain nutritional compositions under contrasting moisture regimes, and to identify superior genotypes for use in breeding and/or production; iii) to analyse the population structure of the Ethiopian finger millet landraces and to identify robust marker-trait associations and quantitative trait nucleotides (QTNs) and haplotypes linked to key agronomic and nutritional and iv) to determine the combining ability, heterosis, and gene action of selected finger millet parents for economic traits in hybrid combinations to guide the selection of best families and new breeding populations. Separate but complementary research activities were conducted to attain the aforementioned objectives.

In the first part of the study, a participatory rural appraisal (PRA) study was conducted in six selected districts of the Southern Nation Nationalities People Region (SNNPR) and Oromia Region in Ethiopia, using 240 and 180 participant farmers through a semi-structured questionnaire and focus group discussion, respectively. The result showed, finger millet was the most important crop in the study areas grown mainly for a combination of uses, including for food, feed and cash (reported by 38.8% of respondent farmers), food and feed (14.5%), food and cash (13.7%), food (11.5%) and food, cash, feed and construction material (9.7%). The main constraints to finger millet production in the study areas were drought stress (reported by 41.3% respondents), lack of improved varieties (12.9%), lack of financial resources (11.3%), small land holdings (10.8%), limited access to seed (10.0%), a shortage of fertilizers (5.4%), poor soil fertility (4.6%), shortage of draught power

(1.3%), labour shortages (1.3%) and high labour costs (1.3%). The most important farmer-preferred traits in a finger millet variety were high grain yield, compact head shape, 'enjera'-making quality, high marketability and early maturity, resolved through principal component analysis. The aforementioned production constraints and farmer-preferred traits are strategic drivers for enhancing finger millet productivity and should be incorporated into Ethiopia's finger millet breeding and technology development.

In the second study, 448 Ethiopian finger millet accessions were evaluated under field conditions for agronomic performance, drought responses and nutrient composition. The study was conducted across three moisture regimes: non-stressed (Arsinegelle: denoted as AN), moderately drought-prone (Maitsebri: SH), and severely drought-stressed (Meiso: MI). Significant variations were recorded among genotype, environment, and genotype × environment interaction for all assessed traits. Grain yield (GY) declined by ~60% at MI site. The test genotypes varied considerably at MI for days to 50% flowering (DTF) (78.5–107.5 days), days to maturity (DTM) (101.0–149.5 days), GY (0.5-3.2 t/ha), iron (Fe) (53.6 – 81.0 ppm) and zinc (Zn) (67.8-83.1 ppm) contents suggesting considerable genetic variation for selection. Black-seeded genotypes maintained higher GY and Fe/Zn under drought, while red-seeded types flowered and matured earlier and produced larger seed size. Broad-sense heritability was > 60% for drought tolerance (Drt) score, DTF, and DTM, but <30% for plant height, starch content and GY. GY was negatively correlated with DTF, DTM, Drt and stay green traits, but positively correlated with seed weight across environments. Principal component analysis explained >67% of the variance for some traits across test sites, and hierarchical clustering grouped genotypes into four clusters. Eight accessions G141 (219819), G423 (AxumColl37), G297 (238326), G247 (237449), G171 (229726), G204 (234176), G294 (238323), and G46 (211473) were identified as promising candidates for breeding and further validation through multi-environment testing and variety evaluation procedures prior to potential release.

In the third study, 448 finger millet genotypes were evaluated across three contrasting environments to characterise their agronomic performance, drought response, and grain micronutrient compositions. A subset of 391 genotypes from this panel was skim-sequenced, generating 24,112 high-quality Single Nucleotide Polymorphisms (SNPs) that were employed for population structure, association mapping and haplotype analyses. Genome-wide association study (GWAS) resolved 70 marker-trait associations, including 15 major QTNs with more than 30% phenotypic variance explained (PVE) for all traits except stay-green score and grain yield. Pleiotropic major QTNs were identified for 50% days to flowering/days to maturity and Fe/Zn on chromosomes 9B and 2B, respectively. Haplotype analysis of major QTNs identified 54 significant haplotype blocks

and 2 additional haplotypes, many of which originated from landraces collected in Tigray and Amhara regions. These findings provide invaluable insights for targeted breeding to enhance finger millet resilience, nutritional profile, and grain yield.

The final part of the study assessed the combining ability, heterosis, and gene action of selected finger millet parents for economic traits in hybrid combinations. A 7 × 10 line × tester mating design was used, and the resultant 70 F1 hybrids and 17 parents were evaluated under well-watered (NST) and drought-stress (ST) conditions across greenhouse and field environments. Significant variations ($p < 0.001$) were observed among lines, testers and their interactions for the assessed traits, indicating both additive and non-additive gene action underlying inheritance of the assessed traits. Additive genetic effect predominantly conditioned the inheritance of DTF, ear length (EL), DTM under ST conditions, whereas non-additive effects affected the number of tillers (NT) and DTM under NST conditions. Broad-sense heritability for GY was higher under ST (0.51) than NST (0.13) conditions, necessitating multiple testing environments for drought tolerance evaluation and selection. Lines such as 235700, 234187 and Addis-01 and testers such as Gute, 24394, Bako-09, Mereb-1, and 215982 exhibited higher general combining ability effects for GY in a desirable trend. Crosses Wama/Kako-1, 234187/24394, Wama/215982, 235700/213835, Addis-01/213835, Addis-01/Gute, Necho/Gute, and Necho/Kako-1 exhibited higher specific combining ability effects and heterosis for GY under ST conditions. The selected parents and the top crosses are recommended for breeding and selection of new generation and drought-adapted finger millet genotypes.

Overall, the present study identified the major production constraints, traits of economic value of finger millet, identified unique genetic resources and genes and developed new breeding populations with better agronomic performance, nutrient compositions and drought tolerance. The new breeds have integrated farmers' preferred traits and will be evaluated across multiple sites for selection and release in the marginal production areas in Ethiopia and similar agro-ecologies.

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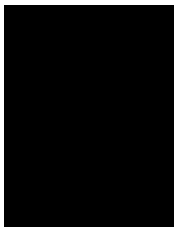
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Declaration

I, Adane Gebreyohannes Woldetensay, declare that,

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been rewritten, but the general information attributed to them has been referenced.
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Signed



……

Adane Gebreyohannes Woldetensay

As the candidate's supervisor, I agree to the submission of this dissertation:

……  ……

Prof. Hussein Shimelis (Supervisor)

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Dedication

This study is dedicated to my wife, Zewdnesh Tadesse, son, Nikodimos Adane, father, Gebreyohannes Woldetensay, mother, Tirunesh Tadesse, and to the people of Dire Dawa City in Ethiopia.

Publications Pertaining to this Thesis

Chapter 1

Gebreyohannes, A., H. Shimelis, J. Mashilo, D.A. Odeny, T. Tadesse and C.O. Ojiewo 2024. Finger millet (*Eleusine coracana*) improvement: challenges and prospects-a review. Plant Breed. 143(3), 350–374. DOI: https://doi.org/10.1111/pbr.13169

Chapter 2

Gebreyohannes, A., H. Shimelis, M. Laing, I. Mathew, D.A. Odeny, H. Ojulong, 2021. Finger millet production in Ethiopia: opportunities, problem diagnosis, key challenges, and recommendations for breeding. Sustainability 13: 13463. DOI: https://doi.org/10.3390/su132313463

Chapter 3

Gebreyohannes, A., H. Shimelis, J. Mashilo, D.A. Odeny, T.T. Mindaye, H. Ojulong and C.O. Ojiewo. 2025. Profiling Ethiopian finger millet (*Eleusine coracana*) accessions for major agronomic traits and nutrient composition under varying drought stress. Euphytica 221: 191. DOI: https://doi.org/10.1007/s10681-025-03642-0

Chapter 4

Gebreyohannes, A., H. Shimelis, D.M. Gimode, P. Gandham, V.K. Valluri, H. Nida, S.M. Moenga, C.O. Ojiewo, B. Kilian and D.A. Odeny 2025. Genetic structure of Ethiopian finger millet landraces and genome-wide association mapping for agronomic and nutritional traits. Theor. Appl. Genet. 138: 111. DOI: https://doi.org/10.1007/s00122-025-04892-1

Thesis Introduction

Background

Finger millet (*Eleusine coracana* [L.] Gaertn.) is an allotetraploid ($2n = 4x = 36$, AABB genome) species belonging to the Poaceae family. It has C_4 photosynthesis and is adapted to growing in the semi-arid tropics. The crop has exceptional genetic plasticity with tolerance to extreme temperatures (Yogeesh et al., 2016; Kudapa et al., 2023), moisture stress (Hittalmani et al., 2017; Ceasar et al., 2018), aluminium toxicity (Brhane et al., 2017), and salinity (Rahman et al., 2014; Divya et al., 2022).

Finger millet has a niche market opportunity due to its popularity among rural and urban populations for its food quality, notable nutritional composition, and human health advantages. It has multiple uses, such as food and beverage preparations and feed. In Ethiopia, the grain is processed to make unleavened bread (locally referred to as *enjera*) and for malting to prepare local drinks such as a distilled spirit '*Areki'* or local beers such as '*tella'* and non-alcoholic drinks such as '*karibu'* and '*shamita'*, while the straw is vital as a livestock feed and for thatching of houses (Assefa et al., 2009; Lule et al., 2012). In Tanzania and Uganda, finger millet flour is used to prepare a staple food such as porridge and traditional beverages, including '*togwa'*, 'obushera', and '*obutoko'* (Mugula et al. 2003; Mukisa et al. 2012). These diverse uses underscore its relevance for food security, health, and economic development (Hawaz et al. 2025).

The grain has extended storage quality (Ceasar et al., 2018), with unique nutritional composition, including high levels of Ca, Fe, Zn, K, Mg, Mn, dietary fibre, phenolic compounds, and essential amino acids (e.g. cystine, methionine, and tryptophan) (Devi et al. 2011; Maharajan et al., 2022; Backiyalakshmi et al., 2023; Kudapa et al., 2023). Finger millet is a gluten-free grain and is a viable dietary alternative for individuals with celiac disease or gluten sensitivity. Finger millet food products are believed to lower blood cholesterol levels and blood pressure (Anitha et al., 2021a) and possess anti-cancer (Chandrasekara & Shahidi, 2011; Devi et al. 2011) and anti-ageing properties (Puranik et al., 2020; Kumar et al., 2021). Further, finger millet diets prevent osteoporosis (Puranik et al., 2017; Anitha et al., 2021b), rickets (Maharajan et al., 2021), diabetics (Devi et al. 2011;

Murtaza et al., 2014; Anitha et al., 2021a), obesity (Murtaza et al., 2014), anaemia (Karkada et al., 2019), celiac (Tadele, 2018), liver disorders, and asthma (Shobana et al., 2009). It also boosts immunity against malaria (Tsehaye et al., 2006; Assefa et al., 2013) and diarrhoea (Tsehaye et al., 2006; Assefa et al., 2013). The human health benefits of finger millet make it a superfood to combat malnutrition and other ailments.

Finger millet is globally produced in more than 2.1 million ha of land, with an annual production of 3.7 million tons when compared with the total area (11 million ha) and annual production (14.6 million tons) allotted to millets (Orr et al., 2016; FAOSTAT, 2020; Gairhe et al., 2021; Indiastat, 2020; MoALD, 2020). The values correspond to finger millet's share of 20% and 26% of the global millets in total area coverage and production, respectively. Ethiopia is the world's second largest producer of finger millet, next to India, with a total production area of 480,511 ha, and an estimated annual production at 1,125,958 tons accounting for an equivalent with 22% and 33% global share of finger millet, indicating the value of finger millet in the agricultural sector (CSA, 2020; Gebreyohannes et al., 2021, 2024). However, the global productivity of finger millet is low, ~1.0 t/ha, compared with the potential productivity reaching up to 8 t/ha (Gebreyohannes et al., 2021, 2024).

The low productivity of the crop in Ethiopia is attributable to a range of biotic and abiotic stresses and socio-economic constraints prevalent in the smallholder production systems. Finger millet blast caused by *Magnaporthe grisea* (Barr) (teleomorph) is the most damaging disease, causing yield losses in the range of 7.3–54.1%, depending on climatic conditions and cultivar susceptibility (Lule et al., 2014). Notable insect pests of the crop include grasshoppers (*Caelifera*) and shoot fly (*Atherigona soccata* (Rondani)) (Assefa et al., 2009), pink stem borer (*Sesamia inferens* (Walker)), finger millet root aphid (*Tetraneura nigriabdominalis* (Sasaki)) and aphids (aphidoidea) (Sasmal, 2018). Yield losses have been reported due to several insect pests such as termites (isopteran) (with a loss of 23%) (Mulualem and Melak, 2013), aphids (35.1%) (Sasmal, 2016) and pink stem borer (56%) (Sasmal, 2018). Weeds cause severe yield loss during the early growth stages of finger millet. In Ethiopia, yield losses of up to 73.5% have been reported due to weeds (Asargew and Shibabawu, 2014).

The major socio-economic impediments to finger millet productivity include a lack of locally adapted, drought-tolerant, disease-resistant, and high-yielding varieties (Gebreyohannes et al., 2021). In most finger millet production areas, notably in sub-Saharan Africa (SSA), including Ethiopia, unimproved traditional varieties or landraces are commonly used for cultivation (Mulualem & Melak, 2013; Kasule et al., 2023). The landrace varieties have excellent eating quality and nutritive value and are highly preferred by growers, consumers, and markets (Gebreyohannes et al., 2021). Also, landraces have better insect and disease resistance due to their co-evolution with major insect pests and diseases (Vetriventhan et al., 2020; Dida et al., 2021; Mbinda & Masaki, 2021). However, landraces are low-yielding, susceptible to drought and lodging, with low grain threshability (Gebreyohannes et al., 2021). Therefore, germplasm maintained by local farmers, regional and international research centres, and gene banks could be an excellent source of novel genetic variation for finger millet pre-breeding and breeding programs.

Recurrent drought stress associated with climate change is the leading constraint affecting finger millet production and other main crops in Ethiopia. The impact of drought stress on finger millet production depends on cultivar susceptibility, the onset date, the intensity and duration of the drought stress and the associated prevailing environmental conditions. Although finger millet is relatively drought-tolerant, 50-100% yield losses can be incurred due to intense and early onset of drought stress (Maqsood & Ali, 2007; Gebreyohannes et al., 2025). Supplementary irrigation, early planting and moisture conservation techniques such as mulching, zero tillage and tie ridging are often used to mitigate drought stress (Wang et al., 2016). However, most smallholder farmers do not have access to irrigation and other resources to manage drought stress. Drought stress also significantly affects grain quality and yield components (Barutçular et al., 2016). Hence, drought-tolerant varieties could be the most economical and environmentally friendly approach to managing drought under smallholder production systems.

Rationale of the Study

Finger millet production and productivity in Ethiopia is severely constrained by the lack of high-yielding, locally adapted, drought-tolerant and disease-resistant varieties. Farmers continue to growing low-yielding landraces under marginal environments characterized by recurrent drought and poor soil fertility. Despite the availability of diverse genetic resources and emerging breeding technologies, genetic improvement of finger millet in Ethiopia has remained slow. This is due to the lack of an integrated breeding framework that links farmer-preferred traits, comprehensive germplasm characterization, trait genetics, and strategic parental selection for variety development. Farmers' perceptions of production constraints and trait preferences have not been systematically documented to guide to farmer- and market-preferred variety development. Participatory rural appraisal (PRA) approaches provide an effective mechanism for identifying farmers' perceived production constraints and the needs and priorities for new varieties to guide breeding. However, such information has rarely been integrated into finger millet breeding program in Ethiopia. At the same time, Ethiopia has genetically diverse finger millet genetic reservoirs, including landraces, wild relatives and released varieties conserved at the Ethiopian Biodiversity Institute and Melkassa Agricultural Research Center. However, these genetic resources were not systematically characterized, and previous efforts used a small and unrepresentative germplasm set, yielding only a modest understanding of phenotypic diversity and market-relevant traits. The genetic basis of key agronomic and nutritional traits also remains poorly understood regarding drought-induced yield losses, micronutrient stability across environments, and the hypothesized tradeoffs between grain yield and micronutrient concentration. Modern breeding innovations, including genomics-assisted breeding, mutation breeding, and genome-editing, offer unique opportunities, but their effective deployment depends on better insights into the genetic compositions, genetic effects, heterosis, and trait inheritance among the genetic pool of finger millet. Furthermore, the limited use of quantitative genetic approaches, such as line × tester analysis, has restricted the identification of superior parental lines and cross combinations for breeding. Therefore, the major challenge to finger millet improvement in Ethiopia is not a lack of improved varieties, farmer inputs, trait knowledge, or genetic characterisation individually, but the failure to integrate these components into a coherent and efficient breeding strategy. Hence, there is a need for a comprehensive finger millet breeding program that combines farmer-centered trait prioritization, extensive phenotypic and genomic characterization, strategic hybridization to accelerate the development of high-yielding, nutrient-dense, and drought-resilient varieties for Ethiopia's diverse and marginal agro-ecologies.

General objective

The overall aim of the study was to establish an integrated breeding framework for Ethiopian finger millet by combining farmer-preferred identification, comprehensive phenotypic and genomic characterization of diverse germplasm, and strategic hybridization of genetically diverse germplasm to accelerate the development of high-yielding, nutrient-dense, and drought-resilient varieties.

Specific objectives

The specific objectives of the study included:

i. To systematically assess finger millet production systems in Ethiopia by identifying key production constraints, opportunities, and farmer-preferred traits and to inform ideotype and variety design for targeted breeding programs.
ii. To evaluate and characterise genetically diverse Ethiopian finger millet accessions for agronomic performance, drought response, and grain nutritional compositions under contrasting moisture regimes, and to identify superior genotypes for use in breeding and/or production.
iii. To analyse the population structure of the Ethiopian finger millet landraces and to identify robust marker-trait associations and quantitative trait nucleotides (QTNs) and haplotypes linked to key agronomic and nutritional traits.
iv. To determine the combining ability, heterosis, and gene action of selected finger millet parents for economic traits in hybrid combinations to guide the selection of the best families and new breeding populations.

Research hypotheses

This study was conducted to test the following hypotheses:

i. In low-moisture finger millet growing areas of Ethiopia, farmers are aware of the finger millet production constraints and have specific trait preferences.
ii. Genetic diversity exists for major agronomic traits, drought response, and nutritional compositions in the core collections of Ethiopian finger millet landraces.
iii. Ethiopian finger millet landraces exhibit distinct population structure and harbour significant marker-trait associations and haplotype blocks governing key drought response, morphological

traits, and nutritional composition, enabling the identification of genomic loci suitable for marker-assisted breeding.

iv. The cross combinations of genetically diverse finger millet parents will exhibit significant variation in combining ability, heterosis and underlying gene action, enabling the identification of superior families and elite parental genotypes for developing high-performing, drought-adapted breeding populations.

Thesis organization

The thesis consists of a comprehensive review of the literature, four experimental chapters, and a concluding overview of the research (Table 0.1). Chapter 1 is written as a separate review paper, while Chapters 2 to 5 are written as independent research papers, each following the format of a stand-alone research paper, followed by a general overview of the research and its implications. The chapters were organised into discrete but interdependent papers according to the University of KwaZulu-Natal's dominant thesis format. Accordingly, there may be limited duplication of introductory text and citations across chapters.

Chapter 1 focused on synthesizing opportunities, constraints, and innovations for improved finger millet cultivars and was published in Plant Breeding 143(3): 350–374. DOI: https://doi.org/10.1111/pbr.13169. Chapter 2 highlights a participatory rural appraisal to diagnose production constraints and identify key farmer-preferred traits, and was published in Sustainability 13: 13463. DOI: https://doi.org/10.3390/su132313463. Chapter 3 emphasises evaluating diverse finger millet for agronomic performance, nutrition content and drought tolerance and was published in Euphytica 221: 191. DOI: https://doi.org/10.1007/s10681-025-03642-0. Chapter 4 focused on linking key genes and haplotypes to superior finger millet traits for targeted breeding and was published in Theoretical and Applied Genetics 138: 111. DOI: https://doi.org/10.1007/s00122-025-04892-1. Chapter 5 attempted to create and evaluate new finger millet cross combinations to select the best parents and hybrids for high yield and drought adaptation.

Table 0.1 Thesis structure

Chapter	Title
-	Thesis Introduction
1	Finger Millet (*Eleusine coracana* [L.] Gaertn.) Improvement: Challenges and Prospects: A Review
2	Finger Millet Production in Ethiopia: Opportunities, Problem Diagnosis, Key Challenges and Recommendations for Breeding
3	Profiling Ethiopian Finger Millet (*Eleusine Coracana*) Accessions for Major Agronomic Traits and Nutrient Composition under Varying Growing Conditions
4	Genetic Structure of Ethiopian Finger Millet Landraces and Genome-Wide Association Mapping for Agronomic and Nutritional Traits
5	Hybrid Performance in Finger Millet (*Eleusine Coracana*) for Grain Yield and Component Traits
-	An overview of research findings and implications for breeding

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Chapter 1. Finger millet (*Eleusine coracana* [L.] Gaertn.) Improvement: Challenges and Prospects: A Review

Abstract

Finger millet is a climate-resilient and highly nutritious small grain crop widely grown in the semi-arid tropics. It has multiple uses, including for food, feed, and beverage preparations. However, finger millet is an under-utilized and under-researched crop with a mean yield of < 1.0 t/ha despite a potential productivity of up to 8 t/ha. The yield gap is attributed to several production constraints, such as biotic and abiotic stresses, a lack of access to improved seeds and production inputs, and poor agronomic management practices. There are valuable genetic resources and genetic variability of finger millet in its centers of diversity and global gene banks for variety design, product development, and commercialization. The genetic variability can be harnessed further to integrate essential traits into candidate varieties through conventional and modern breeding methods. Breeding and genetic innovations such as genomics-assisted breeding, mutation breeding and genome editing would accelerate finger millet breeding and new variety design and deployment. The objective of this review was to document the opportunities, challenges, and prospects of finger millet improvement as a guide for variety development and deployment with enhanced grain yield and nutritional contents. The first section describes global production status and yield gains, major production and productivity challenges in finger millet. This is followed by an in-depth presentation on breeding and genetic progress on variety development with improved agronomic and nutritional quality traits, drought, and salinity tolerance, and fungal diseases, weeds, insect pest resistance. Further, the review summarized finger millet's genetic and genomic resources, reference genomes, whole genome re-sequencing and transcriptomics of finger millet technologies, genetic engineering, and genome editing and their integration with conventional breeding methods for variety design with desired end-use traits. The review provides foundational information to expedite the development of new-generation finger millet cultivars with desirable product profiles, including high grain yield potential, early maturity, desirable seed colour, compact head type, food and feed nutrients quality, and high marketability through modern breeding approaches.

Keywords: finger millet breeding, genetic gain, genome editing, genetic engineering, finger millet global production, production constraints, skim sequencing, whole genome re-sequencing.

1.1 Introduction

Finger millet (*Eleusine coracana* [L.] Gaertn.) is an allotetraploid ($2n = 4x = 36$, AABB) species belonging to the Poaceae family. It has a C_4 photosynthesis and is adapted to growing in the semi-arid tropics. The crop has exceptional genetic plasticity with tolerance to extreme temperatures (Yogeesh et al., 2016; Kudapa et al., 2023), moisture stress (Hittalmani et al., 2017; Ceasar et al., 2018), aluminium toxicity (Brhane et al., 2017a), and salinity (Rahman et al., 2014; Divya et al., 2022). The gluten-free grain has multiple uses, such as food and beverage preparations. The stalk is used as livestock feed, thatching, and bedding material. The grain has extended storage quality (Ceasar et al., 2018), with unique nutritional composition, including high levels of Ca, Fe, Zn, K, Mg, Mn, dietary fibre, phenolic compounds, essential amino acids (e.g. cystine, methionine, and tryptophan) (Devi et al. 2011; Maharajan et al., 2022; Backiyalakshmi et al., 2023; Kudapa et al., 2023).

Finger millet food products are believed to lower blood cholesterol levels and blood pressure (Anitha et al., 2021a) and possess anti-cancer (Chandrasekara and Shahidi, 2011; Devi et al. 2011; and anti-ageing properties (Puranik et al., 2020; Kumar et al., 2021a). Further, finger millet diets prevent osteoporosis (Puranik et al., 2017; Anitha et al., 2021b), rickets (Maharajan et al., 2021), diabetics (Devi et al. 2011; Murtaza et al., 2014; Anitha et al., 2021a), obesity (Murtaza et al., 2014), anaemia (Karkada et al., 2019), celiac (Tadele, 2018), liver disorders, and asthma (Shobana et al., 2009). It also boosts immunity against malaria (Tsehaye et al., 2006; Assefa et al., 2013) and diarrhoea (Tsehaye et al., 2006; Assefa et al., 2013). The human health benefits of finger millet make it a superfood to combat malnutrition and other ailments.

In sub-Saharan African and Asian countries, finger millet is mainly grown by smallholder farmers for household consumption, and the surplus is sold in the local and regional markets. It has a niche market opportunity due to its popularity among rural and urban populations for its human health advantages and food quality. However, limited information and dissemination about its commercial value and human-health benefits have hindered product development and marketing. Integrating finger millet production into the existing cropping systems will diversify the food systems and ensure food and nutrition security and cash income along the value chains (Jerop et al., 2018).

The global total area and production of finger millet are not known precisely. This is because the Food and Agriculture Organization of the United Nations (FAOSTAT) reported finger millet together with pearl millet (*Pennisetum glaucum* [L.] R. Br.), foxtail millet, and other minor millet

types (FAOSTAT, 2020; Gebreyohannes et al. 2021). In some countries such as India, Ethiopia, Nepal, Uganda, and Rwanda, data is available on total area coverage and production of finger millet owing to the economic value of the crop (Orr et al., 2016; CSA, 2020; Indistat, 2020; MoALD, 2020; Gairhe et al., 2021). India is the leading producer of finger millet in the world, with an annual production of 1.8 million tons, followed by Ethiopia (1.2 million tons), Nepal (0.31 million tons), Uganda (0.20 million tons), and Tanzania (0.10 million tons) (Orr et al., 2016; CSA, 2020; FAOSTAT, 2020; Indistat, 2020; MoALD, 2020; Gairhe et al., 2021). Finger millet is an under-utilized and under-researched crop with a mean yield of < 1.0 tons/ha compared with the potential productivity reaching up to 8 tons/ha (Oduori, 2008; Padulosi et al., 2015; Joshi et al., 2023).

The low average global yield of finger millet is attributed to several production constraints: biotic stresses (fungal diseases, insect pests, weeds, and bird damage) and abiotic stresses (drought, heat, poor soil fertility, and salinity). Global finger millet production and productivity are severely constrained by the combined effect of drought and blast disease, whose impact hinges on a complex interplay of varietal susceptibility, crop stage, stress severity, environmental factors, and their intricate interactions. Drought alone causes substantial yield losses, with landraces like Kala Mandua and Safed Mandua in India and TZA-01 in Tanzania experiencing marked yield losses of up to 77% (Maqsood and Ali, 2007; Khatoom and Singh, 2016). Globally, finger millet yield exhibits a substantial reduction in the range of 7 to 90% due to blast disease, driven by a complex interplay of weather conditions and host genotype susceptibility (Nagaraja et al., 2007; Lule et al., 2014; Akech et al., 2016; Mbinda et al., 2021; Mbinda and Masaki, 2021). The severe limitations imposed by drought and disease underscore the critical need to develop highly resilient finger millet cultivars. A lack of access to improved seed and production inputs, poor agronomic management practices, and poor market access are the foremost socio-economic factors hindering finger millet production, especially in less developed countries. Likewise, limited agricultural land for crop production, lack of access to extension services, and absence of integrated disease, insect pest, and weed management, and under-developed pre- and post-harvest technologies and products have a detrimental impact on finger millet productivity and value chains (Jerop et al., 2018; Mbinda and Masaki, 2021).

The major impediments to finger millet productivity include a lack of locally adapted, drought-tolerance, disease-resistant, and high-yielding varieties (Owere et al., 2014; Gebreyohannes et al., 2021; Mbinda et al., 2021). In most finger millet production areas, notably in sub-Saharan Africa (SSA), including Ethiopia, unimproved traditional varieties or landraces are commonly used for

cultivation (Mulualem and Melak, 2013; Kasule, et al., 2023). The landrace varieties have excellent eating quality and nutritive value and are highly preferred by growers, consumers, and markets (Gebreyohannes et al., 2021). Also, landraces have better insect and disease resistance due to their co-evolution with major insect pests and diseases (Vetriventhan et al., 2020; Dida et al., 2021; Mbinda and Masaki, 2021). However, landraces are low yielders, susceptible to drought and lodging with low grain threshability (Gebreyohannes et al., 2021). Therefore, germplasm maintained by local farmers, regional and international research centers, and gene banks could be an excellent source of novel genetic variation for finger millet pre-breeding and breeding programs.

There are valuable genetic resources and genetic variability of finger millet in its centers of diversity and global gene banks. About 40,182 finger millet accessions have been collected and conserved by different gene banks (Dwivedi et al., 2012; PGRC, 2016; ICRISAT, 2017; EBI, 2023). The largest proportions of finger millet accessions are conserved in Asia and African countries, North America, by the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) in India, Kenya and Mozambique. Ethiopia is the center of origin and diversity for finger millet (Harlan, 1971; Hilu et al., 1979; Tesfaye and Mengistu, 2017). The Ethiopian Biodiversity Institute (EBI) and Ethiopian Institute of Agricultural Research (EIAR) - Melkassa Agricultural Research Center (MARC) maintain around 1809 and 400 finger millet accessions, respectively (EBI, 2023). The germplasm is a valuable source of economic traits including grain yield and its component traits (Assefa et al., 2013; Anteneh et al., 2019), nutritional quality (Tsehaye et al., 2006), disease (e.g. blast), heat and drought tolerance, (Assefa et al., 2013; Manyasa et al., 2019), aluminium and acidic toxicity tolerance (Brhane et al., 2017a), bird damage tolerance (Tsehaye et al., 2006) and excellent fermentation quality for brewing (Tsehaye et al., 2006).

Despite substantial genetic diversity, nutritional superiority, and climate resilience of finger millet, genetic gains for grain yield, nutritional quality, and stress adaptation have remained modest in many production environments (Sood et al., 2019; Dida et al., 2021; Marefia et al., 2022; Gupta et al., 2023a). This paradox underscores a persistent breeding bottleneck: despite abundant germplasm diversity and advances in genomic technologies, the development and adoption of high-yielding, farmer-preferred cultivars have progressed slowly (Vetriventhan et al., 2020; Dida et al., 2021). Consequently, a stronger integration of farmers' preferences, phenotypic variation, genomic information, and breeding strategies is required to accelerate genetic gain and cultivar development for diverse production systems (Ceccarelli and Grando, 2007; Varshney et al., 2020). Modern breeding approaches, including genomics-assisted breeding, genome-wide association mapping,

mutation breeding, and genomic selection, have expanded the exploitable genetic variability in finger millet and improved the efficiency of selecting key traits. The greatest progress has been achieved for highly heritable traits such as flowering and maturity time, grain mineral composition (Ca, Fe, and Zn), blast disease resistance, and tolerance to drought and salinity. However, genetic improvement for grain yield and yield stability remains comparatively slow due to complex trait inheritance and strong genotype-by-environment interactions (Hittalmani et al., 2017; Ceaser et al., 2018; Puranik et al., 2020; Kudapa et al., 2023).

Previous studies have generated valuable information on germplasm characterization, trait inheritance, stress tolerance, and molecular genetics in finger millet (Lule et al., 2018; Puranic et al., 2020; Pendergast et al., 2022). However, many investigations have been conducted independently, resulting in limited integration of farmer-preferred traits, field-based phenotyping, genomic analyses, and breeding decision-making. Furthermore, contrasting reports on trait associations, nutritional quality, and stress responses across environments suggest that genotype-by-environment interactions remain inadequately understood and continue to constrain breeding progress (Manyassa et al., 2016; Sharma et al., 2018; Sood et al., 2023b). Addressing these gaps is essential for accelerating genetic gain and developing cultivars that simultaneously combine high yield potential, nutritional quality, and resilience to climate-related stresses (Varshney et al., 2020; Gupta et al., 2023b)

Sustainable genetic improvement of finger millet requires an integrated approach that links production constraints, stakeholder preferences, genetic diversity, phenotypic performance, and modern breeding tools. Participatory approaches are increasingly recognized as effective mechanisms for defining breeding priorities and enhancing cultivar adoption in smallholder farming systems (Ceccarelli and Grando, 2007; Tadelle, 2019). Likewise, multi-environment phenotyping facilitates the identification of stable and adaptive genotypes, while genome-wide association studies and other genomic approaches accelerate the discovery of loci associated with agronomic, nutritional, and stress-adaptive traits (Puranic et al., 2020; Sharma et al., 2022; Pendergast et al., 2022). In parallel, combining ability and hybridization studies provide insights into gene action and parental performance, supporting the design of superior breeding populations and cultivar development strategies (Hallauer et al., 2010; Acquaah, 2012). Together, these complementary approaches provide a robust framework for developing climate-resilient and nutritionally enhanced finger millet cultivars.

The genetic variability of the existing finger millet genetic resources can be harnessed further to integrate winning and essential traits into candidate varieties through conventional and modern breeding methods. Breeding and genetic innovations such as genomics-assisted breeding, mutation breeding, transgenic approaches, and genome editing would accelerate finger millet breeding and new variety design and deployment. Considering the above background, this review aims to provide current and detailed information on the opportunities, challenges, and prospects of finger millet improvement to guide variety development and deployment with enhanced grain yield and nutritional contents. The first section offers detailed data on global production status and yield gains and major production and productivity challenges in finger millet. An in-depth presentation on breeding and genetic progress on cultivar development with improved agronomic and nutritional quality traits, drought and salinity tolerance, and major fungal diseases, weeds and insect pest resistance follows this. This review is supported by several data sets on finger millet breeding and genetic improvement and presents the crop's current breeding and genomic tools and genetic resources. Information presented in the review guides the development of new-generation finger millet cultivars with desirable product profiles, including high grain yield potential, early maturity, desirable seed colour, compact head type, food and feed nutrients quality, and high marketability through modern breeding and genomic tools.

1.2 Global production and productivity of finger millet

Finger millet is grown in more than 50 different countries worldwide, including 27 African countries (Radchuk et al., 2012; Mirza and Marla, 2019; Backiyalakshmi et al., 2021; Maharajan et al., 2021). Figure 1.1 presents countries of finger millet production. Eastern and Southern Africa are the leading finger millet producers in Africa. It is also grown in Southern Chad, Senegal, Ghana, Cameroon, North-Eastern Nigeria and West-Central Africa to a lesser extent. There are 17 main finger millet-producing countries in Asia, including India, Nepal, Sri Lanka, Maldives, Pakistan, Malaysia, China, Bhutan, Taiwan, Myanmar, Iran, Afghanistan, Philippines and Japan (Maharajan et al., 2021). The crop is also grown in some areas of the Americas, specifically in Mexico and the USA. Finger millet is reportedly grown in minor quantities in Europe, such as in the United Kingdom, Germany, Italy and Ukraine (Radchuk et al., 2012; Mirza and Marla, 2019; Backiyalakshmi et al., 2021).

The area and production of finger millet on a global scale are comprehensively collected, analyzed, and summarized in Table 1.1 and Figure 1.2. Finger millet is globally produced in more than 2.1

million ha of land, with an annual production of 3.7 million tons when compared with the total area (11 million ha) and annual production (14.6 million tons) allotted to millets (Orr et al., 2016; FAOSTAT, 2020; Gairhe et al., 2021; Indistat, 2020; MoALD, 2020). The values correspond to finger millet's share of 20% and 26% of the global millets in total area coverage and production, respectively (Table 1.1). India is the world's foremost producer of finger millet, with a total production area of 1 million ha (Indistat, 2020; Gebreyohannes et al., 2021), accounting for 46% of the global share, followed by Ethiopia (with a total production area of 480,511 ha and 22% global share) (Figure 1.2).

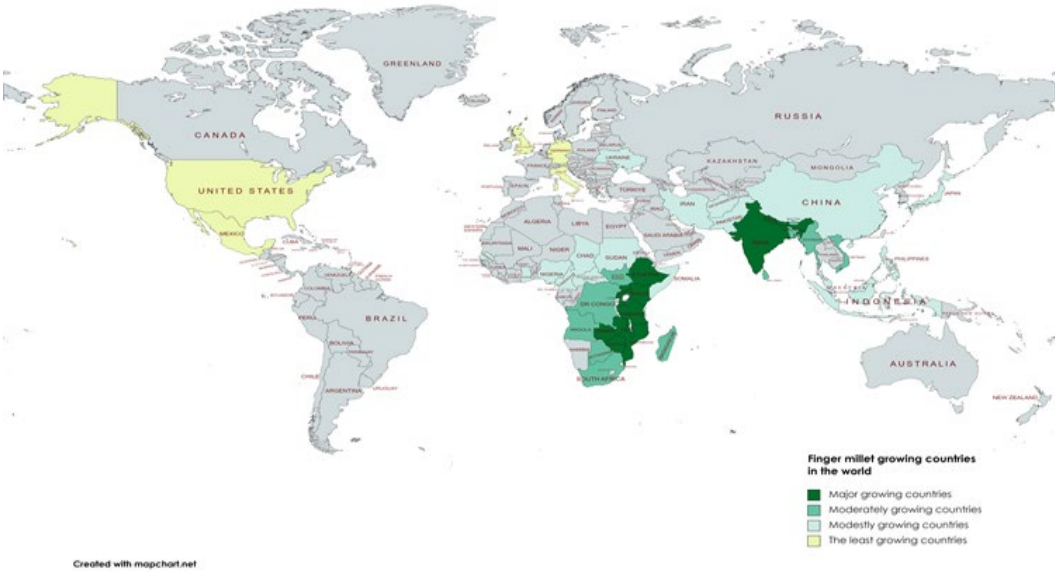


Figure 1.1. Map of finger millet growing countries in the world.

Table 1.1 Total area coverage, production, and mean yield of finger millet and its relative importance compared to other millets (e.g., pearl, finger, foxtail, proso, little, barnyard, kodo and fonio millets) in various major growing countries.

Countries	Relative importance (%)†	Total production area (ha)	Total production (tons)	Yield (t/ha)	References
India	10.3††	1,004,460	1,755,060	1.75	FAOSTAT (2020); Indistat (2020)
Ethiopia	100	480,511	1,218,582	2.54	Orr et al. (2016); CSA (2020); FAOSTAT
Nepal	100	263,261	314,225	1.19	FAOSTAT (2020); Gairhe et al. (2021)
Uganda	94	141,600	197,091	1.39	Orr et al. (2016); FAOSTAT (2020); MoALD
Tanzania	30	81,000	97,500	1.2	
Kenya	45	53,285	68,850	1.29	
Zimbabwe	30	43,349	13,023	0.3	
Zambia	60	39,454	27,003	0.68	
Malawi	60	34,423	29,359	0.85	
Eritrea	20	15,000	5,000	0.33	Orr et al. (2016) ; FAOSTAT (2020)
Mozambique	20	10,695	4,420	0.41	
Rwanda	100	10,637	5,067	0.48	
Finger millet Total/mean		2,177,675	3,735,180	1.03	
The importance of finger millet relative to other millets					
Millets global total/mean		11,140,318	14,585,766	1.32	FAOSTAT (2020)
Finger millets global total/percent/mean		2,177,675 (20)	3,735,180 (26)	1.03	

Note: † = finger millet's production and area coverage compared to other millets, †† = relative importance (%) = (finger millet area /total millet area) x 100, numbers in parenthesis is the percent share of finger millet in relation to other millets

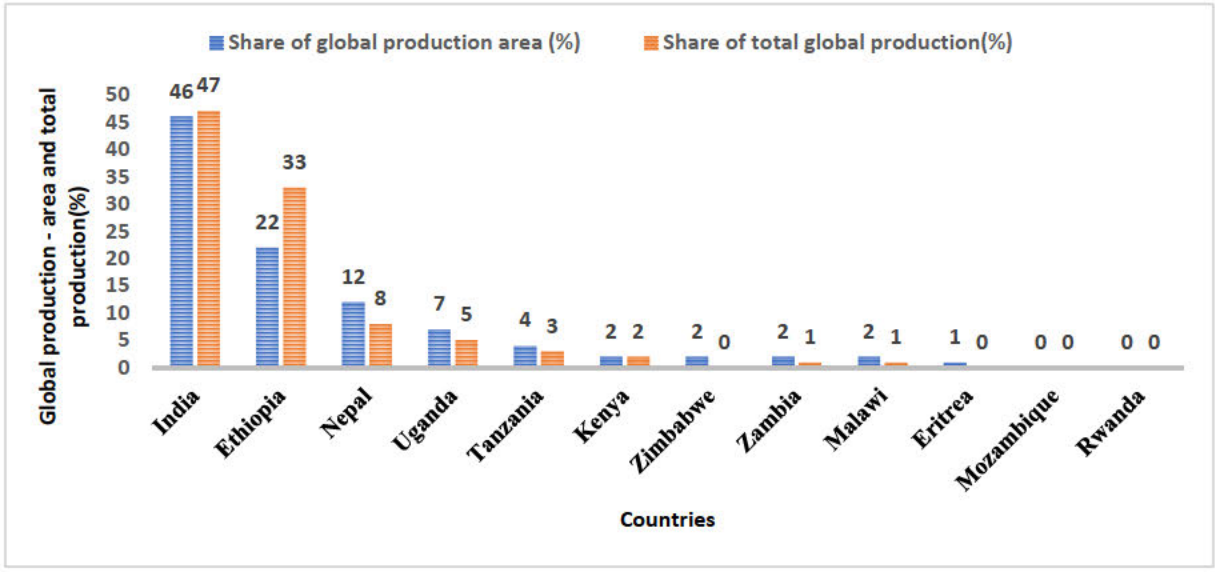


Figure 1.2. Global area and total production (%) share of finger millet in major growing countries

1.3 Genetic gains for agronomic traits and nutritional compositions

Genetic gain refers to the increased performance of genotypes achieved through genetic improvement, resulting in desirable gains for economic traits (Krishnappa et al., 2009; Ganapathy et al., 2011). Genetic gain estimation and documentation support breeding decision-making by highlighting potential features for future improvement and guiding breeding strategies to maximize production (Marefia et al., 2022). Panicle length, number of fingers per ear, plant height, number of productive tillers per plant, 1000 seed weight, threshability, early maturity, large head size, compacted head shape and harvest index are essential traits for finger millet improvement and genetic gains of yield and component traits (Owere et al., 2015; Manyasa et al., 2016; Marefia et al., 2022).

Realised genetic gains reported for agronomic traits in finger millet are presented in Table 1.2. In the past, there were limited breeding efforts that reported the improvement of economic traits, including yield and nutritional compositions in finger millet. Yield reports from Ethiopia (Table 1.2) suggest high yield potential is achievable in finger millet through breeding. Yield-related traits including ear weight plant^{-1} (g), 1000 grain mass (g), straw yield (kg plant^{-1}), number of ears plant^{-1}, number of fingers ear^{-1} and plant height (cm) recorded meagre genetic gains (Table 1.2). Hence, there is a need for breeding and modern production technologies to harness the genetic expression of these vital traits. Finger millet grains composed of the following macro-nutrients in mg/100g: P (130.0-250.0), K (430.0-668.8), Ca (50.0-589.0), S (106.1-149.0), Na (6.3-41.6), and Mg (78.0-201.0) (Puranik et al., 2020; Kumar et al., 2021a; Backiyalakshmi et al., 2023; Teklu et al., 2024). Also, vital micro-nutrients are found in the grains (mg/100g): Fe (2.5-53.4), Mn (17.6-201.0), and Zn (1.0-36.6) (Puranik et al., 2020; Kumar et al., 2021a; Anitha et al., 2021b). Except for calcium content, genetic gains for grain protein, iron, and zinc contents are minimal (Table 1.2). High grain yield of finger millet appears to be closely associated with reduced zinc and protein content but has a positive association with increased calcium content (Table 1.2). For instance, among Indian finger millet cultivars released between 1953 and 2019 (Vadivoo et al., 1998; Udamala et al., 2020), genetic increase for protein content ranged between -0.048 mg/100g year^{-1} and -0.073 g/100g year^{-1} indicating a negative association with yield gains. Likewise, a negative association between grain yield and zinc content were reported (Backiyalakshmi et al., 2023). The genetic gain of protein content was -0.001 mg/100g year^{-1} for Indian finger millet cultivars released between 1976 and 2019 (Table 1.2). Conversely, a positive association has been reported between grain yield and iron and calcium content (Vadivoo et al., 1998; Udamala et al., 2020). The authors reported a genetic gain ranging from 1.336 to 4.110 mg/100g year^{-1} for iron and 0.022 mg/100 g year^{-1} for calcium

contents. Selection response for high yield and Ca and Fe contents can be enhanced through simultaneous trait selection, enabling the creation of finger millet varieties that fulfil the demands of both farmers and consumers. Gene discovery targeting yield and yield components and nutrient profiles using genome-wide association study (GWAS), marker-assisted selection (MAS) and genomic selection methods enable speed and precision breeding. Also, improved farming technologies such as soil fertilizers and water management systems will bolster sustainable crop production and productivity.

Table 1.2. Genetic gains for agronomic traits and nutritional compositions in finger millet

Traits	Country	Years of cultivar release	Mean increase/decrease (unit^{-1} year^{-1})	Genetic gain (% year^{-1})	References
Grain yield (kg ha^{-1})	Ethiopia	1999-2019	27.64	1.35	Marefia et al. (2022)
		1998-2022	43	1.87	MOA (2022)
Ear weight plant $^{-1}$ (g)	India	1959-2016	0.026	0.0005	Aralikatti and Chaturvedi (2020)
1000 grain mass (g)		1959-2016	0.003	0.0001	
1000 grain mass (g)	Kenya	2000-2015	0.43	0.028	Manyasa et al. (2016)
Straw yield plant^{-1} (kg)	India	1959-2016	-0.001	-0.00001	Aralikatti and Chaturvedi (2020)
Number of tillers plant^{-1}	Ethiopia	1999-2019	0.11	0.005	Marefia et al. (2022)
	India	1959-2016	-0.005	-0.0001	Aralikatti and Chaturvedi (2020)
	Kenya	2000-2015	3.02	0.201	Manyasa et al. (2016)
Number of ears plant^{-1}	Ethiopia	1999-2019	0.1	0.005	Marefia et al. (2022)
Number of fingers ear^{-1}	India	1959-2016	-0.012	-0.0002	Aralikatti and Chaturvedi (2020)
	Uganda	1969-2017	0.83	0.017	Owere et al. (2015)
	Kenya	2000-2015	3.39	0.226	Manyasa et al. (2016)
Plant height (cm)	India	1959-2016	-0.006	-0.0001	Aralikatti and Chaturvedi (2020)
Days to maturity		1959-2016	0.027	0.001	
Days to maturity	Ethiopia	2002-2022	-0.58	-0.029	MOA (2022)
Days to 50% flowering	India	1959-2016	-0.033	-0.001	Aralikatti and Chaturvedi (2020)
	Uganda	1969-2017	4.43	0.092	Owere et al. (2015)
Ear head length (cm)	India	1959-2016	0.009	0.0002	Aralikatti and Chaturvedi (2020)
Flag leaf length (cm)		1959-2016	0.029	0.0005	
Finger length (cm)		1959-2016	0.017	0.0003	
Finger length (cm)	Kenya	2000-2015	5.15	0.344	Manyasa et al. (2016)
Panicle exertion (cm)		2000-2015	1.4	0.094	
Protein content (mg/100 g)	India	1976-2019	-0.048	-0.001	Udamala et al. (2020)
Protein content (g/100 g)		1953-1989	-0.073	-0.002	Vadivoo et al. (1998)
Calcium content (mg/100 g)		1953-1989	1.336	0.037	
		1976-2019	4.11	0.096	Udamala et al. (2020)
Iron content (mg/100 g)		1976-2019	0.022	0.001	
Zinc content (mg/100 g)	India	1976-2019	-0.001	-0.00002	

1.4 Constraints to finger millet production

Global finger millet production and productivity are challenged by several biotic and abiotic factors and a lack of modern crop management practices (Mulualem and Melak, 2013; Asargew and Shibabawu, 2014; Lule et al., 2014; Jerop et al., 2018; Manyasa et al., 2019). In sub-Sahara African

countries, farmers are still using low-yielding finger millet varieties, which has resulted in lower crop productivity (< 1 ton/ha). The average productivity of finger millet is 2.5 and 1.4 tons/ha in Ethiopia and Uganda, respectively. This highlights the need for targeted breeding to unleash the crop's true potential on yield and nutritional value (Hussein, 2017). Different studies reported that high grain yield, early maturity, desirable seed colour, compact head type, threshability, end-use quality, and high marketability are preferred traits by finger millet growers and consumers (Owere et al., 2014; Gebreyohannes et al., 2021; Mbinda et al., 2021; Mbinda and Masaki, 2021).

In some countries, there are modest breeding efforts and the development of improved varieties, including selections from landraces. For example, NGRC04789, NGRC04849 and NGRC06490 are landrace selections of finger millet favoured in Nepal for blast resistance, drought tolerance and medicinal value (Luitel et al., 2020). In Zimbabwe, most finger millet production is based on unimproved landrace varieties (Mbanyele et al., 2022). Landraces such as Tsa'ada, Tselim, and Keyih with different seed colours are widely preferred finger millet in Northern Ethiopia, meeting consumers' needs and market demands (Tsehaye et al., 2006). Gangabali, Dengsameli, and Kada are commonly grown finger millet landraces in India (Panda et al., 2021). High-performing and locally adapted varieties, better agronomic management practices, and favourable production conditions can achieve higher yield gains of 4.0 to 8.0 tons/ha in finger millet (Maqsood and Ali, 2007; Oduori, 2008; Padulosi et al., 2015; Puranik et al., 2017; Joshi et al., 2023). Nonetheless, the actual yield of finger millet in SSA is low (Table 1.1) due to the various production constraints outlined below.

1.4.1 Biotic factors

Fungal diseases

Blast disease is the major bottleneck to finger millet production in wet and humid environments. The disease is caused by the heterothallic ascomycete fungus, with two stages of the same pathogen, [teleomorph: *Magnaporthe grisea* (Hebert) Barr] and [anamorph: *Pyricularia grisea* (Cook) Sacc.] (Zhang et al., 2016). Blast inflicts yield loss varying from 7.32 to 90% in finger millet (Lule et al., 2014; Akech et al., 2016). A yield loss of 28 to 36% is reported in India (Nagaraja et al., 2007); 60 to 90% in Uganda (Akech et al., 2016); 7.32 to 54.07% in Ethiopia (Gashaw et al., 2014; Lule et al., 2014) and up to 80% elsewhere (Mbinda and Masaki, 2021). When environmental conditions are favourable, the pathogen infects all parts of finger millet, including the leaves, stem, collar, node, neck, fingers, and roots, resulting in significant crop losses. High temperatures, relative humidity, and rainfall conditions enhance blast infection and disease development. Leaf wetness,

alternate hosts, weeds, crop debris and high planting density promote the spread of blast disease (Gashaw et al., 2014; Lule et al., 2014; Mbinda et al., 2021). Additionally, other fungal diseases that threaten finger millet production include banded sheath blight, caused by *Rhizoctonia solani* Kühn, and foot rot, by *Sclerotium rolfsii* (Nagaraja and Das, 2016; Patro et al., 2018). These pathogens exhibit distinct pathological races. Banded sheath blight manifests as oval lesions on lower foliage, progressing to characteristic brown bands, while foot rot presents with basal stem necrosis, profuse mycelial growth, and sclerotia formation (Nagaraja and Das, 2016).

The use of blast-resistant finger millet varieties is an effective, economical, ecologically friendly and sustainable control strategy (Manyasa et al., 2019; Mbinda and Masaki, 2021). Other blast-controlling options include adjustment of sowing during the first onset of rainfall, intercropping with legumes, weed control, use of fungicides (e.g., tricyclazole, edifenphos, carbendazim and mancozeb), clean seed (Mbinda and Masaki, 2021; Mbinda et al., 2021) and biocontrol methods. Fungal bio-control agents, such as *Trichoderma viride* and *T. harzianum* supress the causative agent of finger millet blast disease (Gashaw et al., 2014).

Insect pests

The most economically important insect pests of finger millet include grasshoppers (Caelifera), shoot flies (*Atherigona soccata* (Rondani)), pink stem borer (*Sesamia inferens* (Walker)), root aphid (*Tetraneura nigriabdominalis* (Sasaki)), and aphids (Aphidoidea) (Mulualem and Melak, 2013; Sasmal, 2018). Insect pests caused yield losses ranging from 23 to 56% in finger millet (Mulualem and Melak, 2013; Sasmal, 2018). Host-plant resistance, pesticides, cultural practices (e.g., managing planting time, field sanitation, crop rotation, deep and frequent ploughing), silicon amendment, and bio-control agents (e.g., predatory spiders and ladybird beetle (coccinellids)) are widely used in insect pests management (Gahukar and Reddy, 2019; Jadhao et al., 2020; Gebreyohannes et al., 2021). Integrating insect pest control involving resistant variety, cultural practices, and biological control methods is the most efficient, cost-efficient, and environmentally friendly option for smallholder farmers to control insect pests of finger millet.

Weeds

Weed infestation causes a yield loss varying from five to 73.5% in finger millet production (Asargew and Shibabawu, 2014; Mahapatra et al., 2021). The notable weed species recorded in finger millet production include *Striga hermonthica* (Delile) Benth, *Digitaria ternata* (A. Rich.), Stapf, *Guizotia scabra* (Vis.) Chiov and *Cyperus rotundus* [L.] (Asargew and Shibabawu, 2014;

Owere et al., 2014). Also, other wild relatives of finger millet, such as *Eleusine indica* (L.) Gaertn., and *E. africana* (L.) Gaertn are regarded as noxious weeds of finger millet. Wild relative weeds are remarkably similar to finger millet and are only distinguishable at the flowering stage.

Finger millet cultivars resistance to the major weeds are the most economical control options. Few *Striga*-resistant cultivars were developed and released by the Kenya Agriculture and Livestock Research Organization (KALRO, 2021). Also, other weed control options include cultural practices (e.g. early planting with the onset of the first rain, crop rotation, trap crops), enhancing soil fertility through the application of nitrogen and phosphorous fertilizers (Mgonja et al., 2013), hand weeding (Asargew and Shibabawu, 2014), application of pre-and post-emergent-herbicides (e.g. butachlor and 2,4-D Na salt) (Mgonja et al., 2013). Integrating weed management, such as resistant variety, bio- and chemical-herbicides and cultural control practices, is the most effective and economical approach to reducing yield and quality losses in finger millet production (Mgonja et al., 2013; Mbinda et al., 2021).

1.4.2 Abiotic factors

Drought stress

Recurrent drought is the major cause of yield and crop losses (Mukami et al., 2019). Drought stress can occur pre-flowering or post-flowering, and its impact is directly related to the crop growth stages (Maqsood and Ali, 2007; Mukami et al., 2019). Pre-flowering drought is associated with reduced leaf number, short plant stature and low canopy size (Maqsood and Ali, 2007). The extent of yield loss varies depending on cultivar susceptibility, the severity and duration of the stress (Mukami et al., 2019). High yield loss is recorded when severe drought occurs at flowering and grain-filling stages (Talwar et al., 2020). Drought at the flowering stage resulted in significant yield loss varying from 40% to 70 % in various crops such as tef, finger millet, and pearl millet (Maqsood and Ali, 2007; Tadele, 2018; Numan et al., 2021).

Developing and deploying finger millet varieties with drought tolerance and enhanced agronomic traits is a novel mitigation approach to drought stress. To pursue food security under drought, farmers adopted some indigenous knowledge systems. For instance, by diversifying the cropping system and integrating finger millet, farmers in the Indian Himalayas safeguarded their food supply even during droughts and famines (Gururani et al., 2021). Other drought mitigation strategies used by farmers include adjustment of sowing date, zero tillage, tie-ridging, mulching and supplemental irrigation.

Salinity stress

Salinity stress threatens finger millet's resilience in arid and semi-arid regions, affecting its development throughout the growth cycle. At the seedling stage, salinity hinders germination, causing chlorosis, leaf scorching, delayed growth, and stunted leaves in finger millet (Mukami et al., 2020; Mbinda and Mukami, 2021). At the vegetative stage, salinity inhibits root and shoot lengths, fresh and dry weights, leaf water potential, and chlorophyll content of finger millet (Satish et al., 2016; Mukami et al., 2020; Divya et al., 2022). Also, salinity disrupts essential physiological and metabolic processes. For example, salinity drastically affected the crop's nutrient and water uptakes (Theerthana et al., 2022). Furthermore, salinity increases root and shoot necrosis, reducing internode lengths (Parida and Das, 2005). These alterations trigger biochemical and molecular changes, impacting functional genes and overall photosynthetic capacity (Rahman et al., 2014).

Climate change and unsustainable agricultural practices exacerbate soil salinity. Rising temperatures and altered precipitation patterns increase salt accumulation, particularly in arid regions. Published data (Mukami et al., 2020; Mbinda and Mukami, 2021) indicated the detrimental effects of salinity on finger millet, but yield loss is not well-quantified. Developing salinity-tolerant finger millet varieties is the most feasible, low-cost, and eco-friendly approach (Mbinda and Mukami, 2021; Divya et al., 2022). Use of fluorescent pseudomonad inoculants as plant growth-promoting rhizobacteria is another approach for a sustainable and economical management of salinity stress in finger millet production (Mahadik and Satyan, 2020). Agronomic management systems (e.g. increasing the soil water content through frequent irrigation, sub-surface drainage, application of calcium or magnesium with nitrate or chloride, and integrated agro-forestry systems) are widely used to mitigate against the effect of salinity stress (Mbinda and Mukami, 2021; Theerthana et al., 2022).

1.4.3 Lack of production inputs and resources, and poor access to markets

Smallholder farmers form the major component of the food systems in SSA. Limited resource access, encompassing finance, land, fertilizers, labor, and draught power, hamper crop productivity (Gebreyohannes et al., 2021). Access to and adoption of scientific innovations and technologies that enhance crop production is vital to promoting sustainable finger millet cultivation (Jerop et al., 2018). Limited market access also poses a significant barrier to smallholder finger millet producers. Unfavourable market conditions, characterized by low prices, price volatility, high transportation costs, and limited access to market information, discourage investment and impede production expansion (Mwema et al., 2017). Marketing bottlenecks can be circumvented through infrastructure

development, streamlined information dissemination, and fair trade, which are crucial to unlock the full potential of finger millet in the global food system and marketplace.

1.5 Breeding goals and variety development in finger millet

Reportedly, the main goals of finger millet breeding are high grain yield potential (Owere et al., 2014; Mwema et al., 2017; Gebreyohannes et al., 2021), enhanced nutritional quality (Puranik et al., 2020; Backiyalakshmi et al., 2023), tolerance to biotic and abiotic stresses (Owere et al., 2014; Mwema et al., 2017; Gebreyohannes et al., 2021; Mbinda and Masaki, 2021; Mbinda and Mukami, 2021), and high marketability (Mwema et al., 2017; Gebreyohannes et al., 2021). Consumer preferences are increasingly shaping finger millet breeding programs, promoting the selection of traits that expand market appeal and ensure the crop's continued relevance in a changing lifestyle and food environment. Targeted breeding efforts focus on key market-driven factors such as grain colour, popping quality, and brewing suitability. For instance, white grain varieties excel in the Indian processing industry, while in Ethiopia, diverse culinary traditions necessitate specific grain colors for traditional staples like “injera” (Tsehaye et al., 2006; Josi et al., 2021). Furthermore, finger millet has high popping potential and offers additional value in India, enabling diverse food applications (Sai and Meera, 2023). This targeted approach maximizes marketability and secures the crop's economic value. Other selection criteria include compact head type, medium plant height, a higher number of fingers per head, longer and wider fingers, increased harvest index, bigger seed weight, and a higher number of productive tillers.

Despite the socio-economic importance of the crop, there is a significant yield gap in finger millet compared to other major cereal crops such as maize, wheat and sorghum (Sood et al., 2016). Finger millet breeding programs in developing countries focus on selection from the landraces to develop improved finger millet varieties. Over 235 improved finger millet varieties have been released globally, with India releasing 149 and Africa 72 (AICSMIP, 2014; Vetriventhan et al., 2020; Dida et al., 2021; MOA, 2022). Globally, the dominant number of improved finger millet varieties (62%) were developed through pure-line selection techniques, while another 32% have emerged from a recurrent selection approach (Dida et al., 2021; Joshi et al. 2022; MOA, 2022; Gupta et al. 2023a,b; Sood et al., 2023a).

Widening the genetic base of finger millet through artificial hybridization presents a critical challenge due to the floral biology (e.g. cleistogamous flower, small florets, and poor

synchronisation of anthesis) (Owere et al., 2016; Nagaraja, et al., 2023). Controlled crosses are the main approach in finger millet breeding programs, especially for genotypes with dominant traits (Owere et al., 2016). However, this method had a limited success rate (2 to 3%), necessitating alternative approaches (Nagaraja, et al., 2023). Treating flower buds with hot water (e.g. 52°C, 3-5 min) and synthetic chemicals such as maleic hydrazide, gibberellic acid, and ethyl induce temporary male sterility in finger millet (Nagaraja et al., 2023).

Molecular markers have been used to assess emasculation efficiency and identify the true hybridity of crosses in finger millet. Krishna et al. (2020) compared hand emasculation and hot water male sterilization methods and assessed the hybrid purity in finger millet using simple sequence repeat (SSR), random amplified polymorphic DNA (RAPD), and inter-simple sequence repeat (ISSR). The authors reported that hot-water treatment of the flowers provided a high success rate (52 to 80% success) than hand emasculation (16 to 40%). The genetic purity of derived hybrids varied from 16 to 80% when assessed using RAPD and SSR markers (Krishna et al., 2020). Seventy-two finger millet varieties were released worldwide using the recurrent selection method with routine crossing and selection (Table 1.3).

Another strategy to enhance hybridization is through the use of male sterility. Developing effective male sterility systems could be vital to harnessing the benefits of heterosis breeding (Vetriventhan et al., 2020). The authors developed INFM 9500, a genetic male-sterile line, through chemical mutagenesis. Developing male sterility systems boosts finger millet production and commercialisation through hybrid breeding.

Mutation breeding is an alternative method for genetic enhancement for finger millet breeding and genetic analysis. Finger millet has small bisexual florets, making artificial emasculation and pollination tedious and time-consuming for genetic recombination and selection. Through mutation breeding, 11 varieties were released and registered in India and Zambia (AICSMIP, 2014; IAEA, 2022). The varieties were reported to be tolerant to stem borer, blast, brown spot and drought. Finger millet variety designated as FMM175, which was derived through mutation breeding, was released in Zambia in 2009 with brewing quality (IAEA, 2022).

Somaclonal variants selected through the tissue culture method were developed and released in India and Ukraine from 2006 and 2017. Cultivars denoted as GN 4 and Dapoli-2, were released in India in 2006 and 2017, respectively, while cultivar, Yaroslav-8(SE7) was released in Ukraine in

2012 (Radchuk et al., 2012; AICSMIP, 2014). Several genes were reported conditioning economic traits in finger millet (Krishnappa et al., 2009; Ganapathy et al., 2011). Nevertheless, genetic engineering has not been pursued to stack candidate genes in desirable varieties due to technical limitations and a lack of priority and support for breeding, genetic research, and innovations. Developing male sterility systems is a potential research area to exploit heterosis in finger millet breeding (Vetriventhan et al., 2020). A genetic male-sterile line of finger millet designated as INFM 95001 has been developed through chemical mutagenesis (Vetriventhan et al., 2020).

Finger millet varieties bred and released globally have enhanced yield potential, adaptability to drought and saline conditions, improved lodging resistance, resistance to insect pests and diseases, and enriched nutritional composition (Tables 1.3, 1.4, 1.5, and 1.6, and Appendix Tables 1.1, 1.2, and 1.3). There is a need for research and development investments to develop and promote the adoption of climate-resilient, consumer-preferred cultivars tailored to the specific needs of SSA. Advanced and precision breeding techniques and innovations such as marker-assisted breeding, genomic selections, genome editing, and genetic engineering can be integrated with classical breeding for impact.

Table 1.3. Finger millet varieties bred and released in different countries.

Country	Number of released varieties	Breeding methods	Characteristic features	References
India	72	PR	High-yielding, drought, salinity, lodging, and cold tolerance, diseases (blast, blight, mosaic, brown spot, viral) and insects (tolerance to stem borer, aphids and tobacco cutworm, myllocerus weevil, earhead caterpillars, and grass hopper), better nutritional quality, photo-insensitive, suitable varieties for irrigable and hilly areas	AICSMIP (2014); Patil and Patel (2018); Madhavilatha et al. (2019); Joshi et al. (2022); Gupta et al. (2023a,b); Sood et al. (2023a)
	66	RS		
	9	MB		
	2	SC		
Ethiopia	27	PR	High-yielding, drought and lodging tolerance, blast, grain mold and insect (stem borer) resistance and excellent nutritional quality	MOA (2022); Teklu et al. (2024)
	1	RS		
Kenya	15	PR	High-yielding, drought, heat, high temperature, striga, and bird damage tolerance, blast and insect resistance, and good nutritional quality	Dida et al. (2021); Vetriventhan et al. (2020)
	4	RS		
Uganda	9	PR	High-yielding, drought and lodging tolerance and resistance to blast	Owere et al. (2014); Vetriventhan et al. (2020)
	4	RS		
Nepal	5	PR	High-yielding, drought and lodging tolerance and resistance to blast	Joshi et al. (2017)
Sri Lanka	5	PR	-	FAO (2011)
Bhutan	3	PR	-	FAO (2011)
Tanzania	3	PR	High-yielding, drought tolerance, and better threshability quality	Ojulong et al. (2016)
Zimbabwe	2	PR		Mirza and Marla (2019)
Zambia	2	MB	High-yielding, and brewing	IAEA (2022); Vetriventhan et al. (2020)
	2	PR		
Malawi	3	PR		ICRISAT (2019)
Ukraine	1	SC	High-yielding	Radchuk et al. (2012); Mirza and Marla (2019)
Total	235			

Note: PR=Pure line selection, RS= Recurrent selection and MB=Mutation breeding and SC=Somaclonal selection

1.5.1 Breeding for drought tolerance

Modest selection progress has been made regarding breeding for drought-tolerant finger millet varieties (Table 1.4). In six countries, including India, Kenya, Ethiopia, Uganda, Nepal, and Tanzania, 59 finger millet varieties have been developed with enhanced drought tolerance. Some 35 drought-tolerant finger millet varieties were released in India, followed by Kenya (13), Ethiopia (3), Nepal (3), Uganda (2), and Tanzania (1) (AICSMIP, 2014; Owere et al., 2014; MOA, 2022; Joshi et al., 2017; KEPHIS, 2023). Yield levels of the drought-tolerant varieties vary from 0.9 to 5.5 in India (AICSMIP, 2014), 1.0 to 6.7 in Kenya (KEPHIS, 2023) and 2.2 to 3.6 in Ethiopia (MOA, 2022). The varieties reportedly possess drought-adaptive traits, including stay-green, robust root system, purple pigmentation, early flowering and maturity. Globally, the highest number of

finger millet varieties have been released in India, with K1 being the first drought-tolerant variety developed in 1939. Varieties such as PR202, Dibya Sinha, Udaya, KMR340, and ML365 are early maturity types (80 to 135 days to maturity). Likewise, varieties Axum, Mereb-1, and Kako-1 are popular drought-tolerant finger millet varieties released in Ethiopia in 2016, with 83 to 147 days to maturity. Early maturing (65 to 138 days) finger millet varieties in Kenya, namely, KNE741, Maseno60D, SDFM1702, and Kat/FM I were developed. Finger millet varieties such as Seremi2 and Gulu-E in Uganda (with maturity of 70 to 80 days) and U-15 in Tanzania (90 to 100 days) have been released for their remarkable earliness. Early maturity is a proxy trait for breeding drought escape genotypes.

Table 1.4. Drought-tolerant finger millet varieties reported globally.

Variety name	Trait description	Breeding method	Days to maturity	Year of release	Yield (t/ha)	Country	References
Mereb-1 (KNE#622)	Drought tolerance	PR	83-121	2016	2.5-3.2	Ethiopia	MOA (2022)
Kako-1 (ACC#203351)			139	2016	2.6-3.0		
Axum (ACC#229355)			147	2016	2.2-3.6		
Dibya Sinha	Drought tolerance	MB	90-100	1971	2.0-2.5	India	Hatakeyama et al. (2018); Aralikatti and Chaturvedi (2020)
K6			100-105	1982	2.3-2.5		
K1 (Kolar Gidda Ragi)		PR	130-135	1939	0.9-1.0		
CO2			110-115	1942	2.0-2.5		
CO1			120-125	1942	2.5-3.0		
Aruna			95-100	1956	1.5-1.8		
Vzm1			105-110	1958	2.0-2.5		
CO8			90-95	1963	1.5-2.0		
CO10			110 – 120	1976	3.5-4.0		
PR202 (Godavari)			110-115	1976	2.5-3.0		
CO11 (EC4849)			110-115	1982	3.5-4.0		
VL204			90-100	1985	1.8-2.0		
Paiyur1			100-110	1985	2.3-2.5		
CO12			120-125	1985	3.5-4.0		
KM13			95-110	1989	2.5-3.0		
PES400 (Pant Mandua3)			95-100	1989	1.8-2.0		
VR520 (Suraj)			85-90	1992	2.0-3.0		
PR230 (Maruthi)			90-100	1998	2.5-3.0		
VR708 (Champavathi)			90-95	1998	2.5-3.0		
Udaya		RS	90-95	1959	2.5-3.0		
Akp2			80-90	1960	2.0-2.2		
CO 9			100-105	1970	2.5-3.0		
INDAF5			105-110	1977	4.5-5.0		
K5			105-110	1982	2.6-3.0		
INDAF8			120-125	1982	2.0-2.5		
INDAF9 (Chitta)			95-105	1985	2.0-2.5		
CO13 (Tnau294)			95-100	1989	2.5-3.0		
ML365			110-115	2008	5.0-5.5		
VL347			90-105	2010	2.0-2.2		
VL352			95-100	2012	3.3-3.5		
KMR340			90-95	2016	3.5-4.0		
KM65	Drought tolerance and blast resistance	PR	95-100	1994	1.8-2.0		
VL146		RS	95-100	1995	2.5-3.0		
GPU26			95-100	1997	3.0-3.5		
GPU45			95-100	2001	2.8-3.0		
Maseno60D (MSUFM60D)	Drought tolerance	RS	80-90	2016	3.1		

Variety name	Trait description	Breeding method	Days to maturity	Year of release	Yield (t/ha)	Country	References
Kacimmi42 (Kak-Wimbi3)			87-130	2016	1.3– 6.4		
Kacimmi49 (KAK-			92-132	2021	1.2-5.7		
P-224		PR	90-120	1981	2.0-5.0		
Kat/FMI			90	2000	1		
KNE741 (EUFM-401)			65-75	2018	1.0-1.4	Kenya	Dida et al. (2021); KEPHIS (2023)
GBK029646A (Kis-Wimbi1)			89-119	2021	1.4-4.4		
AGRY-2 (Mavuno)			90-120	2021	1.8-2.5		
Eufm-8			95-115	2021	1.8-2.2		
U-15 (Maridadi)	Drought tolerance, and blast and striga resistance	PR	90-120	2015	1.1-4.9		
I.E. 4115 (Kak-Wimbi2)			88-131	2016	1.3-6.1		
Okhale-1 (Kak-Wimbi1)			88-138	2016	1.1-6.7		
Kacimmi65 (KAK-Wimbi6)		RS	92-120	2021	1.2-4.3		
SDFM1702 (EUFM-503)	Early maturity, blast resistance and bird damage		90-98	2018	1.5-2.5		
IE-980 (Dalle-1)	Drought tolerance	PR		1980	3.3		
NE1304-43 (Okhle-1)				1980	3.3		
NF-6401-26 (Kabre Kodo-1)				1990	1.8-4.8	Nepal	Joshi et al. (2017)
PR-202 or GE-5176 (Kabre Kodo-2)				2015	2.5		
U-15			90-100	2019	2	Tanzania	Ojulong et al. (2016)
Gulu-E	Drought tolerance, and blast resistance	PR	75-80	1970			
Seremi2 (U15)			70-80	1999	2	Uganda	Mwema et al. (2017)

Note: PR=Pure line selection, RS= Recurrent selection, and MB=Mutation breeding

1.5.2 Breeding for salinity tolerance

Finger millet is a highly preferred crop in arid and semi-arid regions. Reportedly, it possesses polygenes for salinity tolerance and has unique cellular pathways and environmental plasticity (Mbinda and Mukami, 2021). A limited number of salinity-tolerant finger millet varieties were released. For instance, finger millet variety designated as CO 11 (EC 4849) is reportedly high-yielding (3.5 to 4.0 t/ha), drought- and salinity-tolerant, photoperiod-insensitive and early maturing (110 days) (AICSMIP, 2014). Another variety, referred to as Nirmal, has blast resistance and is suitable for production under saline soils with a short maturation period of 110 days (AICSMIP, 2014). Inbred lines such as GBK043094 and GBK043137 were selected by Mukami et al. (2020) for breeding programs. Divya et al. (2022) identified some genotypes (e.g. ML 365, GPU 28, and

GPU 67) with salinity tolerance under controlled environment conditions. Transcriptome analysis through RNA-sequencing was used to identify a finger millet genotype, Trichy 1, for salinity tolerance (Rahman et al., 2014).

1.5.3 Breeding for resistance to fungal diseases

Finger millet blast caused by the fungus *Magnaporthe oryzae* poses a significant threat to global production and productivity. The disease causes a yield loss reaching up to 100% in susceptible varieties. Breeding new varieties with durable blast resistance and product profiles is an overriding goal. For instance, Das et al. (2021) identified five elite lines (IE 2883, IE 2871, IE 6240, IE 2710, and IE 3767) with adequate resistance to finger and neck blasts and desirable agronomic traits. Manyasa et al. (2019) assessed 81 Eastern African finger millet accessions and found three lines (Kafumbata, GBK -00351A, and GBK -011119A) resistant to leaf, neck, and panicle blasts. Among these accessions, GBK-011119A, recognized for its blast resistance and superior yield, was released in Ethiopia as Meba in 2016 (MOA, 2022), marking a significant advancement in disease management and crop production. Wekesa1 et al. (2019) identified blast-tolerant genotypes (e.g. GBK000702, GBK000513, GBK029869, GULU-E, GBK000752, and Busibwabo) in Western Kenya, priming them as donor parents for resistance breeding programs. Lule et al. (2014) reported exceptional blast resistance in cultivated accessions (e.g. Acc. 214995 and PW-001-022) and a wild accession (AAU-ELU-15) among Ethiopian germplasm collections.

Globally, 20 blast-resistant finger millet varieties (Table 1.5) have been developed and released (AICSMIP, 2014; Madhavilatha et al., 2019; MOA, 2022; Dida et al., 2021). About 50% of the released varieties were bred by the All-India Coordinated Research Project on Small Millets (AICSMIP). Five blast-resistant finger millet varieties were released in Ethiopia, one in Nepal, and two in Kenya and Uganda from 1999 to 2020.

Table 1.5. Reported global finger millet varieties with blast resistance

Traits	Mapping methods	Marker types	Number of significant MTAs	Population size	References
Days to 50% flowering, plant height, panicle number, leaf blast severity, and panicle blast incidence at maturity	Bi-parental QTL mapping	SNPs and insertion–deletions	8	151	Pendergast et al. (2022)
Primary root length, shoot dry weight, and total phosphorous content in shoots	Bi-parental QTL mapping	SSRs	92	100	Maharajan et al. (2023)
Stigma, and anther colour	Bi-parental QTL mapping	SNPs	-	294	Devos et al. (2023)
Days to 50 % flowering, basal tiller number, flag leaf width, and plant height	Association mapping	SSRs	5	190	Babu et al. (2014a)
Finger blast, and neck blast resistance	Association mapping	SSRs	7	190	Babu et al. (2014b)
Protein and tryptophan contents	Association mapping	SSRs	3	190	Babu et al. (2014c)
Days to maturity, finger number, grain yield per plant, number of grains per spikelet, productive tiller number, and thousand grain weight	Association mapping	SSRs	16	138	Lule et al. (2018)
Days to 50% flowering, days to maturity, and grain yield	Genome wide association mapping	SNPs	111	113	Sharma et al. (2018)
Grain yield, days to maturity, and seed protein content	Genome wide association mapping	SNPs	81	113	Tiwari et al. (2020)
Iron, zinc, magnesium, sodium, and potassium contents	Genome wide association mapping	SNPs	418	190	Puranik et al. (2020)
Calcium content	Genome-wide association mapping	SNPs	44	202	Sharma et al. (2022)
Days to 50% flowering, days to maturity, plant height, number of basal tillers, flag leaf length, flag leaf width, ear length, ear width, number of fingers, green fodder weight, dry fodder weight, and neck blast	Genome-wide association mapping	SNPs	132	186	Sood et al. (2023b)
Zinc and iron contents	Genome-wide association mapping	SNPs	45	202	Chandra et al. (2024)

Note: PR=Pure line selection, RS= Recurrent selection

1.5.4. Breeding for resistance to insect pests

The major insect pests of finger millet are lower pink stem borer, jassids, aphids, and shooflies (Mulualem and Melak, 2013; Sasmal, 2018). Sasmal et al. (2018) identified few genotypes (e.g. PRM 9002, KOPN 933, OEB 28, RAU 8, and Champabati) exhibiting resistance to lower pink stem borer infestation serving as valuable genetic resources for breeding. Reportedly, a few finger millet genotypes exhibited tolerance to the major insect pests (Appendix Table 1.1). Genotypes, such as PES 110, VR 847 (Srichaitanya), and OEB 532 had, tolerance to broad insect pest resistance. The reported insect pest tolerant genetic resources (Appendix Table 1.1) had grain yield variability, ranging from 2.2 t/ha (OEB 532) to 6.3 t/ha (Ikhule) and other contrasting agronomic traits. Eight insect pest-tolerant finger millet varieties were reported in India. Of these, five were developed through recurrent selection, two through mutation breeding, and one with pure line selection methods (Appendix Table 1.1). Genotype Ikhule, identified and released in Ethiopia, had a marked tolerance to shoot fly (MOA, 2022).

1.5.5 Breeding for *Striga* resistance

Striga is a parasitic weed of significant economic importance, devastating finger millet production in SSA. In SSA there is limited research on *Striga* resistance breeding in finger millet (Sood et al., 2019). Screening for *Striga* resistance typically employs two complementary approaches: namely, pre-attachment and post-attachment resistance screening. Pre-attachment resistance is commonly assessed in the laboratory using the agar-gel technique, where host root exudates are evaluated for their ability to stimulate *Striga* seed germination and radicle growth. Genotypes inducing lower germination rates and shorter germination distances are considered to possess pre-attachment resistance (Makani et al., 2020). Post-attachment resistance, on the other hand, is evaluated in controlled environments such as rhizotrons and greenhouse pot experiments using *Striga*-infested soils. Here, parameters such as the number of attached parasites per plant, time to parasite emergence, and subsequent parasite development are recorded to identify genotypes that inhibit parasite establishment and growth after attachment (Kunguni et al., 2023). Recently, Kunguni et al. 2023) reported *Striga* resistance in the wild finger millet (e.g. genotype LESK10) and the cultivated variety (Okhale-1) with reduced *Striga hermonthica* parasitism. Nyongesa et al. (2018) identified three genotypes (e.g. GBK029661, I.E 2217, and I.E 6537) with an immune reaction to *S. hermonthica* infestation. Makani et al. (2020) reported pre-attachment *Striga* tolerance in the genotype SDMF1702 for *S. asiatica* under controlled environments.

Despite the identification of these promising sources of resistance, limited progress has been made in incorporating these traits into breeding programs. This is likely due to a combination of factors, including the quantitative inheritance of post-attachment resistance, the complexity of the host-parasite interaction, and the absence of effective selection markers (Scholes and Press 2008). Consequently, there is a critical need for robust and high-throughput screening methods to facilitate the efficient transfer of these resistance traits into elite finger millet backgrounds. In Kenya, the following cultivars were released with *Striga* resistance: U-15 (MARIDADI), OKHALE-1 (KAK-WIMBI 1), IE 4115 (KAK-WIMBI 2), KACIMMI 65 (KAK-WIMBI 6), and KACIMMI 42 (KAK-WIMBI 3). These lines were mainly developed through pure line selection, except KACIMMI 42, which was bred through the recurrent selection method. The Kenyan varieties possessed blast and lodging resistance and drought tolerance (KALRO, 2021).

1.5.6 Breeding for nutritional quality traits

Various basic and applied research have characterized finger millet genetic resources for their mineral and protein contents. However, there is no single variety released with unique grain nutrient

profiles. Finger millet's nutritional values have not yet been explored and deployed for the marketplace. Some pre-breeding progresses have been reported on nutrient profiling and dietary value addition (Appendix Table 1.2). India released 6 varieties, followed by Ethiopia (2), Kenya (1), and Zambia (1) based on finger millet pre-breeding for biofortification (Appendix Table 1.2). Early maturing genotype CO 9, selected in India, had a remarkable protein content of 9.6 %, making it an ideal candidate for early harvest and boosting the dietary protein. Genotypes HAMSA and PRM 2 had higher protein levels (>9%), good candidates for quality breeding and deploying nutritionally rich finger millets.

Genotype EUFM-8, selected in Kenya is valued for early maturity and higher contents of calcium and iron. A variety designated as FMM175 and selected in Zambia was recommended for its unique quality in brewing traditional beverages. The diverse products and unique nutrient content of the crop indicated the socio-economic value and the crop's broader significance for product development and commercialisation. Hence, continued breeding efforts are needed to focus on biofortification to develop cultivars rich in essential macro- and micro-nutrients and protein content. Finger millet is a strong candidate for addressing global food and nutrition challenges due to its high level of calcium, iron, dietary fibre, essential amino acids, phenolic compounds, climate resilience (drought, heat, salinity tolerance), C4 photosynthesis pathway, extended storage quality, and gluten-free properties.

1.6 Genetic and genomic resources of finger millet

1.6.1 Genetic resources

Plant genetic resources are the foundation for variety development to meet the increased food demand and mitigate climate change (Ron and Rodiño, 2022). Globally, about 40,182 finger millet accessions have been maintained by various gene banks of different countries and institutions (Dwivedi et al., 2012; PGRC, 2016; ICRISAT, 2017; EBI, 2023). Most accessions are maintained in Asian gene banks. For example, India maintains the largest germplasm of 16,379 accessions, followed by Nepal (869), Japan (565), Sri Lanka (462), and China (300) (Dwivedi et al., 2012). ICRISAT is the highest germplasm repository of finger millet (Table 1.6). ICRISAT in India, Mozambique, and Kenya each maintained 7519, 2068, and 651 accessions, respectively (ICRISAT, 2017). In Africa, Kenya Agricultural and Livestock Research Organization (KALRO) in Muguga maintained the highest number of finger millet accessions (2,875), followed by 2,209 accessions by the Ethiopian Biodiversity Institute (EBI) in Addis Ababa and Melkassa Agricultural Research Center (MARC) in Adama (Dwivedi et al., 2012; EBI, 2023). A higher number of finger millet

accessions is also maintained in the USA, including the University of Georgia (1500), the United States Department of Agriculture (USDA) Agricultural Research Service (ARS) in Griffin, Georgia (1425), and the National Center for Genetic Resources Preservation in Fort Collins (702) (Dwivedi et al., 2012). Most of the collected genetic resources are mainly landrace varieties, which are useful for variety design and development targeting high yield potential, nutrient compositions, and biotic and abiotic stress tolerance.

Crop wild relatives (CWR) possess unique genes for various biotic stress tolerance, including insect pest and disease resistance and enhanced nutritional value (Hajjar and Hodgkin, 2007). 335 wild species of finger millet are maintained in various gene banks. These include at ICRISAT in India, Mozambique, and Kenya, EBI in Addis Ababa, Maseno University in Kenya, and Addis Ababa University in Ethiopia, maintaining 205, 41, 4, 11, 18, and 56 wild species, respectively (ICRISAT, 2017; Dida et al., 2021; EBI, 2023). The species (e.g., *E. coracana* subsp. Africana) and hybrid progenies derived from *subsp. coracana* and *subsp. Africana* are cross-compatible with cultivated finger millet (Lule et al., 2018; Dida et al., 2021). The gene flow between the cultivated and wild accessions would result in genetic admixtures, causing linkage drag or novel genetic combinations for selection (Lule et al., 2018; Dida et al., 2021; Pendergast et al., 2022). Several finger millet varieties known as the "Indaf" series were created through controlled crosses between Indian and African genetic resources. The series possessed desirable traits such as blast and drought tolerance, and enhanced nutritional composition (Hittalmani et al., 2017). There is a need for introgression of farmers' desired traits between the wild and cultivated finger millet varieties. Wild relatives must be collected and conserved for future use in breeding for biotic and abiotic stress tolerance. This requires funding, international cooperation, and public awareness of the importance of CWR.

Phenotypic heterogeneity in finger millet genotypes has been documented for numerous attributes. Marked genetic variation has been recorded on yield and yield component traits, seed colour, glume coverage, tolerance to *Striga*, bird damage and insect pests and disease (blast) (Tsehaye et al., 2006; Owere et al., 2015; Patil and Patel, 2018; Madhavilatha et al., 2019). Finger millet varieties with fist-like ear shapes were reported to be tolerance to bird damage in Kenya (KEPHIS, 2023). Finger millet genotypes with different seed colours are utilized for different purposes. For example, white seeded types are preferred to prepare fermented pancake-like flatbread "injera" in Ethiopia and for the baking and food industries in India (Tsehaye et al., 2006; Joshi et al., 2021). Contrastingly, black and brown seeds have exceptional brewing quality (Tsehaye et al., 2006). Furthermore, the black-seeded types are tolerance to bird damage due to their high tannin content (Xiang et al., 2019).

Finger millet exhibits remarkable genetic variability for agronomic traits, nutritional compositions, and root attributes. Reports indicate variability for grain yield (0.7-8.0 t/ha), plant height (50-180 cm), flowering time (51-96 days), inflorescence dimensions (40-180 mm width, 30-190 mm length), panicle exertion (0-215 mm), number of tillers (3-7 basal tillers), number of fingers (6-9 per ear), root length (68-126 cm), and root weight per plant(14-33 g) (Upadhyaya et al., 2011; Oduori, 2008; David et al., 2021).

Marked genetic diversity were reported in finger millet for nutritional composition, including the contents of dietary fibre (15-20%), protein (5-16%), carbohydrate (72-79%), amylose (29-34%), iron (3-53 mg/100g), magnesium (78-201 mg/100g), zinc (1-37 mg/100g), and potassium (430-490 mg/100g) (Upadhyaya et al., 2011; Puranik et al., 2020; Maharajan et al., 2022; Backiyalakshmi et al., 2023). Higher calcium content was reported in Ethiopian finger millet varieties designated Diga-2 (BKFM0010) and Bareda (BRC-356-1) with 550 to 589 mg/100g (Lule et al., 2020; Teklu et al., 2024), surpassing the previously reported value of 344 mg/100g (Upadhyaya et al., 2011; Puranik et al., 2017, 2020; Maharajan et al., 2022; Backiyalakshmi et al., 2023). The substantial genetic diversity present in finger millet forms the foundation for successful breeding programs. Through targeted selection and hybrid development, cultivars can be tailored for farmer-preferred traits (e.g., yield, drought tolerance) and desirable nutritional attributes.

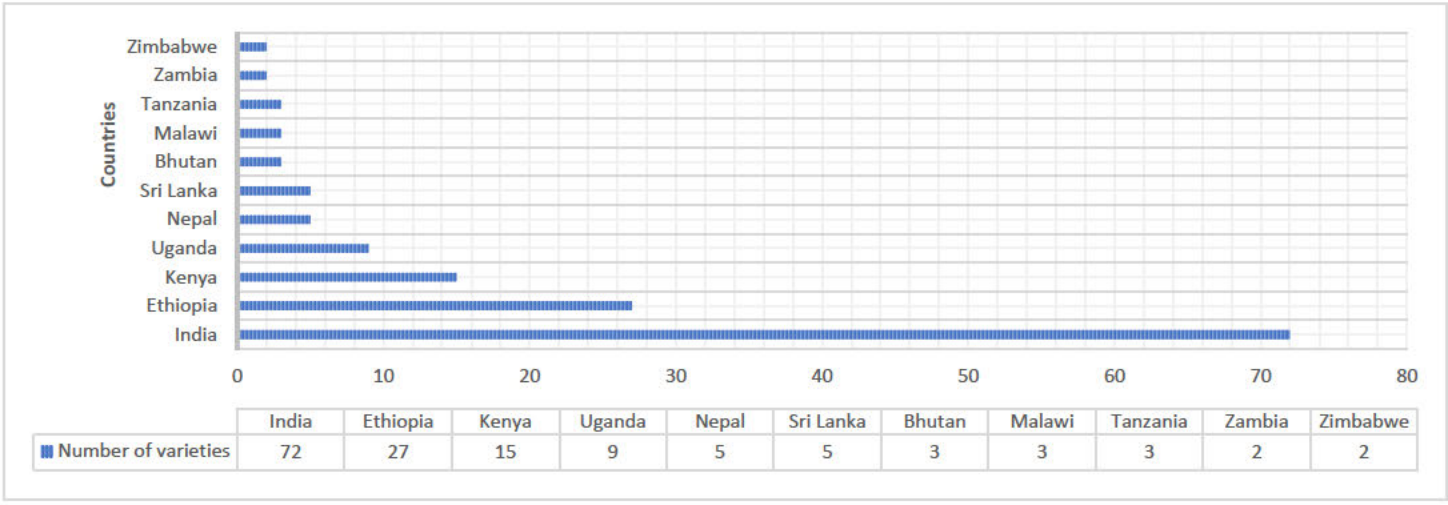
Table 1.6. Important gene banks and databases of finger millet

Gene banks	Location, country	Number of accessions maintained	References
International Crops Research Institute for the Semi-Arid Tropics	Patancheru, India	7519	ICRISAT (2017)
	Nairobi, Kenya	651	
	Bulawayo, Mozambique	2,068	
National Bureau of Plant Genetic Resources	New Delhi, India	9522	Dwivedi et al. (2012)
All India Coordinated Minor Millet Project	Banglore, India	6857	
Kenya Agricultural and Livestock Research Organization	Muguga, Kenya	2875	
Plant Genetic Resources Centre of Sri Lanka	Peradeniya, Sri Lanka	462	PGRC (2016)
Ethiopian Biodiversity Institute and MARC	Addis Ababa and Adama, Ethiopia	2209	EBI (2023)
University of Georgia, USA	Georgia, USA	1500	Dwivedi et al. (2012)
USDA Agricultural Research Service	Griffin, Georgia, USA	1425	
Serere Agricultural and Animal Production Research Institute	Soroti, Uganda	1231	
SADC Plant Genetic Resource Centre	Lusaka, Zambia	1037	

Central Plant Breeding and Biotechnology Division	Kathmandu, Nepal	869	
National Center for Genetic Resources Preservation	Fort Collins, USA	702	
National Institute of Agrobiological Sciences	Kannondai, Japan	565	Dwivedi et al. (2012)
Mt. Makulu Central Research Station	Chilanga, Zambia	390	Dwivedi et al. (2012)
Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences	China/Beijing	300	Dwivedi et al. (2012)
Total		**40,182**	

1.6.2 Impact of in situ collections and gene banks for finger millet varietal development

In situ and gene bank collections are genetic reservoirs for finger millet improvement programs. These collections preserve genetic diversity and facilitate selection of adapted and resilient genetic resources for sustainable plant breeding. Landraces and wild relatives maintained at gene banks are a novel source of genes for drought tolerance, disease and insect pest resistance, and nutritional value (Upadhyaya et al., 2011). Over 150 finger millet varieties have been selected directly from landrace accessions and released in 11 countries across Africa and Asia (Appendix Table 1.3, Figure 1.3). The following gene banks maintain genetically diverse accessions



	India	Ethiopia	Kenya	Uganda	Nepal	Sri Lanka	Bhutan	Malawi	Tanzania	Zambia	Zimbabwe
Number of varieties	72	27	15	9	5	5	3	3	3	2	2

Figure 1.3. Distribution of finger millet varieties released globally that were directly selected from landrace germplasms. (Data sources: AICSMIP 2014; MOA 2022; Dida et al., 2021; Vetriventhan et al. 2020).

of finger millet: ICRISAT/India, NBPG R/India, All India Coordinated Minor Millet Project, KALRO, and EBI. Access to genetically diverse germplasm is the fuel for breeders to develop new varieties that meet local demands and adapt to specific or broad environmental conditions.

1.6.3 Genomic resources of finger millet

Reference genomes, whole genome re-sequencing and transcriptome analysis

Genomic resources are complementary tools for finger millet cultivar design and genetic gain under changing climatic conditions. Genomic tools and databases are essential for trait discovery, gene mining, and markers-assisted breeding. There are three published reference genomes of finger millet, the most recent of which is chromosome-scale (Devos et al., 2023) and is publicly available in Phytozome (Table 1.7). Hittalmani et al. (2017) and Hatakeyama et al. (2018) reported two other scaffold-level reference genomes that were made available in NCBI (Table 1.7). Finger millet's chloroplast genome has been developed, generated, and applied for phylogenetic analysis within the grass family (Liu et al., 2021). Devos et al. (2023) estimated the genome size of finger millet genotype KNE796-S at 1.1 Gb, which was significantly smaller than what was estimated for genotypes ML365 (1.45 Gb) (Hittalmani et al., 2017) and PR202 (1.5 Gb) (Hatakeyama et al., 2018). The availability of the reference genomes enabled the implementation of skim sequencing (Kumar et al., 2021b) and the use of high throughput Single Nucleotide Polymorphism (SNP) markers. Devos et al. (2023) reported the whole genome re-sequencing (WGRS) data from 35 accessions of the subsp. Coracana, 11 from subsp. 41 Africana and two genotypes of *E. indica*. The WGRS data enabled a better understanding of the gene flow between finger millet and progenitors and to discern the genome evolution within the genus *Eleusine*.

Transcriptomics has been used in finger millet for genome annotation, marker and candidate gene discovery. Hatakeyama et al. (2018) generated transcriptome reads to aid in the PR202 genome annotation, while Hittalmani et al. 2017) used transcriptome data to identify drought-induced candidate genes. Devos et al. (2023) used transcriptome data that was publicly available in NCBI to annotate the KNE796-S genome. Kumar et al. (2014) studied the transcriptome of developing spikes and discovered 43,928 and 36,652 SNPs and 24,748 and 21,276 SSRs in the high and low-grain calcium genotypes, respectively. Further, Chandra et al. (2020) used transcriptomics to study Fe and Zn homeostasis of finger millet and identified 15 putative iron and zinc homeostasis pathway candidate genes. Li et al. (2021) deployed transcriptomics and proteomics to determine drought response mechanisms and identified 113 associated differentially expressed genes (DEGs) and differentially expressed proteins (DEPs). Brhane et al. (2022a) exploited transcriptomics for both

marker and trait discovery. They reported differentially expressed genes between Al-tolerant and Al-susceptible finger millet and SNPs and SSR markers. Jadhao et al. (2020) used transcriptomics in finger millet to mine silicon transporter genes linked with defence against pink stem borer (*Sesamia inferens* (Walker)).

The availability of the three finger millet reference genomes, including a recent chromosome-scale assembly, revolutionizes cultivar design and genetic gain under changing climates and market preferences. These resources, complemented by transcriptome data, equip scientists with a powerful toolkit for trait discovery, gene mining, marker development and understanding genome evolution (Sood et al., 2016; Hittalmani et al., 2017; Hatakeyama et al., 2018; Ceasar et al., 2018; Krishna et al., 2022; Devos et al., 2023). Genomic and proteomic tools with advanced breeding techniques will improve the pace and precision of finger millet cultivar development with enhanced nutrient content, stress tolerance, and improved yields.

Table 1.7. Whole genome resources for finger millet

Database	**Website**	**References**
Phytozome	https://phytozomenext.jgi.doe.gov/info/Ecoracana_v1_1	Devos et al. (2023)
NCBI	https://www.ncbi.nlm.nih.gov/assembly/GCA_002180455.1	Hittalmani et al. (2017)
NCBI	https://www.ncbi.nlm.nih.gov/assembly/GCA_021604985.1	Hatakeyama et al. (2018)
NCBI	https://www.ncbi.nlm.nih.gov/nuccore/MW262987.1/	Liu et al. (2021)

Note: NCBI= the National Center for Biotechnology Information

Molecular markers and quantitative trait loci (QTL) mapping in finger millet

Various molecular markers have been used to characterize the genetic diversity and population structure of finger millet. These include Random Amplified Polymorphic DNA (RAPD) (Bezaweletaw, 2011; Pandian et al., 2018), Sequence-Characterized Amplified Region (SCAR) (Reddy et al., 2010), Inter-Simple Sequence Repeats (ISSR) (Brhane et al., 2017b; Pandian et al., 2018), Simple Sequence Repeat (SSR) (Gimode et al., 2016; Lee et al., 2017; Babu et al., 2018), Expressed Sequence Tag-derived Simple Sequence Repeat markers (EST-SSR) (Bwalya et al., 2020; Brhane et al., 2021), and SNP (Gimode et al., 2016; Backiyalakshmi et al., 2021; Brhane et al., 2022b).

Venkatesan et al. (2021) employed ISSR markers for the accurate identification of traditional and hybrid varieties of finger millet, while Krishna et al. (2020) used SSR, RAPD, and ISSR to examine the genetic purity of F1 hybrids. Several studies reported the association of SSR markers with traits of interest (Lule et al., 2018; Ramakrishnan et al., 2018; David et al., 2021). The existing finger millet SSR markers can be integrated into the robust SNP linkage map (Pendergast et al., 2022) to further validate their associations with economic traits.

Marker-trait association (MTA) studies in finger millet have been undertaken using whole genome SNP markers from different skim-sequencing techniques. Through GWAS, SNP markers associated with flowering days (Sharma et al., 2018; Sood et al., 2023b), grain yield (Sharma et al., 2018; Tiwari et al., 2020; Sood et al., 2023b), neck blast (Sood et al., 2023b), micronutrient (Puranik et al., 2020; Sharma et al., 2022; Chandra et al., 2024) and protein contents (Tiwari et al., 2020) were reported. Studies at the University of Georgia have characterized a bi-parental interspecific population (MD-20 x Okhale 1) (Qi et al. 2018) to map for days to flowering, plant height, panicle number per plant and blast disease resistance (Pendergast et al., 2022), and colouration of stigma and anthers (Devos et al., 2023). A mapping population between IE-2606 and PR-202 consisting of 100 individuals was characterized for agro-morphological traits and protein content, identifying several QTLs (Maharajan et al., 2023). Table 1.8 summarizes MTAs conducted in finger millet that used at least 100 genotypes and a minimum of 100 markers in the trait characterization. Future MTA studies in finger millet would require validating the reproducibility of generated datasets. Furthermore, there is a need to deploy larger, genetically diverse, bi-parental populations evaluated across representative environments.

Table 1.8. **A summary of marker-trait association studies in finger millet that used at least 100 genotypes**

Traits	Mapping methods	Marker types	Number of significant MTAs	Population size	References
Days to 50% flowering, plant height, panicle number, leaf blast severity, and panicle blast incidence at maturity	Bi-parental QTL mapping	SNPs and insertion–deletions	8	151	Pendergast et al. (2022)
Primary root length, shoot dry weight, and total phosphorous content in shoots	Bi-parental QTL mapping	SSRs	92	100	Maharajan et al. (2023)
Stigma, and anther colour	Bi-parental QTL mapping	SNPs	-	294	Devos et al. (2023)
Days to 50 % flowering, basal tiller number, flag leaf width, and plant height	Association mapping	SSRs	5	190	Babu et al. (2014a)

Traits	Mapping methods	Marker types	Number of significant MTAs	Population size	References
Finger blast, and neck blast resistance	Association mapping	SSRs	7	190	Babu et al. (2014b)
Protein and tryptophan contents	Association mapping	SSRs	3	190	Babu et al. (2014c)
Days to maturity, finger number, grain yield per plant, number of grains per spikelet, productive tiller number, and thousand grain weight	Association mapping	SSRs	16	138	Lule et al. (2018)
Days to 50% flowering, days to maturity, and grain yield	Genome wide association mapping	SNPs	111	113	Sharma et al. (2018)
Grain yield, days to maturity, and seed protein content	Genome wide association mapping	SNPs	81	113	Tiwari et al. (2020)
Iron, zinc, magnesium, sodium, and potassium contents	Genome wide association mapping	SNPs	418	190	Puranik et al. (2020)
Calcium content	Genome-wide association mapping	SNPs	44	202	Sharma et al. (2022)
Days to 50% flowering, days to maturity, plant height, number of basal tillers, flag leaf length, flag leaf width, ear length, ear width, number of fingers, green fodder weight, dry fodder weight, and neck blast	Genome-wide association mapping	SNPs	132	186	Sood et al. (2023b)
Zinc and iron contents	Genome-wide association mapping	SNPs	45	202	Chandra et al. (2024)

1.7 Genetic engineering and genome editing

Genetic engineering is the transformation of DNA sequence(s) of genomes by a variety of molecular biology methodologies (Lanigan et al., 2020; Ye et al., 2022), notably electroporation, biolistics, micro-injection and *Agrobacterium tumefaciens* (Mir and Patel, 2018). Genetic engineering enables the introduction of a range of traits that may not be transferable through conventional breeding methods. The success of genetic transformation in any crop depends on the ability of the target crop cells to be cultured *in vitro*. Developing an optimum and reproducible tissue culture technique has been a challenge in finger millet, leading to slow progress in genetic engineering. Both somatic embryogenesis and organogenesis have been tested successfully for the regeneration of finger millet plants *in vitro*. Somatic embryogenesis is the formation of an embryo from a cell other than a gamete (Merkle et al., 1995), while organogenesis is the process in which adventitious roots are generated from detached or wounded plant tissues or organs (Chen et al., 2014).

Eapen and George (1989) reported the first finger millet plant regeneration through somatic embryogenesis. Several studies reported the use of somatic embryogenesis in finger millet (Eapen and George, 1990; Ngetich et al., 2018; Venkatesan et al., 2022), using embryoids for genetic engineering. There are successful finger millet plant regeneration using organogenesis (Mukami et al., 2018; Kansara et al., 2023.) and a combination of both organogenesis and somatic embryogenesis (Kashyap et al., 2018; Kansara et al., 2023). The somatic embryogenesis method is the most preferred method of regenerating cereals (Bhaskaran and Smith, 1990) due to the single-cell origin of embryoids that enhances the stability and genetic uniformity of resulting transformants

(Kumar et al., 2001). These successful plant regeneration reports have made it possible to genetically engineer finger millet, albeit with low reproducibility across labs.

Both biolistics and *Agrobacterium*-mediated transformation have been tested for the genetic engineering of finger millet. Gupta et al. (2001) used biolistics and successfully tested the efficiency of various gene promoters in finger millet. Latha et al. (2005) also used biolistics to insert an antifungal gene to improve leaf blast resistance in finger millet. Bayer et al. (2014) used a combination of both biolistics and *Agrobacterium*-mediated transformation to generate finger millet plants with herbicide resistance. Ignacimuthu and Ceasar (2012) reported successful transformation of finger millet using *A. tumefaciens*. The authors pinpointed successful introduction of *rice chitinase* gene into finger millet for leaf blast resistance. Other workers such as Ramegowda et al. (2013) reported successful transgenics for improved zinc concentration; introduced *mannitol-1-phosphate dehydrogenase* (mtID) for improved multiple stress tolerance (Hema et al., 2014); and Jayasudha et al. (2014) and Anjaneyulu et al. (2014) for improving salinity tolerance. The biggest challenge is the reproducibility of the transformation methods across different labs.

Genome editing enables targeted alteration of both the genotypes and phenotypes of the edited organisms. Genome editing, as opposed to genetic engineering, involves the modification of endogenous plant DNA at specified loci by the deletion/insertion and replacement of essential DNA segments. Among several gene editing tools, clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein 9 (Cas9) tools are the most successful in several organisms, including plants (Chen et al., 2019). There are currently no known reports on the use of CRISPR-Cas9 in finger millet, partly due to the lack of an efficient and reproducible transformation system. Genome editing in millets has been extremely slow, except for the recent momentum (Ceasar, 2022). More efficient transformation methods, such as those reported by Satish et al. (2017) and Mukami et al. (2018), will continue to enhance reproducibility across labs and subsequently enable routine genome editing in finger millet in the future. Comparative studies with other more successful cereals, such as rice, will further benefit the application of genome editing in finger millet. An example is deploying methods established in rice to generate male sterile lines (Zhou et al., 2016; Barman et al., 2019), which will be game-changing towards producing hybrids in finger millet. The current well-annotated chromosome-scale reference genome reported by Devos et al. (2023) will be valuable for future genome editing applications in finger millet.

1.8 Conclusion and outlook

Finger millet is a gluten-free, high-potential and niche opportunity crop for its climate resilience, extended storage quality, rich nutritional compositions, and different health benefits. Despite the socio-economic importance of the crop, genetic gains for yield and nutritional compositions of finger millet are low due to the limited research and development support compared with other staple crops. Globally, only a few improved finger millet varieties have been released for consumer-preferred traits, including high grain yield potential, enhanced nutritional quality, high marketability, and tolerance to different biotic and abiotic stresses. Almost all finger millet improvement programs in SSA focus on conventional breeding for pure line selection through germplasm introduction, collection, characterization, selection, and variety recommendation. Very limited research work has been conducted on variety development through mutation, tissue culture, and trait integration using controlled crosses. Investing in robust male sterility systems for finger millet is key to accelerating its breeding progress and enabling its potential to address food security challenges. A male sterility system is an essential strategy for developing hybrid seeds in self-pollinating crop species such as sorghum and rice. Substantial amounts of finger millet genetic resources (cultivated and wild types) are maintained by different gene banks, which is useful in variety design and product development with end-user preferences. The long-term availability of these genetic resources requires germplasm collection and conservation, which depends on availability of funding, international collaboration, and public awareness. A limited number of reported functional genes, QTLs, molecular markers linked to various economic traits and the recently published chromosomal scale reference genome can be employed in finger millet breeding programs. Concurrently, enhancing genomic research and capacity development in developing countries and international collaboration is paramount. There is a need to develop new climate-smart finger millet cultivars tolerance to biotic and abiotic stresses, rich in nutritional value that meet consumers' needs and market demands. Therefore, current and future finger millet improvement programs should integrate yield, nutritional value-attributing traits and local adaptation. This can be achieved by integrating conventional breeding methods with advanced genomic techniques such as marker-assisted selection, genomic-assisted breeding, and genome editing.

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Appendix Table 1.1. Reported global finger millet genotypes with insect pest tolerance

Genotype name/designation	Yield (t/ha)	Breeding methods	Days to maturity	Year of release	Attributes	Country	References
PES 110	3.0-3.5	PR	110-115	1985	Tolerance to stem borer, jassids, aphids and grey weevil, and high-yielding	India	AICSMIP (2014)
BM 11-1 (Rushikulya)	2.5-3.0	MB	110-115	1996	Tolerance to stem borer, moderately resistance to blast and brown spot, and dry spells of 15 to 18 days		
BM 9-1 (Bhairabi)	2.5-3.5	MB	105-110	1999	Tolerance to stem borer and shoot fly, moderately resistance to blast, early maturity, and lodging tolerance		
OEB 10 (Chilika)	2.6-2.7	RS	115-120	2001	Tolerance to stem borer and moderately resistance to blast		
VR 847 (Srichaitanya)	2.6-2.8	RS	110-115	2009	Tolerance to caterpillars and aphids and moderately resistance to blast		
OEB 532	2.2-2.5	RS	110-115	2012	Highly tolerance to myllocerus weevil, earhead caterpillars, stem borer and grasshopper, and moderately resistance to blast		
Indira Ragi-1	2.5-2.6	RS	120-125	2012	Tolerance to stem borer, moderately resistance to neck and finger blast and tolerance to lodging and drought		
KMR 340	3.5-4.0	RS	90-95	2016	Tolerance to stem borer and aphids, resistance to blast and blight diseases		
Ikhule	6.3	PR	131	2021	Tolerance to shoofly and blast	Ethiopia	MOA (2022)

Note: PR=pure line selection, RS= recurrent selection, and MB=mutation breeding

Appendix Table 1.2. Finger millet varieties for nutritional and farmer-preferred traits reported globally

Variety name/designatioin	Breeding methods	Days to maturity	Year of release	Yield (t/ha)	Country	Trait description	References
CO 9	RS	100-105	1970	2.5-3.0	India	Rich in protein content (9.5 to 9.6 %), stay green, and early maturity	AICSMIP (2014)
CO 6		120-125	1935	1.5-2.0		Rich in protein and late maturation	
PR 2614 (SAPTAGIRI)		105-110	1995	2.5-3.0		Excellent for porridge, resistance to blast, tolerance to drought, non-lodging, and medium maturation	
HAMSA	PR	110-120	1967	3.0-3.2		Rich in protein content (9.0 to 9.2 %)	
KALYANI		110-115	1972	2.5-3.0		Resistance to blast, tolerance to drought, non-lodging, and early maturation	
PRM 2		100-105	2010	2.5-2.8		Rich in protein, resistance to finger and neck blast and *Cercospora* leaf spot, and early maturing	
EUFM-8	PR	95-115	2021	1.8-2.2	Kenya	High in Ca and Fe, and early maturing	KEPHIS (2023)
FMM175	MB		2009	4.1	Zambia	Preferred for brewing	IAEA (2022)
Diga-2 (BKFM0010)	PR	164	2018	2.2-3.4	Ethiopia	Rich in Calcium (589 mg/100g), and tolerance to head and leaf blast	Lule et al.(2020); Teklu et al. (2024)
Bereda (BRC-356-1)		146-169	2009	2.0-2.8		Rich in Calcium (550 mg/100g), tolerance to major finger millet diseases	Lule et al.(2020); Teklu et al. (2024)

Note: PR=Pure line selection, RS= Recurrent selection, and MB=Mutation breeding

Appendix Table 1.3. Lists of finger millet varieties released globally from direct selection from the landraces

Variety name	Days to maturity	Year of release	Yield (t/ha)	Attributes	Country	Reference
Tadesse (KNE#1098)	146	1998	2.5	High yielding and compacted head shape	Ethiopia	MOA (2022); Teklu et al. (2024)
Padet (KNE#409)	146	1998	2.4	Tolerance to head blast		
Boneya (KNE#411)	145	2002	2.5-3.0	Tolerance to head blast		
Degu (PGRC/E215874)	137-160	2005	2.3-3.0	-		
Wama (KNE#392)	145-150	2007	1.7-3.5	Tolerance to major finger millet diseases		
Baruda (PW-001-75)	149-159	2007	3.0-3.5	Resistance to grain mold disease		
Gute (ACC#229373)	140-153	2009	2.0-3.5	Tolerance to major finger millet diseases		
Bareda (BRC-356-1)	146-169	2009	2.0-2.8	Tolerance to major finger millet diseases, rich in ca		
Debatsi (Debatsi)	155-167	2010	2.0-2.5	Tolerance to major finger millet diseases		
Necho (PGRC/E203572)	145-175	2011	2.0-3.0	Tolerance to major finger millet diseases		
Tessema (ACC#229469)	145-150	2014	1.8-2.2	Moderately tolerance to major diseases of finger millet		
Gudetu (ACC#215990)	145-150	2014	2.0-2.1	Tolerance to finger millet major diseases (head and leaf blast)		
Mecha (PGRC/E229371)	140-154	2014	2.0-2.9	Tolerance to blast		
Addis-1 (ACC#203544)	145-155	2015	2.6-4.2	Moderately resistance to blast		
Kako-1 (ACC#203351)	139	2016	2.6-3.0	Tolerance to blast and drought		
Mereb-1 (KNE#622)	83-121	2016	2.5-3.2	Resistance to blast (M*agnaporthe oryzea*)		
Meba (GBK-011119A)	132	2016	2.1-3.5	Tolerance to major finger millet diseases		
Axum (ACC#229355)	147	2016	2.2-3.6	Tolerance to major finger millet diseases		
Urgi (ACC#242617)	153-180	2016	1.8-2.7	Tolerance to blast (*Magnaporthe oryzea*)		
Diga-1 (ACC#216036)	140-167	2016	2.2-2.8	Tolerance to blast (*Magnaporthe oryzea*)		
Bako-09 (ACC#214995)	136	2018	3	Tolerance to major finger millet diseases blast		
Diga-2 (BKFM0010)	164	2018	2.2-3.4	Tolerance to head and leaf blast, rich in ca		
Tekeze-1 (SMARCcoll#60)	128-138	2018	2.8-3.5	Moderately tolerance to blast		
Kumsa (BKFM0063 (1))	144	2019	2.5-3.2	-		
Jabe (Acc.229626)	143-168	2019	2.5-3.0	Tolerance to blast and lodging		
Metekili (ACC.05pw-2012)	155	2020	2.8-3.8	Resistance to blast		
Ikhule	131	2021	6.3	Tolerance to blast and shoot fly		
P-224	90-120	1981	2.0-5.0	Tolerance to lodging and blast	Kenya	Dida et al. (2021); Vetriventhan et al. (2020)
Nakuru/FMI	150-210	1996	2	Tolerance to cold and drought		
KAT/FM-1 (KatumaniFM-1)	90	2000	1	Drought tolerance		
U-15 (MARIDADI)	90-120	2015	1.1-4.9	Early maturity; blast, *Striga,* and lodging resistance, and drought tolerance		
Gulu-E	-	2015	-	-		
OKHALE-1 (KAK-Wimbi1)	88-138	2016	1.1-6.7	Blast, *Striga*, and lodging resistance, and drought tolerance		
IE4115 (KAK-Wimbi2)	88-131	2016	1.3-6.1	Blast*, Striga*, and lodging resistance, drought tolerance		
P-283	-	2016	-	-		
KNE741 (EUFM-401)	65-75	2018	1.0-1.4	Super early, drought escape, tolerance to high temperatures		
KNE629 (EUFM-502)	100-120	2018	1.4-2.0	Blast resistance		
SDFM1702 (EUFM-503)	90-98	2018	1.5-2.5	Blast resistance, & tolerance to bird damage due to fist fingers		
EUFM05	120	2019	2.0-3.0	Early maturing		
GBK029646A (KIS-Wibmi1)	89-119	2021	1.4-4.4	Drought tolerance, high yielding, & early maturity		
AGRY-2 (Mavuno)	90-120	2021	1.8-2.5	Resistance to lodging, birds, & blast disease		
EUFM-8	95-115	2021	1.8-2.2	Early maturing, high in Ca and Fe contents		
ACC#14FMB/01WK	-	1987	-	-	Malawi	ICRISAT (2019)
KNE#688	-	1987	-	-		
P224	-	1987	-	-		
U15	90-100	2011	2	-	Tanzania	Ojulong et al. (2016)
P224	100-110	2011	2.8	-		
TARI-FM1 (KNE#689)	100-110	2019	-	-		
GULU-E	75-80	1970	2	Resistance to blast	Uganda	Owere et al. (2014);
Serere1	-	1970	-	-		
Pese1 (P224)	100	1989	2.5-3	Resistance to blast, but susceptible to lodging		

Variety name	Days to maturity	Year of release	Yield (t/ha)	Attributes	Country	Reference
Seremi1 (P249) (PeseII)	100	1999	2.0-3.0	Resistance to blast, & moderately resistance to lodging		Vetriventhan et al. (2020)
Seremi2 (U15)	70-80	1999	2	Resistance to blast, & lodging, early maturing		
Seremi3 (SX17-88)	90-100	1999	2.5-3.0	Resistance to blast, & lodging, drought tolerance		
NAROMIL4	85-90	2017	-	-		
NAROMIL5 (IE2440)	100	2017	-	-		
Ending	-	2018	-	-		
FMV287 (IE2947)	-	1987	-	-	Zambia	IAEA (2022); Vetriventhan et al. (2020)
Lima (IE2929)	-	2009	-	-		
SDEV87001	-	1994	3.5	-	Zimbabwe	Mirza, & Marla (2019)
FMV-1	-	1994	-	-		
LingmithangKongpu-1 (3459)	120	2002	1.6-1.8	-	Bhutan	FAO (2011)
LingmithangKongpu-2 (5459)	140	2002	1.9-2.0	-		
Membja–1 (GPU48)	110-115	2019	5.6	-		
H22	150-155	1918	1.5-2.0	Susceptible to lodging, & long duration	India	AICSMIP (2014); Patil & Patel (2018); Madhavilatha et al. (2019)
ES11 (GIDDARagi)	110-120	1939	1.0-1.2	Highly susceptible to blast, & low yielding		
ES13	115-120	1939	1.5-1.8	-		
K1 (KOLARGIDDARagi)	130-135	1939	0.9-1.0	Stay green character, long duration		
R0870	130-135	1939	1.2-1.5	Long duration		
CO1	120-125	1942	2.5-3.0	Stay green character, long duration, fodder yield		
CO2	110-115	1942	2.0-2.5	Stay green character, & tolerance to drought		
CO4	140-145	1942	2.5-3.0	For irrigated areas, & long duration		
T36B	-	1949	-	-		
CO7	100-105	1953	2.5-3.0	Early duration		
CO5	115-120	1953	2.5-3.0	-		
ARUNA	95-100	1956	1.5-1.8	Non lodging, early duration		
VZM1	105-110	1958	2.0-2.5	Non lodging, suitable for late Kharif, & has stay green character		
VZM2	105-110	1958	2.0-2.5	Non lodging		
AKP2	80-90	1960	2.0-2.2	Extra early		
CO8	90-95	1963	1.5-2.0	Early duration		
HAMSA	110-120	1967	3.0-3.2	Rich in protein content (9.0 - 9.2 %)		
AKP7 (SARADA/IE901)	100-105	1971	2.5-3.0	Resistance to blast, & mosaic diseases		
KALYANI	110-115	1972	2.5-3.0	Resistance to blast & tolerance to drought, non-lodging, good for ball making, & early duration		
CO10	110 - 120	1976	3.5-4.0	Stay green character		
GN1 (GUJARATNAGLI1)	110-115	1976	2.0-2.5	Tolerance to drought		
PR202 (GODAVARI)	110-115	1976	2.5-3.0	Susceptible to blast, tolerance to drought		
VL101 (IE524)	100-105	1978	2.3-3.0	Early duration		
NIRMAL	110-115	1980	1.5-2.0	Resistance to blast, & suitable for saline soils		
CO11 (EC4849)	110-115	1982	3.5-4.0	Photo-insensitive, tolerance to salinity, stay green character, & high yielding		
GN2 (GUJARATNAGLI2)	110-115	1982	2.5-3.0	Moderately resistance to blast, & tolerance to drought		
CO12	120-125	1985	3.5-4.0	Moderately resistance to blast, stay green character, high yielding, & long duration		
BM1 (IE723)	105-110	1985	2.8-3.0	Moderately resistance to blast, & early duration		
PAIYUR1	100-110	1985	2.3-2.5	Moderately resistance to blast, & stay green character		
PES110	110-115	1985	3.0-3.5	High grain density, tolerance to stem borer, jassids, aphids & grey weevil, & high yielding		
PR1044 (RATNAGIRI)	110-115	1985	2.7-3.0	Resistance to blast, & tolerance to drought		
SIMHADRI	105-110	1985	2.5-3.0	Moderately resistance to blast, rich in protein (14.3 mg/100 g)		
VL204	90-100	1985	1.8-2.0	Fingers open at anthesis & closed during seed development, & then partially reopening at maturity, susceptible to finger blast, & early duration		
KM13	95-110	1989	2.5-3.0	Non lodging, synchronous tillering, & early duration		

Variety name	Days to maturity	Year of release	Yield (t/ha)	Attributes	Country	Reference
PES400 (PANTMANDUA3)	95-100	1989	1.8-2.0	Early duration		
TRY1 (SSRC247)	100-105	1989	4.0-4.5	Moderately resistance to blast, tolerance to sodic soils with a PH range of 8.5 and above, early duration, & high yielding		
VL124	100-110	1989	2.0-2.5	Early duration		
VR520 (SURAJ)	85-90	1992	2.0-3.0	Resistance to blast and tolerance to drought, & extra early		
A404	110-115	1993	2.2-2.6	Moderately resistance to blast, & has deep root system		
PPR2350 (PADMAVATHI)	100-105	1993	2.5-3.0	Early duration		
KM65	95-100	1994	1.8-2.0	Resistance to blast, & early duration		
BM2 (BIRSAMARUA2)	105-110	1995	2.5-2.6	Resistance to neck and finger blast, & early duration		
PR230 (MARUTHI)	90-100	1998	2.5-3.0	Resistance to blast, & blight, & early duration		
VR708 (CHAMPAVATHI)	90-95	1998	2.5-3.0	Highly susceptible to blast, photo insensitive, & early duration		
DHRS1	120-125	2005	2.0-2.5	Long duration		
PRM1	110-115	2006	2.0-3.0	-		
VR762 (BHARATHI)	110-115	2006	2.8-3.0	-		
GPU67	115-120	2009	4.0-4.5	Profuse tillering, & non lodging		
PRM2	100-105	2010	2.5-2.8	Resistance to finger, & neck blast, & Cercospora leaf spot, early maturing, & rich in crude protein		
KOPN235 (PhuleNachani-1)	115-120	2011	2.5-2.6	Resistance to blast		
GN-5	120-130	2016	2.5-2.7	Moderately resistance to leaf, & finger blast		
GNN-6	120-130	2016	2.8-3.0	Moderately resistance to leaf blast, & finger blast		
GN-8 (WN585)	105-112	2018	3.1	Moderately resistance to leaf, neck, & finger blast, & foot rot diseases		
VLMandua379 (VL379)	-	2018	-	-		
CFMV1 (Indravathi)	110-115	2020	3.5-4.0	Resistance to neck, & finger blast		
CFMV2 (Gira)	119-120	2020	3.2-3.5	Resistance to blast and stem borer, rich in protein, & iron content		
KMR-316	100-105	2021	2.9-3.5	-		
IE-980 (Dalle-1)	-	1980	3.3	Drought tolerance	Nepal	Joshi et al. (2017)
NE1304-43 (Okhle-1)	-	1980	3.3	Drought & lodging tolerance, & resistance to blast		
NF-6401-26 (KabreKodo-1)	-	1990	1.8-4.8	Drought & lodging tolerance, & resistance to blast		
PR-202orGE-5176 (KabreKodo-2)	-	2015	2.5	Drought & lodging tolerance, & resistance to blast		
GE-5016 (SailungKodo-1)	-	2015	2.5	Lodging resistance		
Ravi	-	-	-	-	Sri Lanka	FAO (2011)
MI301	-	-	-	-		
MI302	-	-	-	-		
Rawana	-	-	-	-		
Co10	-	-	-	-		
KM1	-	-	-	-		

Chapter 2. Finger Millet Production in Ethiopia: Opportunities, Problem Diagnosis, Key Challenges and Recommendations for Breeding

Abstract

Finger millet (*Eleusine coracana* (L.) Gaertn) is a highly nutritious crop, predominantly grown in the semi-arid tropics of the world. Finger millet has a niche market opportunity due to its human health benefits and being rich in calcium, iron and dietary fibre and gluten-free. Ethiopia is the center of the genetic diversity of the crop. However, the productivity of finger millet in the country is low (<2.4 tons ha^{-1}) compared with its potential yield (6 tons ha^{-1}). The yield gap in Ethiopia is due to a range of biotic and abiotic stresses and socio-economic constraints that are yet to be systemically documented and prioritized to guide future production and improved variety development and release. The objective of this study was to systematically assess finger millet production systems in Ethiopia by identifying key production constraints, opportunities, and farmer-preferred traits and to inform ideotype and variety design for targeted breeding programs. A participatory rural appraisal (PRA) study was undertaken in six selected districts of the Southern Nation Nationalities People Region (SNNPR) and Oromia Region in Ethiopia. Data were collected from 240 and 180 participant farmers through a semi-structured questionnaire and focus group discussion, respectively. Finger millet was the most important crop in the study areas grown mainly for a combination of uses, including for food, feed and cash (reported by 38.8% of respondent farmers), food and feed (14.5%), food and cash (13.7%), food (11.5%) and food, cash, feed and construction material (9.7%). Hand weeding was used by 59.2% of the respondent farmers, followed by hand weeding and chemical herbicides (40.8%). Finger millet was mainly planted as a sole crop (reported by 97.0% respondents), mixed (1.7%) and sole and mixed (1.3%). About 75.6% of respondent farmers only practiced finger millet rotation with other crops. Respondent farmers indicated their source of fresh seed was from the Bureau of Agriculture (49.1%), farmer-to-farmer seed exchange (22.1%), own saved seed (7.5%), local producers (7.5%), research institutions (5.8%), unknown sources (4.1%), local market (3.5%) and cooperatives (0.42%). The total cost of finger millet production per hectare was calculated at 1249 USD with a total income of 2139 USD/ha, making a benefit to cost ratio of 1.71:1.00 and indicating the relatively low yield gains using the currently grown varieties. The main constraints to finger millet production in the study areas were drought stress (reported by 41.3% respondents), lack of improved varieties (12.9%), lack of financial resources (11.3%), small land holdings (10.8%), limited access to seed (10.0%), a shortage of fertilizers (5.4%), poor soil fertility (4.6%), shortage of draught power (1.3%), labour shortages (1.3%) and high labour costs (1.3%). The most important farmer-preferred traits in a finger millet variety were high grain yield, compact head shape, 'enjera'-making quality, high marketability and early maturity, resolved through principal component analysis. The above-mentioned production constraints and farmer-preferred traits are strategic drivers to enhance finger millet productivity and need to be incorporated into Ethiopia's finger millet breeding and technology development.

Keywords: *Eleusine coracana*; drought stress; finger millet; participatory rural appraisal; indigenous knowledge

2.1 Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn) is an important cereal crop in the semi-arid and tropical regions of the world. The name finger millet is derived from the appearance of spikes or fingers, which are arranged and appear like human fingers (Byrne, 2023). Compared with other major cereals such as rice, wheat and barley, it is relatively drought-tolerant due to its C4 photosynthesis system and adaption to grow under harsh and marginal agro-ecologies. Agriculture is an important economic sector in Africa, including Ethiopia (Mellor and Dorosh, 2010; Ademe and Mehare, 2023). The sector accounts for 25% of Africa's GDP, 21% of exports, and 65–70% of the workforce supporting the livelihoods of 90% of population (OECD, 2016; World Bank, 2016; Mukasa et al., 2017). In Ethiopia, agriculture contributes to 44% of GDP, 70% of export earnings and 80% of employment opportunity (FAO, 2021). Finger millet is grown mainly for its grain, which is utilized to make traditional food and drinks, while the stalks are used for livestock feed, construction and fuel (Assefa et al., 2009; Lule et al., 2012a).

Finger millet has various human health benefits such as reducing diabetes (Anitha et al., 2021a), obesity and anaemia (Anitha et al., 2021b), osteoporosis (Gupta et al., 2017; Maharajan et al., 2021), and preventing malaria and diarrhea (Tsehaye et al., 2006; Assefa et al., 2013). The health values of finger millet are linked to its high calcium, iron and dietary fibre content and being gluten-free (Jayawardana, et al., 2019; Rathore, et al., 2019). These health benefits will suggest potential for niche health-food markets. Finger millet is cultivated in more than 25 countries in Africa and Asia (Vetriventhan et al., 2015). Ethiopia is the second largest producer of finger millet in the world after India (FAOSTAT, 2019; Indiastat, 2019). In Ethiopia, the grain is processed to make unleavened bread (locally referred to as *enjera*) and for malting to prepare local drinks such as a distilled spirit '*Areki'* or local beers such as '*tella'* and non-alcoholic drinks such as '*karibu'* and '*shamita'*. On the other hand, the straw is vital as a livestock feed and for thatching of houses (Assefa et al., 2009; Lule et al., 2012a).

The global production area and total production for finger millet are not precisely known since independent statistics on finger millet are generally not reported separately. Instead, these statistics are aggregated with those of other millet species in international databases. An estimated total production area of 32,554,127 ha is devoted to millets production worldwide (FAOSTAT, 2019). It is estimated that the share of the global finger millet production area is about 12.5% of the millets. Ethiopia's total finger millet production area is 455,581 ha (CSA, 2019), making an 11.2% global share (CSA, 2019; FAOSTAT, 2019). A total of 3,834,021 tons of finger millet grain is produced

per annum globally (FAOSTAT, 2019), while Ethiopia's output is estimated at 1,125,958 tons (CSA, 2019), equivalent to 29.4% of global production. Finger millet is the sixth most important cereal crop in Ethiopia in total area and production after tef (*Eragrostis tef* (Zucc.) Trotter), maize (*Zea mays* (L.)), sorghum (*Sorghum bicolor* (L.) Moench), wheat (*Triticum aestivum* (L.)) and barley (*Hordeum vulgare* (L.)) (CSA, 2019). It accounts for 5% of the total area allotted to cereal production in Ethiopia (CSA, 2017). Finger millet is grown by more than 1.8 million households on more than 455,000 hectares of land in the northern, north-western, western, the Central Great Rift Valley and West Hararghe zones of Ethiopia (CSA, 2019). In 2017 the total grain production was 1,017,059 tons, increasing by 87% in the preceding 20 years (CSA, 2017).

Despite the importance of finger millet for food security and livelihoods, its productivity is relatively low (2.47 t/ha) (CSA, 2019) in Ethiopia compared with the potential yield of the crop (6 t/ha) achieved under experimental conditions (Upadhyaya et al., 2007). The low productivity of the crop in the country is attributed to a range of biotic and abiotic stresses and socio-economic constraints prevalent in the smallholder production systems. Finger millet blast caused by *Magnaporthe grisea* (Barr) (teleomorph) is the most damaging disease, causing yield losses in the range of 7.32–54.07%, depending on climatic conditions and cultivar susceptibility (Lule et al., 2014). Notable insect pests of the crop include grasshoppers (Caelifera) and shoot fly (*Atherigona soccata* (Rondani)) (Assefa et al., 2009), pink stem borer (*Sesamia inferens* (Walker)), finger millet root aphid (*Tetraneura nigriabdominalis* (Sasaki)) and aphids (aphidoidea) (Sasmal, 2016, 2018). Yield losses have been reported due to several insect pests such as termites (isopteran) (with a loss of 23%) (Mulualem, and Melak, 2013), aphids (35.1%) (Sasmal, 2016) and pink stem borer (56%) (Sasmal, 2018). Weeds cause severe yield loss during the early growth stages of finger millet. In Ethiopia, yield losses of up to 73.5% have been reported due to weeds (Asargew, and Shibabawu, 2014). The most problematic weed species of finger millet in Ethiopia include *Digitaria ternata* (A. Rich.) Stapf, *Guizotia scabra* (Vis.) Chiov, *Cyperus rotundus* L. (Asargew, and Shibabawu, 2014) and *Striga hermonthica* (Delile) Benth (Owere et al., 2014).

Recurrent drought stress associated with climate change is the leading constraint affecting finger millet production and other main crops in Ethiopia. The impact of drought stress on finger millet production depends on cultivar susceptibility, the onset date, the intensity and duration of the drought stress and the associated prevailing environmental conditions. Although finger millet is relatively drought-tolerant, 100% yield losses can be incurred due to intense and early onset of drought stress (Maqsood & Ali, 2007). Supplementary irrigation, early planting and moisture

conservation techniques such as mulching, zero tillage and tie ridging are often used to mitigate drought stress (Wang et al., 2016). However, most smallholder farmers do not have access to irrigation and other resources to manage drought stress. Drought stress also significantly affects grain quality and yield components (Barutçular et al., 2016). Hence, drought-tolerant varieties could be the most economical and environmentally friendly approach managing drought under smallholder production systems.

In Ethiopia, formal research on finger millet improvement started in the early 1980s (Adugna et al., 2011). In the last four decades, finger millet improvement activities in Ethiopia have focused on characterization and evaluation of locally collected and introduced germplasm for pure line selection. As a result, some 23 finger millet varieties have been registered and released for production (MOA, 2018). Two varieties, Tadesse (KNE#1098) and Tessema (ACC#229469), were released with the beneficial traits of wide adaptability, high grain yield potential, good biomass and compact head shape. However, these varieties are late maturing, susceptible to insect pests and diseases, have relatively low human nutrition value and a seed shattering problem. The mean grain yield of improved finger millet varieties in Ethiopia is low at 2.7 t/ha (MOA, 2019), compared with 4.74 and 4.79 t/ha reported for Kenya (Wafula et al., 2016) and India (Bondale, 1993), respectively. Ethiopia is the primary centre of origin and diversity for finger millet (Tesfaye, and Mengistu, 2017). The finger millet landraces grown by farmers are essential genetic resources that are known to hold useful genetic variation for desirable traits. Therefore, these landraces can be evaluated and selected for their desirable characteristics for new variety development, genetic analysis and gene discovery, leading to high yielding varieties that have all the essential farmer-preferred traits (Teklu et al., 2021). The finger millet production opportunities, farming systems, production constraints and preferred traits of the end-users are essential components for variety design and breeding strategies. Incorporating the needs and preferences of farmers would increase the adoption of new varieties of finger millet.

Farmers have a wealth of knowledge about their crops, farming systems and the constraints (Altieri, and Koohafkan, 2008) that can be harnessed through a participatory rural appraisal (PRA). A PRA is a research tool used to gather useful information on farmers and their production systems for designing intervention strategies (Mrema et al., 2016). The PRA approach provides a platform for farmers and breeders to engage in information sharing actively. Plant breeders must understand farmers' situations and choices to design appropriate varieties to meet their needs. Several studies have used the PRA approach to gain insight into farmer production systems and varietal choices to

prioritize breeding objectives, including in tef (Abraha et al., 2016), sorghum (Andiku et al., 2021), wheat (Semahegn et al., 2021), pearl millet (*Pennisetum glaucum* (L.) R. Br) (Rouamba et al., 2021) and finger millet (Mbinda et al., 2021). Studies conducted in sub-Saharan Africa have identified several major production constraints. For example, drought is a major production constraint of finger millet in Uganda (Owere et al., 2014), and sorghum production in Ethiopia (Amelework et al., 2016; Derese et al., 2017). Limited access to improved varieties and quality seed has also been reported for finger millet and sorghum in Uganda (Owere et al., 2014; Andiku et al., 2021), sorghum in Ethiopia (Derese et al., 2017), and groundnut and sesame in Ethiopia (Abady et al., 2019; Teklu et al., 2021). Other important constraints include poor soil fertility and limited arable land in sorghum production in Ethiopia (Amelework et al., 2016) and inadequate access to fertilizer in pearl millet production in Burkina Faso (Rouamba et al., 2021). However, no recent study has documented farmers' perceptions of production constraints and trait preferences in finger millet in Ethiopia. Therefore, the objective of this study was to systematically assess finger millet production systems in Ethiopia by identifying key production constraints, opportunities, and farmer-preferred traits and to inform ideotype and variety design for targeted breeding programs.

2.2 Materials and Methods

2.2.1 Description of the Study Areas

The study was conducted in 2021 in the following two finger millet growing regions in Ethiopia: The Southern Nation Nationalities People Region (SNNPR) and Oromia (Figure 2.1). In SNNPR, two districts, namely, Atote Ulo and Wera, were selected, while four districts (Shala, Siraro, Habro and Daro Lebu) were identified in the Oromia region for the study (Figure 2.1; Table 2.1). The geographical and climatic information for the study areas is presented in Table 2.1 (NMAE, 2021). The study areas fell within the mid to high altitude range between 1200 and 2400 m above sea level. The temperatures (°C) ranged between 12.5 and 29.1 °C with moderate to high mean annual rainfall of between 781.8 and 1103.6 mm $year^{-1}$.

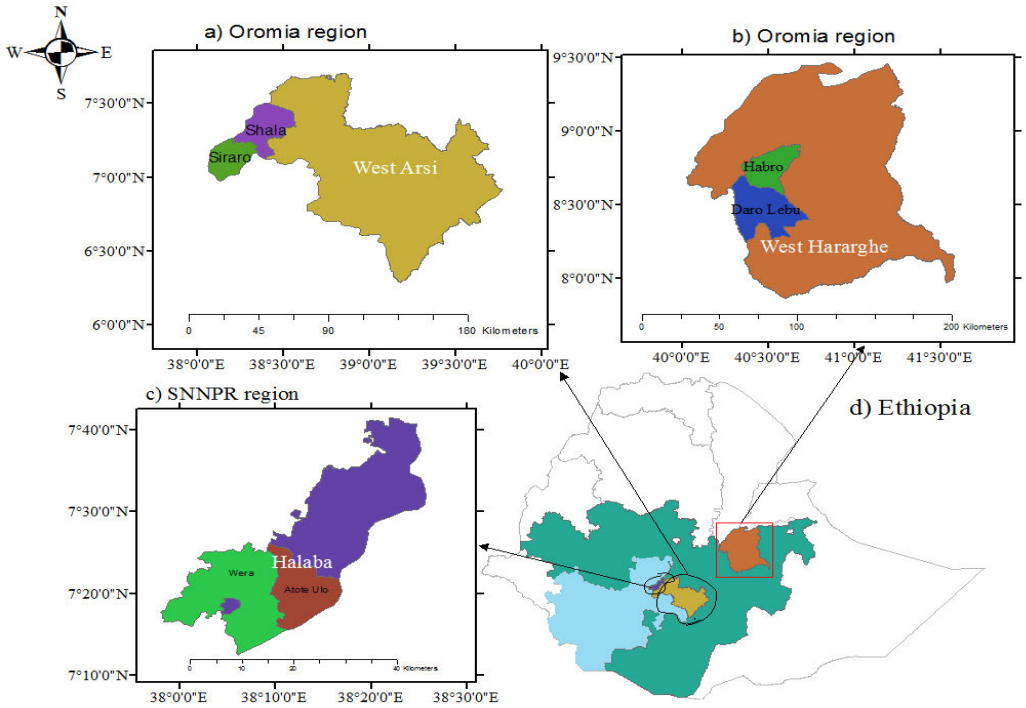


Figure 2.1. Geographical location of the study areas showing the regions, districts and zones.

Table 2.1. Descriptions of the study areas and number of sampled farmers for interviews and focused group discussion.

Regions	Zones	Districts	Peasant Association	Altitudinal Ranges (m.a.s.l.)	Daily Mean Temperature Ranges (°C)	Annual Rainfall (mm year^{-1})	No. of Interviewees			No. of Focused Group Discussants		
							Male	Female	Total	Male	Female	Total
Oromia	West Arsi	Shala	Awara Gema	1500–1900	12.9–26.7	781.8	10	10	20	08	07	15
			Fendi Ejersa				15	05	20	11	04	15
		Siraro	Boye Awarakasa	1500–2075	12.5–27.2	783.0	19	01	20	14	01	15
			Damini Leman				18	02	20	13	02	15
	West Hararghe	Habro	Gadisa	1500–2400	13.4–28.3	1103.6	19	01	20	14	01	15
			Kufa Kas				16	04	20	12	03	15
		Daro Lebu	Gelma Jeju	1200–2000	14.1–29.1	1076.8	16	04	20	12	03	15
			Oda Leku				20	01	20	14	01	15
SNNPR	Halaba	Atote Ulo	1st Ansha	1800–1950	13.1–27.2	787.3	16	04	20	10	05	15
			Girura Bucho				15	05	20	11	04	15
		Wera	Gedeba	1700–2300	13.7–27.3	840.8	17	03	20	12	03	15
			Kufe				19	01	20	13	02	15
Total							199	41	240	144	36	180

Note: m.a.s.l. = meters above sea level; SNNPR = Southern Nation Nationality and Peoples Region.

2.2.2 Sampling Procedures

A multi-stage sampling procedure was used to ensure a good representation of finger millet growers and the diverse agro-ecological zones in Ethiopia. The sampling process involved four sequential stages. These includes (i) selection of major finger millet regions, (ii), selection of representative districts within each region, (iii), selection of peasant associations (PAs) within each district, and (iv), random selection of individual farming households for participation in the survey and focused group discussions. Hence, a purposive sampling procedure was used to capture representative finger millet producing areas, major production opportunities and constraints and different socio-economic challenges. The purposive selection was based on the relative importance of finger millet production, agro-ecological diversity, accessibility, and the need to represent contrasting production environments and farming systems across Ethiopia.

For the study two finger millet growing regions, SNNPR and Oromia, were selected. In the SNNPR region, the study was conducted in the Halaba Zone from which two districts were selected, namely, Atote Ulo and Wera. From each district, two PAs were selected. A peasant association is locally referred to as 'Kebele', which is the smallest unit of administration in Ethiopia. This sampling provided a total of four PAs, including 1st Ansha and Girura Bucho (from Atote Ulo district) and Gedeba and Kufe (Wera district). The study was conducted in two zones in the Oromia region, including West Arsi Zone and West Hararghe Zone. From each zone two districts were selected (Siraro and Shala from West Arsi Zone and Habro and Daro Lebu from West Hararghe Zone). From Shala district, two PAs were selected (Awara Gema and Fendi Ejersa), two PAs from Siraro district (Boye Awarakasa and Damini Leman), two PAs from Habro district (Gadisa and Kufa Kas) and two PAs from Daro Lebu district (Gelma Jeju and Oda Leku).

Following the purposive selection of regions, district and PAs, lists of finger millet-growing households were obtained from local agricultural offices. Respondents were randomly selected from these sampling frames to ensure that all eligible households had an equal probability of inclusion in the study. This transition from purposive site selection to random household selection was employed to improve representativeness while minimizing selection bias.

Participant farmers were randomly selected to represent the various wealth, gender and age group in the finger millet production community. Particular attention was given to including both male and females, as well as different age and socio-economic categories, to capture diverse perspectives

of finger millet production, utilization and varietal preferences. Therefore, in each PA, 20 and 15 farmers were selected for face-to-face interview and focus group discussion (FGD), respectively, making a total of 240 and 180 participant farmers (Table 2.1). The sample size was determined to provide adequate representation across the 12 selected PAs while remaining operationally feasible for detailed household interviews and PRA activities. All selected respondents agreed to participate. In the event of non-response, replacement respondents would have been randomly selected from the same sampling frame to preserve representativeness.

Representativeness was further enhanced through the inclusion of multiple districts spanning diverse agro-ecological zones and major finger millet production systems. Potential selection bias was minimized through the use of random household selection at the final sampling stage and triangulation of information obtained through household interviews and focus group discussions. The PRA approach assumes that farmers possess reliable local knowledge regarding production practices, constraints, and varietal preferences. However, the approach may be influenced by recall bias, subjective perceptions and group dynamics during discussions. Consequently, the findings should be interpreted as reflecting farmers' experiences and perceptions within the selected study areas rather than nationally representative estimates.

2.2.3 Data Collection

Before data collection, enumerators were trained to ensure effective and efficient interviews and focus group discussions. The questionnaire was prepared in English and administered after translation to the local languages through trained enumerators. In the Oromia region, the local languages, namely, Afaan Oromo and Amharic, were used interchangeably to improve communication among researchers, enumerators and respondents, whereas in SNNPR, only the Amharic language was used. The questionnaires were pretested on a few respondents to improve clarity. Two breeders, a socio-economist, a pathologist and an agronomist were involved in facilitating and collecting data. Both primary and secondary data were collected for this study. Semi-structured questionnaire and FGD were used to collect the farmers' responses based on their 2020 finger millet farming experience. Semi-structured questionnaires were used to collect the following data: demographic attributes of the households, crops produced, roles of finger millet, improved varieties and local landraces, cropping system, seed systems, production constraints, drought coping mechanisms and farmers' varietal and trait preferences. FGDs were held to complement and confirm data gathered through interviews. The discussion topics for FGD were crops produced in the study areas, various roles of finger millet, improved varieties and local

landraces, cropping system, seed systems, crop production constraints, coping mechanisms for drought, farmers' varietal and trait preferences and cost and cash income from finger millet production. Secondary data such as long-term weather data were collected from the National Metrological Agency of Ethiopia, while altitude, major crops grown and their area coverage and productivity were collected from the respective district Bureau of Agriculture.

2.2.4 Data Analysis

The qualitative data collected were coded into a suitable category and captured with quantitative data across the variables. Both data sets were subjected to data analysis using the Statistical Package for Social Sciences (SPSS) version 23 (IBM SPSS, 2015). Descriptive statistics such as frequencies and percentages were computed using the cross-tabulation procedure. Chi-square test was applied to categorical frequency data derived from qualitative variables. Contingency chi-square tests were employed to make statistical inference at the 0.05 level of significance to assess the relationship among variables. Conversely, the quantitative data for cost-benefit analysis were summarized using Microsoft excel to calculate the ratios. Regarding the finger millet production constraints and farmers' trait preferences, they were labelled and tallied in a matrix, both in rows and columns, and the scores were obtained from pair-wise ranking based on one-to-one comparisons. The scores are equivalent to the frequency of respondents. Lastly, the scores were counted and used to conduct chi-square analysis and principal component analysis (PCA) for finger millet production constraints and farmers' trait preferences in the same order. PCA plots were developed to summarize the interrelationships of farmers' trait preference and their order of importance. Plots were done using the "FactorMineR" procedure (Lê et al., 2008) of R studio (RStudio, 2016).

2.2.5 Cost-Benefit Ratio Analysis

To appraise the monetary values of finger millet and other major crops production, the benefit to cost ratios were computed based on data collected in the study districts. The benefit to cost ratios were computed following the procedure of Adhikari (2012) and Abraha et al. (2016). Microsoft excel was used to summarize the quantitative data sets of the different variables for the cost-benefit analysis.

$$Cost\ benefit\ ratio = \frac{\textbf{Total income}}{\textbf{Total production cost}}$$

Note: the total income included grain and straw sale, while the total production costs included the costs of seeds for planting, fertilizers, labour for land preparation, weeding, hoeing, thinning, harvesting and threshing.

2.3 Results

2.3.1 Demographic Attributes

The demographic attributes of respondents and their households were summarized during the interviews (Table 2.2). There were significant differences ($X^2 = 17.8$; $p < 0.05$) in gender representation among the different districts. The majority (82.9%) were male farmers across all the study districts. The highest (15) and lowest (3) frequencies of female farmers were interviewed at Shala and Siraro, respectively.

The age groups of farmers did not show significant differences across the sampled districts ($X^2 = 11.0$, p-value = 0.36), with the majority of respondent farmers (72.5%) being between 18 and 40 years old. Only 5% of the farmers were older than 50 years, with none of the famers at Habro older than 50 years. There were significant differences ($X^2 = 38.4$; p-value = 0.000) in family sizes of respondents across the districts. Almost half (48.3%) of the respondents had households with more than five children. Habro and Wera districts had the lowest frequencies of farmers with more than five children, while Atote Ulo, Daro Lebu and Siraro had the lowest number of farmers with less than two children.

There were significant differences across districts ($X^2 = 66.1$, p-value = 0.000) in the levels of education. The highest proportion of farmers (31.3%) had attended school grades 1–5, while 24.6% had not attended any level of formal education. The highest frequency of respondents both with high school and college education was found at Wera at 10 and eight, respectively (Table 2.2).

Table 2.2. Proportion of respondents' gender, age, family size and level of education in the study districts.

Variables	Categories	Districts						Frequency	Percent
		Atote Ulo	Wera	Shala	Siraro	Habro	Daro Lebu		
Gender of household head	Female	9	4	15	3	5	5	41	17.1
	Male	31	36	25	37	35	35	199	82.9
	Chi-square test	$X^2 = 17.8$		df = 5		p-value = 0.003			
Age of household head (year)	18–40	29	31	24	31	33	26	174	72.5
	41–50	8	7	14	8	7	10	54	22.5
	>50	3	2	2	1	0	4	12	5
	Chi-square test	$X^2 = 11.0$		df = 10		p-value = 0.358			
Number of children	≤2	5	18	6	5	13	5	52	21.7
	3–5	14	8	7	11	19	13	72	30
	≥6	21	14	27	24	8	22	116	48.3
	Chi-square test	$X^2 = 38.4$		df = 10		p-value = 0.000			
Educational status of household head	Illiterate	12	5	16	4	16	6	59	24.6
	Read and write	0	2	5	2	4	3	16	6.7
	Grade 1–5	16	10	7	20	7	15	75	31.3
	Grade 6–8	4	5	6	11	6	12	44	18.3
	High school	5	10	6	2	6	3	32	13.3
	College	3	8	0	1	1	1	14	5.8
	Chi-square test	$X^2 = 66.1$		df = 25		p-value = 0.000			

Note: X^2 = chi-square test, df = degree of freedom, p-value = probability value.

2.3.2 Major Crops Grown in the Study Areas

Maize, tef and finger millet were the most important cereal crops grown in the study districts except in Daro Lebu and Habro, where sorghum was the most important and widely grown crop. There were significant differences among districts for a total area of production of finger millet (X^2 = 20.3, p-value = 0.03), maize (X^2 = 96.8, p-value = 0.000) and tef (X^2 = 28.5, p-value = 0.002). Similarly, significant variations were observed among districts for productivity of finger millet (X^2 = 64.392, p-value = 0.00), maize (X^2 = 34.255, p-value = 0.000), tef (X^2 = 31.862, p-value = 0.000) and sorghum (X^2 = 23.424, p-value = 0.009). The majority of the respondents allocated <0.25 ha of agricultural land each to finger millet (68% respondents), tef (51%) and sorghum (67%) production. About 10% of the respondents in Shala, Atote Ulo and Habro allocated a sizeable amount of land (>0.5 ha) to finger millet production. Conversely, about 83% of respondents in Siraro had a smaller land allocation (<0.25 ha) for finger millet (Table 2.3; Figure 2.2). Unlike the other main crops grown in the districts, nearly half of the respondents (46%) allocated large areas (>0.5 ha) of farmland to maize. Only 31% of the farmers in the study areas allocated <0.25 ha for maize production.

Table 2.3. Proportion (%) of respondents' farmland size (ha) allocation and productivity of major crops in the study districts during 2020/21 cropping season.

Districts	Crops											
	Finger Millet			**Maize**			**Tef**			**Sorghum**		
	Production Area (ha) of Crops and Proportion of Respondents (%)											
	<0.25 ha	**0.25–0.5 ha**	**>0.5 ha**	**<0.25 ha**	**0.25–0.5 ha**	**>0.5 ha**	**<0.25 ha**	**0.25–0.5 ha**	**>0.5 ha**	**<0.25 ha**	**0.25–0.5 ha**	**>0.5 ha**
Shala	53	38	10	15	30	55	46	43	11	100	–	–
Siraro	63	28	10	8	36	56	48	29	23	100	–	–
Atote Ulo	70	20	10	16	21	63	24	38	38	–	–	–
Wera	83	18	–	18	30	53	60	28	13	50	50	–
Habro	80	18	3	89	5	5	75	15	10	65	26	10
Daro Lebu	63	38	–	92	4	4	85	8	8	62	29	10
Mean (%)	68	26	5	31	24	46	51	30	19	67	25	8
Chi-square	X^2 = 20.3, df = 10, *p*-value = 0.03			X^2 = 96.8, df = 10, *p*-value = 0.000			X^2 = 28.5, df = 10, *p*-value = 0.002			X^2 = 4.6, df = 10, *p*-value = 0.800		
Districts	Productivity (t/ha) of crops and proportion of respondents (%)											
	<1.5 t/ha	1.5–3.0 t/ha	>3 t/ha	<1.5 t/ha	1.5–3.0 t/ha	>3 t/ha	<1.5 t/ha	1.5–3.0 t/ha	>3 t/ha	<1.5 t/ha	1.5–3.0 t/ha	>3 t/ha
Shala	25	50	25	21	29	50	100	–	–	75	25	–
Siraro	58	33	10	21	64	15	100	–	–	100	–	–
Atote Ulo	8	58	35	3	40	58	87	14	–	57	14	29
Wera	3	33	64	5	47	47	97	3	–	14	43	43
Habro	11	61	29	–	30	70	63	38	–	15	44	41
Daro Lebu	38	38	24	13	33	53	85	15	–	18	55	27
Mean (%)	24	45	31	11	42	48	90	10	–	28	41	31
Chi-square	X^2 = 64.392, df = 10, *p*-value = 0.000			X^2 = 34.255, df = 10, *p*-value = 0.000			X^2 = 31.862, df = 5, *p*-value = 0.000			X^2 = 23.424, df = 10, *p*-value = 0.009		

Note: X^2 = chi-square, df = degree of freedom, t/ha = ton per hectare and *p*-value = probability value.



Figure 2.2. Finger millet seed production in western Ethiopia (photo H. Shimelis).

The majority of the respondent farmers reported yields in the range of 1.5–3.0 t/ha for finger millet and sorghum. A higher proportion of respondent farmers (90%) reported yields <1.5 t/ha for tef. Some 48% respondents reported yields >3.0 t/ha for maize. Farmers in Wera (64%) and Atote Ulo (35%) districts achieved finger millet yields of >3 t/ha (Table 2.3) due to the favorable growing conditions. The use of different crop management methods such as weed management practices, crop rotation and row planting are the most favorable growing conditions and essential drivers for high yield gains. Furthermore, farmers in these districts had access to improved seed through the Bureau of Agriculture and research institutions, which allowed higher yield gains.

2.3.3 Roles of Finger Millet Production in the Study Areas

Finger millet is a multi-purpose crop in the study areas. It is used for household consumption, cash income, feed, construction material and combinations of the various roles of the crop. The roles of finger millet significantly varied across the study districts (X^2 = 101.55; *p*-value = 0.00) (Table 2.4). A relatively higher number of respondent farmers (38.8%) used finger millet for a combination of food, feed and cash, followed by food and feed (14.5%), food and cash (13.7%), food (11.5%) and food, cash, feed and construction material (9.7%). About 11.5% of all the respondent farmers reported using finger millet for food only, while 19.4% in Shala district reported multiple purpose uses. A relatively higher number of farmers (22.5%) in Siraro district used the crop for food only, followed by food and feed 20%). Higher proportions of respondent farmers in Wera (65%), Atote Ulo (55%), Habro (40%) and Daro Lebu (38.9%) used finger millet for a combination of food, feed and cash (Table 2.4).

Table 2.4. Proportion (%) of farmers who grow finger millet for various roles in the study areas.

Roles of Finger Millet	Districts						Mean (%)	X^2	df	*p*-Value
	Shala	Siraro	Atote Ulo	Wera	Habro	Daro Iebu				
Food	8.3	22.5	2.5	5.0	14.3	16.7	11.5			
Feed	–	–	–	–	–	–	–			
Cash	–	–	–	–	–	–	–			
Food and feed	13.9	20.0	15.0	2.5	14.3	22.2	14.5			
Food and cash	8.3	10.0	5.0	7.5	31.4	22.2	13.7	101.55	35	0.00
Food and construction material	5.6	2.5	–	–	–	–-	1.3			
Food, feed and cash	13.9	17.5	55.0	65.0	40.0	38.9	38.8			
Food, feed and construction material	11.1	12.5	5.0	5.0	–	–	5.7			
Food, cash and construction material	19.4	2.5	7.5	–	–	–	4.8			
Food, income, feed and construction material	19.4	12.5	10.0	15.0	–	–	9.7			

Notes: X^2 = chi square test; *p*-value = probability value, df = degree of freedom.

2.3.4 Socio-Economic and Environmental Factors Affecting Finger Millet Production in the Study Areas

Table 2.5 outlines the different constraints affecting finger millet production as perceived by the farmers. Constraints to finger millet production showed significant differences across the study districts (X^2 = 100.5; *p*-value = 0.00) (Table 2.5). About 41.5% of farmers reported drought stress as the foremost constraint affecting finger millet production, followed by a lack of improved varieties (12.9%), a lack of financial resources to purchase inputs (11.3%), land size limitations (10.8%), and limited access to seed (10.0%), shortage of fertilizers (5.4%), poor soil fertility (4.6%), shortage of draught power (1.3%) and labour shortage (1.3%).

Table 2.5. Proportion of farmers (%) who ranked the constraints to finger millet production in six districts of Ethiopia.

Constraints	Districts						Mean (%)	df	X^2	*p*-Value
	Atote Ulo	Daro Lebu	Habro	Shala	Siraro	Wera				
Drought stress	47.5	35.0	35.0	40.0	35.0	55.0	41.3	45	100.5	0.000
Lack of improved varieties	7.5	30.0	12.5	10.0	7.5	10.0	12.9			
Lack of financial resources	15.0	–	–	30.0	22.5	–	11.3			
Land size limitation	10.0	5.0	25.0	2.5	12.5	10.0	10.8			
Limited access to seed	10.0	–	10.0	15.0	12.5	12.5	10.0			
Shortage of fertilizers	2.5	15.0	2.5	–	10.0	2.5	5.4			
Poor soil fertility	–	12.5	10.0	2.5	–	2.5	4.6			
Shortage of draught power	–	2.5	2.5	–	–	2.5	1.3			
Labour shortage	2.5	–	2.5	–	–	2.5	1.3			
High labour costs	5.0	–	0.0	–	–	2.5	1.3			
Mean (%)	100	100	100	100	100	100	100			

df = degree of freedom; X^2 = chi-square; *p*-value = probability level.

2.3.5 Farmers' Trait Preferences of a Finger Millet Variety

Farmers' trait preferences of finger millet were assessed and compared using PCA (Table 2.6). The first three principal components with eigenvalues greater than 1.00 explained 85.3% of the total variability in the desirable attributes of finger millet. The first principal component (PC1) accounted for 44.0% of the total variation, while the second and third PCs explained 26.1 and 15.2% of the variation, respectively. High grain yield (0.99) had the highest positive loading value on PC1, followed by compact head shape (0.94), large head size (0.93), pleasing aroma and taste of food products (0.75) and 'enjera'-making quality (0.60). Tolerance to lodging (−0.89), tolerance to shattering (−0.88), high tillering ability (−0.70), brew-making quality (−0.68), medium plant height (−0.54) and disease resistance (−0.53) had negative contributions to PC1. Insect pest

resistance (0.77), early maturity (0.72), large grain size (0.7) and drought and heat tolerance (0.61) accounted for the highest variation on PC2. The ease of harvest and threshing (−0.84) had a negative loading on PC2. Only tolerance to weeds (0.84) and high marketability (−0.91) made large contributions on the third PC.

Table 2.6. Principal components and their contributions to finger millet agronomic and quality attributes reported in six districts in Ethiopia.

Variables	PC1	Contribution	PC2	Contribution	PC3	Contribution
High grain yield	0.99	12.50	−0.09	0.16	0.02	0.01
Large head size	0.93	10.86	−0.13	0.34	0.09	0.30
Weed tolerance	0.09	0.10	0.36	2.79	0.84	25.65
Disease resistance	−0.53	3.54	−0.31	2.05	0.40	5.82
Ease of harvest and threshing	−0.27	0.94	−0.84	14.87	0.36	4.85
Large grain size	0.64	5.10	0.70	10.29	0.33	4.02
Compact head shape	0.94	11.03	0.17	0.58	0.28	2.89
Insect pest resistance	−0.57	4.04	0.77	12.65	0.27	2.69
Tolerance to lodging	−0.89	9.92	−0.30	1.94	0.23	1.89
Brew-making quality	−0.68	5.87	−0.61	7.91	0.13	0.57
High tillering ability	−0.70	6.23	0.59	7.47	−0.06	0.11
Early maturity	0.59	4.34	0.72	10.87	−0.08	0.26
Pleasing aroma and taste of food products	0.75	7.13	−0.57	6.91	−0.18	1.19
Drought and heat tolerant	−0.20	0.51	0.61	8.03	−0.23	1.95
Medium plant height	−0.54	3.72	0.45	4.39	−0.26	2.47
Tolerance to shattering	−0.88	9.65	−0.09	0.18	−0.36	4.74
'Enjera'-making quality	0.60	4.46	−0.55	6.51	−0.54	10.53
High marketability	−0.07	0.06	0.31	2.08	−0.91	30.05
Eigenvalues	7.9		4.7		2.7	
% of total variance	44.0		26.1		15.2	
Cumulative variance (%)	44.0		70.1		85.3	

PC = principal component, bold face values denote high score values.

Figure 2.3 presents the variables and study areas where the variables are connected with the biplot origin through the line vectors. The plot shows that high grain yield has the smallest angle with large head size followed by compact head shape, pleasing aroma and taste of food products, 'enjera'-making quality, large grain size and early maturity. Furthermore, the variables mentioned above have an angle less than 90° with high grain yield. On the other hand, the rest of the variables have an angle greater than 90° with high grain yield.

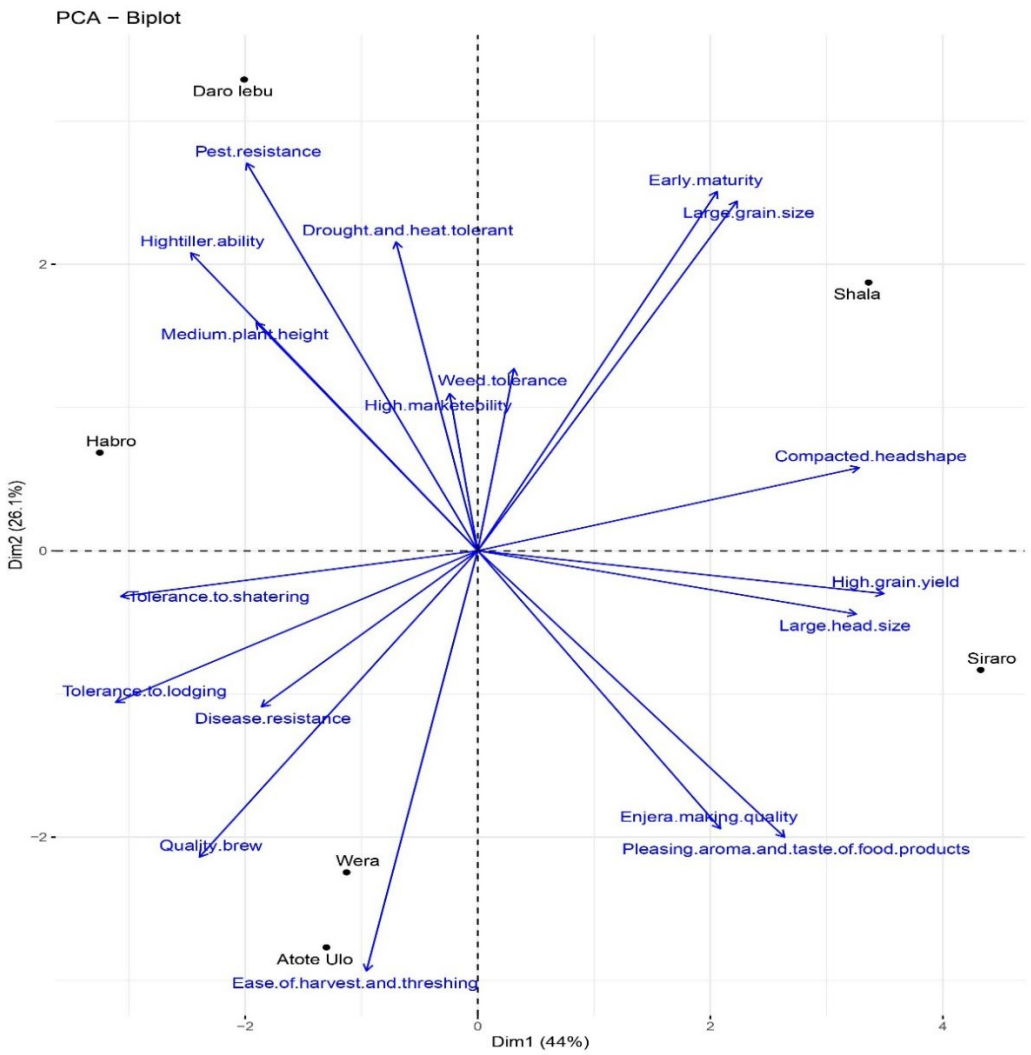


Figure 2.3. Biplot showing the interrelationships among the variables.

2.3.6 Crop Management Practices in Finger Millet Production

Respondent farmers reported the common crop management practices of finger millet. There were significant differences in finger millet growers' management practices across the districts (Table 2.7). About 40.3% of the respondents used a combination of hand weeding and chemical herbicides to control weeds, while 59.2% used hand weeding only. The largest proportion of respondent farmers (78.8%) used hand weeding in the Daro Lebu district. Shala and Siraro districts had the highest proportion of farmers at 65 and 55%, respectively, who controlled weeds using a combination of hand and chemical methods. Finger millet was planted as a sole crop by 97.0% of farmers. In all districts, a higher proportion of finger millet farmers (75.6%) practiced crop rotation with haricot bean, green pepper and potato. In Habro district, there were a lower proportion of farmers 20%) who practiced crop rotation. Direct field sowing was the major planting method of

finger millet reported by 69.1% of respondents, followed by transplanting seedlings at 4–6 leaf stage. About 88.0% of the respondent farmers used row planting, while 12% practiced broadcasting. Some 51.4 and 15.4% of respondent farmers in Habro and Daro Lebu, respectively, used a broadcasting method of finger millet sowing (Table 2.7).

Table 2.7. The proportion (%) of respondents who used different crop management practices in finger millet production across the districts during 2020/20121 cropping season.

Districts	Crop Management											
	Weeding			Cropping System			Crop Rotation		Transplanting		Planting Methods	
	Hand Weeding	Chemical Herbicides	Hand Weeding and Chemical	Sole	Mixed	Sole and Mixed	Yes	No	Yes	No	Row	Broadcasting
Atote Ulo	55.0	−	45.0	100.0	−	−	100.0	0.0	−	100.0	100.0	−
Wera	77.5	−	22.5	100.0	−	−	100.0	0.0	−	100.0	95.0	5.0
Shala	35.0	−	65.0	91.9	2.7	5.4	100.0	0.0	100.0	−	100.0	−
Siraro	45.0	−	55.0	97.5	−	2.5	72.5	27.5	80.0	20.0	97.5	2.5
Habro	67.5	2.5	30.0	−	−	−	20.0	80.0	−	100.0	48.6	51.4
Daro Lebu	78.8	−	21.2	100.0	5.4	−	58.8	41.2	−	82.5	84.6	15.4
Mean (%)	59.2	0.5	40.3	97.0	1.7	1.3	75.6	24.4	30.9	69.1	88.0	12.0
Chi-square test	$X^2 = 30.7$ df = 10 *p*-value = 0.00			$X^2 = 12.7$ df = *p*-value = 0.24			$10X^2 = 111.3$ df = *p*-value = 0.00		$5X^2 = 203.0$ df = *p*-value = 0.00		$5X^2 = 70.4$ df = 5 *p*-value = 0.00	

Notes: X^2 = chi-square test; *p*-value = probability value, df = degree of freedom.

2.3.7 Finger Millet Varieties Grown and Sources of Seed

Attributes of varieties cultivated by the farmers

There have been 20 finger millet varieties officially released in Ethiopia since 1998. However, only a few of these varieties are presently grown in the study areas (Table 2.8), such as Tadesse, Tessema, Axum, Meba and Bareda. However, late maturity, susceptibility to disease (head blast), insect pests and shattering problems were among the released varieties' major drawbacks (Table 2.8).

Table 2.8. Lists of released finger millet varieties and landraces, their preferred traits and drawbacks reported by respondent farmers in 2020/21 cropping season.

Name of Variety or Designation	Preferred Traits	Drawbacks
Released Varieties		
Tadesse (KNE#1098)	Easy to thresh, high yielding, medium plant height, lodging resistance, compact head, large grain size, high biomass, erect tillers, good for feed	Late maturing, susceptible to insect pests and diseases, shattering problem, low human health value
Tessema (ACC#229469)	High yield, compact head, high biomass, easy to thresh	Susceptible to insect pests and diseases, late maturing, low medicinal value
Axum	High yielding, drought tolerance	Susceptible to root rot disease, low human health value
Meba	Disease resistant	Low yielding
Bareda	High yield, good biomass	Low human health value
Landraces		
Amharacha	Good food quality, insect and disease resistance, human health value	Low yield, susceptible to lodging, low biomass production
Dagusa	Good food quality, insect and disease resistant, human health	Difficult to thresh
Dima (red seed type)	Good food quality, insect and disease resistant, better in medicinal value	Low biomass
Dalecha (dark brown seed)	High tillering capacity, medicinal value	Low yielding
Ejeru	Lodging resistance, early and good 'enjera'-making quality	Susceptible to disease
Guracha (black seed)	Good for 'enjera' and high yielding	Susceptible to drought
Habesha	Good food quality	Low yield
White	High yield and good for 'enjera'-making	Susceptible to disease, late maturing

Farmers also cultivated landrace or local finger millet varieties (Table 2.8). The main distinguishing features used in the selection of the local varieties were local names and seed colour. Respondent farmers preferred the landraces for their higher perceived nutritional and human health values than the released varieties. The farmers mentioned that the local finger millet varieties are also preferred for their tolerance to disease and insect pests. However, the local landraces are cultivated on small areas because they have low yield and biomass production, susceptibility to lodging and are difficult to thresh. The harvested seed from the local landraces is not true-to-type due to genetic admixtures.

Sources of Finger Millet Seed

There were significant differences ($X^2 = 191.597$, p-value = 0.000) among respondent farmer seed sources (Table 2.9). The Bureau of Agriculture (BOA) was the primary source of finger millet seed. About 49.1% of respondent farmers across the districts accessed seed from the BOA. In the Atote Ulo and Wera districts, 88 and 93% of respondents, respectively, used BOA as their seed source.

The next important source of seed was farmer-to-farmer exchange. On average, 22% of the respondents used seed obtained from other farmers. Daro Lebu (reported by 50% of respondents) and Siraro (35%) had the highest frequencies of farmers who exchanged seed with other farmers. Research institutions such as the Ethiopian Institute of Agricultural Research (EIAR) and Oromia Agricultural Research Institute (OARI), local producers and self-saved seed were also mentioned as seed sources by 32, 28 and 22% of respondents at Shala, Siraro and Habro, in that order (Table 2.9).

Table 2.9. The proportion (%) of respondents and corresponding seed sources of finger millet varieties in the study districts in 2020/21 cropping season.

Seed Sources	Districts						Mean (%)
	Atote Ulo	Wera	Shala	Siraro	Habro	Daro Lebu	
Research institutions	5.0	–	32.0	–	2.7	–	5.8
Bureau of Agriculture	87.5	92.5	35.50	22.5	35.1	15.8	49.1
Local producers	2.5	2.5	6.50	27.5	2.7	2.6	7.5
Farmer-to-farmer seed exchange	2.5	–	22.60	35.0	24.3	50.0	22.1
Own saved seed	-	5.0	–	–	21.6	18.4	7.5
Cooperatives	2.5	–	–	–	–	–	0.4
Local market	–	–	–	7.5	5.4	7.9	3.5
Unknown source	–	–	3.20	7.5	8.1	5.3	4.1
Chi-square test	$X^2 = 191.597$, df = 35, *p*-value = 0.000						

2.3.8 Cost-Benefit Analysis of Finger Millet in the Study Areas

The economic importance of the major crops grown in the study areas was assessed through cost-benefit analysis. In this regard, the principal crops were compared concerning achieved yield (t/ha), total income realized from sales of grain and straw in United States dollars per hectare (USD/ha), total production costs (USD/ha), revenue (USD/ha) and benefit to cost ratios. The highest grain yield (3.00 t/ha) was obtained from finger millet followed by maize (2.93 t/ha) and sorghum (2.20 t/ha). Conversely, tef had the least yield (0.65 t/ha) followed by haricot bean (1.74 t/ha). The total income (USD/ha) generated from finger millet was the highest at 2139 USD/ha followed by sorghum (1612 USD/ha) and haricot bean (1033 USD/ha). Total income generated from haricot bean and maize sales were 1033 and 1003 USD/ha, respectively, lower than the average price of all crops (1329.8 USD/ha) (Table 2.10).

The total cost of finger millet production (1249 USD/ha) was at least twice as high as the average cost of production of all other crops grown (691.6 USD/ha) in the study areas. Sorghum was the most profitable crop, with an average profit of 923 USD/ha, followed by finger millet (890

USD/ha). Tef growers realized significantly lower profits of 353 USD/ha, while maize growers attained the least profit of 259 USD/ha (Table 2.10).

The principal crops were also compared in terms of benefit/cost ratio. On average, haricot bean producers with a higher benefit to cost ratio of 3.85 had the highest benefit, followed by sorghum growers (2.34). The benefit/cost ratios for finger millet, tef and maize were 1.71, 1.69 and 1.35, respectively. The significant costs of finger millet production were the costs of the seed for planting, fertilizers, labour for land preparation, weeding, hoeing, thinning, harvesting and threshing.

Table 2.10. Income, cost and cost-benefit analysis of finger millet and other major crop production in the 2020/21 cropping season in the study districts.

Crops	Price of Grain (USD/ton)	Grain Yield (t/ha)	Income from Grain Sell (USD/ha)	Income from Straw Sell (USD/ha)	Total Income (USD/ha)	Total Production Cost (USD/ha)	Profit (USD/ha)	Benefit/Cost Ratio
Finger millet	630.67	3.00	1892.00	247.00	2139.00	1249.00	890.00	1.71
Haricot bean	566.67	1.74	986.00	47.00	1033.00	268.00	765.00	3.85
Maize	303.75	2.93	890.00	113.00	1003.00	743.00	259.00	1.35
Sorghum	646.36	2.20	1422.00	190.00	1612.00	689.00	923.00	2.34
Tef	1189.23	0.65	773.00	89.00	862.00	509.00	353.00	1.69
Mean	667.30	2.10	1192.60	137.20	1329.80	691.60	638.00	2.19

2.3.9 Cultural Practices to Cope with Low Moisture Stress

The respondent farmers developed a range of agronomic solutions to finger millet production challenges, mainly drought stress (Table 2.11). As a result, farmers in the study areas used various cultural methods to cope with moisture stress. Ploughing varied in terms of frequency, depth and date as a moisture stress coping strategy. Hoeing at the right stage, weed control and supplemental irrigation, if available, were also used to mitigate moisture stress. Moreover, adjustment of sowing dates, tie ridging and relatively deep sowing were used to manage moisture stress. Farmers planted at higher than recommended seeding rates to attain optimal plant populations. Varietal selection, application of inorganic fertilizers and the use of mulching and cattle dung were also used to manage moisture stress (Table 2.11).

Table 2.11. Various methods used by finger millet growers to cope with moisture stress, reported during the focus group discussion.

Methods to Cope with Moisture Stress	Perceived Advantages
High ploughing frequency before the onset of rainfall	Assists in infiltrating the available soil moisture, exposure to sunlight of eggs of insect pests present in the soil.
Deep ploughing by using tractor	Improves moisture-holding capacity of the soil, exposure to sunlight of eggs of insect pests present in the soil
Early ploughing and land preparation as soon as the onset of the first rain shower after harvesting	Effective use of the available soil moisture
Hoeing at the right stage	Maintains the available soil moisture
Weed control	Protects the crop from the competition of the soil moisture and other nutrients
Irrigation if available	Provides supplemental moisture required by the crop
Adjustment of sowing date	Manages flowering time so as not to coincide with drought times and utilizes the available soil moisture
Sowing in tie ridging	Holds available soil moisture
Row planting	Manages the appropriate plant population
Sowing the seed relatively deep in the soil	Assists the seed to access the available soil moisture for germination
Use of higher seed rate than the recommended one	Assists to get the required plant population during low moisture period
Soil mulching using different grass species	Increases soil fertility and water holding capacity and lowers soil temperature
Use of cattle dung and application of urea fertilizer after the first weeding and when there is a relatively good soil moisture	Increases soil fertility and moisture-holding capacity and provides healthy and vigorous crop to cope with low moisture stress period
Varietal selection	Better and cheap alternative to alleviate the problem of low moisture stress

2.4 Discussions

2.4.1 Demographic Attributes

The demographic characteristics of the respondents were documented (Table 2.2) because they influence farming practices, intervention strategies and technology adoption among farming communities. The most significant proportion of respondents were male, which is concomitant with the fact that most households in the study area were male headed (Table 2.2). Patriarchy is dominant in the study area, with a negligible number of females having decision-making powers. This gender disparity was evident not only in household headship but also in participation in key agricultural activities. During focus group discussions, women consistently reported having limited influence over decisions regarding variety choice, input purchases, and the marketing of

finger millet, despite their active participation in weeding, harvesting, and processing. For instance, in all six districts, FGD participants noted that men predominantly made decisions on the sale of finger millet grain, while women often had to negotiate for a share of the income to meet household food needs. The disenfranchisement of females, as discovered in other PRA studies, also reflects their peripheral roles in decision-making in agricultural activities and their ongoing exclusion from social services such as training and agricultural extension services (Aazami et al., 2011), despite their active participation in farming operations such as ploughing, weeding and harvesting. In this study, women's participation in extension training was reported to be significantly lower than men's, with only 12% of female respondents having attended any agricultural training in the past 3 years, compared with 68% of male respondents. This disparity has implications for technology adoption, as women may lack access to information about improved varieties and agronomic practices.

In terms of age, most of the interviewed farmers were within the active age group of 18–40 years (Table 2.2). This group consists of young and middle-aged adults that participate in the economy by providing labour and engaging in economic activities, such as trade, and in decision-making. The young adults in this group can adopt new agricultural technologies, given their higher literacy level and potential openness to innovation (Jerop et al., 2018). Middle-aged adults in the active, productive group were involved in decision-making and influenced choices of agricultural technologies, which, in turn, have an impact on crop production and productivity (Mrema et al., 2016).

The respondent farmers had large families of more than five children per household, which positively impacts the provision of labour for crop production but is a concern for food security in the study districts. Large families provide readily available labour for farming activities in subsistence farming systems because the farmers cannot afford to hire external labour (Derese et al., 2017). Smaller households struggle to implement essential activities such as ploughing and weeding, given that most operations in smallholder farming are manual. Provision of labour is also related to the age of family members. Families composed mostly of young children struggle to provide the required labour. However, large families require more food for sustenance, and the risk of food insecurity increases in subsistence farming, where crop productivity is generally low. Tadele (2017) noted that large families have an adverse impact on food security, especially in Africa, where the population growth rate is very high.

The low literacy levels among the sampled farmers are of concern, especially for the successful introduction of new technologies and dissemination of information. A low level of education has been identified as a significant factor leading to poor adoption of agricultural technologies and access to information in rural and smallholder farming communities. Interventions such as farmer training and information provision have a lower impact on agricultural systems where farmers have low literacy levels (Aazami et al., 2011; Tadesse et al., 2021). Farmers with higher literacy are more likely to adopt improved technologies and improve their farming practices to increase crop productivity and have the potential to engage in more profitable markets or negotiate better prices with service providers (Jerop et al., 2018; Mengistu et al., 2018).

2.4.2 Dominant Crops Cultivated in the Study Areas

Crop production was dominated by maize and finger millet (Table 2.3), consistent with previous reports showing that smallholder farmers cultivated mainly maize and other cereals crops (Sime, and Aune, 2018). The land allocated for finger millet production by a household was equivalent to the national average of 0.25 ha (17 CSA, 2017), showing that the selected study sites could represent finger millet production systems in Ethiopia. The production of finger millet is essential for mitigating the impact of drought stress on food security. Finger millet is more drought tolerant than crops such as maize. However, the dominance of cereals is a concern for nutritional security. Cereal-based diets are carbohydrate-rich, leading to hidden hunger caused by deficiencies in essential nutrients such as specific amino acids, minerals and vitamins. Finger millet, and sorghum to an extent, are high in micronutrients, and farmers in the study areas get the various health benefits in their food sources from the two crops. The farmers reported trading their grains for cash income generation to buy other foods containing proteins, vitamins and minerals to supplement their cereal diets. However, low productivity and a lack of surplus grain yield frequently limit potential income generation. Yields below 1.5 t/ha have been commonly recorded in the study areas, below the national average for all crops. The dominance of maize in production systems of the study areas has been enhanced by its potential due to its early sowing dates, where green maize is grown to avert food shortages in the lean season (when the previous season's grain harvest becomes depleted but the new crop is not available), and its relative ease of marketing compared to finger millet or other cereals.

2.4.3 Various Uses of Finger Millet

Foremost, finger millet is used as a food crop in the study areas (Table 2.4). It is commonly ground into flour for making leavened bread known locally as 'enjera'. However, finger millet has relatively poor 'enjera'-making qualities and the farmers usually blend the finger millet flour with maize flour. Alternatively, finger millet is coarsely ground to make porridge. However, porridge made from finger millet is not common in Habro and Daro Lebu districts, where the farmers mentioned that they do not use finger millet to make porridge. Cultural differences and access to information influence the uses of finger millet. Training and awareness campaigns on the potential uses of finger millet and bio-fortification of finger millet could improve its utilization and contribute to food security.

Finger millet straw is also vital for livestock feed (Table 2.4). The farmers have small land holdings, and their livestock are raised on communal grazing lands. After harvest, the livestock are allowed into the fields to graze on crop residues. Most of the farmers in the study areas harvested the stover to feed the livestock when there was scarcity. While this stover's nutritional value and palatability are relatively low relative to a green fodder crop (Feedipedia 2019), its impact on animal health is vital given the lack of alternative grazing in the dry season. Mululam and Melak 2013) reported that 69% of farmers in North-Western Ethiopia used finger millet straw for animal feed, while 12% used the straw as a construction material. Studies in China showed that the replacement of other straws like corn straw with finger millet straw improved the growth of sheep and was recommended in fattened lamb production (Chen et al., 2020).

2.4.4 Socio-Economic and Environmental Factors Affecting Finger Millet Production

While the ranking of the importance of production constraints varied across the districts, erratic rainfall, a lack of improved varieties, a lack of financial resources to procure inputs, land shortages, a limited supply of seeds of improved varieties, a lack of access to fertilizers and declining soil fertility were the most common challenges affecting finger millet production (Table 2.5). Erratic rains were also identified as a major production constraint in Kenya (Mwenda et al., 2019), Myanmar (Mar et al., 2018) and Ethiopia (Abeje, and Alemayehu, 2019; Wendimu, 2021). A lack of financial resources has been previously identified as the single most crucial socio-economic challenge affecting crop production in most sub-Saharan African countries (Kayira, 2019). Limited access to agricultural inputs such as fertilizers, pesticides and improved seeds is related to limited financial resources and has been widely reported in Africa (Tadele, 2018) and,

particularly, Ethiopia (Mesfin, and Zemedu, 2015; Yimer, and Babege, 2018; Tadesse et al., 2021).

Smallholder farmers face a multitude of production constraints that limit crop productivity. Biotic and abiotic constraints, such as pests and diseases and declining soil fertility, may be mitigated with breeding for varieties with the necessary resistance or tolerance level to support crop production in stress-prone environments. On the other hand, socio-economic constraints can be rectified by implementing necessary policy changes, training intervention and improving extension services. Both policy regulations to improve the socio-economic environment and breeding are still lagging, which significantly compromises crop production in general, particularly finger millet.

2.4.5 Farmers' Trait Preferences of a Finger Millet Variety

The most desirable traits of finger millet were compared and their order of importance were assessed via PCA. The biplot shows the interrelationship among the variables. The cosine of the angle between the vectors of two variables is almost equal to the correlation coefficient between them (Yan, and Kang, 2003). The angle between the two variables is an indication of how closely or distantly related the variables are. Therefore, the smaller the angle between them the stronger the relationship they have and vice versa. Comparison of the angles in Figure 2.3 and the principal component analysis of Table 2.6 showed a high correspondence between them. Identifying farmer-preferred traits is an essential step for variety design and development. High grain yield, '*injera'*-making quality, large head size and compacted head shape can be prioritized in variety development to meet the aspirations of the farmers (Table 2.6). The inclusion of farmer-preferred traits in variety development is essential to promote cultivar adoption but also to mitigate production constraints. Traits such as insect pest and disease resistance and drought and heat tolerance are vital for inclusion in new varieties, given that the farmers alluded to the impact of biotic and abiotic constraints on finger millet production (Table 2.6). While the ranking of farmer-preferred traits varied across the districts, the identified traits were consistent and could potentially be pyramided into a single variety. After identifying farmer-preferred traits in finger millet, the next step would be to understand the genetic basis of the traits and devise suitable strategies for their improvement in new cultivars. Traits such as high grain yield and drought tolerance are quantitative traits that are difficult to improve due to their polygenic nature and high environmental variance. They will require the collection of diverse genetic resources for evaluation and selection to develop suitable varieties**.** For traits such as blast disease resistance,

additive gene action has been predominant for finger millet and showed that progress would be made through recurrent selection (Owere et al., 2016).

Similarly, traits like high '*enjera'*-making quality are likely to be governed by a few major genes; the selection process and variety development may be relatively easier and faster than high yield and drought-tolerant variety development. Given that farmers desired multiple traits in a single finger millet variety, breeding an ideal variety will not be a straightforward process. This complexity arises because the simultaneous improvement of multiple farmer-preferred traits depends on their genetic and phenotypic relationships. While traits such as grain yield, large and compact head size, and market-preferred grain characteristics are often positively associated. However, trade-offs may occur between early maturity, drought adaptation, and yield potential under certain environments. Therefore, the development of an ideal finger millet variety requires a balanced multi-trait selection strategy that exploits favourable correlations while minimising undesirable genetic associations among target traits (Ceccarelli and Grando, 2007; Lule et al., 2012; Varshney et al., 2020). This process of soliciting information from farmers can be conducted periodically and iteratively at all stages of variety design to incorporate new ideas and insights and respond to changes in environment and lifestyle. Owere et al. 2014) also reported that high grain yield, compact head shape and early maturity were the most preferred attributes of finger millet. Likewise, high yield, drought tolerance, early maturity and big heads were key farmer-preferred traits reported by Ojulong et al. (2017) and Tracyline et al. (2020).

2.4.6 Cropping Patterns of Finger Millet and its Management Practices

Weed control was one of the major tasks carried out by farmers, and the use of manual labour to control weeds is both inefficient and time-consuming (Table 2.7). The combination of herbicides and manual labour is more efficient but was limited by the farmers' shortage of inputs and lack of financial resources. Finger millet was planted as a sole crop, which agreed with another report showing that finger millet is commonly grown as a sole crop (Tsehaye et al., 2006). Unlike maize, which is sometimes intercropped with legumes, there are very few cases where finger millet is intercropped with legumes. The most common practice is to rotate finger millet with other cereals or legumes, which farmers in the study areas practiced. During group discussions, the respondents pointed out that finger millet was planted as a sole crop but in rotation with haricot bean and hot pepper. In addition to crop rotation, farmers used double cropping systems involving tef and haricot bean. However, the double cropping system was not possible with finger millet because the currently cultivated finger millet varieties are too late-maturing to fit into a double cropping

system. Developing and deploying early maturing varieties would facilitate its inclusion in a double cropping system for enhanced food production.

2.4.7 Seed Source of Finger Millet

Currently, there is a poorly developed seed system industry for finger millet in Ethiopia. A significant dependence on BOA and farmer-to-farmer seed exchange is linked to poor access to seeds of improved varieties (Table 2.9). Farmer saved seeds are not pure, have low germination rates and often carry seed-borne diseases (Mamiro, and Clement, 2014), contributing to yield losses. While the BOA was a seed source for most farmers, it often has limited supplies and cannot reach all the farmers simultaneously for planting. It is imperative that as breeding programs commence, they can be developed in parallel with a commercial seed system to ensure efficient and effective distribution. There are also few registered finger millet varieties in Ethiopia despite the importance of finger millet as a crop. This is concordant with previous reports on the neglect of traditional cereals in breeding programs compared to crops such as maize and wheat. Of the 23 released varieties, only five were in production, which begs the question why the farmers poorly adopt them. A possible reason is lack of farmer involvement in previous breeding programs that focused on product development with little regard to farmer input. Recently, most programs have developed varieties that were high yielding but lacked other vital and complementary attributes desired by farmers, leading to their rejection by the market. In this regard, Jerop et al. (2018) reported that the significant seed sources of finger millet in Kenya were self-saved seed and the government extension program, which corroborate the findings of this study. Tsehaye et al. (2006) reported that most farmers in Northern Ethiopia also used self-saved seed or obtained seed from the local informal market.

2.4.8 Cost-Benefit Analysis of Finger Millet in the Study Areas

The high cost of production for finger millet was probably driven up by the high labour costs for weeding due to its susceptibility to weed competition during its early stages of growth. Manual weeding was practiced at a higher frequency for finger millet than other crops, requiring more man hours and increasing production costs. In addition to weeding, harvesting and threshing of finger millet are tedious and labour-intensive. In general, weeding, harvesting and winnowing were the significant labour demanding tasks in finger millet production. Even though finger millet is a highly profitable crop (890 USD/ha), the respondents expressed reluctance to produce it on a large scale, citing the high labour requirements as an impediment. Higher labour requirements for

finger millet production than other crops have been identified as a major deterrent to its production, productivity and market potential (Rouamba et al., 2021). In India, the average cost of production for finger millet was estimated to be 544.3 USD/ha, with average yield productivity of 1.44 t/ha and a net profit of 138.1 USD/ha (Kaushal and, Choudhary, 2020). The cost-benefit ratio calculated for finger millet was similar to 1.05 reported by Adhikari 2012) and within the range of 1.05–2.15 that was reported by Kaushal and Choudhary (Kaushal and, Choudhary, 2020). There is a need to increase the benefit to cost ratio to motivate the farmers to adopt finger millet production. Improved resistance to weeds, increased thresh ability and early maturity would reduce labour costs associated with the respective agronomic practices and encourage farmers to adopt the crop. Therefore, there is a need for finger millet improvement to deliver high yielding and farmer-preferred varieties to enhance the economic benefits of the crop. Maize is one of the major crops in Ethiopia, including in the study areas. Nevertheless, farmers are not deriving profits from the production and marketing of this crop due to various reasons. The primary reason is that, in the country, the grain prices of maize are unpredictable due to the high market supply during the production season. This condition is the major constraint for maize farmers given that most of them have access to the local markets to sell maize (Abera et al., 2013). In addition, there are no adequate postharvest infrastructures in the country, including transport, storage and processing.

2.4.9 Cultural Methods to Cope with Low Moisture Stress

Production of drought-tolerant crops such as finger millet has been promoted as a strategy for climate change mitigation (Lule et al., 2012b). Farmers in the study areas were aware of climate change, its adverse effects and possible mechanisms to cope with its effects. As a result, they used various strategies to cope with low moisture stress to minimize crop loss and food insecurity. These included various soil moisture conservation and soil fertility enhancement technologies (Table 2.11). The frequency, depth and period of ploughing and the timing of crop management practices such as planting, weeding, and adjusting plant population were used to mitigate the impact of moisture stress, with various levels of success. Similarly, during the period of low moisture stress, most farmers in South and North Welo grew early maturing sorghum to escape drought stress (Amelework et al., 2016). The breeding of short duration finger millet varieties would also help the crop to escape drought stress. Mulching and the use of tie ridges were practiced because these practices are commonly used for moisture conservation. Early planting, use of organic inputs, adoption of new tillage practices and applying tied ridges have been previously reported among strategies used by smallholder farmers to mitigate the impact of low soil moisture (Yvonne et al., 2016).

2.5 Conclusions

Finger millet is one of the staple food crops in Ethiopia, but its productivity is constrained by a range of biotic and abiotic stresses and socio-economic factors. Drought stress was considered to be the most important constraint in all the districts, followed by a lack of farmer preferred improved varieties, limited access to seed and a lack of financial resources. Land size limitations, poor soil fertility and a lack of access to fertilizers were also ranked important constraints affecting finger millet production. The most critical farmer-preferred traits in finger millet were high grain yield, compact head shape, 'enjera'-making quality, high marketability and early maturity. Therefore, to enhance finger millet productivity, plant breeding aimed at solving the above-mentioned production constraints and incorporating the farmer-preferred traits needs to be undertaken in Ethiopia.

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Chapter 3. Profiling Ethiopian Finger Millet (*Eleusine Coracana*) Accessions for Major Agronomic Traits and Nutrient Composition under Varying Growing Conditions

Abstract

Finger millet (*Eleusine coracana* L. Gaertn) is a drought-resilient cereal with notable agronomic and nutritional value, yet remains underutilized due to limited research and product development. The objective of this study was to evaluate and characterise genetically diverse Ethiopian finger millet accessions for agronomic performance, drought response, and grain nutritional compositions under contrasting moisture regimes, and to identify superior genotypes for use in breeding and/or production. This study evaluated 448 Ethiopian accessions (landraces and improved varieties) for agronomic performance, drought responses and nutrient composition across three moisture regimes: non-stressed (Arsinegelle: AN), moderately drought-prone (Maitsebri: SH), and severely drought-stressed (Meiso: MI). Field trials employed a row-column design (64×7 with two replications). Significant ($P < 0.001$) effects of genotype, environment, and genotype × environment interaction were detected for all traits. Grain yield (GY) declined by ~60% at MI site. The test genotypes varied considerably at MI for key traits: days to 50% flowering (DF) (78.5–107.5 days), days to maturity (DM) (101.0–149.5 days), grain yield (GY) (0.5-3.2 t/ha), grain iron (53.6 – 81.0 ppm) and grain zinc (67.8-83.1 ppm) suggesting considerable genetic variation for selection. Black-seeded genotypes maintained higher GY and Fe/Zn under drought, while red-seeded types flowered and matured earlier and produced larger seed size. Broad-sense heritability exceeded 60% for drought tolerance (Drt) score, DF, and DM, but remained below 30% for plant height, starch content and GY. GY was negatively correlated with DF, DM, Drt and stay-green traits, but positively correlated with seed weight across environments. Principal component analysis explained >67% of the variance in key traits across test sites, and hierarchical clustering grouped genotypes into four clusters. Eight accessions (G141, G423, G297, G247, G171, G204, G294, and G46) were identified as promising candidates for breeding and further validation through multi-environment testing and variety evaluation procedures prior to potential release.

Key words: Agronomic traits, Cluster analysis, drought tolerance, Finger millet, grain colour, nutritional composition, principal component analysis

3.1 Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn.; 2n = 2x = 18) is an underutilized but high-potential cereal crop valued for its resilience to climate stress and superior nutritional profile. It is naturally gluten-free and rich in calcium, iron, dietary fibre, essential amino acids, and phytochemicals, including polyphenols, flavonoids, and antioxidants (Devi et al. 2014; Chandra et al. 2016; Gebreyohannes et al. 2021, 2024; Kaur et al. 2024). The crop is well-adapted to arid and semi-arid regions, tolerating heat and drought stress (Ceasar et al. 2018; Kudapa et al. 2023).

Globally, finger millet is cultivated on approximately 2.1 million hectares, producing an estimated annual yield of 3.7 million tons (FAOSTAT 2022; Indiastat 2022). It accounts for around 20% of the global millet cultivation area and 26% of total production (Gebreyohannes et al. 2024). In East Africa, it serves as a multipurpose crop for food, feed, and beverage production (Hilu et al. 1979; Tesfaye and Mengistu 2017). In Ethiopia, its grains are used to make traditional alcoholic and non-alcoholic drinks, as well as unleavened bread. The straw is also valued for animal feed and roofing material (Tsehaye et al. 2006; Lule et al. 2012). In Tanzania and Uganda, finger millet flour is used to prepare a staple food such as porridge and traditional beverages including ‘togwa’, ‘obushera’, and ‘obutoko’ (Mugula et al. 2003; Mukisa et al. 2010, 2012). These diverse uses underscore its relevance for food security, health, and economic development (Hawaz et al. 2025).

The market potential of finger millet is rapidly increasing due to its exceptional food value and superior nutritional profile, which provides valuable human health benefits (Devi et al. 2014; Chandra et al. 2016). Lifestyle changes and consumer preference for healthy and alternative nutrient-dense crops drive a shift from traditional staple crops to economical and nutritious food and feed sources, such as finger millet. The demand for finger millet products highlights the need for product diversification, strategic marketing, and commercialisation (Mugula et al. 2003; Tsehaye et al. 2006; Lule et al. 2012; Mukisa et al. 2012). Designing value-added products would leverage the crop’s benefits, with the potential of amplifying its market value and stimulating economic growth. Therefore, there is a need for targeted research and development on finger millet that would include the design of market-preferred varieties integrating both climate resilience and superior nutritional profiles.

Finger millet grain productivity remains below 1 ton/ha in Africa and Asia, far less than the attainable yields reaching 6 to 8 tons/ha (Gebreyohannes et al. 2021; 2024). This yield gap arises from a complex interplay of biotic, abiotic, and socio-economic factors (Sasmal 2018; Mukami et

al. 2019; Mahapatra et al. 2021; Mbinda et al. 2021). Lack of high yielding varieties, severe recurrent drought, fungal disease (e.g. blast caused by *Magnaporthe grisea* [Barr] and insect pests (e.g. grasshoppers, shoot flies [*Atherigona soccata* [Rondani]]), pink stem borer (*Sesamia inferens* [Walker]), root aphid (*Tetraneura nigriabdominalis* [Sasaki]) and aphids (*Aphidoidea*)) are the major constraints to sustainable production and yield gains (Sasmal 2018; Mbinda, and Masaki 2021; Mbinda, and Mukami 2021; Mahapatra et al. 2021; Mbinda et al. 2021).

Recurrent and severe drought conditions are the major production constraint of dryland millets, curtailing yield and quality (Maqsood and Ali 2007; Mukami et al. 2019). For example, yield losses ranging from 40 to 77% were reported in finger millet due to drought stress (Maqsood and Ali 2007; Khatoom and Singh 2016). Drought stress disrupts key physiological processes such as photosynthesis, stomatal regulation, and nutrient uptake, leading to premature senescence and impaired growth. Its agronomic consequences include delayed flowering, shortening grain filling, reduced biomass, and poor yield stability with the severity depending on whether stress occurs at pre- or post-flowering stages (Maqsood and Ali 2007; Ceasar et al. 2018; Mukami et al. 2019; Sood et al. 2019). These adverse effects highlight the need to evaluate finger millet across diverse environments to identify genotypes with adaptive resilience and stable productivity under varying water stress conditions.

A lack of and poor adoption of improved finger millet varieties with desirable product profiles, including enhanced climate resilience, high-yielding capacity and superior nutritional profiles, limits sustainable crop production. Also, poor access to agricultural inputs and inadequate infrastructure contribute to the persistent yield disparities (Owere et al. 2014; Jerop et al. 2018). Therefore, to mitigate the above multifaceted constraints, there is a need for strengthening research and development investment, multi-institutional collaboration, and an inclusive innovation system that integrates breeding, agronomy, and socio-economic interventions. A strategic approach that leverages the rich genetic diversity of finger millet genetic resources is critical to mitigate production constraints and bridge the yield gap.

Finger millet is believed to have originated in the East African highlands, with both Ethiopia and Uganda recognised as primary centres of genetic diversity (Harlan 1971; Hilu et al. 1979; Tsehaye et al. 2006; Tesfaye and Mengistu 2017). The Ethiopian Institute of Biodiversity maintains an estimated 2200 collections of finger millet genetic resources, which were collected from the diverse agro-ecologies (i.e., Tigray, Amhara, Oromia, Benishangul & Gumuz and the Southern

Nations, Nationalities and Peoples' Region) of the country. Also, the Ethiopian Institute of Agricultural Research (EIAR)-Melkassa Agricultural Research Centre maintains an additional set composed of 400 accessions (EBI 2024; Gebreyohannes et al. 2024). These collections are composed mainly of landraces, crop-wild relatives (i.e., *E. coracana* subsp. Africana) and released varieties offering a vital genetic reservoir for enhancing yield, drought tolerance, and nutritional quality. Hence, the diverse genotypes should be systematically characterised for breeding climate-resilient and nutritious cultivars (Tsehaye et al. 2006; Assefa et al. 2013; Brhane et al. 2017; Dida et al. 2021).

Despite Ethiopia being recognised as one of the primary centre of origin and diversity for finger millet, the country's extensive germplasm resources remain largely underexploited for crop improvement (Hillu et al., 1979; Tsehaye et al., 2006; Dida et al., 2021). Previous studies were generally limited in germplasm coverage, environmental representation, and trait scope, focusing predominantly on agronomic performance while giving comparatively less attention to drought adaptation, grain nutritional quality, and their interactions across environments (Chemeda and Gemechu 2010; Bezaweletaw 2011; Tesfaye, and Mengistu 2017; Lule et al. 2018; Anteneh et al. 2019). Consequently, critical information on the magnitude of genetic variability, genotype x environment interaction, and nutritional traits remains inadequate. This knowledge gap impedes the effective utilisation of Ethiopian finger millet genetic resources in breeding programmes to address climate change, food insecurity, and malnutrition. Therefore, a more comprehensive assessment involving a larger and more diverse germplasm of finger millet genetic resources across representative growing environments is required to appraise useful genetic variants for economic traits and diverse market segments. The objective of this study was to evaluate and characterise genetically diverse Ethiopian finger millet accessions for agronomic performance, drought response, and grain nutritional compositions under contrasting moisture regimes, and to identify superior genotypes for use in breeding and/or production. The research aims to assess unique genetic resources and vital data to develop drought-resilient and nutritionally enhanced varieties.

3.2 Materials and methods

3.2.1 Plant materials and the study sites

The study used 448 finger millet accessions, and they were purposefully selected based on three explicit criteria. First, geographic spread: accessions were sourced from five major finger millet

growing regions of Ethiopia; namely, Tigray, which comprised of the highest accessions at 168 followed by Amhara (145), Oromia (86), the Southern Nations, Nationalities, and Peoples' Region (SNNPR) (17), and Benishangul & Gumuz (9) to capture the broad agro-ecological diversity of the country. Second, landrace status: the collection comprised predominantly landrace accessions (425) preserved by the Ethiopian Biodiversity Institute (EBI), supplemented by 23 officially released improved varieties obtained from national and regional research centres in Ethiopia. This enables the comparative evaluation of farmer-maintained versus elite genetic materials. Third, grain colour diversity: accessions represented six distinct seed colours, including white, light brown, brown, dark brown, red and black (Appendix Table 3.1). This allows investigation of trait associations with seed pigmentation, particularly for drought response and nutritional composition.

Three sites were selected for the study, namely: Arsinegelle (designated as AN), Maitsebri (SH) and Meiso (MI) (Table 3.1). Together, these three sites capture the full spectrum of Ethiopian drought scenarios from high-rainfall, secure environments (AN) through moderate moisture stress (SH) to low-reliability areas (MI). The specific sowing and harvesting months for each location during the 2019 growing season are provided to define the experimental timeline. Soil analyses were conducted following the standardized procedures according to Estefan et al. (2013). The analysis revealed that the AN site was characterized by loam soil with moderate fertility, including 2.10% total organic carbon, 0.16% total nitrogen, and a soil pH of 6.5. The MI site has clay loam soil with low organic carbon (1.20%) and nitrogen content (0.08%), and a pH of 7.03, indicating slightly alkaline soil. MI had higher clay content (36%) compared to AN (26%). The SH site, as reported by Redda and Abay (2015), possesses Vertisols with clay-texture, moderate acidity (pH of 6.1), low organic carbon (1.1%), and total nitrogen (0.1%). AN received the highest annual rainfall (1223.45 mm) and had the lowest mean 20.34°C), minimum (7.73°C), and maximum (32.94°C) temperatures. Conversely, MI exhibited the highest mean (22.47°C) and maximum (35.67°C) temperatures, with the lowest rainfall (394.20 mm), which is characteristic of an arid environment. SH, was notably warmer, recording an average temperature of 21.72°C and moderately dry (with 632.81 mm annual rainfall). Overall, the sites represented a diverse range of agro-ecological conditions, which are crucial for agronomic evaluation and stability tests.

Table 3.1. Description of the study locations.

Parameter	Location		
	Arsinegelle (AN)	**Maitsebri (SH)***	**Meiso (MI)**
Soil texture	Loam	Clay	Clay loam
pH	6.5	6.1	7.0
Total organic carbon (%)	2.1	1.1	1.2
Total nitrogen (%)	0.2	0.1	0.1
Clay (**wt/wt**) (%)	26.0	42.0	36.0
Sand (wt/wt) (%)	37.0	25.0	27.0
Silt (wt/wt) (%)	37.0	33.0	37.0
Latitude	N07°19.541'	N13°41.303'	N09°13.713'
Longitude	E038°39.494'	E038°10.329'	E040°45.442'
Altitude (**masl**)	1933.0	1445.0	1326.0
Mean temperature (°C)	20.3	21.7	22.5
Maximum temperature (°C)	32.9	34.9	35.7
Minimum temperature (°C)	7.7	8.6	9.3
Annual rainfall (mm/year)	1223.4	632.8	394.2
Relative humidity (%)	67.0	56.0	61.0
Distance from Addis Ababa (km)	240.0	939.0	296.0
Sowing month	May/2019	July/2019	July/2019
Harvesting month	November/2019	November/2019	December/2019

Note: wt/wt = weight by weight, masl= meter above sea level; * source: Redda and Abay 2015)

3.2.2 Experimental design and field management

The 448 finger millet genotypes were evaluated using a 64 x 7 row-column experimental design, replicated twice at each site. The field study was conducted in 2019/20 growing season. Individual plots comprised of a single 3 m row with an inter-row spacing of 0.4 m and an intra-row spacing of 10 cm. To optimize early growth, a basal application of di-ammonium phosphate (DAP, 18% N, 46% P_2O_5) fertilizer was administered at a rate of 100 kg/ha during sowing. Urea (46% N) was not applied to facilitate natural expression and prevent lodging.

3.2.3 Data collection

Agronomic data

Data on agronomic traits were collected following the protocols described by the International Board for Plant Genetic Resources (IBPGR) (1985), with some minor modifications. Plant height (PH) was determined in cm by measuring five randomly selected and tagged plants per plot from ground level to the inflorescence apex at the dough developmental stage. Days to 50% flowering (DF) and maturity (DM) were quantified as the number of days from sowing until 50% of the main tillers within each plot exhibited emerged ears and fully mature ears, respectively. Grain yield

(GY) was determined by harvesting the total grain from a 1.2 m^2 plot, and then adjusting the weight to a standard moisture content of 12.5% and converting the result to tons per hectare. Thousand seed weight (TW) was determined gravimetrically (g) for a random sample of 1000 seeds.

Drought tolerance

Drought stress was naturally occurring under rainfed field conditions, reflecting the moisture-limited environments commonly experienced by finger millet in target production areas. Evaluating drought tolerance (Drt) and stay-green (SG) under naturally occurring drought conditions enhances the realism of phenotypic assessment and provides a more representative measure of genotype performance under farmers' field conditions. In this study, SG and Drt scores were assessed at the post-flowering stage using visual scales widely applied in finger millet and related cereals (Jordan et al. 2012; Borrell et al. 2014; Hoang et al. 2019; Kamal et al. 2019; Shin et al. 2020). The SG was visually scored on a scale of 1 to 5 at maturity as follows: a score of 1 indicates excellent SG and denotes strong drought tolerance, as the canopy remains fully green (Figure 3.1); a score of 2 represents good SG and reflects moderate to high drought tolerance characterized by a largely green canopy with slight yellowing; a score of 3 indicates an intermediate drought response, where noticeable yellowing occurs but partial upper-canopy greenness remains; a score of 4 signifies poor SG and indicates low drought tolerance evidenced by substantial canopy senescence; a score of 5 denotes very poor SG and high drought sensitivity, as the canopy is completely senescent. Furthermore, Drt is a composite measure of key morphological and physiological indicators, including SG ability, earliness, leaf wilting, and plant canopy vigour. It was visually assessed at maturity on a standardised scale of 1 to 5; where a score of 1 indicates high tolerance, where plants remain green with minimal wilting or leaf rolling, exhibit early maturity and retain good biomass; a score of 2 reflects tolerance with a largely green canopy and only mild yellowing or wilting; a score of 3 denotes moderate tolerance, characterized by partial canopy senescence, moderate leaf wilting, and delayed maturity; a score of 4 represents susceptibility, with widespread yellowing, poor canopy maintenance, and reduced vigour; a score of 5 denotes high susceptibility, marked by severe wilting, complete canopy senescence, stunted growth, or plant death.

Nutrient composition

Post-harvest nutritional composition analysis was performed at Melkassa Agricultural Research Centre (MARC) food and nutrition laboratory in Ethiopia. Representative grain samples (150 to

200g) were collected per accession from replicated plots across test sites. Samples were subjected to rigorous cleaning to eliminate extraneous materials. Moisture loss and contamination were minimized by storing cleaned samples in hermetically sealed containers. Prior to non-destructive Near-Infrared Reflectance Spectroscopy (NIRS) analysis, instrument calibration was conducted using a polystyrene reference plate with a known spectral signature. NIRS analysis was performed using a Perten IM 9500 analyser (Perten Instruments AB, Sweden) by placing the subsamples in the sample hopper. Duplicate spectral acquisitions were performed per sample, and the mean values were used to enhance data reliability. Of note, the units (% for Fe/Zn, and ppm for amylose and starch) correspond directly to NIR instrument's internal calibration output. Finally, grain colour of the test genotypes was categorized as follows: 1 = white, 2 = light brown, 3 = brown, 4 = dark brown, 5 = red, and 6 = black.



Figure 3.1 A picture showing the stay green phenotype in finger millet. The mature fingers can be seen on plants with a majority of green leaves.

3.2.4 Data analysis

Diagnostic Bartlett's test of homogeneity of variance (Bartlett 1937) was conducted in each test environment, followed by a combined analysis of variance using a linear mixed model in SAS 9.4 (SAS Institute, Inc.). The mixed model treated environment as a fixed effect, and genotypes and genotypes by environment interaction as random effects to partition the phenotypic variation into its constituent components: environmental, genotypic, and their interaction effects (SAS 2013). The linear mixed model across multiple test environments was defined as follows:

$$Y_{IJKLM} = \mu + g_I + s_J + (gs)_{IJ} + b_{JK} + r_{JKL} + c_{JKM} + \epsilon_{IJKLM}$$

Where:

- Y_{IJKLM} is the value of the variable measured from the I^{th} genotype in K^{th} replicate in L^{th} row and M^{th} column nested in the J^{th} environment.
- μ is the overall mean.
- g_I is the random effect of genotype I, $N(0, \sigma^2_g)$.
- s_J is the fixed effect of environment J.
- $(gs)_{IJ}$ is the effect of the interaction between genotype i and environment J, $N(0, \sigma^2 gs)$.
- b_{JK} is the random effect of replicate K within environment J, $N(0, \sigma^2 b)$.
- r_{JKL} is the random effect of row L within replicate K within environment J, $N(0, \sigma^2 r)$.
- c_{JKM} is the random effect of column M within replicate K within environment J, $N(0, \sigma^2 c)$
- ϵ_{IJKLM} is the residual effect, $N(0, \sigma^2_e)$.

Genetic parameters

Variance components, broad-sense heritability and genetic advance were computed to assess the magnitude of genetic variability and the potential for selection among finger millet accessions across three environments.

Variance components

The variance components, namely phenotypic, genotypic, and environmental variances, were computed using the expected mean squares from ANOVA summary results by following the procedure outlined by Holland et al. (2003) from the linear mixed model. To estimate the total phenotypic variance, the model integrates contributions from genotypic effects, genotype- by-location interactions, and residual errors, structured differently for multi-location and single-location analyses. Following the classical principles of variance partitioning (Fisher, 1918), the total variance (σ^2_p) was computed dynamically using the specific agricultural multi-location application described by Gebreyohannes et al. (2018) as follows: $\sigma^2{}_p = \sigma^2{}_g + \frac{\sigma^2{}_{gs}}{J} + \frac{\sigma^2{}_e}{KJ}$, where: σ^2_g, σ^2_{gs}, and σ^2_e represent variance due to genotype, genotype x environment interaction, and residual error, respectively; J, and K denote the number of environments and replications in that order. The genotypic variance (σ^2_g) was calculated as $\sigma^2 g = \frac{MS_g - MS_{gs}}{JK}$, where MS_g, and MS_{gs} denote mean square due to genotypes, and genotypes x environment interaction; J, and K are the number of environments, and replications in that order. The environmental variance (σ^2_E)

was computed as $\sigma^2{}_E = \frac{\sigma^2{}_{gs}}{J} + \frac{\sigma^2{}_e}{JK}$, where σ^2_{gs}, and σ^2_e are the variance due to genotype x environment interaction and residual error, respectively; J, and K represent the number of environments and replications, in the same order.

Genetic parameters, correlation, principal component and cluster analyses

Genetic parameters, including broad-sense heritability (H^2), genetic advance (GA) and genetic advance as percent of mean (GA%) were computed according to Johnson et al. (1955) and Holland et al. (2003). The (H^2) was calculated across and single locations: $H^2 = \frac{\sigma^2{}_g}{\sigma^2{}_g + \frac{\sigma^2{}_{gs}}{K} + \frac{\sigma^2{}_e}{KJ}}$ (multi-locations), and $H^2 = \frac{\sigma^2{}_g}{\sigma^2{}_g + \frac{\sigma^2{}_e}{K}}$ (single-location), where: σ^2_g, σ^2_{gs}, and σ^2_e represent variance due to genotype, genotype x environment interaction, and residual error; J, and K denote the number of environments and replications, respectively. The GA and GA% were estimated following the procedure described by Johnson et al. (1955). GA was computed using the formula: $GA = K \times H^2 \sqrt{\sigma^2{}_p}$, where K is the selection intensity at 5% (2.06), σ^2_p = Phenotypic variance, while GA% was computed as $GA\% = \frac{GA}{\mu} x100$, where GA = genetic advance and μ = the overall mean.

Multivariate analysis

Phenotypic Pearson correlation analysis was determined to discern the pattern and magnitude of association for assessed agronomic, nutritional traits and drought-tolerant traits for each environment using the corrplot package (Wei and Simko 2024). Hierarchical clustering and a red-blue diverging scale facilitated the interpretation of positive and negative associations, enabling the identification of key trait combinations relevant for breeding (Kassambara 2017).

Principal component analysis (PCA) was done to dissect interrelationships of the finger millet genotypes within the agronomic and nutritional traits, and drought tolerance characteristics using the FactoMineR (Lê et al. 2008) and factoextra (Kassambara and Mundt 2016) packages in R version 4.1.2 (R Core Team 2021). Eigenvalues and eigenvectors were computed to derive the percent variation explained by the respective principal components (PC's) and variable loading

scores, which assorts individual trait contributions. Subsequently, PC biplots were constructed to visualize genotype-trait associations.

Hierarchical clustering with complete linkage was applied to the standardised trait data, and genotypes were assigned to four clusters. Cluster membership was extracted using the cutree function, and genotype names within each cluster were listed to characterise group composition. To further describe cluster properties, mean values of traits were calculated for each cluster using the aggregate function (Kaufman and Rousseeuw 2009; Kassambara 2017).

3.3 Results

3.3.1 The effect of genotypes, environments, and their interaction on agronomic traits, drought response and nutritional profiles

Table 3.2 summarises the results of the combined analysis of variance for agronomic traits. Highly significant ($P < 0.001$) differences were observed among the main effects of genotypes, environments, and their interactions for all the agronomic traits. The coefficient of variation (CV) ranged from 2.3% for days to 50% flowering to 13.5% for grain yield, while the proportion of explained variance (R^2) varied from 88.5% for thousand seed weight to 99.0% for days to 50% flowering. Further, genotypes, environment, and their interactions significantly affected SG score (SG) and drought tolerance (Drt) score (Table 3.2). The CVs ranged from 16.0% for Drt to 21.8% for SG, while the R^2 values varied from 90 (SG) to 92% (Drt). The nutritional parameters, such as amylose (Am), starch (Stc), iron (Fe), and zinc (Zn) concentrations, were significantly ($p < 0.01$) affected by genotypes, environments, and genotype by environment interaction. The CV values were low 2.3% (for AM) to 10.9% (Fe), while the R^2 values ranged from 71% (Stc) to 92% (Zn) (Table 3.2).

Table 3.2. Combined analysis of variance showing mean square values and level of significance for the studied agronomic traits, drought parameters and nutritional profiles of 448 finger millet accessions evaluated at Arsinegelle, Maitsebri and Meiso sites in Ethiopia

Sources of variation		Agronomic traits					Drought parameters		Nutrition profiles			
	Degree of freedom	DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Fe	Zn
		Mean squares and significant tests										
Genotypes	447	119.4**	469.5**	330.6**	1.9**	0.3**	2.6**	5.1**	0.7**	71.7**	253.1**	38.5**
Environments	2	250327.8**	581367.3**	202375.9**	768.7**	33.5**	205.2**	56.0**	98.3**	2760.0**	43789.8**	2708.7**
GEI	894	17.5**	314.7**	46.7**	1.0**	0.1**	1.1**	0.7**	0.4**	47.1**	105.9**	15.9**
Columns (Rep)	12	36.0^{NS}	415.6**	92.6^{NS}	0.1^{NS}	0.02^{NS}	0.5*	0.4*	0.4**	41.2^{NS}	187.9**	18.8**
Rows (Rep)	126	5.7^{NS}	120.1^{NS}	15.8^{NS}	0.1^{NS}	0.04*	0.2^{NS}	0.2^{NS}	0.2^{NS}	2476^{NS}	38.4^{NS}	5.4^{NS}
Rep(E)	2	94.4**	805.0**	266.5**	0.7**	0.2*	3.0**	3.1**	1.0**	12.7**	167.8*	37.0
Error	1116	5.5	99.2	14.8	0.1	0.03	0.3	0.2	0.2	29.8	46.1	5.4
Trial statistics												
CV (%)		2.3	9.2	2.8	13.5	8.9	21.8	16.0	2.3	10.9	10.8	3.1
R^2 (%)		99.0	93.2	97.1	97.3	88.5	90.1	92.2	80.3	71.4	85.2	86.1
LSD (5%)		2.7	11.3	4.4	0.3	0.2	0.6	0.5	0.5	6.2	7.7	2.6

Note: ^{NS}, * & ** denotes non-significant, significance at the 5, and 1% probability levels, respectively, GEI = Genotypes by environment interactions, Columns(Rep) = columns nested in replication, Rows(Rep)= rows nested in replication, Rep(E), replication nested in environment, CV% = coefficient of variation, R^2(%) = coefficient of determination, LSD = least significant difference at 5% level of significance, DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn=zinc content (%).

3.3.2 Mean performance of test genotypes for the assessed traits

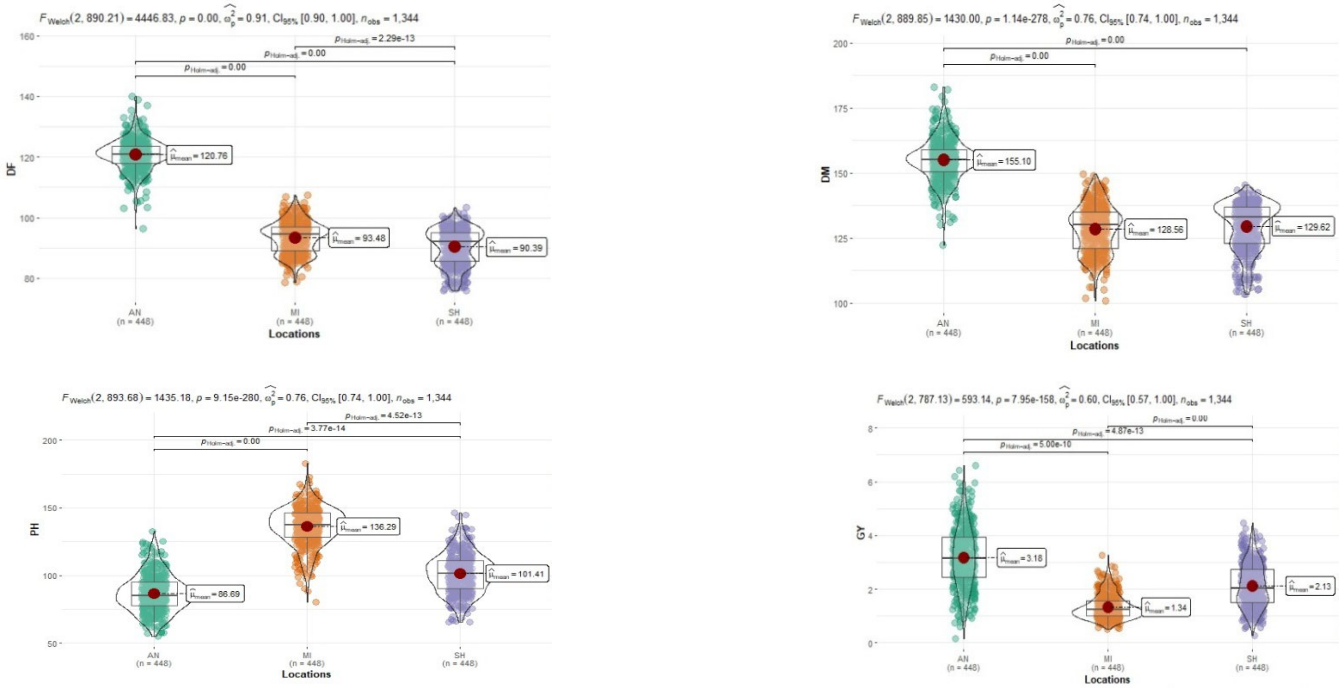
Agronomic traits

Figure 3.2 and Appendix Table 3.1 summarise agronomic traits across three locations, namely: Arsinegelle (denoted as AN, non-stressed environment), Maitsebri (SH, moderately drought-stressed), and Meiso (MI, highly drought-stressed). Drought significantly impacted agronomic traits at the MI site compared to the non-stressed environment (AN) and moderate stress environment (SH). At MI, drought stress led to a 17.4% reduction in thousand-grain weight (Figure 3.2 and Appendix Table 3.2). Furthermore, grain yield at MI was significantly affected by drought stress. Overall, yield reductions varied from 33.0% (SH) to 60.0% (MI) relative to AN.

The top ten best-performing and bottom five poor-performing were selected based on grain yield response under stressed conditions (MI) (Appendix Table 3.2). The top performers were G141, G423, G297, G247, G18, G432, G195, G223, G435, and G171 with higher grain yield of > 2.5 t/ha, and early flowering (< 90 days) and maturity (< 122 days). The mean grain yield of the best-performing genotypes was 2.69 t/ha at MI and 3.46 t/ha at AN, corresponding to an average yield loss of approximately 22.25% due to drought stress (Table 3.3). Of the test genotypes, G141, G423, G297, and G247 were high yielding at 3.2, 2.9, 2.8, and 2.7 tons/ha, respectively, in MI. The genotypes G257, G198, G361, G296, and G333 were high-yielding and recorded grain yields of 6.6, 6.4, 6.2, 6.0, and 6.0 tons/ha, in the same order, at AN. None of the released finger millet varieties were ranked among the top ten performers at the non-stressed environment, AN. However, in a stressed environment, MI, genotypes G432 and G435, officially released as cultivar Mecha (229371) and Meba (GBK011119A), demonstrated superior performance for grain yield at 2.6 t/ha and 2.5 t/ha, respectively (Figure 3.2). These high-yielding genotypes at MI were early flowering, with 85 to 96 days to 50% flowering and 113 to 133 days to maturity. These genotypes were moderately tall (122.5 to 149.0 cm) with moderate to higher seed weight (1.5 to 2.8 g/1000 seed). The grain colour was predominantly dark brown (38.8%), black (37.1%), and brown (12.7%) accounting for the total assessed finger millet genotypes. In contrast, the bottom five performing genotypes at MI, including G239, G49, G128, G37, and G50, displayed consistently low yields with a mean of 0.56 tons/ha compared to 1.68 t/ha at AN, which resulted in a yield penalty of 66.7%. Furthermore, the genotypes showed slightly delayed flowering (94 to 101 days) and maturity (128 to 142 days).

Table 3.3 presents the variation in agronomic traits in grain colour groups across three environments. The common grain colours of the finger millet accessions were dark brown, black,

brown, white, and red. There were variations in grain colour, panicle and nodal pigmentations (Figure 3.3A-E). Across locations, black and dark brown grain colour groups consistently demonstrated superior agronomic performance, notably associated with higher grain yield. Furthermore, genotypes with red grains displayed the shortest time to flowering (89 to 111 days), and maturity (115 to 141 days) across the test environments. At AN, black seeded types achieved the highest grain yield (3.4 t/ha), while red types matured earlier (141.3 days), and had higher thousand seed weight (2.7 g). In SH, grain yields across grain colour groups were relatively moderate (2 tons/ha). However, genotypes with black and dark brown grain colours exhibited relatively better performance, particularly in terms of grain yield (2.1 to 2.2 tons/ha). Overall, the lowest grain yield was observed in the MI site; however, the black and red types demonstrated comparatively better performance, maintaining slightly higher grain yield (1.4 to 1.6 tons/ha) compared to other groups.



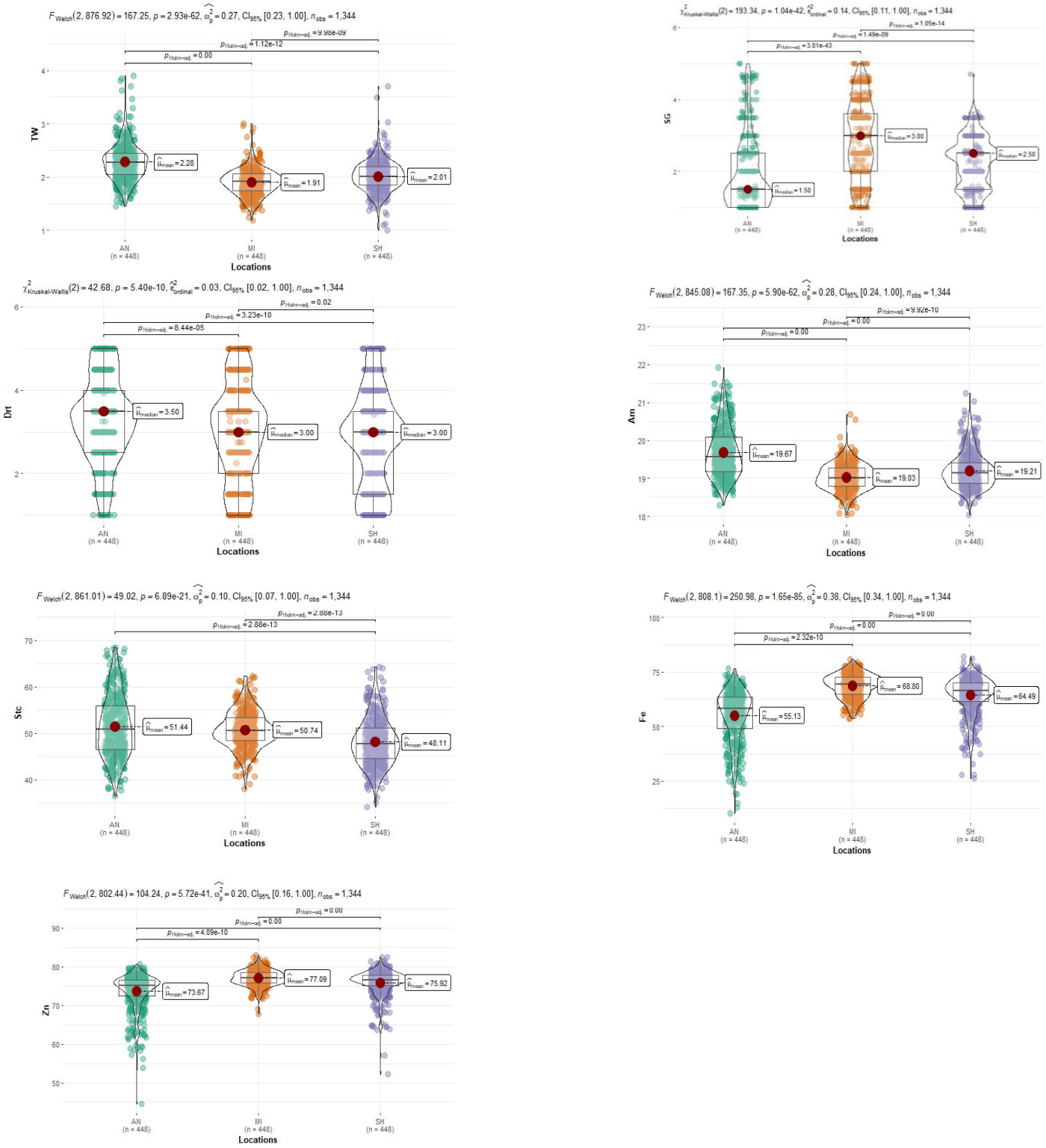


Figure 3.2. Distribution of agronomic, drought-responsive, and nutritional traits of 448 finger millet genotypes across three locations in Ethiopia. Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn=zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri.

Nutritional profiles

Figure 3.2 displays the mean performance of finger millet genotypes for the nutritional profiles across the contrasting test sites. Unlike most agronomic and drought-related traits that were affected by drought stress, certain nutritional traits, such as iron and zinc concentrations were unaffected under drought conditions at MI compared to the other environments. While the stressed environment, MI, maintained relatively higher levels of iron and zinc, which declined more significantly under the potential environment, AN. However, the concentrations of the amylose and starch contents appeared to remain relatively stable across the test environments (Figure 3.2).

The top ten best grain yield performing genotypes displayed higher amylose content, which varied between 18.3 and 19.2%, starch content of 45.0 to 55.1%, iron concentration of 62.0 to 74.7 ppm, and zinc concentration of 75.4 and 80.2 ppm at MI (Figure 3.2). Genotypes G163, G16, G259, G106, and G340 recorded higher amylose content of 20.7, 20.5, 20.1, and 19.9% at MI, respectively. Similarly, genotypes G431, G166, G240, G49, and G173 expressed higher amylose content at AN with values of 21.9, 21.5, 21.5, 21.4%, respectively. Genotypes G106 and G163 displayed superior performance for both amylose and starch contents at MI recording values of 19.9 and 20.7%, and 62.1 and 59.3%, in that order. The bottom five performing genotypes at MI did not consistently rank as the lowest performing across all traits and environments. For instance, the iron concentration of genotype G37 showed marked variation across environments, ranging from 24.7 ppm at AN to 57.1 ppm in MI, and peaking at 64.9 ppm in SH. Likewise, G37 recorded the lowest zinc values in AN (58.9 ppm), MI (72.8 ppm), and SH (75.3 ppm). In contrast, some of the lowest-yielding genotypes for grain yield, such as G49, demonstrated relatively higher iron content (56.9 ppm) in MI. For starch content, G423 consistently showed lower values (AN: 42.6%, MI: 51.5%, SH: 46.8%). Amylose content remained relatively stable across the least performing genotypes for grain yield, with slight variations, for example, G49 (AN: 21.4%, MI: 19.6% and SH: 19.3%).

Grain colour had distinct patterns in nutritional trait expression across environments. Table 3.3 presents the differential responses in carbohydrate stability and micronutrient accumulation under varying moisture conditions. Amylose content exhibited remarkable environmental and phenotypic stability, consistently ranging from 18.9 to 20.6% across diverse environments and grain colours. In contrast, starch content showed greater variability, with notably elevated levels exceeding 58% in light brown and red seeds at AN. Dark-seed genotypes exhibited relatively

higher micronutrient levels in low moisture environments. At MI, black seeds recorded the highest values, reaching 69.7 ppm iron and 77.4 ppm of zinc, signalling the influence of test environments on genotype performance.

Response to stay-green and drought

Drought tolerance (Drt) score and the stay-green (SG) traits were essential parameters for discriminating finger millet genotypes under water-limited conditions (Figure 3.2). The top 10 genotypes, selected based on better grain yield under the drought-prone condition, MI, displayed lower drought scores and more favourable SG scores compared to the bottom five performers. For instance, high-yielding genotype G141 scored a drought score of 2.5 and a SG score of 2.0 at MI, while genotype G239 from the lower-performing group had a significantly higher drought score (5.0) and SG score (4.5). This trend was consistent across environments, with superior genotypes maintaining lower average drought scores (e.g., 3.0 at AN, 2.8 at SH) and better chlorophyll retention.

Grain colour groups showed notable variation in drought-related traits across environments (Table 3.3), providing additional insight into the genotypic plasticity under stress. Black and dark brown-seeded genotypes consistently recorded higher SG and drought scores, averaging 2.0 and 3.4 at AN and 2.9 and 3.0 at MI, in that order, compared to light brown and red groups, which tended to score higher on both scales. In particular, light brown genotypes, despite having higher starch content, displayed poor drought responses with mean drought scores of 4.1 and 3.4 and SG scores of 2.3 and 2.9 at AN and MI locations, respectively. White-seeded types performed moderately, maintaining relatively balanced SG and drought scores across sites.

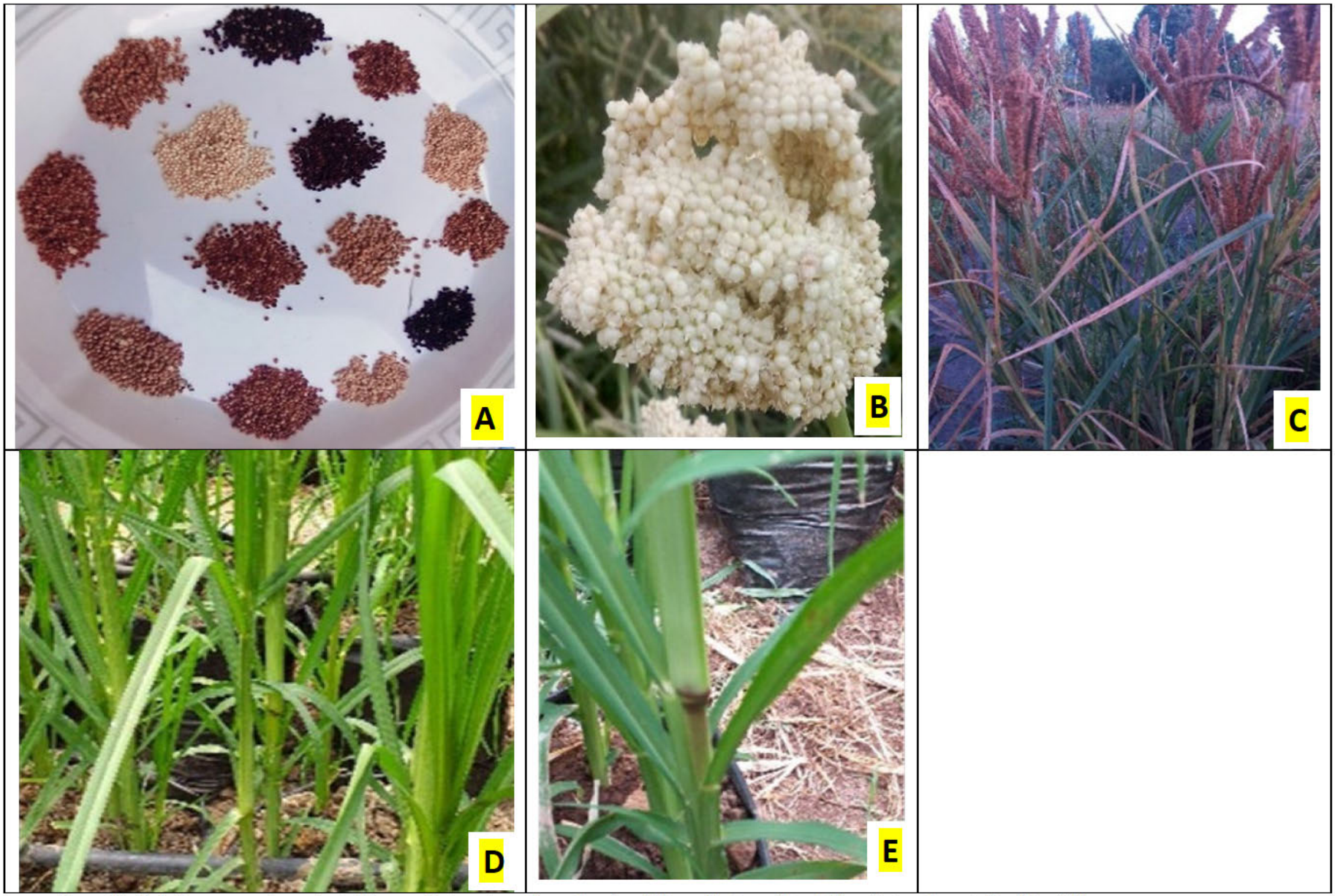


Figure 3.3. Variations among the evaluated finger millet genotypes for grain colour (A), panicle types (B and C), and stem pigmentation (D and E)

Table 3.3. Mean values for agronomic traits, drought parameters, and nutritional profiles of 448 finger millet genotypes evaluated across three test environments in Ethiopia based on seed coat colours.

Grain colour	Locations	Agronomic traits					Drought parameters		Nutrition profiles			
		DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Iron	Zinc
Black	AN	121.4	88.1	156	3.4	2.3	2.0	3.4	19.4	49.0	59.9	75.7
Red	AN	111.2	74.4	141.3	3.2	2.7	1.0	1.8	20.6	58.4	37.3	66.9
Dark brown	AN	119.9	85.8	153.8	3.3	2.3	1.9	3.1	19.6	50.1	57.8	75.2
Brown	AN	121.8	86.3	156.9	2.9	2.4	2.0	3.5	20.3	56.6	41.9	69.1
Light brown	AN	124.6	88.9	161.5	2.1	2.3	2.3	4.1	20.5	59.9	38.4	65.5
White	AN	120.4	86.2	154.3	2.9	2.2	1.7	3.2	19.9	57.5	49.5	67.4
Mean	AN	119.9	85.0	154	3.0	2.4	1.8	3.2	20.1	55.3	47.5	70.0
Black	SH	90.6	101.7	130.1	2.1	2.0	2.3	2.8	19.0	46.2	67.9	77.2
Red	SH	82.1	99.0	115.3	1.8	2.3	1.7	1.6	19.5	52.0	58.9	73.7
Dark brown	SH	89.4	99.8	128	2.2	2.0	2.3	2.6	19.1	47.2	67.3	76.9
Brown	SH	92.0	102.2	131.9	2.3	2.2	1.9	3.1	19.7	51.4	54.9	73.1
Light brown	SH	94.6	100.6	135.3	1.8	2.0	2.1	3.6	19.8	53.2	53.1	71.8
White	SH	91.8	108.2	132.3	1.8	1.9	2.1	3.0	19.7	54.4	54.7	70.7
Mean	SH	90.1	101.9	128.8	2.0	2.1	2.1	2.8	19.5	50.7	59.5	73.9
Black	MI	93.3	138.4	128.3	1.4	1.9	2.9	3.0	19.0	51.0	69.7	77.4
Red	MI	88.7	130.9	120.4	1.6	2.2	1.7	1.4	18.9	51.2	68.6	77.3
Dark brown	MI	92.6	136.3	127.1	1.3	1.9	2.8	2.9	19.0	50.3	69.2	77.3
Brown	MI	95.5	133.4	132.2	1.3	2.0	2.8	3.1	19.1	51.0	67.1	76.5
Light brown	MI	97.7	128.3	135.5	1.2	1.9	2.9	3.4	19.2	50.7	65.4	76.1
White	MI	94.4	134.6	130.1	1.3	1.8	3.1	3.3	19.2	51.4	66.3	76.0
Mean	MI	93.7	133.7	128.9	1.4	2.0	2.7	2.9	19.1	50.9	67.7	76.8

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn = zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri.

3.3.3 Genetic parameters for the assessed traits

Agronomic traits

Genetic parameter estimates for agronomic traits are summarised in Table 3.4. At AN, phenotypic variance was notably high for plant height (184.54 cm), and days to maturity (59.84), with genotypic variance following a similar trend, particularly for plant height (114.86 cm), and days to maturity (47.49). Heritability estimates were relatively high ($H^2 > 0.6$) across traits, especially for grain yield (0.90), days to 50% flowering (0.79) and days to maturity (0.79). Genetic advance (GA) was the highest for plant height (17.42), and days to maturity (12.65). Likewise, genetic advance as a percent of mean (GA%) was remarkably high for grain yield (59.95%) (Table 3.4). In SH, a comparable pattern was observed, where the largest phenotypic variances were recorded

for plant height (160.05) and days to maturity (75.05), and genotypic variances were higher for days to maturity (68.90) and plant height (113.52). Environmental variances remained comparatively low for most traits, further supporting the genetic basis of observed variability. Heritability estimates were consistently high, ranging from 0.71 for plant height to 0.93 for grain yield. GA was the highest for days to maturity (16.38), and plant height (18.48), while GA% was highest for grain yield (65.81%). At MI, phenotypic variation was most pronounced in plant height (165.87), and days to maturity (68.25), and this was closely mirrored by genotypic variance, with notable values in plant height (112.67), and days to maturity (59.16). Despite moderate contributions from environmental variance such as for plant height (53.20), heritability estimates remained high for most traits, including days to maturity (0.87), and grain yield (0.82). GA was the highest for days to maturity (14.75), and plant height (18.02), while GA% reached higher for grain yield (52.20%). In the combined analysis across environments, phenotypic variance remained high for plant height (150.08), and days to maturity (65.73), whereas genotypic variances were comparatively lower across most traits (Table 3.4). Heritability was high (>0.6) only for days to 50% flowering (0.71), and days to maturity (0.72), while moderate values (0.3 to 0.6) were observed for thousand seed weight. Traits such as plant height, and grain yield exhibited low heritability (<0.3). The GA for key agronomic traits varied from 0.25 for thousand seed weight to 12.02 for days to maturity, while GA% spanned from a low 4.02% for plant height to moderate 17.89% for grain yield (Table 3.4).

Nutritional composition

The summary of genetic parameters for nutritional traits is presented in Table 3.4. Unlike agronomic traits, nutritional profiles presented variable trends. At AN, phenotypic variance was high for iron (164.27), and starch concentrations (60.98), with genotypic variance showing a similar pattern, especially for iron (83.01). Environmental variance surpassed genotypic variance for amylose concentration and was remarkably more pronounced for starch concentration at 41.60%. In contrast, zinc, and iron contents displayed higher genotypic variance, though environmental influence was relatively more evident in iron concentration (Table 3.4). Broad sense heritability estimates were moderate (0.3 to 0.6) for the majority of nutritional traits except for zinc concentration (0.67). The GA for nutritional traits varied from 0.66 in Am to 13.34 in iron content, while the GA% ranged from a low of 3.37% for amylose content to a moderate value of 24.20% for iron concentration. In SH, genetic influence was notably high for the two nutritional traits, except for starch concentration, which was the highest due to the environment (Table 3.4). Broad-sense heritability varied from 0.45 (starch content) to (0.45) to 0.75 (iron

concentration. The estimates of GA and GA% followed a similar pattern to that observed in Arsinegelle. In Meiso, both amylose, and starch contents were more strongly influenced by the environment, as evidenced by their respective variance components. Notably, starch was affected by the environment (10.28) with its genetic variance (5.22), leading to a reduced heritability (0.34). In contrast, iron, and zinc contents showed more stable genetic expression, reflected in relatively high heritability estimates of 0.71, and 0.61, respectively. When pooled across environments, nutritional traits revealed a more complex interaction. Starch content was more influenced by environmental effect (13.62 vs. genotypic 4.10), resulting in a very low heritability (0.23), and a marginal genetic advance of 4.01%. Amylose content showed low heritability (0.27). However, micronutrients retained some breeding potential: iron ($H^2 = 0.39$), and zinc ($H^2 = 0.38$) presented moderate to low genetic control, with respective GA of 10.21%, and 3.26%.

Drought parameters

At the AN test site, stay-green (SG) and drought tolerance (Drt) scores displayed a strong genetic basis with genotypic variances of 0.69 and 0.75, markedly exceeding environmental variance of 0.24, and 0.21, in that order (Table 3.4). Heritability in the broad sense was remarkably high for both traits (0.74 for stay-green, and 0.78 for drought score). This was supported by high GA% (75.63% for stay-green, and 47.73% for drought score). In contrast, genotypes at the MI site displayed remarkably high heritability values for SG (0.88) and drought score (0.86), supported by higher genotypic variances (0.89, and 0.86, in that order). However, the genetic advance values (1.82 for stay-green, and 1.77 for drought score) and their GA% (63.41% and 59.45%), respectively, were somewhat lower than those observed in AN. At SH, the variance components for SG and drought score showed a clear contribution of the genetic effect, with genotypic variances (stay-green: 0.28, and drought score: 1.04), far greater than their corresponding environmental variances (stay-green: 0.14 and drought score: 0.09), in that order. This strong genetic influence was further substantiated by high heritability estimates (SG score: 0.67, and drought score: 0.92). The GA values (SG score: 0.90, and drought score: 2.02), coupled with considerable GA% (SG score: 40.33%, and drought score: 71.98%) recorded for these traits. In the combined analysis across environments, both SG and drought scores showed a decline in genotypic variance at 0.25 and 0.73 in comparison with the increased environmental variability 0.45 and 0.28, in that order, resulting to high heritability for drought score (0.72) while moderate heritability was recorded for SG score (0.36). Notwithstanding this, the genetic advance for both traits remained high for drought score (GA:1.50, GA%: 49.45%), and SG score (GA: 0.62, GA%: 26.42%).

Table 3.4. Genetic parameters for agronomic and drought parameters, and nutritional traits for finger millet accessions tested across three environments in Ethiopia during the 2019 /2020 main rainy season.

Genetic parameters	Locations	Agronomic traits					Drought parameters		Nutritional traits			
		DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Fe	Zn
Phenotypic variance	AN	24.44	184.54	59.84	1.07	0.13	0.93	0.96	0.51	60.98	164.27	23.52
Genotypic variance	AN	19.38	114.86	47.49	0.96	0.10	0.69	0.75	0.23	19.38	83.01	15.81
Environmental variance	AN	5.06	69.68	12.35	0.11	0.03	0.24	0.21	0.28	41.60	81.26	7.71
Heritability in broad sense (H^2)	AN	0.79	0.62	0.79	0.90	0.76	0.74	0.78	0.45	0.32	0.51	0.67
Genetic advance	AN	8.07	17.42	12.65	1.91	0.55	1.47	1.57	0.66	5.11	13.34	6.71
Genetic advance as a % of mean	AN	6.69	20.09	8.15	59.95	24.17	75.63	47.73	3.37	9.94	24.20	9.11
Mean	AN	**120.76**	**86.70**	**155.10**	**3.18**	**2.29**	**1.94**	**3.29**	**19.67**	**51.43**	**55.13**	**73.67**
Phenotypic variance	SH	30.95	160.05	75.05	0.54	0.08	0.42	1.13	0.20	23.14	66.05	9.38
Genotypic variance	SH	28.34	113.52	68.90	0.50	0.06	0.28	1.04	0.13	10.32	49.83	6.86
Environmental variance	SH	2.61	46.53	6.16	0.04	0.02	0.14	0.09	0.07	12.82	16.22	2.52
Heritability in broad sense (H^2)	SH	0.92	0.71	0.92	0.93	0.73	0.67	0.92	0.64	0.45	0.75	0.73
Genetic advance	SH	10.49	18.48	16.38	1.40	0.41	0.90	2.02	0.58	4.42	12.63	4.62
Genetic advance as a % of mean	SH	11.61	18.23	12.64	65.81	20.38	40.33	71.98	3.04	9.19	19.59	6.08
Mean	SH	**90.39**	**101.41**	**129.62**	**2.13**	**2.03**	**2.22**	**2.80**	**19.21**	**48.11**	**64.49**	**75.92**
Phenotypic variance	MI	22.38	165.87	68.25	0.17	0.06	1.02	1.00	0.11	15.50	26.04	3.70
Genotypic variance	MI	19.44	112.67	59.16	0.14	0.05	0.89	0.86	0.05	5.22	18.60	2.27
Environmental variance	MI	2.94	53.20	9.10	0.03	0.01	0.13	0.14	0.07	10.28	7.44	1.43
Heritability in broad sense (H^2)	MI	0.87	0.68	0.87	0.82	0.82	0.88	0.86	0.41	0.34	0.71	0.61
Genetic advance	MI	8.47	18.02	14.75	0.70	0.40	1.82	1.77	0.28	2.73	7.51	2.43
Genetic advance as a % of mean	MI	9.06	13.22	11.47	52.20	20.69	63.41	59.45	1.47	5.38	10.91	3.15
Mean	MI	**93.48**	**136.29**	**128.56**	**1.34**	**1.91**	**2.87**	**2.98**	**19.04**	**50.74**	**68.80**	**77.09**
Phenotypic variance	Combined	23.90	150.08	65.73	0.62	0.07	0.70	1.02	0.18	17.72	62.12	9.92
Genotypic variance	Combined	16.98	25.80	47.32	0.15	0.03	0.25	0.73	0.05	4.10	24.53	3.77
Environmental variance	Combined	6.92	124.28	18.42	0.47	0.04	0.45	0.28	0.13	13.62	37.58	6.15
Heritability in broad sense (H^2)	Combined	0.71	0.17	0.72	0.24	0.45	0.36	0.72	0.27	0.23	0.39	0.38
Genetic advance	Combined	7.16	4.34	12.02	0.39	0.25	0.62	1.50	0.24	2.01	6. 41	2.46
Genetic advance as a % of mean	Combined	7.04	4.02	8.71	17.89	12.25	26.42	49.45	1.25	4.01	10.21	3.26
Grand mean	**Combined**	**101.63**	**107.90**	**138.00**	**2.20**	**2.07**	**2.33**	**3.03**	**19.30**	**50.07**	**62.80**	**75.57**

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn=zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri.

3.3.4 Correlations among phenotypic and nutritional traits

Associations among agronomic traits under drought

The correlation heatmap (Figure 3.4) revealed variable trends and magnitudes of associations among agronomic traits. A strong and positive association was computed between days to 50% flowering and days to maturity across all environments. However, days to 50% flowering, and days to maturity revealed consistent negative correlations with grain yield (r = -0.35 at MI, while -0.47, and -0.43 at the SH and AN sites), in that order. Moreover, thousand seed weight displayed substantial and negative associations with days to 50% flowering (r= -0.13) and days to maturity

(r= -0.13) at MI. In contrast, there existed a positive correlation between thousand seed weight and grain yield (r = 0.13 to 0.24) across locations. Conversely, plant height had poor associations with most traits, including grain yield, and days to 50% flowering in MI, except for a positive and strong correlation with days to 50% flowering (r = 0.27) at AN. Furthermore, grain colour revealed a weak and negative correlation with phenological traits in some environments. For instance, grain colour was negatively associated with days to 50% flowering and days to maturity at MI (r = −0.11), and at SH (r = −0.08 and -0.07), in that order (Figure 3.4).

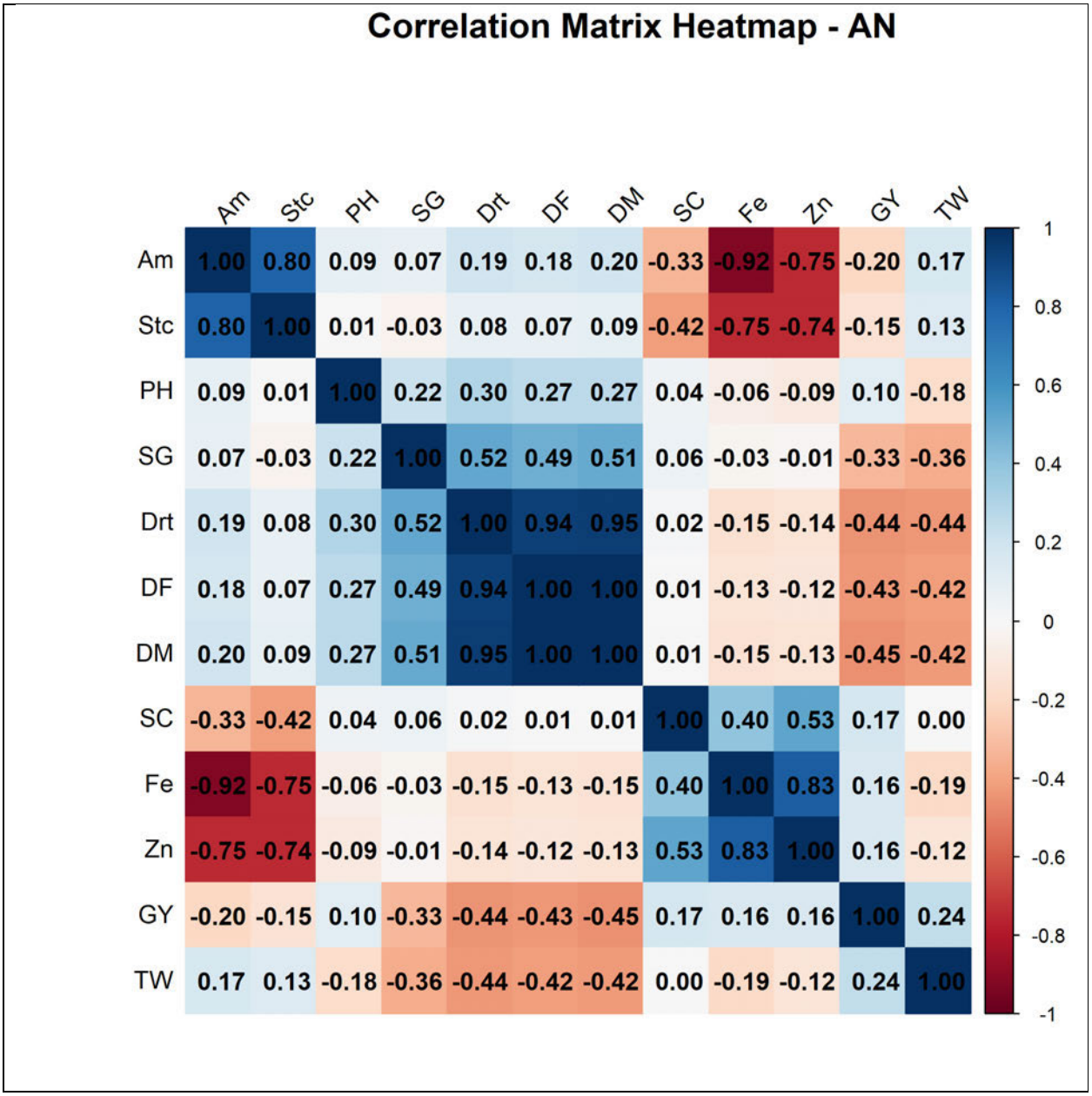
Association between nutritional composition

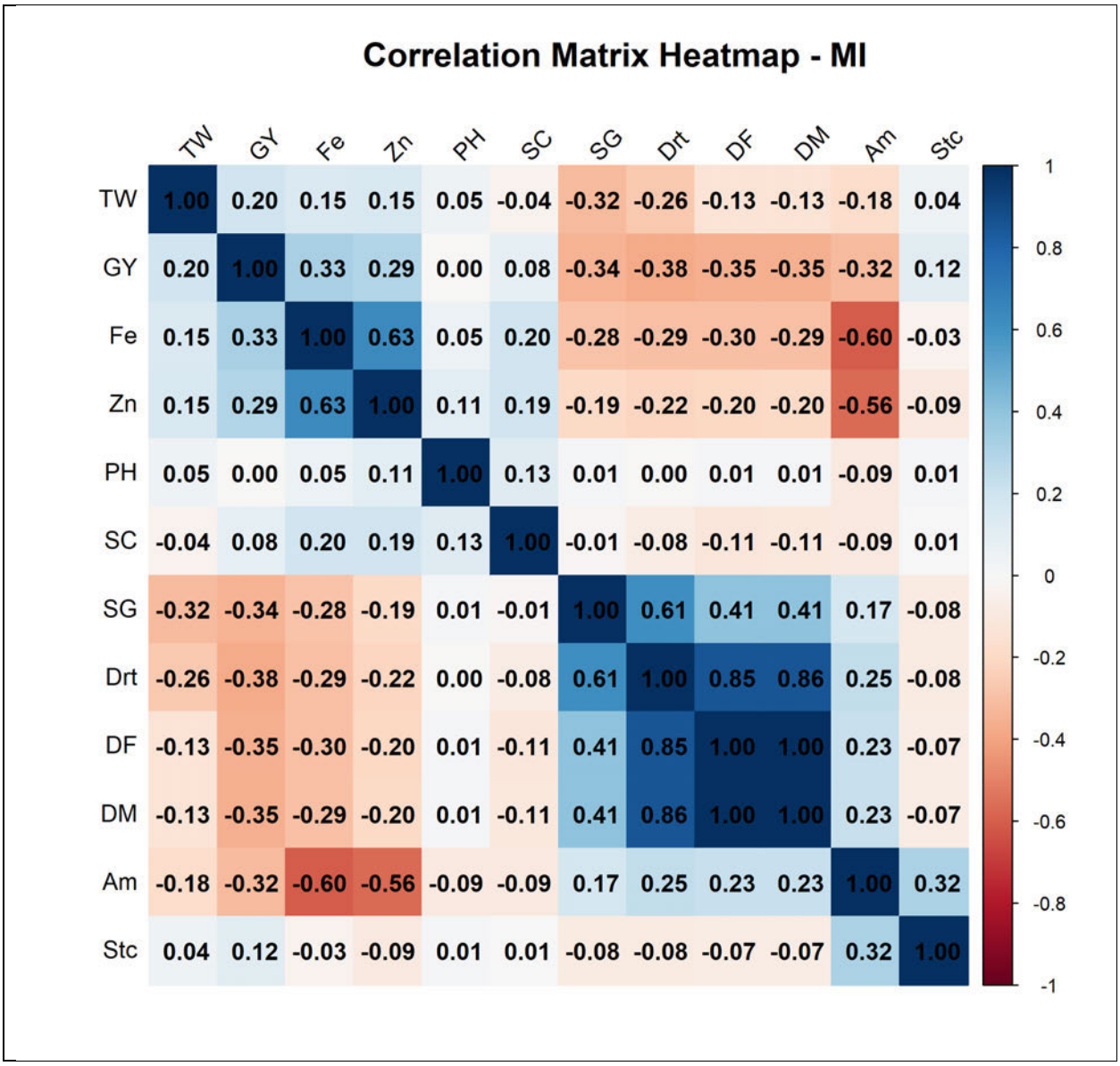
The nutritional traits, namely, amylose, starch, iron, and zinc contents, presented uniform pattern of association across all environments, although the magnitude of these correlations varied (Figure 3.4). Amylose content was strongly and positively related to starch content at all sites (r = 0.32 to 0.80), but exhibited a marked negative interaction with both iron (r = -0.92 to -60) and zinc (r = -0.75 to -0.56) contents. Similarly, starch content was negatively associated with iron (r = -0.75 to -0.03) and zinc (r = -0.74 to -0.09). Remarkably, iron and zinc were highly and positively correlated at all sites (r = 0.63 to 0.83). Moreover, among agronomic and drought-related traits, grain yield highlighted a modest but remarkable positive connection with both iron and zinc content at AN and MI (r = 0.16 to 0.33). Drought tolerance score displayed a consistent and noteworthy positive association with amylose content, specifically at AN (r = 0.19), MI (r = 0.25), and SH (r = 0.21). In contrary, stay-green had variable correlations with amylose and starch contents, with weak and inconsistent associations (r = 0.17) at MI and (r = –0.13) at SH for amylose, and mildly negative with starch content at both MI (r = –0.08) and SH (r = –0.15) (Figure 3.4). Grain colour was positively correlated with iron and zinc content, making it a good morphological marker for indirectly selecting for these traits. The correlation was also significantly lower for MI.

Associations of drought parameters

The association heatmap across the three test locations displayed consistent relationships among drought parameters and key agronomic traits in finger millet. Stay-green (SG) score showed a strong and positive association with drought tolerance score across all environments, with (r = 0.52 at AN, r = 0.61 at MI, and r = 0.35 at SH). Additionally, SG score showed marked positive correlation with days to 50% flowering (r = 0.49 at AN, r = 0.41 at MI, and r = 0.36 at SH), and days to maturity (r = 0.51 at AN, r = 0.41 at MI, r = 0.36 at SH). Likewise, drought tolerance score was strongly and positively associated with days to 50% flowering (r = 0.94 at AN, r = 0.85

at MI, r = 0.95 at SH) and days to maturity (r = 0.95 at AN, r = 0.86 at MI, and r = 0.93 at SH). Contrarily, both SG and drought tolerance score revealed significant negative correlations with grain yield (stay-green: r = −0.33 at AN, r = −0.34 at MI, r = −0.37 at SH; drought tolerance: r = −0.44 at AN, r = −0.38 at MI, and r = −0.47). Additionally, both drought-related parameters were inversely correlated with thousand seed weight and grain colour at several locations, though the strength and significance of the associations varied (Figure 3.4).




Correlation Matrix Heatmap - MI
TW GY Fe Zn PH SC SG Drt DF DM Am Stc
TW 1.00 0.20 0.15 0.15 0.05 -0.04 -0.32 -0.26 -0.13 -0.13 -0.18 0.04
GY 0.20 1.00 0.33 0.29 0.00 0.08 -0.34 -0.38 -0.35 -0.35 -0.32 0.12
Fe 0.15 0.33 1.00 0.63 0.05 0.20 -0.28 -0.29 -0.30 -0.29 -0.60 -0.03
Zn 0.15 0.29 0.63 1.00 0.11 0.19 -0.19 -0.22 -0.20 -0.20 -0.56 -0.09
PH 0.05 0.00 0.05 0.11 1.00 0.13 0.01 0.00 0.01 0.01 -0.09 0.01
SC -0.04 0.08 0.20 0.19 0.13 1.00 -0.01 -0.08 -0.11 -0.11 -0.09 0.01
SG -0.32 -0.34 -0.28 -0.19 0.01 -0.01 1.00 0.61 0.41 0.41 0.17 -0.08
Drt -0.26 -0.38 -0.29 -0.22 0.00 -0.08 0.61 1.00 0.85 0.86 0.25 -0.08
DF -0.13 -0.35 -0.30 -0.20 0.01 -0.11 0.41 0.85 1.00 1.00 0.23 -0.07
DM -0.13 -0.35 -0.29 -0.20 0.01 -0.11 0.41 0.86 1.00 1.00 0.23 -0.07
Am -0.18 -0.32 -0.60 -0.56 -0.09 -0.09 0.17 0.25 0.23 0.23 1.00 0.32
Stc 0.04 0.12 -0.03 -0.09 0.01 0.01 -0.08 -0.08 -0.07 -0.07 0.32 1.00
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

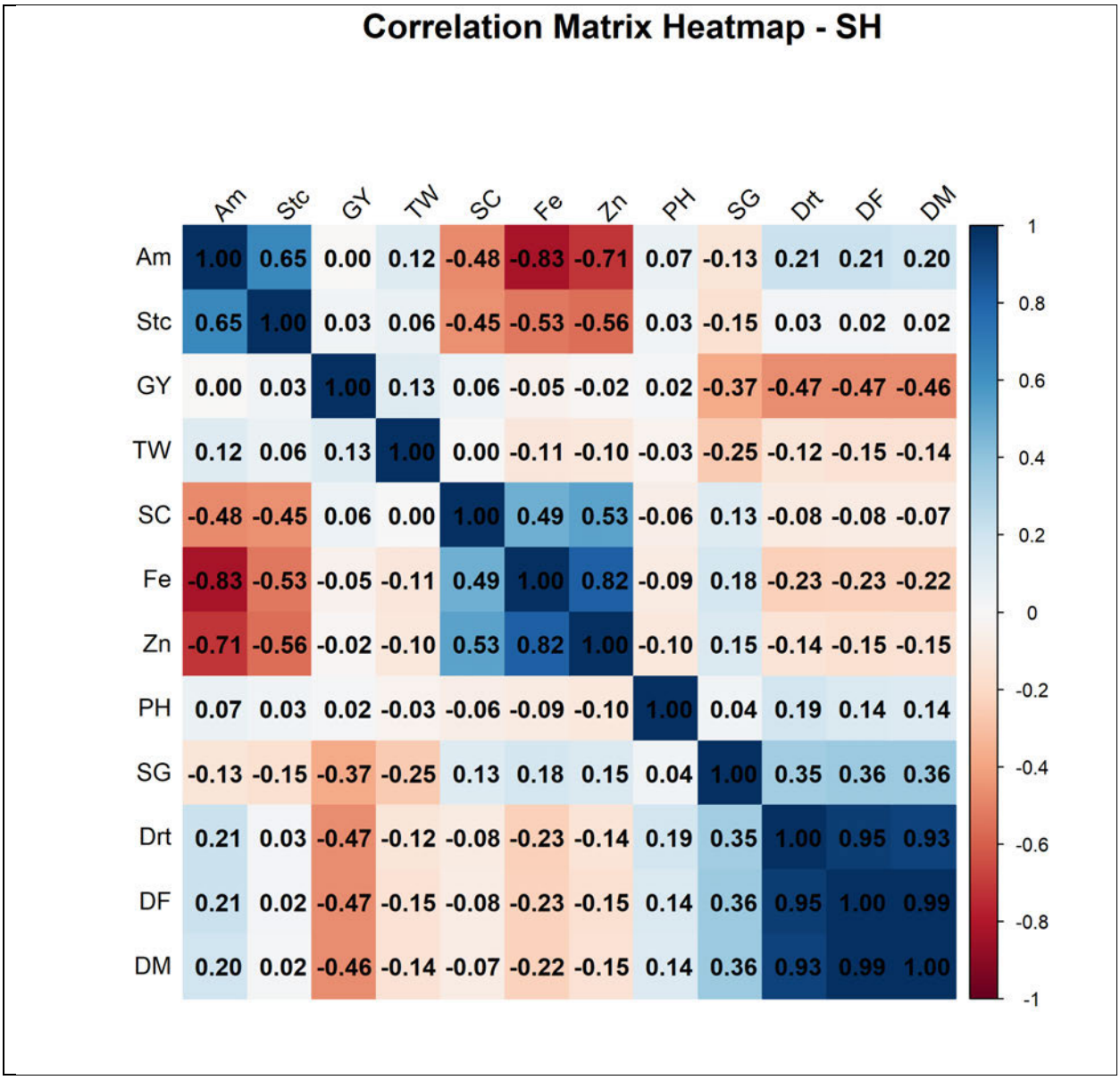


Figure 3.4. Correlation matrix heatmap of the various agronomic, drought parameters and nutritional profiles of finger millet accessions evaluated at Arsinegelle (AN) and Meiso (MI), and Maitsebri (SH) in Ethiopia. Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), Zn=zinc content (%), and SC=grain colour.

3.3.5 Principal component and biplot analyses

Principal component analysis showing eigenvalues (> 1.0), percent and cumulative variation for agronomic, nutritional traits, and drought response parameters is presented in Table 3.5. In the

potential environment, Arsinegelle (AN), three principal components were identified by PCA, which accounted for 73.1% of the total variance. Notably, days to 50% flowering and days to maturity were strong contributors to PC-1, while plant height and grain yield contributed to PC-3. Uniquely, grain colour (SC) was moderately loaded across PC-3 and PC-2, contributing to genotype differentiation. At AN (Figure 3.5A), genotypes sourced from Amhara region and released varieties were closely clustered with grain yield, plant height and thousand seed weight, while genotypes from Tigray region were more linked with days to flowering, and grain colour, and genotypes from Oromiya region showed proximity with days to maturity. In the intermediate stress environment (Maitsebri - SH), a similar pattern to AN was observed where PC-1, PC-2 and PC-3 cumulatively accounted for 67.7% of the total variation. PC-1 captured days to 50% flowering (14.2%) and days to maturity (13.8%) effects alongside grain colour (6.7%), while thousand seed weight and plant height dominated PC-3 with 39.6% and 23.4% contributions, respectively (Table 3.5). At SH, genotypes obtained from Amhara region showed close association with grain yield and thousand seed weight, while released genotypes were linked with plant height, and SNNP and Tigray regions genotypes were positioned towards grain colour (Figure 3.5B). Four PCs were identified in the stressed environment (Meiso - MI), cumulatively explaining 68.0% of the total variation. Starch significantly contributed to PC-4, while plant height and grain colour were prominent traits across two groups of principal components (PC-3 and PC-4). Notably, grain colour also showed strong associations with PC-3 and PC-4, and plant height contributed to PC-4. Under the stress condition, MI (Figure 3.5C), genotypes from Amhara region were associated with thousand seed weight and days to maturity. Released genotypes-maintained association with plant height, and SNNP region continued to link with grain colour (Figure 3.5C).

Nutritional traits revealed distinct differentiation across environments, particularly under moderate and severe stress. At AN, PC-2 captured most variation for iron (13.3%), starch (13.2%), zinc (12.6%), and amylose (11.5%) (Table 3.5). The biplot for AN showed that Benishangul & Gumz and SNNP regions genotypes clustered near starch and iron contents, while accessions from Oromiya region were associated with amylose concentrations (Figure 3.5A). At SH, although the trait loadings differed, nutritional traits remained influential where iron (14.0%), amylose (13.6%), and zinc (12.0%) were co-expressed in PC-1, while starch was also moderately involved in PC-2 (9.6%) (Table 3.5). In SH, genotypes obtained from Benishangul & Gumuz region maintained a strong association with iron contents, while those genotypes from SNNP region remained near starch content, and released accessions were relatively close to Zinc

contents (Figure 3.5B). Under the MI environment, starch had a strong contribution to PC-4 (40.9%), while zinc (21.0%), amylose (22.2%), and iron (15.7%) dominated PC-2. Figure 3.5C confirms these trends, where genotypes from Benishangul & Gumuz, SNNP, and Oromiya regions clustered around high concentrations of amylose, iron and zinc contents.

Traits related to drought response, namely stay-green (SG) and drought tolerance (Drt) scores, played a prominent role in genotype discrimination across environments. At AN, drought response contributed strongly to PC-1 (14.4%), with SG trait loading moderately across PC-1 and PC-2. at AN, SG and drought response scores showed weaker associations across genotypes under the favourable conditions (Figure 3.5A). Similarly, at SH, drought response (13.7%) was again a key contributor to PC-1, co-loading with SG score (11.4%) in PC-2. At SH, genotypes sourced from Oromiya and Tigray regions were closely aligned with SG and Drt traits (Figure 3.5B). In MI, drought response remained influential in PC-1 (18.4%), while SG was significantly associated with PC-3 (11.4%). Figure 3.5C further illustrates the spatial separation of drought-resilient genotypes, where accessions with higher SG and drought response scores aligned away from yield-related traits. The genotype sources that showed strong drought associations at SH exhibited similar patterns at MI (Figure 3.5C).

Table 3.5. Trait loadings of agronomic traits, drought parameters, and nutritional profiles on principal component axes, showing eigenvalues, percentage and cumulative variation for 448 finger millet genotypes evaluated at three diverse environments in Ethiopia.

Traits	Trait category	Arsinegelle (AN)			Maitsebri (SH)			Meiso (MI)			
		PC-1	PC-2	PC-3	PC-1	PC-2	PC-3	PC-1	PC-2	PC-3	PC-4
DF	Agronomic	14.2	8.7	0.0	14.2	11.7	2.0	17.5	8.3	6.4	1.6
DM		14.8	8.5	0.0	13.8	11.7	2.0	17.5	8.4	6.4	1.7
PH		1.8	1.2	55.7	1.0	0.1	23.4	0.1	2.4	3.3	27.6
GY		6.7	1.1	32.8	3.4	8.6	7.3	8.5	0.2	4.3	2.5
TW		2.1	9.1	1.1	0.0	3.1	39.6	2.9	0.0	39.0	3.0
SC		2.6	6.3	8.2	6.7	6.0	7.1	0.9	2.6	27.7	16.2
SG	Drought response	5.5	6.1	0.0	0.7	11.4	11.1	9.9	2.1	11.0	0.5
Drt		14.4	8.4	0.2	13.7	11.1	2.9	18.4	7.5	0.2	0.5
Am	Nutritional composition	10.9	11.5	1.0	13.6	8.5	0.1	7.4	22.2	0.2	4.6
Stc		7.7	13.2	0.0	6.8	9.6	4.1	0.0	9.6	1.7	40.9
Fe		10.0	13.3	0.8	14.0	8.6	0.2	9.7	15.7	0.0	0.3
Zn		9.3	12.6	0.2	12.0	9.6	0.1	7.1	21.0	0.0	0.5
Explained variance (eigenvalue)		4.2	3.4	1.1	3.9	3.2	1.0	4.0	1.9	1.1	1.1
Proportion of total variance (%)		35.3	28.4	9.4	32.6	26.4	8.7	33.4	15.7	9.6	9.3
Cumulative variance (%)		35.3	63.6	73.1	32.6	59.0	67.7	33.4	49.1	58.7	68.0

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), Zn=zinc content (%), and SC=grain colour. PC-1 = principal component 1; PC-2 = principal component 2; PC-3 = principal component 3; and PC-4 = principal component 4

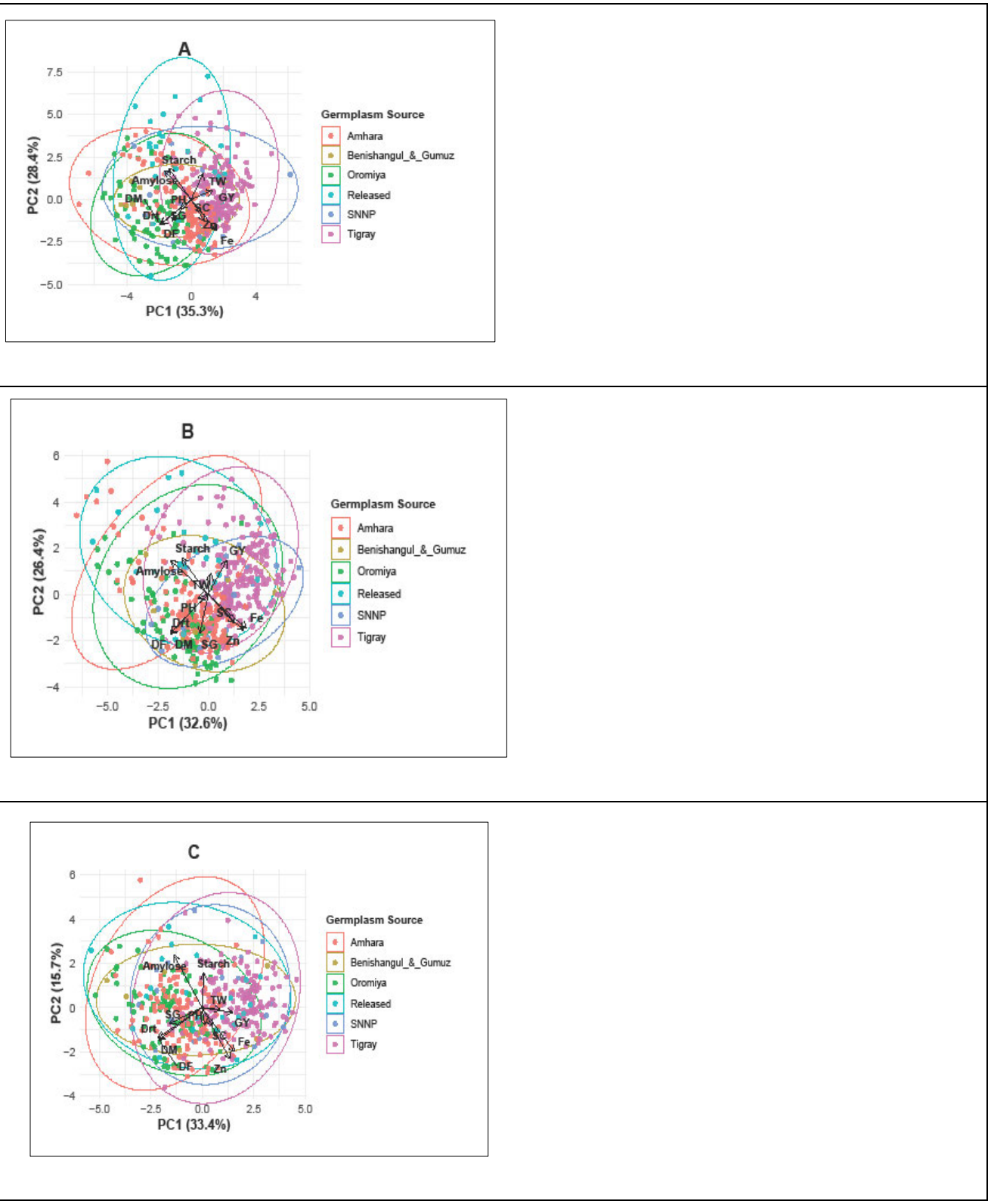


Figure 3.5. Principal component biplot showing the distribution of 448 finger millet genotypes and 12 traits at A: Arsinegelle, B: Maitsebri, and C: Meiso locations in Ethiopia. Note DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain

yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Fe = iron content (%), Zn=zinc content (%), and SC=grain colour.

3.3.6 Clustering finger millet genotypes for simultaneous selection

Cluster analysis revealed unique pattern for some key genotypes (Table 3.6). Cluster 1 encompassed the majority of genotypes in all three locations, including those from regions such as Benishangul & Gumuz, Amhara, Oromia, Tigray, and SNNP. This cluster grouped genotypes such as G1–G5, G14, G21–G25, G34, G48, G58, G83, G91–G92, G100, G110–G112, and G125–G135. Cluster 2 grouped the genotypes G6, G11, G13, G41, G52, G84, G107, G164, and G240, across the test environments. Genetically differentiated genotypes including G10, G16–G18, G26–G31, G60, G73–G75, G95–G99, G149–G159 were grouped in Cluster 3. A small subset formed cluster 4, comprising G143, G235, G303, and G418 (Table 3.6).

Table 3.6. Clustering of 448 Ethiopian finger millet genotypes for agronomic and nutritional traits at three testing environments with variable rainfall.

Clusters	Arsinegelle (AN)	Maitsebri (SH)	Meiso (MI)
1	G1, G2, G3, G4, G5, G7, G8, G9, G14, G20, G21, G22, G23, G24, G25, G32, G34, G36, G37, G38, G39, G40, G48, G49, G50, G51, G58, G64, G67, G80, G83, G85, G90, G91, G92, G100, G106, G108, G109, G110, G111, G112, G114, G115, G116, G117, G118, G119, G120, G121, G122, G123, G124, G125, G126, G127, G128, G129, G130, G131, G132, G133, G134, G135, G137, G152, G153, G161, G162, G163, G167, G168, G170, G173, G179, G182, G183, G184, G185, G202, G227, G228, G236, G239, G243, G264, G266, G268, G269, G270, G307, G312, G320, G325, G329, G331, G335, G336, G337, G342, G373, G374, G375, G376, G377, G378, G379, G380, G381, G383, G384, G385, G436, G437, and G446	G1, G2, G3, G4, G10, G11, G12, G14, G15, G17, G20, G21, G22, G23, G24, G25, G26, G27, G28, G29, G30, G31, G32, G34, G35, G38, G40, G43, G44, G48, G50, G53, G54, G55, G56, G57, G58, G60, G62, G63, G64, G65, G66, G71, G72, G74, G75, G77, G78, G79, G80, G81, G82, G83, G85, G86, G87, G88, G89, G91, G92, G93, G94, G95, G96, G97, G98, G99, G100, G101, G102, G103, G104, G105, G110, G111, G112, G113, G114, G115, G116, G117, G118, G119, G121, G123, G124, G125, G126, G128, G129, G130, G131, G132, G135, G136, G137, G138, G141, G148, G149, G150, G151, G152, G154, G155, G157, G158, G159, G160, G161, G165, G166, G167, G169, G172, G175, G176, G177, G178, G179, G180, G181, G183, G184, G185, G187, G191, G192, G193, G194, G198, G199, G200, G201, G202, G203, G205, G207, G213, G215, G217, G218, G219, G228, G230, G232, G237, G238, G239, G241, G242, G243, G246, G250, G253, G254, G255, G256, G258, G262, G263, G265, G266, G267, G272, G274, G275, G279, G281, G282, G283, G284, G286, G292, G295, G296, G297, G299, G300, G306, G307, G308, G309, G310, G311, G312, G318, G319, G320, G321, G322, G324, G326, G327, G328, G329, G331, G332, G333, G334, G335, G336, G337, G338, G339, G341, G342, G344, G351, G355, G366, G368, G369, G371, G372, G373, G375, G376, G378, G379, G380, G381, G384, G385, G391, G400, G426, and G446	G1, G2, G3, G4, G5, G7, G8, G12, G13, G14, G15, G16, G21, G23, G24, G33, G34, G35, G38, G39, G43, G44, G48, G51, G52, G53, G55, G56, G57, G58, G62, G65, G66, G68, G71, G72, G73, G75, G77, G78, G80, G82, G83, G84, G89, G90, G91, G92, G94, G95, G96, G97, G98, G100, G102, G103, G106, G107, G108, G109, G110, G111, G112, G113, G114, G115, G117, G118, G120, G121, G122, G125, G126, G127, G128, G129, G130, G132, G133, G134, G135, G137, G140, G149, G150, G151, G152, G153, G157, G160, G161, G162, G165, G167, G168, G170, G175, G177, G178, G181, G183, G184, G185, G189, G191, G193, G194, G205, G207, G214, G216, G217, G218, G236, G237, G239, G243, G254, G257, G262, G263, G265, G266, G267, G268, G271, G277, G295, G299, G305, G306, G307, G309, G310, G311, G312, G313, G318, G319, G320, G321, G322, G323, G324, G325, G328, G330, G331, G332, G333, G335, G336, G337, G338, G339, G340, G341, G342, G364, G367, G368, G369, G370, G372, G373, G374, G375, G378, G379, G380, G381, G382, G383, G384, G385, G386, G391, G404, G407, G426, G436, G437, and G446
2	G6, G11, G13, G19, G41, G42, G46, G52, G61, G70, G79, G84, G107, G113, G139, G142, G160, G164, G165, G166, G188, G195, G197, G211, G229, G230, G240, G241, G246, G247, G252, G257, G261, G282, G296, G299, G300, G305, G313, G315, G317, G323, G324, G330, G338, G340, G356, G359, G361, G362, G364, G365, G370, G372, G382, G386, G387, G394, G396, G399, G402, G407, G408, G412, G414, G421, G422, G424, G427, G428, G429, G431, G432, G433, G434, G435, G438, G439, G440, G441, G442, G443, G444, G447, and G448	G5, G7, G8, G9, G13, G33, G37, G39, G41, G49, G51, G52, G67, G70, G76, G84, G90, G106, G107, G109, G120, G122, G127, G133, G134, G139, G143, G144, G153, G163, G164, G168, G170, G173, G174, G182, G186, G229, G236, G240, G257, G264, G268, G269, G270, G277, G305, G313, G315, G323, G325, G330, G340, G362, G364, G365, G370, G374, G377, G382, G383, G386, G427, G428, G430, G431, G433, G436, G437, G438, and G439	G6, G10, G11, G17, G18, G19, G20, G22, G25, G26, G27, G28, G29, G30, G31, G32, G40, G42, G45, G46, G47, G50, G54, G59, G60, G61, G63, G64, G67, G70, G74, G76, G79, G81, G85, G86, G87, G88, G93, G99, G101, G104, G105, G116, G119, G123, G124, G131, G136, G138, G139, G141, G143, G144, G145, G146, G147, G148, G154, G155, G156, G158, G159, G164, G166, G169, G171, G172, G176, G179, G180, G182, G186, G187, G188, G190, G192, G195, G196, G197, G198, G199, G200, G201, G202, G203, G204, G206, G208, G209, G210, G211, G212, G213, G215, G219, G220, G221, G222, G223, G224, G225, G226, G227, G228, G230, G232, G233, G234, G238, G240, G241, G242, G244, G245, G246, G247, G248, G250, G251, G252, G253, G255, G256, G258, G261, G272, G273, G274, G275, G276, G278, G279, G280, G281, G282, G283, G284, G285, G286, G287, G288, G289, G290, G291, G292, G293, G294, G296, G297, G298, G300, G301, G302, G303, G308, G314, G316, G317, G326, G327, G329, G334, G343, G344, G345, G346, G347, G348, G349, G350, G351, G352, G354, G355, G356, G357, G358, G360, G361, G362, G363, G365, G366, G371, G376, G387, G388, G389, G390, G392, G393, G394, G395, G396, G397, G398, G399, G400, G401, G402, G403, G405, G406, G408,

			G409, G410, G411, G412, G413, G414, G415, G416, G417, G418, G419, G420, G421, G422, G423, G424, G425, G429, G431, G432, G434, G435, G439, G440, G441, G442, G443, G444, G447, and G448
3	G10, G12, G15, G16, G17, G18, G26, G27, G28, G29, G30, G31, G33, G35, G43, G44, G45, G47, G53, G54, G55, G56, G57, G59, G60, G62, G63, G65, G66, G68, G69, G71, G72, G73, G74, G75, G76, G77, G78, G81, G82, G86, G87, G88, G89, G93, G94, G95, G96, G97, G98, G99, G101, G102, G103, G104, G105, G136, G138, G140, G141, G144, G145, G146, G147, G148, G149, G150, G151, G154, G155, G156, G157, G158, G159, G169, G171, G172, G174, G175, G176, G177, G178, G180, G181, G186, G187, G189, G190, G191, G192, G193, G194, G196, G198, G199, G200, G201, G203, G204, G205, G206, G207, G208, G209, G210, G212, G213, G214, G215, G216, G217, G218, G219, G220, G221, G222, G223, G224, G225, G226, G231, G232, G233, G234, G237, G238, G242, G244, G245, G248, G249, G250, G251, G253, G254, G255, G256, G258, G259, G260, G262, G263, G265, G267, G271, G272, G273, G274, G275, G276, G277, G278, G279, G280, G281, G283, G284, G285, G286, G287, G288, G289, G290, G291, G292, G293, G294, G295, G297, G298, G301, G302, G304, G306, G308, G309, G310, G311, G314, G316, G318, G319, G321, G322, G326, G327, G328, G332, G333, G334, G339, G341, G343, G344, G345, G346, G347, G348, G349, G350, G351, G352, G353, G354, G355, G357, G358, G360, G363, G366, G367, G368, G369, G371, G388, G389, G390, G391, G392, G393, G395, G397, G398, G400, G401, G403, G404, G405, G406, G410, G411, G413, G415, G416, G417, G419, G420, G423, G425, G426, G430, and G445	G6, G16, G18, G19, G36, G42, G45, G46, G47, G59, G61, G68, G69, G73, G108, G140, G142, G145, G146, G147, G156, G162, G171, G188, G189, G190, G195, G196, G197, G204, G206, G208, G209, G210, G211, G212, G214, G216, G220, G221, G222, G223, G224, G225, G226, G227, G231, G233, G234, G235, G244, G245, G247, G248, G249, G251, G252, G259, G260, G261, G271, G273, G276, G278, G280, G285, G287, G288, G289, G290, G291, G293, G294, G298, G301, G302, G303, G304, G314, G316, G317, G343, G345, G346, G347, G348, G349, G350, G352, G353, G354, G356, G357, G358, G359, G360, G361, G363, G367, G387, G388, G389, G390, G392, G393, G394, G395, G396, G397, G398, G399, G401, G402, G403, G404, G405, G406, G407, G408, G409, G410, G411, G412, G413, G414, G415, G416, G417, G418, G419, G420, G421, G422, G423, G424, G425, G429, G434, G435, G441, G442, G443, G444, G445, G447, and G448	G9, G36, G37, G41, G49, G69, G163, G173, G174, G229, G259, G264, G269, G270, G315, G359, G377, G427, G428, G430, G433, G438, and G445
4	G143, G235, G303, G409, and G418	G432, and G440	G142, G231, G235, G249, G260, G304, and G353

Note: See Appendix Table 3.1. for descriptions of genotypes.

3.4 Discussion

Finger millet is an important drought-resilient cereal with exceptional nutritional value and broad adaptation in sub-Saharan Africa, particularly in Ethiopia. Ethiopia's diverse finger millet germplasm comprising landraces, wild relatives, and improved varieties represents a rich genetic reservoir for developing high-yielding, climate-resilient, and nutrient-dense cultivars. In this study, Ethiopian finger millet accessions were systematically evaluated under drought condition to profile genetically diverse finger millet accessions for major agronomic traits, drought response, and nutritional compositions in relation to adaptation under contrasting drought stress conditions to select genotypes for breeding or production. In the current study, there were significant effects of genotype (G), environment (E), and their interaction (GEI) observed for agronomic, drought response, and nutritional traits (Table 3.2). The extensive genotypic diversity has previously been reported in finger millet, concurring with present findings (Tesfaye and Mengistu 2017; Kumari et al. 2018; Singh et al. 2024). The genotypes were varied for grain yield, and genotypes such as G141, G423, G247, G171, G46, G294, and G204 were identified with high yield potential, with grain yield exceeding 3.0 tons per hectare. Further, these genotypes were high-yielders compared to the widely cultivated genotypes in the country, including Tadesse (G441), Tesema (G442), Necho (G433), and Diga-2 (G446). These genotypes also showed superior performance for major agronomic traits, including early flowering, heavier seed, stay-green (SG) trait. The SG trait is particularly valuable for drought avoidance and biomass retention under moisture-limited conditions (Jordan et al. 2012; Borrel et al. 2014; Danful et al. 2019; Shin et al. 2020; Gebreyohannes et al. 2025). These genotypes represent promising genetic resources for future breeding programs and warrant further validation through multi-environment testing and variety evaluation procedures prior to potential release.

The significant effects of environment on the studied agronomic and nutritional traits in finger millet revealed that genotype performance is strongly shaped by contrasting agro-ecological conditions, such as edaphic factors, rainfall and temperature. Specifically, environments like Arsinegelle (AN), characterized by higher rainfall, moderate temperatures, and fertile, well-drained soils with adequate organic matter (Table 3.1) tend to favour genotypes with high yield development and late maturity. Conversely, Meiso (MI), with its arid climate, heat stress, and nutrient-poor, often alkaline or saline soils with low water-holding capacity, amplifies the expression of drought tolerance and early flowering. Maitsebri (SH), representing an intermediate zone, with balanced soil texture and moderate fertility, supports both stress resilience and

productivity traits. This environmental heterogeneity particularly in rainfall patterns, temperature regimes, and soil characteristics plays a vital role in trait expression of genotypes and supports earlier observations by Anuradha et al. (2022), and Lanjewar et al. (2025), who emphasized that stress gradients across test sites can trigger significant GEI. The observed significant GEI for most traits indicates that genotype performance varied widely across locations, reflecting differential and spatial adaptability. This necessitates the identification of location-specific superior genotypes, enabling breeders to recommend best-performing accessions for specific environments. For instance, genotypes excelling in MI may be drought-resilient but less suitable for high-potential areas like AN. Recognizing and exploiting such patterns is vital for designing targeted breeding and deployment strategies, ultimately enhancing genetic gains and production stability across diverse growing regions (Mulualem 2022; Gangashetty et al. 2023; Tesfaye et al. 2023). However, further GEI analyses are required to identify genotypes with specific and broad adaptation across the tested environments.

Heritability is a useful measure of the degree of association between an individual's breeding value and its observable phenotypic traits, whereas genetic advance predicts the effectiveness of selection for specific traits in crop breeding programs (Falconer and Markey 1996). The observed high broad-sense heritability estimates (>60%) for days to 50% flowering, days to maturity, and drought-related traits (stay-green and drought tolerance score) are consistent with reports by Ketema et al. (2025) and Kannababu et al. (2025). This suggests that these traits are under strong genetic control, with genetic factors accounting for a substantial proportion of the observed phenotypic variation despite environmental influences. Consequently, they are promising targets for phenotypic selection in breeding programs. The drought tolerance score showed high genetic advance as a percentage of the mean, making it highly responsive to direct selection. However, this should be interpreted cautiously, as visual scoring may influence the magnitude of GA% in addition to underlying genetic variation. In contrast, days to 50% flowering and days to maturity showed low genetic advance as a percent of mean (GA%) despite their high heritability, suggesting constrained genetic variability or non-additive effects, which necessitates later-generation selection (Sharma et al. 2018; Nagaraja et al. 2024; Brhane et al. 2024). In contrast, traits like plant height, and grain yield, amylose, and starch concentrations showed low heritability and low genetic advance and GA%, underscoring strong environmental influence and polygenic inheritance, as alluded by Naveen et al. (2024).

The NIR-based estimates of nutritional composition exhibited an acceptable level of accuracy, mainly given the high cost and labour-intensive nature of the wet chemistry procedure. However, there is a need to validate the current results through conventional wet chemistry analysis. Sood et al. (2019) highlighted that the integration of advanced plant phenomics and genomics has meaningfully enhanced genetic gains and strengthened the understanding of key agronomic, adaptive, and nutritional traits in finger millet. Furthermore, the recent multi-omics studies in finger millet provide complementary insights into Fe and Zn homeostasis, highlighting the potential of integrating omics-driven biofortification with modern breeding strategies (Chandra et al. 2020). Moderate heritability and GA% values for thousand seed weight (TW), SG, and micronutrients (Fe, Zn) point to the potential for steady genetic improvement via recurrent selection. Despite moderate heritability, the low genetic advance for micronutrients indicates limited short-term gains, emphasizing the need for biofortification breeding strategies such as genomic selection and hybridization to exploit heterosis to enhance nutritional traits (Fred et al. 2021; Teklu et al. 2023a, b). In addition, this study corroborates earlier reports in finger millet (Marefia et al. 2022; Mulualem 2022) that emphasize high heritability for phenological traits but limited selection efficiency for yield and quality traits. Therefore, to optimize genetic gains in finger millet across Ethiopia's variable climates, a stratified breeding strategy is essential-combining direct selection for high-heritability traits, recurrent breeding for moderately complex traits, and genomic-assisted or hybrid approaches for low-heritability traits. This approach ensures both selection precision and adaptability of genotypes across diverse agro-ecological zones.

Breeding for drought tolerance is crucial to improve yield stability, ensure food and nutritional security under variable and water-limited conditions of Ethiopia and similar agro-ecologies in sub-Saharan Africa. Environmental effects were pronounced at MI, where intense drought stress during critical growth stages especially flowering accelerated phenological progression and caused a substantial reduction in grain yield, reaching nearly 60%, relative to the more favorable conditions observed at AN. This outcome is consistent with earlier reports in cereals, where drought stress at flowering resulted in 40–70% yield loss in tef, finger millet, and pearl millet (Maqsood and Ali 2007; Tadele 2018; Numan et al. 2021). Consistent with the current result, early flowering and maturity finger millet genotypes such as G141, G423, G297, G247, and G171 performed better under severe drought (MI site), reflecting a drought-escape strategy that enables completion of their life cycle before peak water stress (Tadelle 2018; Panda et al. 2023). Remarkably, several genotypes exhibited consistence performance across these contrasting

environments, indicating inherent adaptability and potential for breeding heat and drought-resilient cultivars. These genotypes G141, G423, G297, G247, and G171, which exhibited excellent drought-adaptation, can be used as parents in hybridization programs to introgress early maturity and stress-resilient traits into diverse and cultivated backgrounds, or as donor lines in recurrent selection to enhance population performance. The genotypes' consistency makes them ideal candidates for multi-environment trials and release for broad cultivation in Ethiopia and similar environments. A notable pattern emerged in relation to seed pigmentation such that genotypes with black or dark brown grains consistently exhibited superior performance for grain yield, drought resistance, and SG ability, particularly under stress-prone conditions (Table 3.3). This observation suggests that the association between darker grain pigmentation and superior drought performance may reflect pleiotropic effects or tight genetic linkage with stress-resilience loci rather than a direct causal effect of pigmentation itself (Vadivoo et al. 1998; Singh et al. 2024). Black or red seeds generally show superior drought tolerance because their pigmentated seed-coats are rich in phenolics and flavonoids that enhance antioxidant protection, regulate water uptake, and improve seedling vigor under stress (Radchuk and Borisjuk 2014; Dabravolski and Isayenkov 2023; Li and Ahammed 2023; Zhang et al. 2023). Genotypes with darker pigmentation such as G141, G423, G297, G247, G171, G204, G294, and G46 were noted as top performers under the harsh conditions of MI, combining several desirable traits, including early flowering and maturity, high yield potential, large seed size, SG characteristics, and strong drought tolerance. Notably, they also exhibit superior nutritional quality, with high zinc and iron content. Their multi-trait excellence and proven stability make them valuable assets for breeding climate-resilient and nutrient-rich cultivars.

Trait correlation analyses resolved interesting associations for finger millet improvement (Figure 3.4). Negative association was detected between grain yield and stress adaptive traits across the test locations, suggesting targeted selection under stress-prone environments. High-yielding finger millet genotypes tend to mature early and show reduced drought sensitivity, aligning with previous findings in finger millet (Manyasa et al. 2016; Kumari et al. 2018; Mulualem 2022) and other cereals such as sorghum (Haussmann et al. 2012), pearl millet (Yadav et al. 2021), and maize (Talabi, et al. 2017). Early maturity linked with drought escape is a proxy trait for drought tolerance breeding. Furthermore, the negative association between stay-green and grain yield is beneficial, as lower SG scores (1-2) were linked to higher productivity under drought, highlighting their value in selecting drought-tolerant genotypes. Therefore, breeding strategies should prioritise early flowering and drought resilience. Additionally, integrating location-

specific selection indices that consider local drought scenarios, maturity, and nutritional goals will be instrumental in developing climate-smart and nutritionally superior finger millet cultivars (Sharma et al. 2022; Pramanick et al. 2024).

Principal component analysis (PCA) clearly revealed how key traits drive the adaptation and differentiation of finger millet genotypes across Ethiopia's contrasting environments. PCs with eigenvalues > 1.0 were retained, and the number of components varied across environments depending on their eigenvalues (Table 3.5). At AN, a high-potential site, three PCs accounted for > 70% of the total variation, with genotypes primarily differentiated by grain yield, plant height (PH), and nutritional traits, including Fe, Zn and amylose contents. At MI, a drought-prone environment, four PCs were retained, due to the fourth component captured additional meaningful variation in starch content, plant height and grain colour. At MI, early flowering (DF), and maturity (DM), and drought tolerance were the most defining traits, with the four PCs collectively explaining 68.0% of the total variation. At SH, an intermediate environment, three PCs explained 67.7% of the variation, with both resilience-related and grain nutritional quality contributing substantially to genotype separation. This spatially explicit trait clustering highlights distinct adaptation strategies, with genotypes excelling either in stress avoidance and early maturity or in high productivity and nutritional quality. Such patterns, consistent with previous studies in finger millet and other cereals (Admas and Tesfaye 2017; Kumari et al. 2018; Negash et al. 2019; Kumar et al. 2020), underscore the need for environment-specific breeding pipelines. Prioritizing early-maturing, drought-tolerant lines in harsh zones and yield- and nutrient-rich lines in favorable areas offers a strategic, resource-efficient path to maximize genetic gains and climate resilience.

Cluster analysis of 448 Ethiopian finger millet genotypes revealed distinct genotypes groupings under contrasting environments. Cluster 1 contained the majority of genotypes, originating from diverse regions such as Amhara, Oromia, Tigray, SNNP, and Benishangul & Gumuz, suggesting shared trait combinations and consistent grouping across environments, which may reflect similar phenotypic responses under contrasting agro-ecological conditions. Cluster 2 comprised moderately distinct genotypes that showed some degree of environmental adaptability across sites. In contrast, Cluster 3 contained highly divergent genotypes with unique trait combinations, making them valuable candidates for targeted trait-specific breeding. A small, unique subset formed Cluster 4, representing rare or extreme trait expressions. Similar clustering of finger millet germplasms based on multivariate trait data has been reported by Kumari et al. (2018), in

other millets species, pearl and foxtail millet (Backiyalakshmi et al. 2021; Rao et al. 2024). The observed cluster structure demonstrates phenotypic diversity among Ethiopian finger millet genotypes and provides a useful basis for selecting genetically distinct parents for further evaluation and breeding.

3.5 Conclusions and recommendations

The study profiled the 448 Ethiopian finger millet accessions under varying drought stress conditions for agronomic, drought-responsive, and nutritional traits. The findings revealed marked genotype by environment interactions and substantial yield reduction (60%) under a severe stress growing condition, highlighting the need for drought tolerance breeding. Drought adaptive traits such as early flowering, stay-green score (SG), and drought tolerance scores (Drt), were significantly associated with yield gains. Notably, days to flowering, days to maturity, and drought tolerance score exhibited relatively high broad-sense heritability ($H^2 > 60\%$), suggesting their reliability and potential for genetic improvement under drought stress. Black-seeded finger millet genotypes had high yield and elevated micronutrient content (iron and zinc), while red-seeded, early maturing and heavier grain weight was related to drought tolerance. Significant associations of SG and Drt with grain yield across environments indicated that genotypes with lower scores, early flowering, delayed senescence, and reduced stress symptoms were more productive under drought-prone conditions. The trait associations were further supported by principal component analysis (PCA), where DF, DM, and Drt accounted for the largest explained variance across environments. Also, cluster analysis delineated four distinct genotype groups based on agronomic performance, drought response parameters and nutritional profiles. In this context, the NIR-based analyses of nutritional content offered a rapid and cost-effective option with acceptable accuracy; yet, validation through conventional wet chemistry remains recommended for ensuring data accuracy. Integrating agronomic, drought-responsive, and nutritional traits with PCA and clustering analyses provided a robust data set for the identification of unique genotypes such as G141, G423, G297, G247, G171, G204, G294, and G46, and breeding programs warrant further validation through multi-environment testing and variety evaluation procedures prior to potential release.

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Appendix Table 3.1. Names, region of collection and grain colour of 448 finger millet genotypes used in the study

Genotype code	Genotype name	Grain color	Regions of collection
G1	24268	Dark brown	Benishangul & Gumuz
G2	24269	Dark brown	Benishangul & Gumuz
G3	24270	Brown	Amhara
G4	24392	Dark brown	Oromia
G5	24393	Light brown	Oromia
G6	24394	Brown	Oromia
G7	24395	Light brown	Oromia
G8	24396	Light brown	Oromia
G9	100064	Brown	Oromia
G10	100065	Black	Oromia
G11	100092	Black	Oromia
G12	100093	Black	Oromia
G13	100095	Brown	Oromia
G14	100097	Brown	Oromia
G15	207543	Black	Amhara
G16	207591	Black	Tigray
G17	207593	Black	Tigray
G18	207897	Black	Tigray
G19	207900	Black	Tigray
G20	207960	Black	Oromia
G21	207961	Black	Oromia
G22	207962	Black	Oromia
G23	207963	Black	Oromia
G24	207964	Dark brown	Oromia
G25	208013	Brown	Amhara
G26	208015	Dark brown	Amhara
G27	208016	Dark brown	Amhara
G28	208438	Black	Amhara
G29	208439	Black	Amhara
G30	208440	Black	Amhara
G31	208442	Dark brown	Amhara
G32	208443	Black	Amhara
G33	208444	Dark brown	Amhara
G34	208445	Dark brown	Amhara
G35	208446	Black	Amhara
G36	208447	Dark brown	Amhara
G37	208448	Light brown	Amhara
G38	208724	Dark brown	Oromia
G39	208725	Brown	Oromia
G40	208726	Dark brown	Oromia
G41	208727	Brown	Oromia
G42	208728	White	Oromia
G43	208729	Dark brown	Oromia
G44	208730	Black	Oromia
G45	211029	Black	Tigray
G46	211473	Black	SNNP
G47	211474	Dark brown	SNNP
G48	211504	Black	Oromia
G49	211505	Brown	Oromia
G50	211506	Black	Oromia
G51	212461	Brown	Oromia
G52	212462	White	Oromia
G53	212692	Dark brown	Amhara
G54	212693	Black	Amhara
G55	212694	Black	Amhara
G56	213032	Black	SNNP
G57	213033	Dark brown	SNNP
G58	213034	Dark brown	SNNP
G59	213035	Dark brown	SNNP
G60	213228	Black	Tigray
G121	216038	Dark brown	Oromia
G123	216040	Black	Oromia
G124	216041	Black	Oromia
G125	216045	Black	Oromia
G126	216046	Black	Oromia
G127	216047	Black	Oromia
G128	216048	Black	Oromia
G129	216049	Black	Oromia

Genotypes code	Genotypes name	Grain color	Regions of collection
G61	213835	Brown	SNNP
G62	215017	Black	Oromia
G63	215798	Dark brown	Oromia
G64	215802	Dark brown	Oromia
G65	215804	Dark brown	Oromia
G66	215805	Black	Oromia
G67	215829	White	Amhara
G68	215837	White	Amhara
G69	215841	White	Amhara
G70	215843	Light brown	Amhara
G71	215844	Black	Amhara
G72	215847	Black	Amhara
G73	215848	White	Amhara
G74	215850	Dark brown	Amhara
G75	215867	Dark brown	Amhara
G76	215869	Dark brown	Amhara
G77	215872	Black	Amhara
G78	215873	Dark brown	Amhara
G79	215875	Black	Amhara
G80	215878	Dark brown	Amhara
G81	215879	Black	Amhara
G82	215883	Dark brown	Amhara
G83	215887	Dark brown	Amhara
G84	215889	White	Amhara
G85	215896	Dark brown	Amhara
G86	215908	Dark brown	Amhara
G87	215916	Dark brown	Amhara
G88	215962	Dark brown	Amhara
G89	215963	Black	Amhara
G90	215966	Brown	Amhara
G91	215967	Dark brown	Amhara
G92	215968	Dark brown	Amhara
G93	215970	Dark brown	Amhara
G94	215973	Dark brown	Amhara
G95	215976	Black	Amhara
G96	215981	Dark brown	Amhara
G97	215982	Black	Amhara
G98	215984	Black	Amhara
G99	215985	Black	Amhara
G100	215986	Black	Amhara
G101	215989	Black	Amhara
G102	215992	Black	Amhara
G103	215994	Black	Amhara
G104	215996	Black	Amhara
G105	216020	Black	Oromia
G106	216021	Brown	Oromia
G107	216023	white	Oromia
G108	216024	white	Oromia
G109	216025	White	Oromia
G110	216026	Black	Oromia
G111	216027	Black	Oromia
G112	216028	black	Oromia
G113	216029	Dark brown	Oromia
G114	216030	Dark brown	Oromia
G115	216031	Black	Oromia
G116	216032	Black	Oromia
G117	216033	Black	Oromia
G118	216034	Black	Oromia
G119	216035	Black	Oromia
G120	216037	Dark brown	Oromia
G122	216039	Dark brown	Oromia
G185	230562	Black	Oromia
G186	234148	white	Tigray
G187	234149	Black	Tigray
G188	234151	Black	Tigray
G189	234154	Black	Tigray
G190	234157	Black	Tigray
G191	234158	Black	Tigray

Genotype code	Genotype name	Grain color	Regions of collection
G130	216050	Black	Oromia
G131	216051	Black	Oromia
G132	216052	Brown	Oromia
G133	216053	Brown	Oromia
G134	216054	Brown	Oromia
G135	216055	Brown	Oromia
G136	216057	Brown	Oromia
G137	219503	Dark brown	Amhara
G138	219807	Black	Tigray
G139	219817	white	Tigray
G140	219818	Black	Tigray
G141	219819	Black	Tigray
G142	219821	Dark brown	Tigray
G143	219824	Brown	Tigray
G144	219831	Brown	Tigray
G145	221697	Dark brown	Tigray
G146	223145	Dark brown	Tigray
G147	223146	white	Tigray
G148	225892	Black	Amhara
G149	225894	Black	Amhara
G150	225895	Black	Amhara
G151	227165	Black	Amhara
G152	227166	Dark brown	Amhara
G153	227973	white	SNNP
G154	227974	Dark brown	SNNP
G155	227975	Dark brown	SNNP
G156	228202	white	Amhara
G157	228304	Dark brown	Amhara
G158	228305	Black	Amhara
G159	228306	Black	Amhara
G160	228309	Dark brown	Amhara
G161	228901	Dark brown	Oromia
G162	228902	white	Oromia
G163	229718	white	Amhara
G164	229719	white	Amhara
G165	229720	Dark brown	Amhara
G166	229721	Dark brown	Amhara
G167	229722	Dark brown	Benishangul & Gumuz
G168	229723	Dark brown	Benishangul & Gumuz
G169	229724	Dark brown	Benishangul & Gumuz
G170	229725	Dark brown	Benishangul & Gumuz
G171	229726	Dark brown	Benishangul & Gumuz
G172	229728	Dark brown	Benishangul & Gumuz
G173	229729	Brown	Amhara
G174	229730	white	Amhara
G175	229731	Dark brown	Amhara
G176	229732	Dark brown	Amhara
G177	229733	Black	Amhara
G178	229734	Dark brown	Amhara
G179	229735	Dark brown	Amhara
G180	229736	Black	Amhara
G181	229738	Dark brown	Amhara
G182	230255	Brown	Benishangul & Gumuz
G183	230560	Dark brown	Oromia
G184	230561	Black	Oromia
G247	237449	Dark brown	Tigray
G248	237450	Dark brown	Tigray
G249	237452	Dark brown	Tigray
G250	237458	Dark brown	Tigray
G251	237459	Dark brown	Tigray
G252	237461	Dark brown	Tigray
G253	237462	Dark brown	Tigray
G254	237463	Black	Tigray
G255	237466	Black	Tigray
G256	237467	Dark brown	Tigray
G257	237468	Brown	Tigray
G258	237471	Dark brown	Tigray
G259	237473	Dark brown	Tigray
G260	237474	Dark brown	Tigray
G261	237476	Dark brown	Tigray
G262	237477	Black	Tigray
G263	237582	Dark brown	Oromia
G264	237583	Light brown	Oromia

Genotypes code	Genotypes name	Grain color	Regions of collection
G192	234159	Black	Tigray
G193	234160	Black	Tigray
G194	234162	Black	Tigray
G195	234165	Black	Tigray
G196	234168	Black	Tigray
G197	234169	Brown	Tigray
G198	234170	Black	Tigray
G199	234171	Black	Tigray
G200	234172	Dark brown	Tigray
G201	234173	Black	Tigray
G202	234174	Dark brown	Tigray
G203	234175	Black	Tigray
G204	234176	Black	Tigray
G205	234178	Black	Tigray
G206	234179	Black	Tigray
G207	234183	Black	Tigray
G208	234184	Dark brown	Tigray
G209	234185	Dark brown	Tigray
G210	234186	Dark brown	Tigray
G211	234187	Brown	Tigray
G212	234188	Dark brown	Tigray
G213	234190	Black	Tigray
G214	234192	Black	Tigray
G215	234193	Dark brown	Tigray
G216	234194	Dark brown	Tigray
G217	234198	Dark brown	Tigray
G218	234201	Black	Tigray
G219	234202	Black	Tigray
G220	234203	Black	Tigray
G221	234204	Dark brown	Tigray
G222	234205	Dark brown	Tigray
G223	234206	Dark brown	Tigray
G224	234207	Dark brown	Tigray
G225	234208	Black	Tigray
G226	234209	Dark brown	Tigray
G227	234210	Dark brown	Tigray
G228	235140	Dark brown	Amhara
G229	235141	Brown	Amhara
G230	235151	Black	Tigray
G231	235153	Brown	Tigray
G232	235154	Dark brown	Tigray
G233	235155	Dark brown	Tigray
G234	235699	Black	SNNP
G235	235700	Dark brown	SNNP
G236	235782	white	Amhara
G237	235783	Black	Amhara
G238	235828	Dark brown	Amhara
G239	235833	Black	Amhara
G240	235835	Brown	Amhara
G241	235836	Black	Amhara
G242	235838	Dark brown	Amhara
G243	235846	Dark brown	Amhara
G244	237443	white	Amhara
G245	237446	black	Tigray
G246	237447	Dark brown	Tigray
G309	238342	Black	Amhara
G310	238343	Dark brown	Amhara
G311	238344	Dark brown	Amhara
G312	238345	Dark brown	Amhara
G313	238346	Dark brown	Amhara
G314	238460	Dark brown	Tigray
G315	240506	Brown	SNNP
G316	241768	Brown	SNNP
G317	241769	Dark brown	SNNP
G318	242105	Black	Amhara
G319	242106	Black	Amhara
G320	242107	Black	Amhara
G321	242108	Brown	Amhara
G322	242109	Black	Amhara
G323	242111	white	Amhara
G324	242112	Black	Amhara
G325	242113	Brown	Amhara
G326	242114	Dark brown	Amhara

Genotype code	Genotype name	Grain color	Regions of collection
G265	237584	Dark brown	SNNP
G266	237969	Black	Oromia
G267	237970	Dark brown	Oromia
G268	237971	white	Oromia
G269	237972	Light brown	Oromia
G270	237973	Brown	Oromia
G271	238297	Black	Tigray
G272	238298	Black	Tigray
G273	238300	Black	Tigray
G274	238302	Black	Tigray
G275	238303	Black	Tigray
G276	238304	Black	Tigray
G277	238305	Brown	Tigray
G278	238306	Dark brown	Tigray
G279	238307	Black	Tigray
G280	238308	Black	Tigray
G281	238309	Dark brown	Tigray
G282	238310	Dark brown	Tigray
G283	238311	Black	Tigray
G284	238312	Black	Tigray
G285	238313	Dark brown	Tigray
G286	238314	Dark brown	Tigray
G287	238316	Dark brown	Tigray
G288	238317	Black	Tigray
G289	238318	Dark brown	Tigray
G290	238319	white	Tigray
G291	238320	Black	Tigray
G292	238321	Dark brown	Tigray
G293	238322	Dark brown	Tigray
G294	238323	Dark brown	Tigray
G295	238324	black	Tigray
G296	238325	Black	Tigray
G297	238326	Black	Tigray
G298	238328	Black	Tigray
G299	238329	Black	Tigray
G300	238331	Dark brown	Tigray
G301	238333	Black	Tigray
G302	238334	Dark brown	Tigray
G303	238335	Black	Tigray
G304	238336	Dark brown	Tigray
G305	238337	Brown	Tigray
G306	238338	Dark brown	Amhara
G307	238340	Dark brown	Amhara
G308	238341	Dark brown	Amhara
G371	243639	Black	Amhara
G372	243640	Dark brown	Amhara
G373	243641	Dark brown	Amhara
G374	243642	Dark brown	Amhara
G375	243643	Dark brown	Amhara
G376	243644	Dark brown	Amhara
G377	244798	Light brown	SNNP
G378	245084	Black	Oromia
G379	245085	Black	Oromia
G380	245086	Black	Oromia
G381	245087	Black	Oromia
G382	245088	white	Oromia
G383	245089	Brown	Oromia
G384	245090	Brown	Oromia
G385	245091	Dark brown	Oromia
G386	245092	Light brown	Oromia
G387	AxumColl1	Dark brown	Tigray
G388	AxumColl2	Dark brown	Tigray
G389	AxumColl3	Dark brown	Tigray

Genotypes code	Genotypes name	Grain color	Regions of collection
G327	242115	Dark brown	Amhara
G328	242117	Dark brown	Amhara
G329	242118	Brown	Amhara
G330	242119	Brown	Amhara
G331	242120	Brown	Amhara
G332	242121	Dark brown	Amhara
G333	242122	Dark brown	Amhara
G334	242123	Dark brown	Amhara
G335	242125	Black	Amhara
G336	242126	Dark brown	Amhara
G337	242127	Dark brown	Amhara
G338	242128	Dark brown	Amhara
G339	242129	Black	Amhara
G340	242130	Brown	Amhara
G341	242131	Dark brown	Amhara
G342	242132	Dark brown	Amhara
G343	242133	Dark brown	Amhara
G344	242134	Dark brown	Amhara
G345	242135	white	Amhara
G346	242611	Black	Tigray
G347	242612	Black	Tigray
G348	242615	Black	Tigray
G349	242616	Dark brown	Tigray
G350	242618	Dark brown	Tigray
G351	242619	Black	Tigray
G352	242620	Dark brown	Tigray
G353	242621	Dark brown	Tigray
G354	242622	Dark brown	Tigray
G355	242624	Black	Tigray
G356	242626	Brown	Tigray
G357	242627	Black	Tigray
G358	242628	Black	Tigray
G359	243615	Brown	Amhara
G360	243616	white	Amhara
G361	243617	white	Amhara
G362	243629	white	Amhara
G363	243630	Dark brown	Amhara
G364	243631	Brown	Amhara
G365	243632	white	Amhara
G366	243633	Dark brown	Amhara
G367	243634	Black	Amhara
G368	243635	Black	Amhara
G369	243637	Black	Amhara
G370	243638	Brown	Amhara
G432	Mecha(229371)	Brown	Released
G433	Necho (203572)	white	Released
G434	Axum (ACC#229355)	Brown	Released
G435	Meba (GBK011119A)	Light brown	Released
G436	Bareda (BRE356-10)	Brown	Released
G437	Baruda(Pw01-075)	Brown	Released
G438	Boneya (KNE#411)	Brown	Released
G439	Debatsi (Debatsi)	Light brown	Released
G440	Padet (KNE#409)	Brown	Released
G441	Tadesse (KNE#1098)	Red	Released
G442	Tesema (ACC 229469)	Light brown	Released
G443	Wama(KNE-392)	Brown	Released
G444	Kako-1(203351)	Light brown	Released
G445	Bako-09 (ACC#214995)	Brown	Released
G446	Diga-2 (BKFM0010)	Black	Released
G447	Mereb-1 (KNE#622)	Red	Released
G448	Tekeze-1 (SMARC coll#60)	Dark brown	Released

Genotype code	Genotype name	Grain color	Regions of collection	Genotypes code	Genotypes name	Grain color	Regions of collection
G390	AxumColl4	Black	Tigray				
G391	AxumColl5	Black	Tigray				
G392	AxumColl6	Black	Tigray				
G393	AxumColl7	Dark brown	Tigray				
G394	AxumColl8	Dark brown	Tigray				
G395	AxumColl9	Dark brown	Tigray				
G396	AxumColl10	Dark brown	Tigray				
G397	AxumColl11	Black	Tigray				
G398	AxumColl12	Dark brown	Tigray				
G399	AxumColl13	Red	Tigray				
G400	AxumColl14	Dark brown	Tigray				
G401	AxumColl15	Dark brown	Tigray				
G402	AxumColl16	Black	Tigray				
G403	AxumColl17	Black	Tigray				
G404	AxumColl18	Black	Tigray				
G405	AxumColl19	Dark brown	Tigray				
G406	AxumColl20	Dark brown	Tigray				
G407	AxumColl21	Black	Tigray				
G408	AxumColl22	Black	Tigray				
G409	AxumColl23	Red	Tigray				
G410	AxumColl24	Black	Tigray				
G411	AxumColl25	Black	Tigray				
G412	AxumColl26	Dark brown	Tigray				
G413	AxumColl27	Dark brown	Tigray				
G414	AxumColl28	Brown	Tigray				
G415	AxumColl29	Dark brown	Tigray				
G416	AxumColl30	Black	Tigray				
G417	AxumColl31	Black	Tigray				
G418	AxumColl32	Red	Tigray				
G419	AxumColl33	Black	Tigray				
G420	AxumColl34	Dark brown	Tigray				
G421	AxumColl35	Dark brown	Tigray				
G422	AxumColl36	Dark brown	Tigray				
G423	AxumColl37	Dark brown	Tigray				
G424	AxumColl38	Brown	Tigray				
G425	AxumColl39	Dark brown	Tigray				
G426	Degu (215874)	Black	Released				
G427	Addis-01 (ACC#203544)	Red	Released				
G428	Urgi (242617)	white	Released				
G429	Diga-1(216036)	Dark brown	Released				
G430	Gudetu(215990)	Brown	Released				
G431	Gute (229373)	Brown	Released				

Appendix Table 3.2 Means values for five agronomic traits, four nutritional and two drought-related parameters and grain colour of 448 finger millet genotypes showing the top 10 and five bottom performing genotypes when evaluated across three diverse test environments in Ethiopia, ranked according to their grain yield (t/ha) performance under stressed environment, Meiso (MI).

Env	TrT	Top 10 genotypes											Bottom five genotypes				Mean*	CV (%)	LSD (5%)
		G141	G423	G297	G247	G18	G432	G195	G223	G435	G171	G239	G49	G128	G37	G50			
AN		120.0	113.5	120.5	115.0	121.0	123.0	113.5	119.5	120.5	121.0	123.5	129.5	124.0	133.0	127.0	121.0	1.9	4.4
MI	DF	90.0	86.5	93.5	84.5	94.0	96.0	90.5	87.0	94.0	90.5	100.5	99.0	94.5	98.5	93.5	93.5	2.6	4.8
SH		89.0	83.0	92.0	79.0	86.0	90.5	86.0	84.0	84.0	85.0	97.5	103.5	97.5	100.0	97.5	90.4	2.5	4.5
AN		153.5	143.5	154.5	146.0	155.0	158.0	144.0	153.0	154.5	155.0	159.0	170.0	160.0	174.5	167.0	155.0	2.3	6.9
MI	DM	122.0	116.5	128.0	113.0	129.0	133.0	123.0	117.5	129.0	123.0	141.5	138.5	130.0	137.0	128.0	129.0	3.3	8.4
SH		128.5	118.0	133.0	110.0	124.0	131.0	124.0	120.0	120.0	122.0	139.5	145.5	139.5	142.0	139.5	130.0	2.7	6.9
AN		73.5	80.0	73.8	77.0	76.3	87.5	80.0	90.0	104.0	85.0	92.5	89.0	117.5	64.5	104.5	86.7	9.6	16.0
MI	PH	131.5	123.3	142.0	133.5	122.5	147.5	131.5	142.5	140.0	149.0	137.5	112.5	143.5	100.5	136.0	136.0	7.6	20.0
SH		110.0	106.5	95.0	100.5	110.0	67.5	104.5	111.0	106.5	98.0	84.5	89.5	101.0	76.3	107.5	101.0	9.5	19.0
AN		3.7	3.0	3.7	4.6	3.9	2.7	3.0	3.6	2.3	4.1	3.3	1.7	3.5	1.4	1.5	3.2	11.0	0.7
MI	GY	3.2	2.9	2.8	2.7	2.6	2.6	2.6	2.5	2.5	2.5	0.6	0.6	0.6	0.5	0.5	1.3	18.0	0.5
SH		3.1	3.5	0.9	1.9	1.7	2.0	2.7	2.6	2.6	2.8	1.5	1.6	0.9	1.6	1.6	2.1	14.0	0.6
AN		2.3	2.4	2.1	2.8	2.4	3.0	2.2	2.9	2.9	2.8	2.0	1.9	2.1	1.8	2.4	2.3	7.9	0.4
MI	TW	2.1	2.2	2.1	2.1	1.9	2.8	1.5	2.1	2.0	1.8	1.8	1.4	1.5	1.8	2.1	1.9	7.9	0.3
SH		2.2	2.3	2.1	2.3	1.9	3.7	1.7	1.9	2.4	1.0	2.4	1.4	2.2	1.6	2.1	2.0	10.0	0.4
AN		1.4	1.0	1.0	1.0	1.5	1.5	1.5	1.0	1.0	1.0	2.5	3.7	2.5	2.5	3.7	1.9	25.0	0.9
MI	SG	2.0	1.5	1.5	1.0	1.5	1.0	2.5	2.5	1.0	2.0	4.5	3.5	3.5	4.5	3.7	2.9	17.0	1.0
SH		1.5	2.0	3.0	1.2	1.5	1.5	2.0	2.5	1.0	2.0	3.0	2.0	2.5	1.0	4.7	2.2	23.0	1.0
AN		3.0	1.5	3.5	2.0	3.0	3.5	1.5	3.0	3.5	3.5	4.0	5.0	4.0	5.0	5.0	3.3	14.0	0.9
MI	Drt	2.5	1.0	2.5	1.0	2.5	1.5	3.0	2.5	1.0	2.5	5.0	4.5	3.0	4.5	3.0	3.0	18.0	1.0
SH		3.0	1.0	3.0	1.0	2.5	3.0	2.5	1.5	1.5	2.0	4.5	5.0	4.5	5.0	4.5	2.8	15.0	0.8
AN		19.9	19.1	19.1	19.8	19.2	21.0	19.9	19.1	20.0	18.7	19.1	21.4	20.2	21.2	20.1	19.7	2.7	1.0
MI	Am	19.2	18.7	18.3	19.1	18.9	18.7	18.8	18.7	18.7	18.7	19.2	19.6	19.1	19.7	19.3	19.0	1.9	0.7
SH		18.5	18.7	18.7	18.8	19.2	19.7	19.0	19.7	20.3	19.1	19.2	19.3	18.9	19.7	18.9	19.2	1.9	0.7
AN		52.1	42.6	42.9	63.9	42.4	63.3	55.7	45.0	51.2	45.1	45.9	63.7	46.9	65.9	53.9	51.4	13.0	13.0
MI	Stc	53.0	51.5	50.3	54.4	55.1	45.0	45.1	50.5	51.0	48.3	49.1	51.8	48.7	53.4	49.0	50.7	8.9	8.9
SH		40.4	46.8	46.1	42.5	44.8	56.4	45.5	49.8	53.4	48.3	48.1	46.9	43.9	54.3	39.5	48.1	11.0	10.0
AN		53.5	66.0	63.0	60.9	64.6	30.7	53.0	60.7	41.8	68.2	61.9	34.1	56.4	24.7	53.5	55.1	16.0	18.0
MI	Fe	62.0	67.4	72.8	71.6	74.4	67.7	70.2	74.5	71.5	74.7	63.1	56.9	81.0	57.1	62.1	68.8	5.6	7.6
SH		70.4	72.3	70.5	65.0	65.8	57.4	66.5	60.1	40.2	60.8	63.6	53.8	68.9	64.9	66.0	64.5	5.7	11.0
AN		74.1	76.1	75.6	73.8	76.8	65.1	72.5	75.7	69.1	78.4	76.1	68.1	74.4	58.9	75.8	73.7	3.8	5.5
MI	Zn	79.2	78.0	78.0	79.0	80.0	75.4	77.4	77.8	77.2	80.2	76.0	74.0	75.4	72.8	76.1	77.1	2.2	3.3
SH		76.5	78.6	78.9	76.1	77.6	74.5	76.4	75.7	67.6	76.7	77.4	73.3	77.7	75.3	77.8	75.9	3.0	4.4
	SC	6	4	6	4	6	3	6	4	2	4	6	3	6	2	6			

Note: See Appendix Table 3.1 for genotypes descriptions., * = overall mean, and DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn=zinc content (%), grain colour (SC):1 = white, 2 = light brown, 3 = brown, 4 = dark brown, 5 = red, & 6 = black. TrT= traits, SC= grain colour, Env=environments, AN = Arsinegelle, MI = Meiso, and SH = Maitsebri.

Chapter 4: Genetic Structure of Ethiopian Finger Millet Landraces and Genome-Wide Association Mapping for Agronomic and Nutritional Traits

Abstract

Finger millet (*Eleusine coracana* subsp. *coracana*) (2n=4x=36) remains one of the most important millets in East Africa (EA), where it was most likely domesticated along the highlands of Ethiopia and Uganda**.** The goal of the current study was to analyse the population structure of the Ethiopian finger millet landraces and to identify robust marker-trait associations and quantitative trait nucleotides (QTNs) and haplotypes linked to key agronomic and nutritional traits. In a field evaluation across three environments, 448 genotypes were assessed for days to flowering (DTF), days to maturity (DTM), thousand seed weight (TSW), grain yield (GY), stay-green score (STG), and drought score (DrtSc). The harvested grain was analyzed for Fe and Zn contents. A subset of 391 genotypes was skim-sequenced, generating 24,112 high-quality SNPs that were employed for population structure, association mapping and haplotype analysis. Seventy marker-trait associations were detected including 15 major QTNs with more than 30% phenotypic variance explained (PVE) for all traits except STG and GY. Pleiotropic major QTNs were identified for DTM/DTF and Fe/Zn on chromosomes 9B and 2B respectively. Haplotype analysis of major QTNs identified 54 significant haplotype blocks and 2 additional haplotypes for a *multidrug ABC transporter gene family like* protein on chromosome 4A that was associated with PTH. Favorable haplotypes from pleiotropic DTM/DTF and Fe/Zn QTNs were present in 13 and 12 genotypes respectively, majority from Tigray. Two genotypes from Tigray and one from Amhara harbored favorable haplotypes for DTM/DTF and Fe/Zn. These findings provide invaluable insights for targeted breeding to enhance finger millet resilience, nutritional profile, and yield.

Key messages: The evaluation of unimproved Ethiopian finger millet genotypes reveal untapped agronomic and micronutrient diversity that should be exploited in breeding programs for improved genetic gain and biofortification.

Keywords: *Eleusine*, biofortification, Fe, Zn, QTN, stay-green, haplotype, pleiotropy

4.1 Introduction

Finger millet {2n=4x=36; *Eleusine coracana* (L.) Gaertn} is an important cereal crop cultivated on ~2.1 m ha with an annual production of ~3.7 m tons globally (Indiastat 2020; FAOSTAT 2021). It represents 20% of the global millet area and 26% of the total global millet production respectively (Gebreyohannes et al. 2024). It is the most important millet in East Africa, where it is believed to have been domesticated along the sub-humid highlands (Hilu et al. 1979; Tsehaye et al. 2006; Tesfaye and Mengistu 2017). Its adaptability to extreme weather conditions, extended storage quality, rich nutritional profile, high seed multiplication rate, and diverse health benefits make finger millet a desirable climate resilient crop for food and nutrition security (Ceasar et al. 2018; Kudapa et al. 2023; Gebreyohannes et al. 2024).

Finger millet exhibits outstanding adaptability due to its C4 photosynthetic pathway. This metabolic advantage, as documented by Yogeesh et al. (2016), Hittalmani et al. (2017), Ceasar et al. (2018), and Kudapa et al. (2023), allows finger millet to thrive in diverse and often challenging climates characterized by high temperatures, intense heat, and limited moisture availability. Beyond its climatic resilience, finger millet demonstrates additional stress tolerance. Studies by Hatti et al. (2018) report its ability to perform well in depleted soils, while Krishnamurthy et al. 2014) highlight its salinity tolerance. This inherent adaptability is further emphasized by Dida and Devos (2006), who describe finger millet's success in various agro-ecological zones, performing well under low rainfall in drylands and on a wide range of tropical soils.

Finger millet boasts an exceptional nutritional profile, which is particularly rich in a range of nutrients such as calcium (50 – 589mg/100g), potassium (430 – 669 mg/100g), iron (3 – 53 mg/100g), phosphorus (130 – 250 mg/100g), sulfur (106 – 149mg/100g), sodium (6 - 42 mg/100g), and magnesium (78 - 201 mg/100g) (Backiyalakshmi et al. 2023; Teklu et al. 2024). This impressive array of nutrients, along with rich sources for essential amino acids, dietary fibre (18%), and phenolic compounds (0.3-3%), has earned finger millet the title as a "superfood" (Devi et al. 2014; Krishnan 2024). The grain is gluten-free and has extended storage quality due to the polyphenol content (Xiang et al. 2019; Odeny et al. 2020; Gebreyohannes et al. 2021), thus an important cereal for famine reserves. After grain harvest, the finger millet stover is an important source of fodder for livestock, enhancing feed security in areas that rely on crop and livestock farming. Micronutrient deficiencies, often referred to as the hidden hunger, affect over 2 billion people worldwide, primarily in low-income developing countries (Gupta et al. 2017; Sheoran et al. 2022; Teklu et al. 2023a). Micronutrient deficiencies are particularly severe in sub-

Saharan African countries, where many populations lack access to a diverse diet. A recent study by Gebremedhin et al. (2021) reported that in Ethiopia, 37.3% of children aged 6–23 months had not received any recommended micronutrient sources. Therefore, finger millet is a healthy alternative for managing nutrition deficiencies, especially when the affected families adopt and cultivate high micronutrient-containing varieties.

Despite its agronomic and nutritional importance, finger millet productivity remains low relative to its genetic potential. Drought stress, poor soil fertility, disease, and limited access to improved cultivars continue to constrain production. Yield losses exceeding 50% have been reported due to drought stress, impacting both grain quality and key yield components (Maqsood and Ali 2007). Furthermore, breeding progress has been slow because many economically important traits, including grain yield, drought adaptation, flowering time, maturity, iron and zinc concentration, are quantitatively inherited and strongly influenced by genotype x environment interactions. Although substantial phenotypic diversity has been reported among Ethiopian finger millet landraces; however, the underling genetic architecture controlling these traits remains inadequately understood. Consequently, breeders lack sufficient genomic information to efficiently implement marker-assisted selection, genomic-assisted breeding, or precision introgression of favorable alleles into elite backgrounds.

Ethiopia represents one of the most important centres of diversity for finger millet and harbors a rich reservoir of landraces that have evolved under diverse agro-ecological conditions. These landraces potentially contain unique alleles for adaptation, productivity, and nutritional quality. However, previous studies investigating the genetic basis of agronomic and nutritional traits in finger millet have relied on relatively small germplasm panels, low-density marker systems, or limited environmental testing, thereby restricting the discovery of robust and transferable marker-trait associations (Sharma et al., 2018; Puranic et al., 2020; Tiwari et al., 2020; Sharma et al., 2022). Moreover, limited information exists regarding the population structure, linkage disequilibrium patterns, favourable haplotypes, and genomic regions controlling key agronomic and micronutrient traits within Ethiopian finger millet germplasms. This knowledge gap remains a major constraint to the effective utilisation of indigenous genetic resources in modern breeding programmes.

Advances in next-generation sequencing technologies have transformed crop genetic research by enabling the generation of large-scale genome-wide marker datasets at relatively low cost. The availability of reference genome assemblies for finger millet (Hittalmani et al., 2017; Hatakeyama et al., 2018; Devos et al., 2023) and the development of skim-sequencing approaches now permit rapid discovery of thousands of single nucleotide polymorphisms (SNPs) distributed across the genome (Kumar et al., 2021). Skim-sequencing provides a cost-effective strategy for high-density genotyping and has been successfully applied in several crops for genetic diversity analysis, genome-wide association studies (GWAS), and

candidate gene discovery (Malmberge et al., 2018; Kumar et al., 2021; Long et al., 2022). However, its application in Ethiopian finger millet germplasm remains largely unexplored.

GWAS have emerged as one of the most powerful approaches for dissecting the genetic basis of complex quantitative traits. Unlike conventional bi-parental quantitative trait locus (QTL) mapping, GWAS exploits historical recombination events accumulated over many generations and therefore provides higher mapping resolution and greater allelic diversity (Huang and Han, 2014; Alqudah et al., 2019). By leveraging linkage disequilibrium between molecular markers and functional loci, GWAS enables the identification of marker-trait associations, quantitative trait nucleotides (QTNs), candidate genes, and favorable haplotypes underlying complex phenotypes. The approach has been widely used in cereals to identify genomic regions controlling yield, drought adaptation, nutritional quality, and stress tolerance traits, thereby accelerating marker-assisted breeding and genomic selection strategies (Puranic et al., 2020; Sharma et al., 2022; Bančič et al., 2023). Nevertheless, the success of GWAS depends on accurate characterization of population structure and relatedness among genotypes because unaccounted population stratification can generate spurious associations. Therefore, assessing population structure, genetic diversity, and linkage disequilibrium is a critical prerequisite for reliable association mapping.

Although several GWAS studies have been conducted in finger millet, significant knowledge gaps remain regarding Ethiopian germplasms, which represent one of the largest and most diverse repositories of finger millet genetic resources globally. In particular, robust genomic regions governing drought adaptation, grain yield, and related agronomic traits, as well as iron and zinc concentrations, have not been comprehensively identified. Furthermore, little information is available on the distribution of favourable haplotypes and candidate genes within Ethiopian landraces. Addressing these gaps is essential for accelerating marker-assisted selection and developing climate-resilient, nutrient-dense finger millet cultivars. Therefore, the objective of the study was to analyse the population structure of the Ethiopian finger millet landraces and to identify robust marker-trait associations and quantitative trait nucleotides (QTNs) and haplotypes linked to key agronomic and nutritional traits. Specifically, the study tested the hypothesis that: (i) Ethiopian finger millet landraces possess distinct genetic population structure and substantial genomic diversity; (ii) significant marker-trait associations and QTNs exist for major agronomic, drought-adaptive, and nutritional traits; (iii) favourable haplotypes associated with superior trait performance can be identified and utilised in marker-assisted breeding. The findings are expected to provide valuable genomic resources and molecular breeding tools for the development of high-yielding, drought-resilient, and nutrient-rich finger millet varieties adapted to Ethiopian and similar agro-ecologies.

4.2 Materials and methods

4.2.1 Description of the experimental sites

Three different sites were used in the study; Arsinegelle (E1), Maitsebri (E2), and Meiso (E3) in Ethiopia (Figure 4.1). E1 is characterized by loam soils, slightly acidic pH, higher total organic carbon and nitrogen content, moderate clay content, and relatively high annual rainfall. E2 experiences moderate annual rainfall. E3 is characterized by clay loam soil, neutral pH, lower total organic carbon and nitrogen content, highest clay content, and lowest annual rainfall (Table 3.1). The study areas varied in altitudes, which spanned from 1323 to 1933 meters above sea level. Before planting, soil samples were taken across the three sites from various depths ranging from 0 to 60 cm. The soil samples were thoroughly mixed and transported to Melkassa Agricultural Research Center (MARC, Adama, Ethiopia) for physicochemical analysis employing the Estefan et al. (2013) method. Nutritional composition analysis was also carried out at MARC, at the food and nutrition laboratory immediately following harvest.

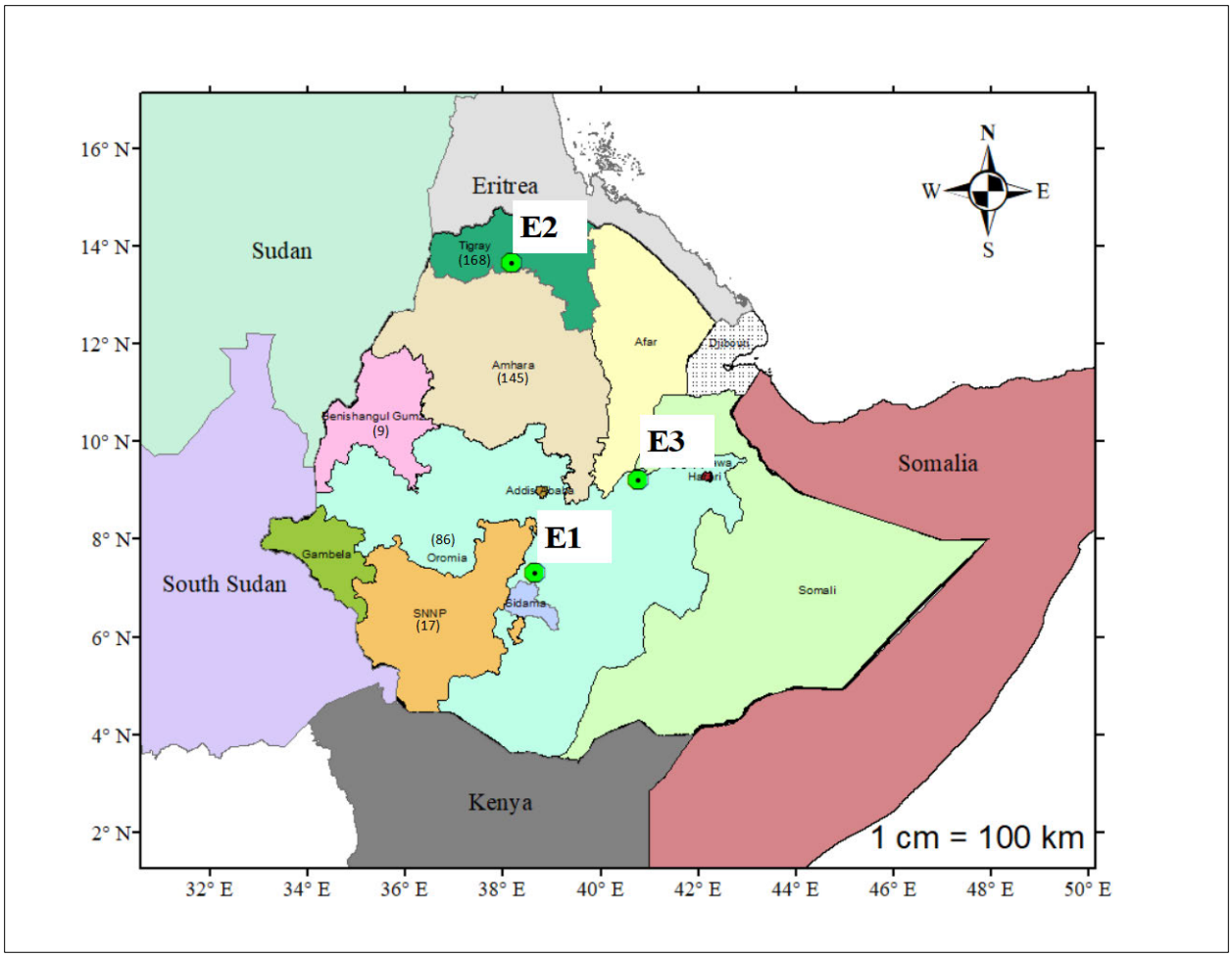


Figure 4.1 A map of Ethiopia showing finger millet landraces collection regions, including Tigray, Amhara, Benishangul & Gumuz, Oromia and Southern Nation, Nationalities, and People (SNNP). The number of genotypes from each region is indicated in brackets. The evaluation sites are designated as E1= Arsinegelle, E2= Maitsebri, and E3= Meiso.

4.2.2 Plant material

A comprehensive collection of 448 finger millet accessions, including 425 diverse landraces and 23 improved varieties was assembled for the present study (Appendix Table 3.1). The germplasm was sourced from various regions and research centers across Ethiopia, representing the country's rich diversity in finger millet (Figure 4.1). Tigray contributed the highest number of germplasm collection (168 entries), followed closely by Amhara (145 entries) and Oromia (86 entries), The Southern Nation Nationalities People Region (SNNPR; 17 entries) and Benishangul & Gumuz (9 entries) (Appendix Table 3.1). The study additionally included 23 released varieties developed

by the Ethiopian regional and national research institutes, encompassing research centers namely, Bako, Melkassa, Pawe, Adet, Jinka, Shire-Maitsebri, and Axum (Appendix Table 3.1).

4.2.3 Experimental design, planting and managing the field experiments

A row-column design with two replicates was employed at each location with each replicate consisting of 64 rows and 7 columns. Each plot consisted of three meters of a single row with a row spacing of 0.4 meters and a plant-to-plant spacing of 10 centimeters. To minimize lodging risk, only Di-ammonium Phosphate (DAP) fertilizer was applied during sowing at the rate of 100 kg/ha. No additional nitrogen fertilizer (urea), herbicide and insecticide were applied during the subsequent growth stages. Weeding was performed manually.

4.2.4 Phenotyping for agro-morphological traits

Agro-morphological and drought related data were collected following the procedures already described in IBPGR (1985) with minor modifications. Plant height (PTH; cm) was measured from ground level to the tip of the inflorescence (ear) at the dough stage on five randomly selected plants within each plot. Days to 50% flowering (DTF) was recorded as the number of days from sowing to when half of the main tillers in a plot had emerged ears. Similarly, days to 50% maturity (DTM) were recorded as the number of days from sowing to the day when 50% of the main tillers in a plot had fully mature ears. Thousand seed weight (TSW) was determined by drying 1000 randomly chosen seeds to a standard moisture content of 12.5% and recording their weight in grams (g). Grain yield (GY; t ha^{-1}) was measured as the total grain weight of a plot (1.2 m^2) harvested at 12.5% moisture content and then converted to t ha^{-1}. Stay-green score (STG) was rated using a visual score on a scale of 1 to 5 per plot basis representing plant canopy greenness at maturity, with 1 indicating fully stay-green (drought tolerant) (Figure 3.1), and 5 indicating completely senesced (drought sensitive). Finally, Drought Score (DrtSc) was assessed using a visual score on a scale of 1 to 5 per plot basis, representing overall drought tolerance, where 1 refers to highly tolerant, and 5 indicating highly sensitive. It is essential to note that drought tolerance is a complex trait encompassing multiple physiological and morphological attributes, including stay-green, earliness, and late maturity with associated stay-green characteristics.

4.2.5 Phenotyping for nutrient content

Nutritional composition analysis of the crop was conducted at MARC, at the food and nutrition laboratory, immediately after harvest. A representative grain sample of 150-200 g per accession was carefully and independently collected from all plots at each testing site for G × E analysis during the 2019/2020 harvesting period. The seeds were cautiously inspected to ensure they were clean and free from any inert matter, dust, or grains from other crops. To prevent moisture loss and contamination, the clean seeds were stored in airtight containers. Prior to Near Infra-Red (NIR) analysis, a standardization step was performed using a reference plate made of polystyrene, a material with a known NIR spectrum. This step calibrated the instrument to match the NIR spectrum of the reference plate, ensuring accurate NIR spectrum measurements of the samples. For non-destructive NIR analysis, a representative amount of the seed sample (150 – 200g) was added into the sample hopper of the NIR analyzer (Perten Instruments AB, Sweden). The NIR analysis process was then initiated, and the Perten IM 9500 measured the NIR spectrum of the sample. This measurement process was repeated twice, and the average of the two readings was used for each sample to enhance accuracy. The machine recorded data on iron (Fe) (mg/100g), and zinc (Zn) (mg/100g) contents.

4.2.6 Leaf tissue sampling, DNA extraction, library preparation and sequencing

To guarantee seed purity and uniformity, three rounds of single-seed descent were conducted for each genotype before phenotyping. Subsequently, 3-4 seeds were sown in six '72 cavity seedling trays' at MARC, Ethiopia. Thinning was done to ensure only one healthy and vigorous seedling was retained per cavity. Leaf tissue samples were collected 3-4 weeks after planting and placed in individual wells of a 96-well plate for efficient sample handling and storage. The collected samples were deep-frozen at -80°C for 24 hours, before being subjected to freeze-drying (lyophilization) using the Martin Christ Alpha 1-2 LDplus (Donau lab, Ukraine) for 24 hours. The lyophilized leaf samples were carefully packaged and shipped to the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Genomics laboratory unit in Nairobi (Kenya) for DNA extraction. DNA was extracted using the Isolate II plant DNA extraction kits (Bioline Pty Ltd, Nottingham, UK) according to manufacturer's instructions. The purity and quantity of the extracted DNA were determined using gel electrophoresis and a Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA) respectively with final dilution to 50 ng/µl. DNA samples were sent to Psomagen (USA) for library preparation and next-generation sequencing. Libraries were constructed using the RIPTIDE kit (Twist Bioscience, San Francisco, CA, USA)

according to the manufacturer's protocol. The libraries were subjected to paired end sequencing on the Illumina Novaseq6000.

4.2.7 Quality control and SNP calling

Raw sequencing reads were trimmed to remove adapter sequences and poor-quality reads using Trimmomatic (version 0.39) as per Bolger et al. (2014). The high-quality reads were aligned to the chromosome scale finger millet reference genome (Devos et al. 2023) and SNPs called using GATK (version 4.2.5.0) (McKenna et al. 2010). High-throughput genotyping via skim-sequencing initially generated 17, 401, 572 raw SNPs across the 391 diverse Ethiopian finger millet genotypes. Haplosweep, a tool specifically designed for filtering high-quality SNPs from polyploid crops was used to eliminate homeologous SNPs (Clevenger et al. 2018). Additional filtering was done to retain SNPs with a minor allele frequency (MAF) > 5%, < 20% missing data, and heterozygosity of less than 25%. Only SNPs that mapped to finger millet's 18 chromosomes were retained for downstream analysis. This stringent quality filtering and linkage disequilibrium (LD) pruning yielded a final dataset of 24,112 highly informative, high-quality SNPs, subdivided into 10,246 markers from sub-genome A and 13,866 from sub-genome B. Given a total genome size of approximately 1.5 Gb, this yielded an average marker density of 16 SNPs per megabase pair (SNPs/Mbp).

4.2.8 Population structure and linkage disequilibrium

Filtered SNPs were used to undertake Principal Component Analysis (PCA) in the SNP & Variation Suite (SVS version 8.9.0). To establish the differences and likely effects of each of the finger millet sub-genomes, whole genome SNPs were first used for a separate PCA analysis. Subsequently, additional analyses were conducted using SNPs generated from sub-genomes A and B. Ten principal components (PCs) and the additive model were used to generate Eigen values. The first three principal components of the variation were plotted and visualized in R software using the scatterplot3d 0.3-41 package (Ligges and Machler 2003). The first three PCs were sufficient to capture and explain the most significant portion of the population's genetic variation (ranging from 43.3% to 51.5% across marker sets). The Discriminant Analysis of Principal Components (DAPC) was done using the adegenet v. 2.1.10 package in R software by retaining the first three principal components (Jombart 2010). LD decay was also done for whole

genome, sub-genomes A and B SNPs independently. LD decay was estimated by using linkage disequilibrium analysis from Tassel v5 (Bradbury et al. 2007) program with a sliding window of 10 kb. The resulting LD R^2 values were plotted using R script. The r^2 threshold was set to 0.2 as a standard baseline to determine the physical distance over which markers remain significantly correlated for high-resolution mapping. The whole-genome SNPs exhibited a moderate LD decay distance of 2.1 Mb, with sub-genome B decaying at an even slower 3.2 Mb, and sub-genome A decaying more rapidly at 1.2 Mb.

4.2.9 Phenotypic data analysis

Analysis of variance (ANOVA), means, and variances for each quantitative trait was done using R (R core team, 2021). Best linear unbiased predictions (BLUPs) and thereafter variance components within environments were estimated in the lme4 package (Bates et al. 2015) in R (R core team, 2021) by manipulating the REstricted Maximum Likelihood (REML) method using the model:

$$Y_{ijk} = \mu + r/\alpha i + r/\beta_j + \varepsilon_{ijk}$$

where Y_{ijk} is the k^{th} observation for the i^{th} row and j^{th} column; μ is the overall mean; $r/\alpha i$ and r/βj are the effect of i^{th} and j^{th} rows and columns nested in replicates, respectively.

ε_{ijk}: Random error term.

BLUP variance components estimated within environments were appropriated to calculate Broad-sense heritability (H^2) for respective traits per location using the formula:

$$H^2 = \frac{\sigma^2 g}{\left(\sigma^2 g + \sigma^2 e/r\right)}$$

H^2 scores were classified according to Robinson et al. (1949) as follows: 0 – 30% = low; 30 – 60% = moderate; > 60% = high. BLUPs were further used to generate frequency distribution curves and input as trait in GWAS. Pearson's correlation coefficients between all possible trait pairs were analyzed using the Proc corr function in SAS (SAS 2008).

4.2.10 Marker-trait associations

Marker trait associations (MTAs) were calculated by combining the filtered SNP dataset of the genotypes with the corresponding BLUPs in R software using the Genome Association and Prediction Integrated Tool (GAPIT) version 2 package (Tang et al. 2016). A combination of statistical models was employed, including BLINK, CMLM and MLM. All the models used the first three principal components (PCs) as the fixed effect to correct for population structure. Manhattan and quantile-quantile (Q-Q) plots were generated using the R package qqman (Turner 2018) to visualize the results. Manhattan plots provide a scatterplot representation of GWAS results, showing the distribution of SNPs across the chromosome, while Q-Q plots assess the GWAS model's ability to account for population structure and familial relationships. A stringent Bonferroni-corrected *P* values (0.05/no. of markers) were used as the threshold for retaining markers with significant associations. Putative candidate genes within LD distance of the significant SNPs were identified based on the KNE796-1 reference genome available in Phytozome (https://phytozomenext.jgi.doe.gov/info/Ecoracana_v1).

4.2.11 Haplotype analysis

The most rapid LD decay distance obtained after LD analysis was used to build haplotype blocks around all major quantitative trait nucleotides (QTNs). This LD-based approach facilitates the identification of linked marker combinations that capture underlying causal variants and is widely applied in haplotype-assisted association mapping and genome analyses (Hao et al., 2012; Mathew et al., 2018). All markers that were within the LD decay distance of 1.2 Mb (600 Kb up- and downstream) of the major QTN (based on the rapid decay of sub-genome A) were considered for the analysis based on the minimum LD distance calculated (Appendix Figure 4.1). The use of LD decay distance to define candidate genomic intervals around significant QTNs is a standard approach in association mapping studies (Yu et al., 2006; Korte and Farlow, 2013). Genes that were co-localized with a minimum of two SNPs around the major QTN haplotype blocks were analyzed for gene-specific haplotypes. Haplotype-based analyses were employed because they capture the combined effects of linked variants and can provide greater power than the single-marker analyses (Morris, and Kaplan, 2002; Lorenz et al. 2010). Phenotypic data was categorized based on the identified haplotypes and used to test for haplo-phenotype association in individual and across environments. One way ANOVA with Duncan's test as a post hoc test was used to identify significant associations and measure specific differences between pairs of means in R using package DescTools (Signorell et al. 2025). Only haplotypes that were present in at least

five genotypes were considered for the statistical analysis. This threshold minimises the influence of rare haplotype classes and enhances the reliability of association estimates (Balding, 2006; Bush and Moore, 2012)

4.3 Results

4.3.1 Phenotypic variation

Highly significant differences were observed across locations (Loc), genotypes (Gen) and their interactions (Gen x Loc) for all traits under study at $P < 0.001$ (Table 4.1). DTF, DTM, GY, and DrtSc demonstrated high heritability across all environments (E1, E2, E3), with values ranging from 0.7 to 0.9. PTH and Fe content also displayed consistent moderate to high broad sense heritability across all environments (0.5-0.6). Mean DTF demonstrated marked environmental dependence, with E1 (120.8 days) and E2 (90.4 days) reporting contrasting extremes. The highest range and mean (0.2 - 6.6 tons/ha; 3.2 tons/ha) for GY was reported in E1 and the lowest (0.5 – 3.3 tons/ha; 1.2 tons/ha) from E3 (Table 4.1). Mean Fe and Zn reported similar and increasing patterns of variations from E3 to E1 (Table 4.1). Strong negative correlations were reported between DTF, DTM, STG, and DrtSc with grain yield (GY) and component trait (TSW) across all environments (Appendix Table 4.1). Fe and Zn displayed consistent and location-independent positive association with correlation coefficients ranging from 0.76 to 0.81 (Appendix Table 4.1). However, there was no correlation between Fe and Zn with all the agronomic traits, except for a once-off weak positive correlation (0.09) between Fe and GY at E3 (Appendix Table 4.1). Frequency distribution histograms for all traits from each environment and across all environments are presented in Figure 4.2.

Table 4.1 Descriptive statistics for all traits measured across the three environments

Location		DTF (days)	PTH (cm)	DTM (days)	GY (tons/ha)	TSW (g)	STG (1 – 5)	DrtSc (1 – 5)	Fe (mg/100g)	Zn (mg/100g)
Arsinegelle (E1)	Range	96.5 – 140.0	55.0 – 132.5	122.5–183.0	0.2 – 6.6	1.5-3.9	1 - 5	1 – 5	1.0 – 7.7	4.5 – 8.1
	Mean	120.8	86.6	155.1	3.2	2.3	1.9	3.3	5.5	7.4
	SE	1.9	7.0	2.9	0.2	0.1	0.4	0.4	0.7	0.2
	H^2	0.8	0.6	0.8	0.9	0.8	0.8	0.8	0.5	0.7
Maitsebri (E2)	Range	76.0-103.5	62.3-146.5	103.5-145.5	0.3-4.5	1.0-3.7	1.0-4.7	1.0-5.0	2.6-8.2	5.2-8.3
	Mean	90.4	101.3	129.7	2.1	2.0	2.2	2.8	6.5	7.6
	SE	1.6	7.7	2.5	0.2	0.2	0.4	0.3	0.4	0.2
	H^2	0.9	0.6	0.9	0.9	0.6	0.6	0.9	0.6	0.6
Meiso (E3)	Range	78.5-107.5	80.0-182.5	101.0-149.5	0.5-3.3	1.2-3.0	1.0-5.0	1.0-5.0	5.4-8.1	6.9-8.3
	Mean	93.5	136.4	128.6	1.3	1.9	2.9	3	6.9	7.7
	SE	93.5	136.4	128.6	1.3	1.9	2.9	3	6.9	7.7
	H^2	0.8	0.6	0.8	0.7	0.7	0.8	0.8	0.6	0.5
Source of variation	Location	***	***	***	***	***	***	***	***	***
	Genotypes	***	***	***	***	***	***	***	***	***
	Gen x Loc	***	***	***	***	***	***	***	***	***

H^2=broad sense heritability; Means were calculated based on Best linear unbiased predictions (BLUPS); SE=standard error; Gen x Loc = genotype by location interaction, ***= significant difference at $P< 0.001$

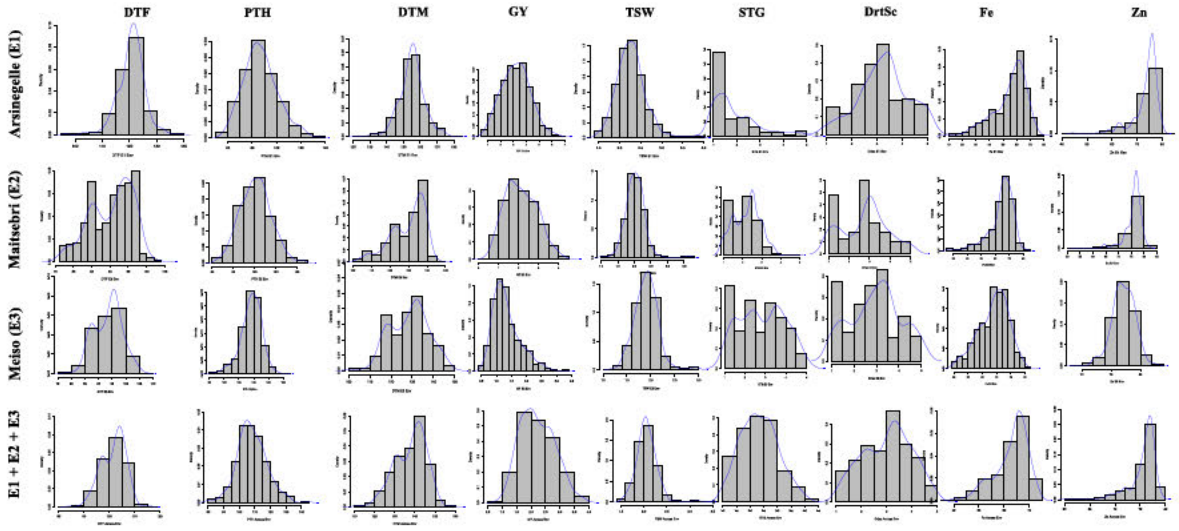


Figure 4.2 Frequency distribution graphs for each of the traits across all environments. The graphs were drawn using BLUPs

None of the top 10 best yielders in each of the environments was an improved variety except Mecha (229371) and Meba (GBK011119A) at Meiso (Table 4.2). The top three best yielders in E1 surpassed the potential yield of 6 tons/ha and were from Tigray and Amhara (Table 4.2). Most of the top ten yielders in each of the locations were from Amhara and Tigray (Table 4.2). All the top 10 genotypes having the most abundant Fe and Zn were landraces, majority from Tigray (Table 4.3).

Table 4.2 A summary of the top ten best yielders in each of the environments and their origin

Arsinegelle (E1)			Maitsebri (E2)			Meiso (E3)		
Accession	**Origin**	**Yield (tons/ha)**	**Accession**	**Origin**	**Yield (tons/ha)**	**Accession**	**Origin**	**Yield (tons/ha)**
237468	Tigray	6.61	AxumColl22	Tigray	4.46	219819	Tigray	3.24
234170	Tigray	6.42	AxumColl21	Tigray	4.25	AxumColl37	Tigray	2.86
243617	Amhara	6.18	242115	Amhara	4.12	238326	Tigray	2.81
242122	Amhara	5.97	234186	Tigray	4.07	237449	Tigray	2.67
238325	Tigray	5.96	237461	Tigray	4.01	207897	Tigray	2.62
238297	Tigray	5.85	AxumColl28	Tigray	3.97	Mecha*	Amhara	2.62
234162	Tigray	5.73	235835	Amhara	3.92	234165	Tigray	2.56
238321	Tigray	5.69	243631	Amhara	3.89	234206	Tigray	2.53
AxumColl17	Tigray	5.68	AxumColl33	Tigray	3.88	Meba*	Oromia	2.48
237452	Tigray	5.64	235828	Amhara	3.80	229726	Benishangul & Gumuz	2.47

*****_Improved varieties_

Table 4.3 A summary of the top ten accessions with the highest Fe and Zn content in each of the environments

Environment	Accession	Origin	Fe (mg/100g)	Accession	Origin	Zn (mg/100g)
Arsinegelle (E1)	223145	Tigray	7.66	234159	Tigray	8.08
	242612	Tigray	7.41	234203	Tigray	7.99
	238319	Tigray	7.36	215982	Amhara	7.97
	235700	SNNP	7.35	243639	Amhara	7.97
	215805	Oromia	7.34	235700	SNNP	7.97
	238316	Tigray	7.33	238316	Tigray	7.97
	221697	Tigray	7.30	215805	Oromia	7.96
	238304	Tigray	7.24	221697	Tigray	7.95
	228306	Amhara	7.20	238319	Tigray	7.94
	229734	Amhara	7.16	223145	Tigray	7.94
Maitsebri (E2)	229735	Amhara	8.20	229735	Amhara	8.26
	215875	Amhara	8.10	215805	Oromia	8.16
	207963	Oromia	7.94	208730	Oromia	8.14
	234183	Tigray	7.80	238333	Tigray	8.13
	238323	Tigray	7.75	245085	Oromia	8.09
	238297	Tigray	7.68	238342	Amhara	8.09
	238317	Tigray	7.67	229728	Bennishangul & Gumuz	8.08
	234171	Tigray	7.63	219503	Amhara	8.05
	215805	Oromia	7.63	238313	Tigray	8.05
	223145	Tigray	7.61	238335	Tigray	8.02
Meiso (E3)	216048	Oromia	8.10	241769	SNNP	8.31
	234202	Tigray	7.94	242118	Amhara	8.25
	208730	Oromia	7.87	216032	Oromia	8.20
	238337	Tigray	7.84	100095	Oromia	8.18
	242122	Amhara	7.84	234154	Tigray	8.12
	211029	Tigray	7.84	215867	Amhara	8.11
	234207	Tigray	7.83	238313	Tigray	8.09
	234175	Tigray	7.81	242108	Amhara	8.09
	234171	Tigray	7.80	234193	Tigray	8.07
	243637	Amhara	7.80	216057	Oromia	8.04

4.3.2 Linkage disequilibrium, genetic diversity and population structure

Skim-sequencing generated 17,401,572 raw SNPs from 391 genotypes and retained 24,112 high quality SNPs after filtering and LD pruning. Out of the 24,112 markers, 10,246 markers were

from sub-genome A, while 13,866 were from sub-genome B. Assuming a genome size of 1.5 Gb, the overall density of the markers across the genome would be 16 SNPs/Mbp. LD varied depending on the SNP sets used. Whole genome SNPs reported moderate LD decay at 2.1 Mb, with sub-genome B reporting the slowest decay point (3.2 Mb), and sub-genome A revealing the most rapid decay at 1.2 Mb (Appendix Figure 4.1). A detailed analysis of LD across markers of each chromosome is provided in Appendix Table 4.2.

PCA using all markers and markers from each of the sub-genomes confirmed that the markers retained were informative and were able to differentiate the genotypes (Figure 4.3). Sub-genome B markers were the most informative, explaining 51.5% genetic variation across the genotypes within the first 3 principal components (PCs), followed by whole genome SNPs (45.6%) and lastly the sub-genome A SNPs (43.3%) (Figure 4.3C). While most genotypes clustered as admixtures, there was relatively distinct clustering of genotypes from Oromia and Tigray (Figure 4.3). Genotypes from SNNP always clustered together with Oromia genotypes, which is consistent with the neighbouring locations of these two regions (Figure 4.1 & Figure 4.3).

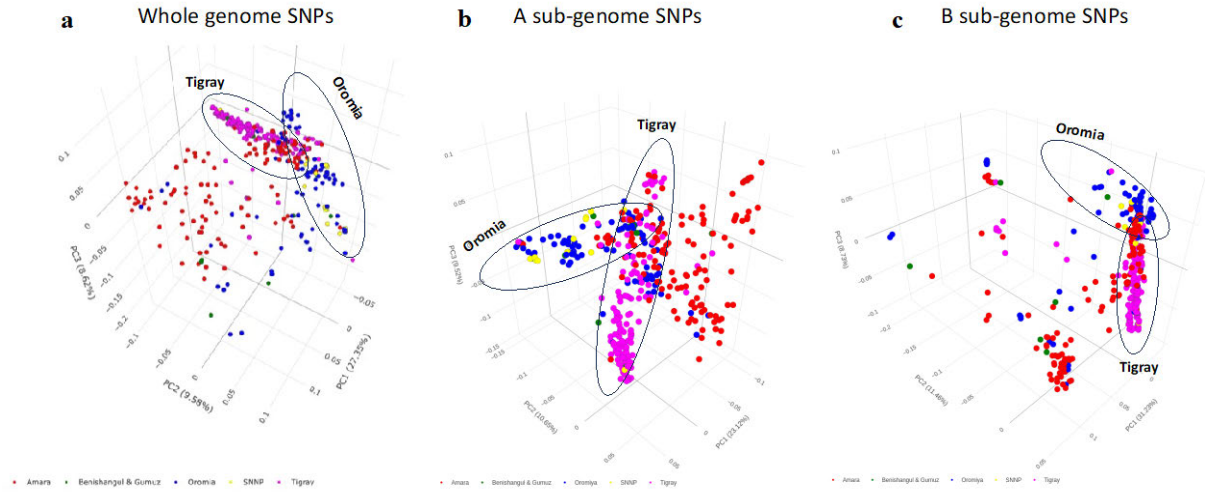


Figure 4.3 PCA using the retained markers across 391 genotypes. **a.** PCA done using whole genome SNPs in which the first 3 PCs explain 45.6% genetic variation. **b.** PCA done using sub-genome A SNPs across the 391 genotypes where the first 3 PCs explain 43.3% genetic variation. **c.** PCA done using sub-genome B SNPs. The first 3 PCs explain 51.5 genetic variation across individuals.

To gain a deeper understanding of population structure, DAPC analysis was subsequently employed. The three categories of markers clustered the 391 genotypes into 4 sub-populations with different memberships (Figure 4.4). Sub-populations generated by whole genome SNPs

were based on regions of origin, with clusters 2 and 3 being the most distinct and having genotypes predominantly from Amhara and Tigray respectively (Figure 4.4A), while cluster 1 was predominantly consisting of genotypes from Amhara (69 out of 145) (Appendix Table 4.3). The most distinct sub-populations generated by the sub-genome A SNPs (Figure 4.4B) was cluster 2 that consisted of majority genotypes from Tigray (100 genotypes), while genotypes from Amhara were split into 2 sub-populations (cluster 1 and 3) (Appendix Table 4.3). Sub-genome B SNPs were the most informative in distinguishing genotypes from Tigray, which were grouped into cluster 1 (108 genotypes), but the same set of SNPs were not informative for genotypes from Amhara that were clustered in each of the four sub-populations (Figure 4.4C; Appendix Table 4.3). An overview of sub-population membership is presented in Appendix Table 4.3.

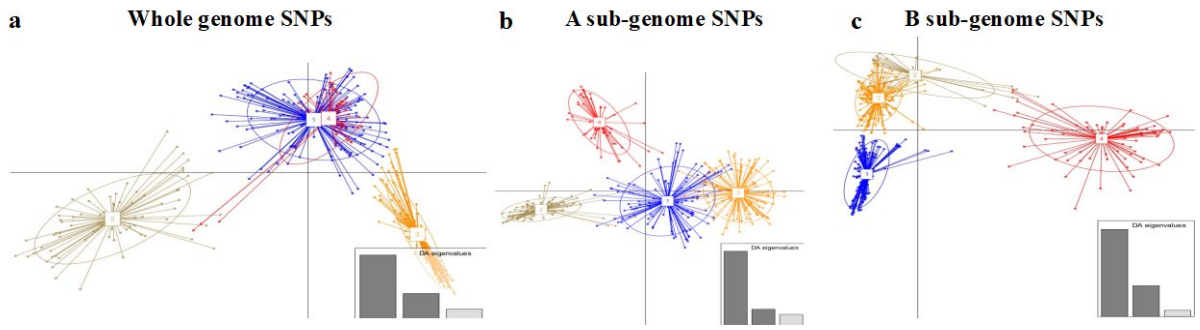


Figure 4.4 Discriminant analysis of principal components (DAPC) analysis using different marker categories. **a.** Whole genome SNPs separated the genotypes into 4 sub-populations but sub-populations 1 and 4 were not distinct. **b.** Sub-genome A SNP marker successfully separated the 4 sub-populations into distinct clusters. **c.** Sub-genome B SNP markers distinguished clearly the sub-population 4 from the rest of the sub-populations. Membership in each of the clusters is described in Appendix Table 4.3.

4.3.3 Genetic diversity of released varieties

Although the different marker categories clustered most of the released varieties uniquely, they all revealed that the released varieties have been developed using a very narrow set of genotypic diversity, and almost always overlapped with genotypes from SNNP (Figure 4.5). Whole genome SNPs showed a single cluster (16 out of the 22) of the released varieties that overlapped with genotypes from SNNP and was flanked by genotypes predominantly from Oromia (Figure 4.5A). Sub-genome A SNPs followed a similar pattern and clustered most of the released varieties in between a sub-cluster of Oromia genotypes that also contained SNNP genotypes (Figure 4.5B). Sub-genome B SNPs clustered the released varieties with an admixture set of genotypes from Oromia, SNNP, Amhara and Benishangul & Gumuz (Figure 4.5C). There were hardly any released varieties clustering under the predominant clusters from Tigray (pink; Figure 4.5) and

Amhara (red; Figure 4.5) for both whole genome and sub-genome A SNP marker. Although a cluster of Amhara genotypes was not as distinct using sub-genome B markers, there were not many overlaps between released varieties and Amhara genotypes (red; Figure 4.5). The same scenario was observed for genotypes from Tigray, which might suggest that most of the collections from Tigray and Amhara are yet to be used in breeding programs for crop improvement.

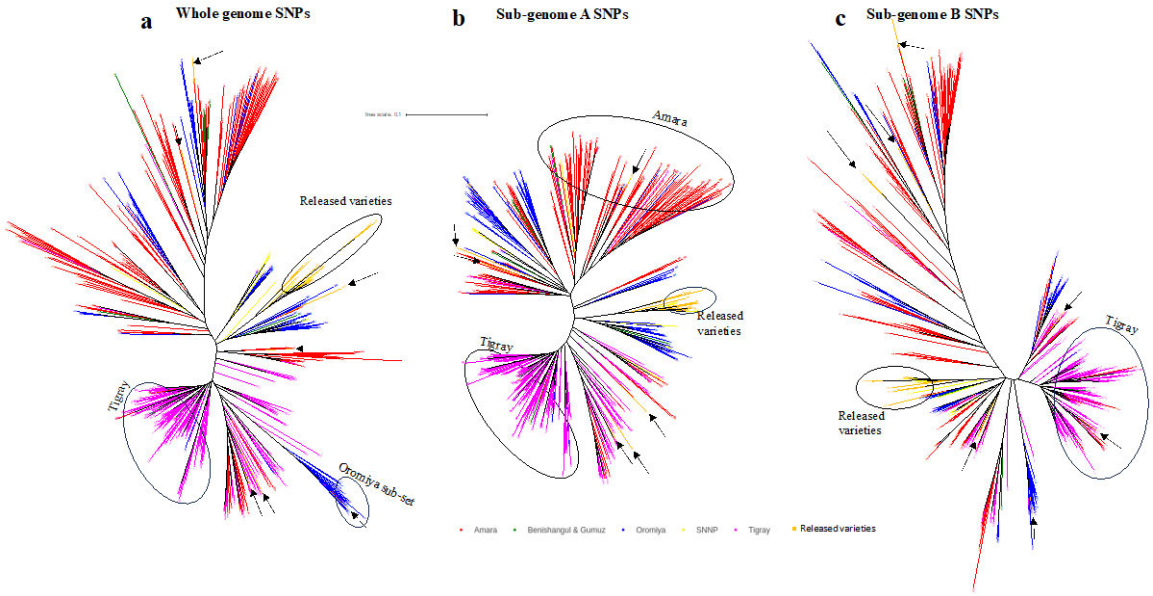


Figure 4.5 Dendrograms showing the clustering of released varieties in the background of all germplasm used in the current study. All released varieties clustering individually are shown with arrows. **a.** Clustering of released varieties using whole genome SNPs. **b.** Clustering of released varieties using sub-genome A SNPs. **C.** Clustering of released varieties using sub-genome B SNPs.

4.3.4 Marker-trait associations (MTA)

Seventy (70) MTAs were detected across the nine traits from at least one of the environments using the stringent Bonferroni threshold of $P<2.07366E-06$ for whole genome SNPs, $P<4.8E-06$ for sub-genome A, and $P<3.6E-06$ for sub-genome B (Table 4.4). Sixty-two of the 70 MTAs were detected using whole genome SNPs while the remaining 8 MTAs were major (≥30% phenotypic variation explained) QTNs detected using sub-genome A and sub-genome B SNPs independently (Table 4.4). Out of the 70 MTAs, 8 markers were significant for more than one trait, resulting in a non-redundant set of 62 QTNs.

Whole genome MTAs

Fifty-five of the 62 non-redundant QTNs were detected using whole genome SNPs, of which 8 were major QTNs detected in association with DTM (40.6% phenotypic variation explained; PVE), TSW (35.8%, 38.1%, 56.1% & 60.6% PVE), DrtSc (33.8% PVE), Zn (44.5% PVE) and Fe and Zn (30.6% PVE; 32.9% PVE) (Table 4.4). The 4 major QTNs detected for TSW were on different chromosomes; 1B (SNP 1B_64659309; 56.1% variation VE), 5B (SNP 5B_3150126; 35.8% PVE), and two on chromosome 6B (SNP 6B_24190829, 60.6% PVE; SNP 6B_40602961, 38.1% PVE) (Figure 4.6; Table 4.4). The highest number of MTAs (13) was reported for TSW, followed by 10 MTAs for Zn and nine for PTH (9) (Table 4.4). The lowest number was reported for STG, for which the QTN was specifically detected in E3 (Table 4.4). MTAs were detected in at least one environment for all the traits except STG. One major QTN (SNP 2B_35281485) was detected for both Fe and Zn (Table 4.4).

Sub-genome specific MTAs

Only major QTNs were reported for the sub-genome specific MTAs in Table 4.4. Sub-genome A SNPs detected five additional major QTNs, 3 localised on chromosome 8A and 1 on chromosome 4A. The 5 major QTNs were detected for DTF (SNP 8A_18375210; 55.6% VE); PTH (SNP 4A_3954933; 33.8% VE); TSW (SNP 8A_22146023; 33.8% and 62.8% VE), DrtSc (SNP 8A_23730370; 38.7% VE) and Fe quality (SNP 8A_14715050; 42% VE) (Table 4.4). All the major QTNs detected using sub-genome A markers were not detected as major QTNs using whole genome SNPs (Table 4.4). Despite having fewer markers than sub-genome B (13,866), the use of sub-genome A markers (10,246) alone added more information and new major QTNs that were not detected while using whole genome SNPs.

Sub-genome B SNPs detected additional 2 major QTNs, same SNP (9B_20268455) for DTF (35.9% PVE) and DTM (34.7% PVE), and another SNP (6B_27369367; 72.3% PVE) for TSW (Table 4.4). The two major QTNs for DTF were only detected when the sub-genome SNPs were used and were totally missed when whole genome SNPs were deployed for analysis (Table 4.4). STG MTAs were better detected using sub-genome B or whole genome SNPs as opposed to sub-genome A SNPs. The highest PVE by a marker was reported on chromosome 6B (SNP 6B_27369367) for TSW in E1 at 72.3% PVE followed by another marker downstream on the

same chromosome (SNP 6B_24190829) for the same trait in E3 at about 60.0 % VE using both CMLM and MLM (Figure 4.6).

Table 4.4 Marker trait associations detected using whole genome and sub-genome SNPs across different models

Trait	SNP	*P* values			PVE (%)	Locations
		BLINK	CMLM	MLM		
Using whole genome SNPs						
DTF	1A_41691781	1.48E-06	-	-	11.8	E3
	6B_17245025	7.72E-07; 1.70E-07	-	-	2.0; 1.2	E2; E1+E2+E3
	7A_42035020	3.38E-07	-	-	17.8	E1
	7B_29006305	1.31E-06	-	-	1.6	E1+E2+E3
	8A_6485125	8.23E-10	-	-	6.7	E1
PTH	4B_50601501	6.51E-09; 1.30E-06	-	-	1.5; 4.8	E3, E1+E2+E3
	5B_27829128	1.29E-07	-	-	2.5	E3
	6A_29685470	5.27E-07	-	-	16.1	E2
	6B_2712127	2.97E-08	-	-	2.1	E3
	7A_35748697	9.979E-07	-	-	16.7	E1+E2+E3
	8B_59128846	9.16E-07	-	-	1.3	E3
	9A_40793867	4.13E-07	-	-	1.0	E3
	9B_15553707	9.84E-09	-	-	9.0	E3
	9B_19836556	2.59E-09	-	-	8.4	E3
DTM	4A_3946408	5.11E-08	-	-	7.3	E1
	5B_65558510	1.33E-06	-	-	40.6	E3
	6B_16874563	1.17E-06	-	-	10.3	E2
	6B_17245025	6.30E-08	-	-	1.4	E1+E2+E3
	7A_42035020	2.72E-07	-	-	16.4	E1
	7B_29006305	8.81E-08	-	-	1.8	E1+E2+E3
GY	3A_22037946	3.72E-09; 1.02E-06	-	-	7.2; 4.7	E1; E1+E2+E3
	4A_40121282	1.25E-06	-	-	1.9	E1+E2+E3
	5B_55857122	2.61E-07	-	-	1.3	E1+E2+E3
	6A_14427382	3.18E-11; 3.26E-11			10.6; 5.9	E1; E1+E2+E3
TSW	**1B_64659309**	-	3.77E-07	3.77E-07	56.1	E1+E2+E3
	1B_7786365	1.95E-06; 4.60E-08	-	-	4.8; 4.3	E1; E1+E2+E3
	2A_34244148	1.23E-07	-	-	1.8	E3
	3B_35970259	1.26E-09	-	-	1.4	E1+E2+E3
	3B_45474371	1.40E-06; 4.51E-08	-	-	15.1; 29.6	E1; E1+E2+E3
	5B_28252956	2.04E-07	-	-	2.5	E1
	5B_3150126	1.51E-15; 1.55E-07; 4.16E-14	-	-	22.1; 35.8; 10.6	E1; E2; E1+E2+E3
	6A_40922437	1.92E-07; 1.50E-06	-	-	5.4; 1.9	E2; E1+E2+E3
	6B_24190829	-	1.66E-06	1.66E-06	60.6	E3
	6B_40602961	1.35E-16	-	-	38.1	E3
	7A_13129745	1.74E-07	-	-	0.8	E1
	7B_49045901	1.61E-06	-	-	6.7	E3
	8B_12513208	2.389E-07	-	-	1.1	E1+E2+E3
STG	6B_10864215	1.58E-07	9.90E-08	7.54E-07	21.3	E3
DrtSc	1A_41691781	2.71E-10	-	-	6.3	E3
	1A_47690818	1.47E-06	-	-	20.2	E2
	4A_2499716	5.34E-07	-	-	19.4	E2
	5B_35573546	1.02E-07	-	-	33.8	E3
	7A_42035020	1.72E-07	-	-	10.1	E1
	9A_6603556	5.02E-09	-	-	13.5	E1
Fe	2B_35126324	-	1.04E-06	1.04E-06	4.6	E2
	2B_35281485*	2.01E-11; 2.38E-08	1.14E-07	1.14E-07	1.9 - 32.9	E1; E2
	2B_37326032	-	1.05E-06	1.05E-06	2.6	E2
	3B_49895136	3.61E-07	-	-	2.5	E1
	7B_22082060	4.37E-07	-	-	5.0	E1
	8A_14715050	5.87E-07	-	-	2.8	E1
	8A_34625287	1.11E-08	-	-	6.2	E1
	9A_44001813	5.65E-08	-	-	4.5	E1
Zn	2B_35126324	-	1.19E-06	-	12.0	E2
	2B_35281485*	2.76E-27; 2.50E-08	6.31E-07; 5.65E-07	6.31E-07	8.1 – 30.6; 2.1 - 8.9	E1; E2

Trait	SNP	*P* values			PVE (%)	Locations
		BLINK	CMLM	MLM		
	2B_35342493	-	7.74E-07	-	0.1	E2
	3A_38743459	3.30E-07	-	-	2.1	E1
	5A_62694353	9.73E-08	-	-	1.9	E1
	5A_65700827	2.50E-07	-	-	2.2	E1
	7B_14800902	5.00E-13	-	1.61E-06	7.4 – 44.5	E2
	8B_30935289	1.60E-06	-	-	4.6	E2
	9A_42427372	9.97E-07	-	-	1.5	E1
	9B_11179336	2.78E-07	-	-	7.3	E1
Additional Major QTNs detected using Sub-genome A specific MTAs						
DTF	**8A_18375210**	3.55E-06	-	-	55.6	E1
PTH	**4A_3954933**	-	2.01823E-06	2.01823E-06	33.8	E1+E2+E3
TSW	**8A_22146023**	4.92E-09; 5.00E-09	-	-	62.8; 33.8	E1; E1+E2+E3
DrtSc	**8A_23730370**	1.85E-15	-	-	38.7	E3
Fe	**8A_14715050**	5.56E-07	-	-	42	E1
Additional Major QTNs detected using Sub-genome A specific MTAs						
DTF	**9B_20268455***		1.37E-06	1.37E-06	35.9	E1+E2+E3
DTM	**9B_20268455***		1.67E-06	1.67E-06	34.7	E1+E2+E3
TSW	**6B_27369367**	-	2.49E-06	2.49E-06	72.3	E1

**Same QTN is reported for Fe and Zn, and for DTF and DTM. SNPs in bold are considered major QTNs reporting >=30% PVE in at least one environment*

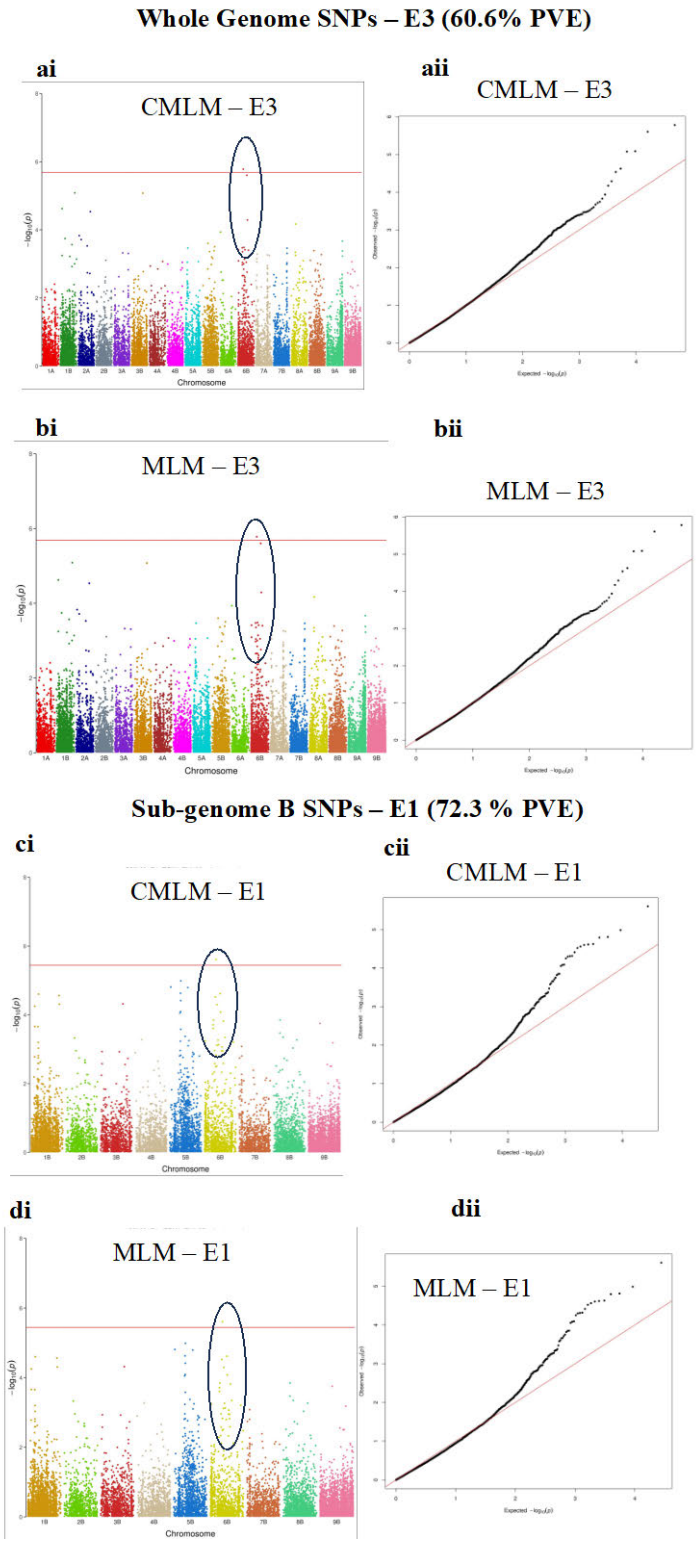


Figure 4.6 Manhattan and QQ plots showing the TSW major QTNs explaining ~60.6% and 72.3% phenotypic variation. **ai & bi.** Manhattan plots drawn using CMLM and MLM models with whole genome SNPs and showing significant association with TSW for E3. **aii & bii.** The corresponding QQ plot to the Manhattan plot in Ai and Bi plotted based on phenotypic data generated from E3. **ci & di**. Manhattan plots showing the detected major QTN for TSW (72% PVE) for E1 using CMLM and MLM models. **cii & dii**. The corresponding QQ plots to the Manhattan plots in Cii and Dii. Sub-genome A chromosomes are represented by odd numbers while sub-genome B are represented by even numbers.

A QTN hotspot for Zn and Fe was detected on chromosome 2B using CMLM and MLM (Figure 4.7; Table 4.4). The hotspot QTN was detected across E1 and E2 only (Figure 4.7; Table 4.4) and not in E3.

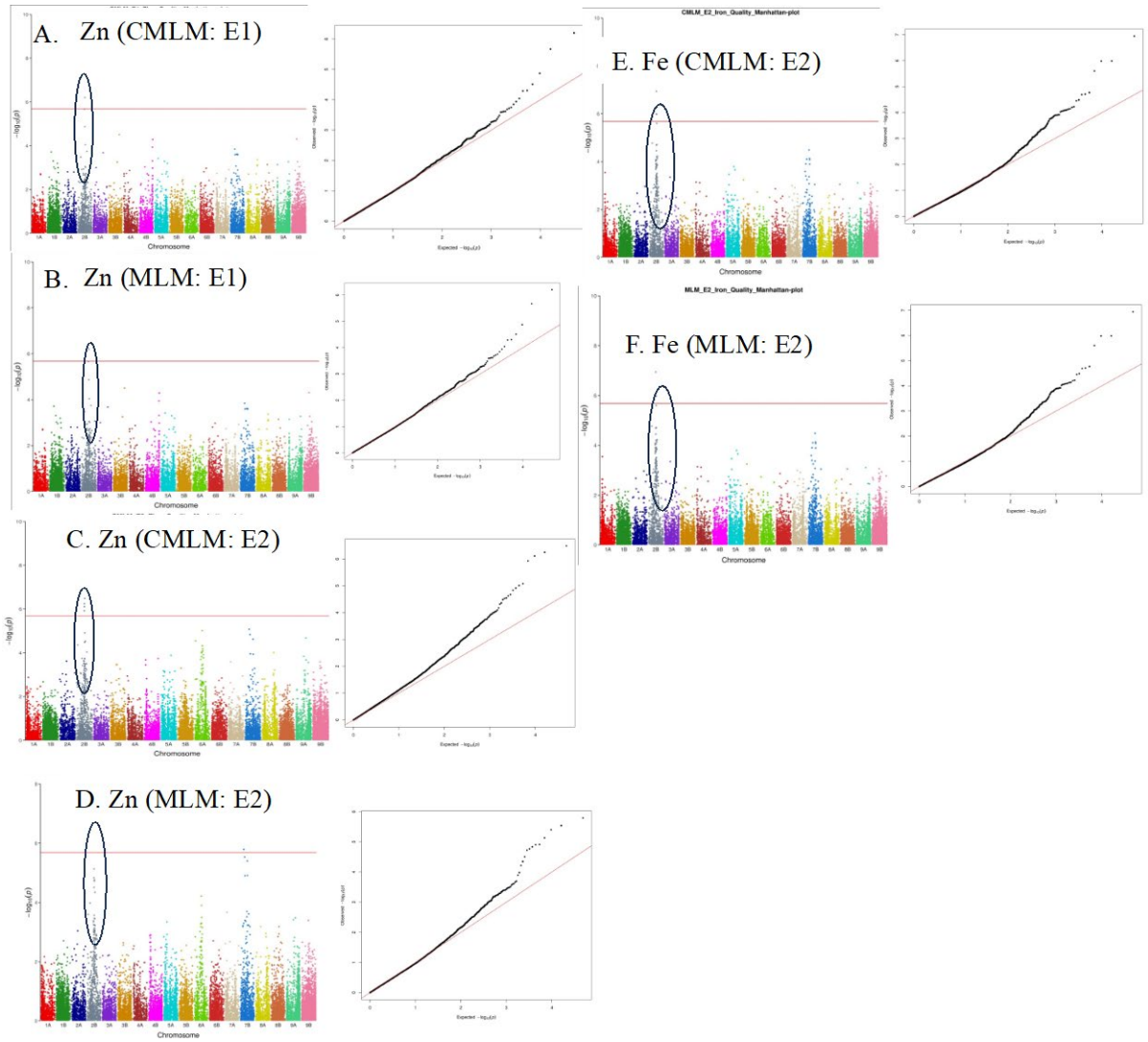


Figure 4.7 Manhattan and QQ plots revealing the QTN hotspot for Fe and Zn on chromosome 2B. **A, B, C, D.** Manhattan plots and corresponding QQ plots drawn using Zn quality data from E1 and E2 as shown using CMLM or MLM GWAS models. **E & F**. Manhattan plots and corresponding QQ plots drawn using Fe quality data from E2 as shown using CMLM and MLM GWAS models.

A major QTN on chromosome 9B (SNP 9B_20268455) for DTF (35.9% PVE) and DTM (34.7% PVE) was detected across the three environments using sub-genome B specific markers (Table

4.4). All major QTNs were plotted on the finger millet marker density map as shown on Figure 4.8.

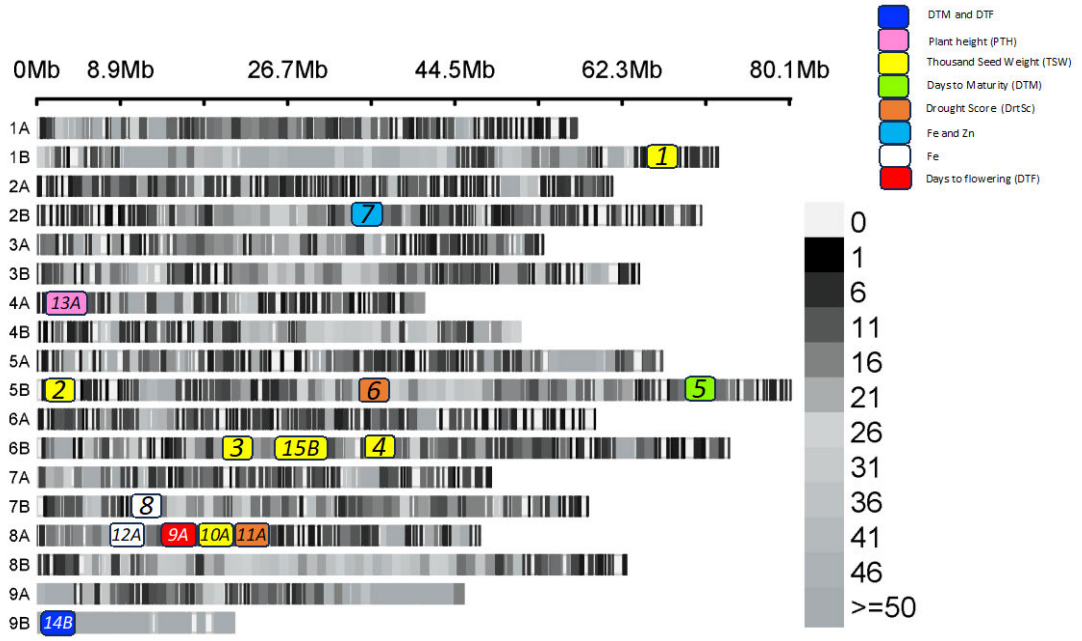


Figure 4.8 The overall SNP density and the locations of major QTNs for which candidate genes were detected. The SNP density is indicated by the grey to black scale. The colour key for each QTN is plotted within the figure. Major QTN locations are estimates and not drawn to scale. Major QTNs detected using sub-genome A SNPs only are denoted with "*A*" and those detected using sub-genome B SNPs only denoted with "*B*".

4.3.5 Haplotype analysis

Haplotype analysis of all major QTNs revealed 54 haplotype blocks having significant association with the respective traits of interest (Table 4.5). The maximum number of haplotypes detected per locus was 5 while the longest haplotype comprised of 16 nucleotides (Table 4.5).

Table 4.5 Haplotypes detected from major QTNs with significant association with the traits

Trait	Major QTN	Haplotypes
DrtSc	1. 5B_35573546	1. GG
		2. AG
		3. GT
	2. 8A_23730370	1. GCG
		2. ACG
		3. GCA
		4. GTG
DTF	8A_18375210	1. CCG
		2. TCC
		3. CAG
		4. CCC
DTF & DTM	9B_20268455	1. CGCCAACAGGAAACTT
		2. TGTAGCTGTAGTTTCC
		3. CACCAACAGGAAACTT
DTM	5B_65558510	1. CT
		2. CG
		3. TT
Fe	8A_14715050	1. AGC
		2. CGT
		3. CGC
		4. CAC
Fe & Zn	2B_35281485	1. AG
		2. GA
		3. GG
Zn	7B_14800902	1. CGG
		2. TGA
		3. TAA
PTH	4A_3954933	1. TTCC
		2. CCGT
		3. TTGT
TSW	1. 1B_64659309	1. GAG
		2. AAG
		3. GAA
		4. GGG
	2. 5B_3150126	1. TGCGG
		2. TGTAA
		3. GGCGG
		4. TACGG
	3. 6B_24190829	1. GAGGT
		2. GGGAG
		3. GGGGG
		4. AAGGT
		5. GGAGG
	4. 6B_27369367	1. GGC
		2. AAC
		3. GGG
	5. 6B_40602961	1. ACGCG
		2. GCGTG
		3. GTGCG
		4. ACACG
		5. GCGCG
	6. 8A_22146023	1. AGCC
		2. AGCT
		3. GATC

One way ANOVA of different haplotype pairs detected 195 significant associations with target traits, majority (136) of which were significant at $P<0.001$, 35 at $P<0.05$, and 24 at $P<0.01$. Box plots showing comparisons between pairs of haplotypes at each test location and across

environments revealed that most of the favorable haplotypes were rare and present in a smaller percentage of individuals (Appendix Figure 4.2). Pleiotropic haplotypes associated with both DTM and DTF identified on chromosome 9B revealed the largest block containing 16 SNPs (Figure 4.9). The most favorable haplotype for DTM and DTF at the pleiotropic QTN on chromosome 9B (9B_20268455) was H3 (CACCAACAGGAAACTT), which was present in 13 individuals (Figure 4.9 C & D).

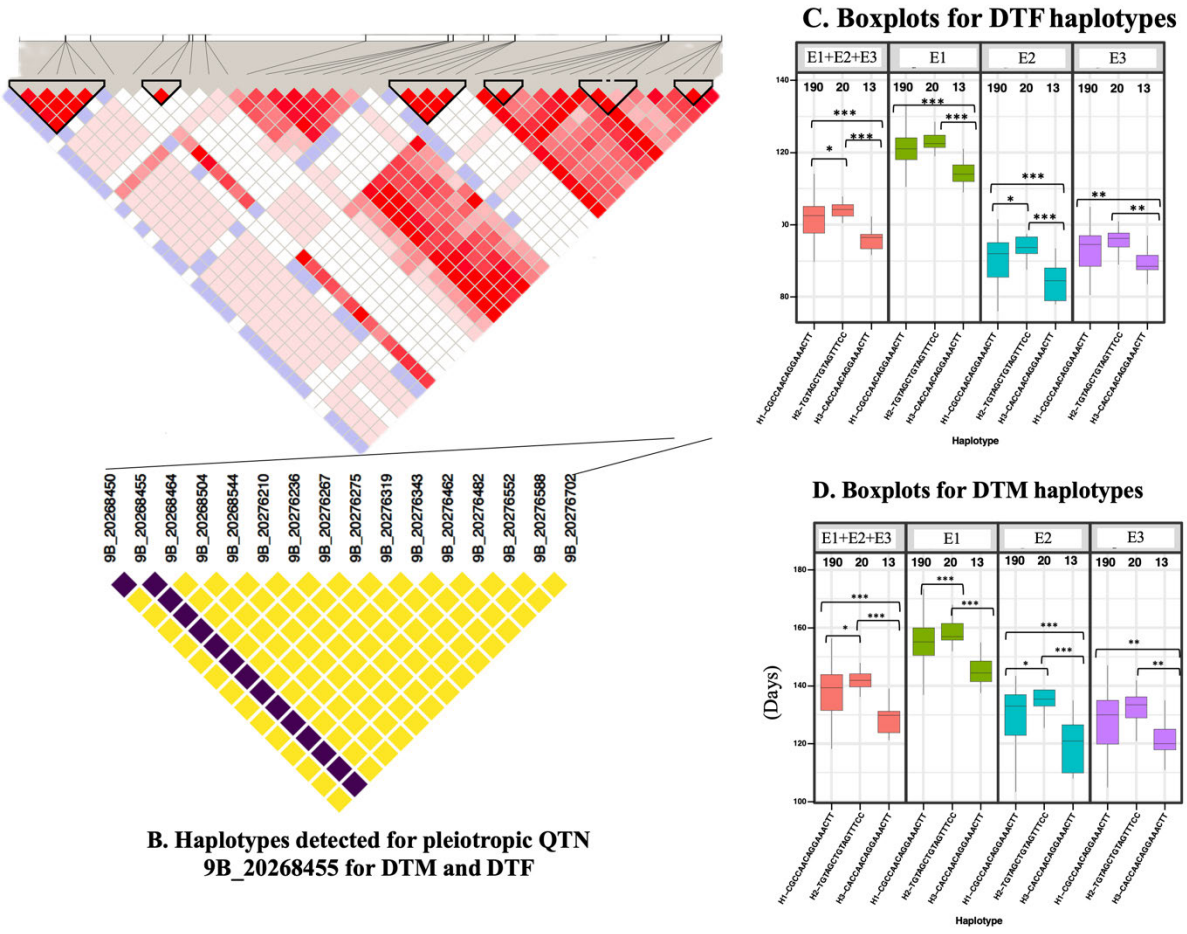


Figure 4.9 Graphical representation of haplotype blocks across chromosome 9 and around the pleiotropic QTN 9B_20268455 for DTM and DTF. **A.** Haplotype blocks across the whole chromosome 9B. **B.** Haplotypes detected for pleiotropic QTN 9B_20268455 for DTM and DTF. **C.** Boxplots showing the performance of genotypes harboring various haplotypes with respect to DTF. **D.** Boxplots showing the performance of individual genotypes harboring various haplotypes with respect to DTF. All haplotypes are significantly different at **P*<0.05; ***P*<0.01; ****P*<0.001.

The other pleiotropic haplotype associated with Fe and Zn was revealed on chromosome 2B (2B_35281485), was having two nucleotides, with the most favorable haplotype being GG that was present in 12 individuals (Figure 4.10).

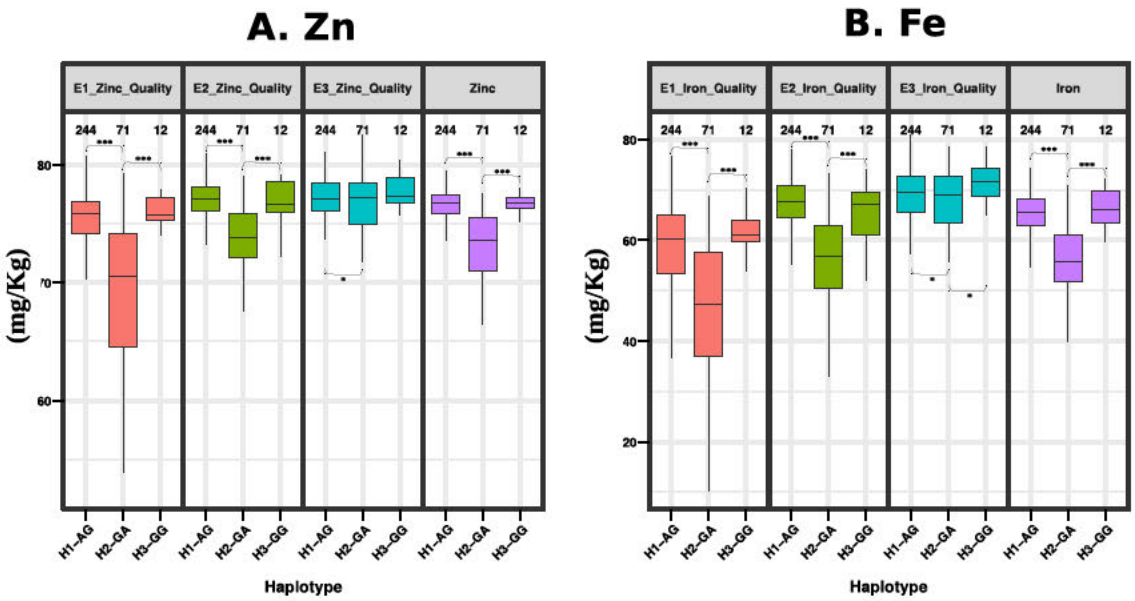


Figure 4.10 Boxplots showing differences in performances of individuals harboring different haplotype blocks generated based on a major QTN that was associated with both Fe and Zn. **A.** Differences in haplotypes detected for pleiotropic QTN 2B_35281485 for Zn. **B.** Differences in haplotypes detected for pleiotropic QTN 2B_35281485 for Fe. All haplotypes are significantly different.

4.3.6 Regional distribution of genotypes having favorable haplotypes around the pleiotropic QTNs

Using data across the 3 environments, majority of the 13 and 12 genotypes harboring favorable haplotypes for DTM/DTF and Fe/Zn respectively were from Tigray (Table 4.6), consistent with the enrichment of superior performing genotypes in the same region (Tables 4.2 & 4.3). Three genotypes (243635, AxumColl25 and AxumColl31) uniquely harbored both the DTM/DTF and Fe/Zn favorable haplotypes (Table 4.6). Only one released variety (Tekeze-1) was among the list of genotypes having superior pleiotropic haplotypes (Table 4.6).

Table 4.6 Distribution of genotypes harboring favorable pleiotropic haplotypes for DTM/DTF and Fe/Zn

Trait & locus	Haplotype	Genotypes	Region of collection
DTM/DTF 9B_20268455	H3: CACCAACAGGAAACTT	100065	Oromiya
		208442	Amhara
		211029	Tigray
		215850	Amhara
		215887	Amhara
		234186	Tigray
		237473	Tigray
		243635*	Amhara
		AxumColl25*	Tigray
		AxumColl27	Tigray
		AxumColl31*	Tigray
		Tekeze-1	Tigray
Fe & Zn 2B_35281485	H3: GG	219831	Tigray
		234185	Tigray
		235153	Tigray
		238337	Tigray
		243635*	Amhara
		AxumColl13	Tigray
		AxumColl25*	Tigray
		AxumColl28	Tigray
		AxumColl29	Tigray
		AxumColl31*	Tigray
		AxumColl35	Tigray
		AxumColl3	Tigray
		AxumColl7	Tigray

**Genotypes having both DTM/DTF and Zn/Fe favorable haplotypes*

4.3.7 Functional QTNs and gene-specific haplotypes

Ten genes were found to co-localise with major QTNs, two of which contained more than 1 SNP (Chromosomes 4A and 9B; Table 4.7). Four of the genes were associated with PTH, one gene (*glycosyltransferase*) with TSW, two genes with Fe and one gene with DTM/DTF (Table 4.7). The two genes that harbored at least two SNPs were *ABC transporter family protein* (ELECO.r07.4AG0303600) and *ankyrin repeat family protein* (ELECO.r07.9BG0703480) and were associated with PTH and TSW (Table 4.7). The study identified 2 haplotypes (H1-ATA, H2-GCG) for ELECO.r07.4AG0303600 and 4 haplotypes (H1-CCGGCGAG, H2-TTAACAGA, H3- CCGGTGAG, H4-CTAACAGA) for ELECO.r07.9BG0703480. Mean comparison tests between haplotypes of ELECO.r07.9BG0703480 revealed no significant differences (P<0.05) between genotypes and were therefore dropped from further analysis. Significant association between ELECO.r07.4AG0303600 haplotypes were observed in E1 (P<0.05), E2 (P<0.05), E3 (P<0.01) and across environments (P<0.001) (Figure 4.11).

Table 4.7 Genes colocalizing with major QTNs

Gene Id	Gene description	Trait	Allele	Pos
ELECO.r07.4AG0303570	RPM1-interacting protein 4-like protein	PTH	C/G	3404460
ELECO.r07.4AG0304200	Polygalacturonase QRT3	PTH	C/T	3940479
ELECO.r07.4AG0304230	30S ribosomal protein S17	PTH	C/T	3955182
ELECO.r07.4AG0304420	Shikimate/quinate hydroxycinnamoyl transferase	PTH	T/C	4204724
ELECO.r07.4AG0303600*	Multidrug resistance protein ABC transporter family protein	PTH	A/G	3454764
			T/C	3454863
			A/G	3454904
ELECO.r07.5BG0413640	Glycosyltransferase	TSW	G/A	2841435
ELECO.r07.8AG0623600	4'-phosphopantetheinyl transferase	Fe	C/T	14459510
ELECO.r07.8AG0623750	Receptor kinase 1	Fe	T/A	15284945
ELECO.r07.9BG0703480*	Ankyrin repeat family protein	DTF and DTM	C/T	19836545
			C/T	19836552
			G/A	19836556
			G/A	19836782
			C/T	19836804
			G/A	19836808
			A/G	19836813
			G/A	19836895
			G/A	20349730

**Highlights genes for which gene-based haplotype analysis was done*

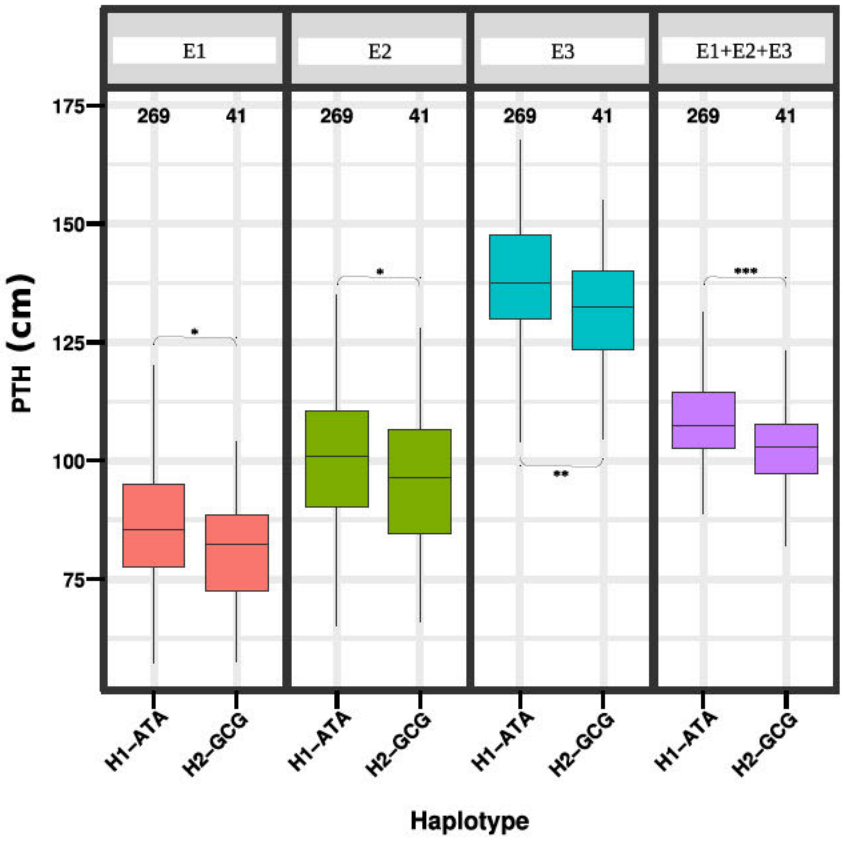


Figure 4.11 Boxplots showing differences in performances of individuals harboring the two different haplotypes for PTH within the gene ELECO.r07.4AG0303600 associated with plant height.

4.3.8 Identification of all other candidate genes from major QTNs using whole genome and sub-genome A SNPs

Three hundred and nineteen (319) genes were retrieved from chromosomes 1B (TSW), 2B (Fe and Zn), 5B (DrtSc and DTM), 6B (TSW) and 7B (Zn content) based on whole genome SNP analysis, and a further 149 candidate genes (15 for DTF; 4 for TSW; 8 for DrtSc, 23 for Fe and 99 for PTH) from using sub-genome A SNPs only and 10 genes (4.6 for DTF and DTM; 4 for TSW) from using sub-genome B SNPs only. The four major QTNs for TSW detected using whole genome SNPs revealed 269 candidate genes, with the first QTN on chromosome 1B having a cluster of *Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein* family and *Katanin p80 WD40 repeat-containing subunit B1 homolog*. The second TSW major QTN on chromosome 5B reported an abundance of *Ubiquitin carboxyl-terminal hydrolase* 12,

O-methyltransferase-like protein and *glycosyltransferases,* while the third TSW QTN revealed abundance of *serpins*. An additional *Ubiquitin family protein* was also identified in the TSW major QTN on chromosome 8A that was detected using the sub-genome A SNPs only. The additional candidate genes detected for TSW on chromosome 6B contained four genes, two of which had been detected in other TSW QTNs. GDSL esterase/lipase gene detected on chromosome 6B for TSW was also detected on chromosome 5B major QTN for TSW; GRF zinc finger family protein was also detected upstream within LD of another TSW QTN (6B_40602961).

The DTM QTN showed abundance of *Calmodulin-binding protein,* as well as *Transmembrane protein* families. Two additional *Transmembrane protein* families were identified for DTF on chromosome 8A using sub-genome A SNPs. The major QTN for Fe detected using sub-genome A markers revealed a cluster of 3 *Cysteine protease genes* that were ~0.5 Mb upstream of the significant marker. The same Fe major QTN on chromosome 8A also harboured 2 *cytochrome P450* genes and one *Cytochrome P450 reductase*. One *Receptor protein kinase* was reported for Fe major QTN on chromosome 7B, while 2 *Receptor protein kinases* were reported for the same trait on chromosome 8A.

4.4 Discussion

The findings of this research demonstrate tremendous genetic variation for both agronomic and nutrition related traits for Ethiopian finger millet germplasm evaluated across three different environments. Our study is the first comprehensive GWAS for both agronomic and nutrition-related traits for finger millet in Africa using more than 300 genotypes. Beyond identifying significant MTAs, we also identified promising candidate genes and favorable haplotypes for the target traits that could be deployed right away into breeding programs. Overall, results confirm earlier studies that there is adequate genetic variation among finger millet germplasm to select for several traits such as drought, agro-morphological and micronutrient content (Lule et al. 2012; Assefa et al. 2013; Backiyalakshmi et al. 2023; Chandra et al. 2024).

4.4.1 Phenotypic variation for the target traits

The present investigation revealed highly significant phenotypic variation between genotypes for all the traits studied across and within each of the locations. The current findings confirm that the assembled set of genotypes were ideal for trait discovery and paves the way for their

utilization in other studies. Ethiopia is considered a primary center of diversity for finger millet (Purseglove 1985; Tsehaye et al. 2006; Tesfaye and Mengistu 2017), therefore likely to harbour important agronomic diversity required for crop improvement. Confirming this high extent of agronomic diversity among Ethiopian germplasm was also important for finger millet, in which the yields are extremely low and the gap between potential yield (6 – 8 tonnes/ha) and farmers' yields (<2.5 tonnes/ha) is extremely high (Oduori, 2008; Padulosi et al., 2015; Gebreyohannes et al. 2021; Joshi et al., 2023; Gebreyohannes et al. 2024). Our study identified unimproved material yielding much more than the released cultivars, especially in Arsinegelle, suggesting that the existing native agronomic potential of Ethiopian finger millet has not been exploited to the farmers' advantages. Furthermore, most of the top ten best yielders and those harboring the highest concentration of micronutrient content were from Amhara and Tigray, the two regions from which the study could confirm minimal clustering with released varieties. Therefore, future efforts will need to introduce these promising landraces into breeding programs and design relevant agronomic and management packages that are appropriate for farmers in enhancing their yields (Beres et al. 2020).

Relatively high broad sense heritability (H^2) for most of the traits was identified in each of the environments, an indication of greater genetic control for the traits studied. Previous studies in finger millet that included at least 100 genotypes also reported similar H^2 values for some of the traits such as DTF (Lule et al. 2012; Eric et al. 2016), DTM (Anteneh et al. 2019), GY (Owere et al. 2015; Eric et al. 2016), PTH (Lule et al. 2012; Eric et al. 2016) and TSW (Lule et al. 2012). To the best of our knowledge, this was the first reported large-scale screening for the stay-green trait (STG) in finger millet, for which very high H^2 values were recorded. The stay-green trait has been used in several crops, including sorghum (Borell et al. 2014), to select for drought tolerance but is yet to be exploited in finger millet. Recording high H^2 values is promising and indicates the potential for genetic improvement of drought tolerance in finger millet using STG. Significant correlation between STG and drought score was also observed in E2 and E3, suggesting that the observed STG contributes to drought tolerance in these sites. More studies will need to be done to ensure that the stay-green trait being introduced into breeding programs is functional (Jordan et al. 2012) and not cosmetic (Myers et al. 2018).

The NIR based estimates of Fe and Zn showed a moderate level of H^2 (0.5-0.7). This is a good level of accuracy considering the prohibitive nature of the costs of wet chemistry. Although these results will still need to be validated through wet chemistry, the range of Fe content recorded in

the current study was higher than reported for the global finger millet core collection (Upadhyaya et al. 2011) but comparable to Puranik et al. 2020), who analyzsed a diverse set of genotypes that had been evaluated in Kenya. The Zn content reported in this investigation exceeds most of the previous reports and only comparable to previous studies in which plants had been grown in Zn treated soils (Yamunarani et al. 2016; Teklu et al. 2024). A recent study on agronomic biofortification of Fe and Zn in Ethiopia reported up to 21.4% increase in grain Fe and Zn content following the application of Zn and Fe fertilizer (Teklu et al. 2023b). Previous studies reported higher Fe grain concentrations than Zn (Upadhyaya et al. 2011; Puranik et al. 2020; Fred et al. 2021; Teklu et al. 2024) in contrast to our study where Zn concentrations were higher. The relatively higher Zn concentrations were consistent across the 3 locations and therefore reveal a likely unique germplasm set for improving grain Zn content in breeding programs. Our results might also suggest that there could be abundant genetic variation for Zn content in Ethiopia that may not have been captured within the global collections.

4.4.2 Genetic variation, population structure and linkage disequilibrium

We stringently filtered our markers to retain a highly informative marker set for further characterization of the genotypes. The study also chose to conduct all the genetic analysis using whole genome, sub-genome A and sub-genome B sets of markers, following interesting results from previous studies (Bančič et al. 2023; Devos et al. 2023). The retained markers explained more than 45% genetic variation between the genotypes and successfully defined four sub-populations across the germplasm irrespective of which marker set was used. The marker density of 16 SNPs/Mb was twice higher than reported in Bančič et al. (2023). Retaining an informative set of SNP markers is a pre-requisite for population structure analysis and for determining differences between individuals. The results of the present study successfully showed that most of the genotypes from Tigray and Amhara have not been actively used in breeding programs based on the minimal clustering of the released varieties within the Tigray and Amhara clusters. The germplasm used is, therefore, a unique resource that should be introduced into breeding programs to enrich the pool of breeding lines, and will also need to be well maintained and conserved to ensure the allelic richness is available in the future. Being native to Ethiopia, there is likely to be diverse cultivated and wild finger millet accessions that are growing alongside each other with regular gene flow between them (Tsehaye et al. 2006; Tesfaye and Mengistu 2017; Lule et al. 2018; Dida et al. 2021; Pendergast et al. 2022). Gene flow can enhance adaptation and increase genetic variation for traits of interest that should be

regularly captured through focused collection missions. Despite being an important center of diversity for finger millet, there are currently only ~30 finger millet genotypes from Ethiopia that are conserved in the ICRISAT global germplasm collection (ICRISAT 2024). This study reveals a need to have better representation of both Tigray and Amhara finger millet collection and characterization within the local and global gene banks.

All the three sets of markers revealed four sub-populations using DAPC analysis, although the sub-genome marker sets revealed more distinct clusters. The four clusters are consistent with Bančič et al. (2023) who studied 423 cultivated finger millet accessions from India, Nepal, East Africa and Southern Africa using whole genome SNPs. Devos et al. (2023) performed a similar analysis with the addition of wild accessions and reported two distinct clusters irrespective of which marker set was used. A repeat analysis of the same dataset in addition to existing datasets of wild accessions will be interesting in confirming the results reported by Devos et al. (2023). The clear difference in our study was the ability of the sub-genome markers to separate the sub-populations more clearly than the whole genome SNPs.

We also observed a huge difference in the LD decay points between the two sub-genomes, which would need to be studied further in more diverse germplasm sets. Using naïve models, the study confirmed that LD decayed more rapidly in the sub-genome A (1.2 Mb) in comparison to sub-genome B (3.2 Mb), which is consistent with a previous study in which LD decayed much faster in the sub-genome A with or without genetic structure correction (Bančič et al. 2023). LD is important in association mapping as it determines the level of optimal resolution required for an association study. Although LD has not been studied much in finger millet, the reported slow decay is not surprising given the highly self-pollinating nature of this crop. The difference in LD between the two sub-genomes could also be traced back to the progenitors. It is known that the A sub-genome donor is a wild weedy species, *Eleusine indica* (Zhang et al. 2019), hence a more rapid decay would be expected. LD decays more rapidly in wild populations than in cultivated crops (Sela et al. 2014).

4.4.3 Marker-trait associations, haplotype analysis and candidate genes

Our stringent filtering of markers and the use of Bonferroni threshold paid off in detecting major QTN regions. Some of the major QTNs detected in the current study were extremely novel and will form the basis for routine breeding and further research on the respective traits. Bančič et al. (2023) and Sood et al. (2023) detected several MTAs while studying agronomic traits in

finger millet, but none of the reported associations explained >20% phenotypic variation. Our study revealed major QTNs for DTM, DTF, TSW, DrtSc, Fe and Zn alongside several other significant QTNs. The major QTNs were associated with economically important traits in finger millet, all of which are still being improved using traditional methods for most part. We additionally chose a stringent 30% PVE as a cut-off for major QTNs to enhance the immediate application of our results into molecular breeding. There are studies reporting as low as 10% PVE as major QTLs (Pandey et al. 2020). A major QTL/QTN is one that is detected in more than one environment and has a large effect on the phenotype. Most studies recommended at least 15 to 20% PVE for the locus to be considered as major (Du et al. 2015). This study employed a high threshold of 30% PVE as a cut-off to reduce the numbers of false positives when the associated markers are introduced into breeding programs for genomics-assisted selection and introgression. While recent advances in next generation sequencing (NGS) have led to the development of Quality Control (QC) markers in finger millet, markers associated with economically important traits are still lacking. These major QTNs will add significant value towards early generation and genomic selection in structured finger millet breeding programs.

The potential reliability of the major QTNs for breeding was further validated using haplotype analysis. Haplotype analysis has been reported to improve the identification of genes of interest in other cereal crops including rice (Yang et al. 2023) and wheat (Taranto et al. 2023) but not yet exploited in finger millet, partly due to the previous lack of high-quality reference genome. Using a chromosome scale reference genome (Devos et al. 2023), we detected significant associations of different haplotype pairs with the target traits across all major QTNs. Associated haplotypes would enhance the precision of selection and introgression and improve breeding efficiency. Our results also provide opportunity to stack different favorable haplotypes into superior elite backgrounds for better performance. In some cases, we identified individuals harboring more than one favorable haplotype making such genotypes obvious candidates for immediate release, or introduction into various breeding programs. While a more comprehensive haplotype analysis of all QTNs identified will still be required to demonstrate the potential benefits of the QTNs detected, the results obtained from major QTLs form a baseline from which future similar studies will be anchored. Haplotype based breeding (HBB) promises to enhance genetic gain (Sivabharathi et al. 2024), especially in an under-researched crop such as finger millet.

The highest numbers of major QTNs were reported for TSW, which is one of the important determinants of grain yield in finger millet (Wolie and Dessalegn 2011). Haplotype analysis for seven major QTNs for TSW revealed clear differences in haplotypes demonstrating the readiness of all the markers identified for immediate use in breeding programs. Low yields in finger millet have been reported as one of the limiting factors to commercialization of the crop. Field evaluation, genetic diversity and haplotype analysis results provide new knowledge and reveal that grain yield in finger millet has not been studied and exploited sufficiently. In rice (*Oryza sativa* L.), where seed weight has been extensively studied, three major genes have been reported for TSW. The first TSW locus in rice, *GS3*, encodes a transmembrane protein (Fan et al. 2006), while the second, *GW5*, encodes a calmodulin binding protein (Liu et al. 2017). A third locus encodes a transcription repressor *OsBZR1*, which represses *FZP* (*Frizzy Panicle*) expression (Bai et al. 2017). This study identified 3 copies of *calmodulin binding proteins* and 4 *transmembrane proteins* in the DTM major QTN. DTM was found to be positively correlated with TSW. A major TSW QTN was also found colocalized with a *glycosyltransferase* gene on chromosome 5B in our study. These interesting candidate genes make a priority list for functional validation towards increasing grain size and yield in finger millet. Finger millet researchers will now have the favorable haplotypes and unique high yielding landraces to deploy in their programs and improve genetic gain as soon as research investments are made available.

Gene-specific haplotype analysis done for two major QTNs reported promising results and suggests that future studies should consider all the significant QTNs for gene specific haplotype analysis in the future. The two haplotypes identified for *ELECO.r07.4AG0303600* for PTH are promising for immediate deployment in selection for and/or against the trait. Tall plants in finger millet have been associated with lodging, which is one of the breeding objectives (Lule et al. 2012). Wolie and Dessalegn (2011) reported negative correlation between PTH and grain yield (dwarf plants are better yielding) and a positive correlation with biomass. It has been argued that the introduction of dwarf plants into cereals may have saved more lives than any other scientific development (Hedden 2003). The clear differences in PTH of each of the haplotype pools is proof that this gene-specific haplotype has the potential to play a huge role if introduced into breeding programs, either for grain yield or biomass. Haplotype GCG of *ELECO.r07.4AG0303600* should be studied further alongside TSW haplotypes for improving yields. Finger millet for fodder also remains an underexploited field that could take advantage of haplotype ATA of the gene *ELECO.r07.4AG0303600. ELECO.r07.4AG0303600* codes for ABC transporter gene family that is not well characterized in finger millet. However, there are

several reports in many crops demonstrating the involvement of ABC transporter genes in dwarfism (Busov et al. 2008; Wang et al. 2017; Ye et al. 2013; Zhu et al. 2019). The identification of a putative ABC transporter in PTH opens a new chapter for both haplotype-based breeding and functional characterization to confirm its role in finger millet.

Drought tolerance is also an important trait in finger millet that can result in significant yield penalty (Krishnamurthy et al. 2016). This study identified a major QTN for drought tolerance and a relatively minor one for the stay green trait (21.3% PVE). Haplotype analysis on the major QTNs for DrtSc on chromosomes 5B and 8A revealed highly significant haplotypes that should be deployed right away in breeding programs. The most applicable would be the negative selection against drought sensitive haplotypes, which were very consistent across environments. The stay-green QTN will also need to be explored further because it revealed significant contribution to the phenotype. Natural variation in the promoter region of a rice stay-green gene has been exploited in breeding and led to delayed senescence and increased grain yield (Shin et al. 2020). Similar studies can be designed in finger millet to further characterize the stay-green QTN alongside the stable DrtSc QTNs and haplotypes.

The pleiotropic QTNs detected between DTM and DTF and between Fe and Zn were not surprising. There is evidence of positive correlation between Fe and Zn in pearl millet (Govindaraj et al. 2022), finger millet (Ojulong et al. 2021), as well as in several other crops (Cichy et al. 2009; Velu et al. 2017; Singh et al. 2018; Sanjana Reddy et al. 2010; Diaz et al. 2022). Our results further confirm a common major QTN for both traits in finger millet for the first time providing more evidence for joint genomics-assisted selection for Fe and Zn. Malnutrition has been identified among the top priority problems that result in high levels of maternal and infant mortality in Ethiopia (Kassebaum et al. 2014). The QTNs identified here can be immediately deployed for the selection of genotypes enriched for the two elements. Once validated, such markers could also be used in the varietal release process as a standard to ensure only high Fe and Zn varieties are released, or recommended as a biofortification solution to the malnutrition cases, not only in Ethiopia, but in all finger millet producing countries. Both DTF and DTM are traits responsible for earliness, therefore a confirmation of a common QTN is a great validation of our results. Immediate validation and introduction of these markers will make it possible to improve the correlated traits simultaneously.

All the major QTNs detected while using whole genome SNPs were from the sub-genome B. The major QTNs on chromosome 8A were only detected when sub-genome A markers alone were used in the QTN analysis. Bančič et al. (2023) also detected significant QTNs only in the sub-genome B when whole genome SNPs were used in the analysis. This result was not surprising given the differences observed in LD pattern for the different sub-genomes, as well as for the whole genome SNPs. The appropriate MTA threshold would vary depending on both population- and genome-specific factors such as LD pattern and minor allele frequency (MAF) (Kaler and Purcell 2019). Given the rapid rate of LD decay in sub-genome A and the relatively fewer numbers of markers, the Bonferroni threshold used for the whole genome SNPs may have resulted in several false negatives for sub-genome A that could be detected when sub-genome A SNPs alone were used for the analysis. Although there are not many GWAS reports for finger millet using cultivated species that distinguish the two sub-genomes, it will be important for future studies to take this point into consideration in order to ensure that no potential associations are missed out.

4.5 Conclusion

This study significantly advanced our understanding on the genetic basis of important agronomic and nutrient traits in finger millet. The use of skim-sequencing SNPs alongside a comprehensive and stringent GWAS approach identified major QTNs, favorable haplotypes and promising candidate genes which are all novel discoveries in finger millet. To ensure the identified MTAs, haplotypes and candidate genes translate into practical applications, allelic and functional characterization will be required for their validation. Once validated, the markers reported in the current study will be great candidates for genomics-assisted selection and haplotype-based breeding in finger millet, in which there are currently none. To enhance conservation efforts and promote utilization in global breeding programs, further characterization of the Ethiopian finger millet germplasm is recommended. Ethiopian breeding program will likely benefit tremendously from integrating exotic germplasm into their conservation and breeding programs to enhance the diversity of finger millet breeding accessions for the benefit of breeders. Simultaneous improvement of agronomic and nutritional traits in finger millet breeding programs will pave the way towards making finger millet the desired global food security and climate resilient crop.

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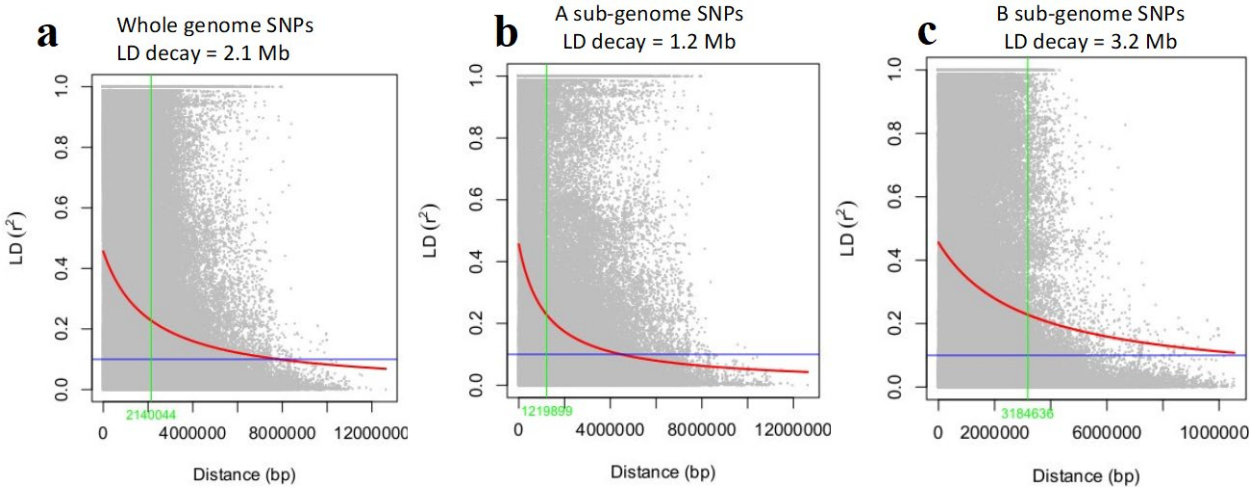
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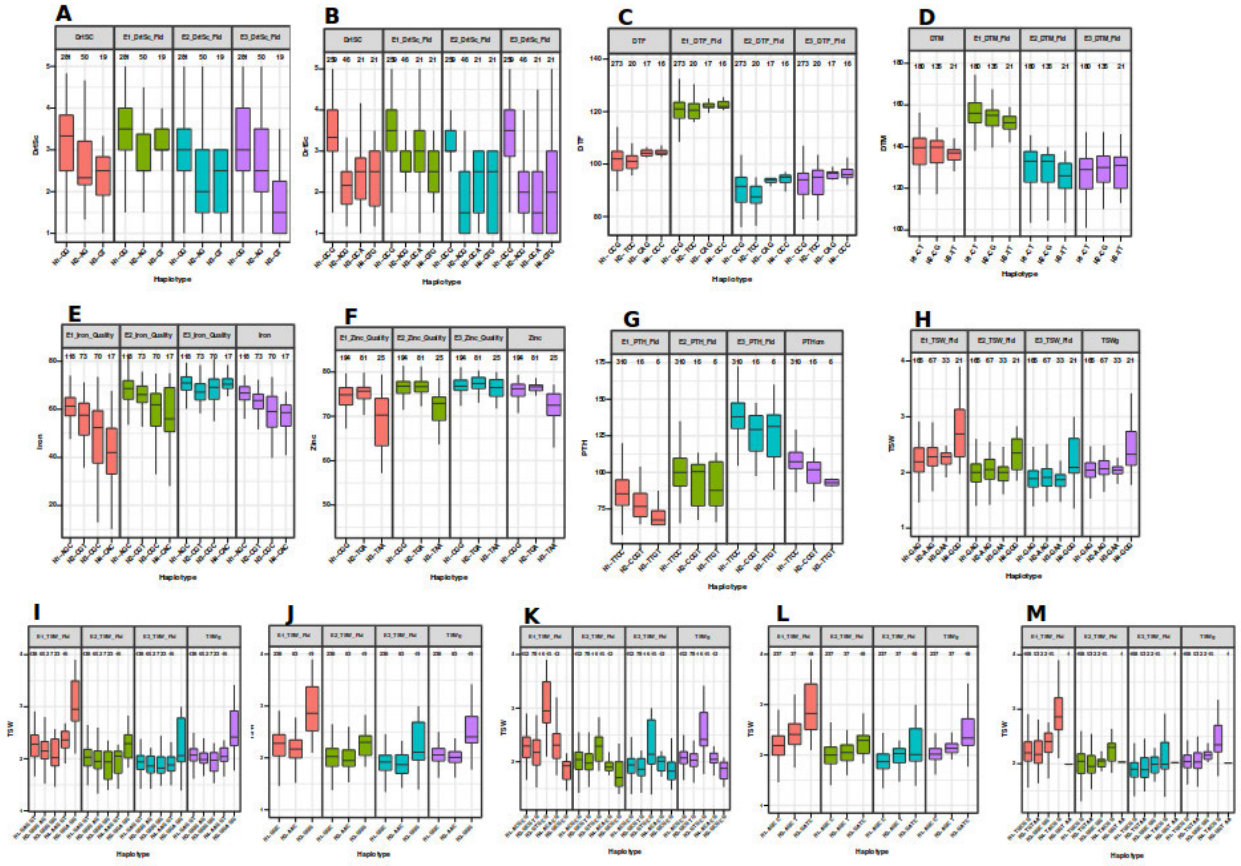
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Appendix Figure 4.1 LD decay plots showing differences in the LD decay distance. **a.** Whole genome overall LD decay distance of 2.1 Mbp. **b.** LD decay distance of 1.2 Mb for sub-genome A. **c.** LD decay distance of ~3.2 Mb for sub-genome B.



Appendix Figure 4.2 Boxplots showing differences in performances of individuals harboring different haplotype blocks generated from major QTNs. A. DrtSc haplotypes detected for chromosome 5B (5B_35573546) B. DrtSc haplotypes detected for chromosome 8A (8A_23730370) C. DTF haplotypes detected for chromosome 8A (8A_18375210). D. DTM haplotypes detected for chromosome 5B (5B_65558510). E. Fe content haplotypes detected for chromosome 8A (8A_14715050). F. Zn content haplotypes detected for chromosome 7B (7B_14800902). G. PTH haplotypes detected for chromosome 4A (4A_3954933). All TSW haplotypes detected were plotted for 1B_64659309 (H), 5B_3150126 (I), 6B_24190829 (J), 6B_27369367 (K), 6B_40602961 (L) and 8A_22146023 (M).

Appendix Table 4.1. Pearson correlation coefficients(r) of the various agronomic, drought related and nutritional composition traits of finger millet genotypes conducted/collected from the locations Arsingelle (E1), Maistebri (E2) and Meiso (E3)

Traits	r	DTF	DTM	PTH	GY	TSW	STG	DrtSc	Iron	Zinc
DTF	E1	1	0.99**	0.20**	-0.41**	-0.39**	0.43**	0.92**	0.04^{NS}	0.03^{NS}
	E2	1	0.99**	0.11**	-0.44**	-0.12**	0.31**	0.93**	0.04^{NS}	0.03^{NS}
	E3	1	0.99**	0.02^{NS}	-0.31**	-0.12**	0.38**	0.82**	0.01^{NS}	0.01^{NS}
DTM	E1		1	0.21**	-0.43**	-0.40**	0.45**	0.94**	0.04^{NS}	0.03^{NS}
	E2		1	0.11**	-0.44**	-0.12**	0.31**	0.91**	0.05^{NS}	0.03^{NS}
	E3		1	0.02^{NS}	-0.31**	-0.12**	0.37**	0.83**	0.01^{NS}	0.01^{NS}
PTH	E1			1	0.12**	-0.14**	0.18**	0.24**	-0.03^{NS}	-0.05^{NS}
	E2			1	0.04^{NS}	-0.02^{NS}	0.03^{NS}	0.15**	-0.02^{NS}	-0.00^{NS}
	E3			1	-0.00^{NS}	0.04^{NS}	0.01^{NS}	0.00^{NS}	-0.01^{NS}	-0.02^{NS}
GY	E1				1	0.23**	-0.31**	-0.41**	0.01^{NS}	0.01^{NS}
	E2				1	0.11**	-0.33**	-0.44**	-0.01^{NS}	-0.01^{NS}
	E3				1	0.19**	-0.31**	-0.34**	0.09**	0.04^{NS}
TSW	E1					1	-0.34**	-0.40**	-0.06^{NS}	-0.04^{NS}
	E2					1	-0.20**	-0.10**	0.003^{NS}	0.03^{NS}
	E3					1	-0.27**	-0.22**	0.02^{NS}	0.02^{NS}
STG	E1						1	0.45^{NS}	0.01^{NS}	0.03^{NS}
	E2						1	0.30**	0.04^{NS}	0.05^{NS}
	E3						1	0.58**	-0.03^{NS}	-0.02^{NS}
DrtSc	E1							1	0.02^{NS}	0.01^{NS}
	E2							1	0.04^{NS}	0.03^{NS}
	E3							1	0.01^{NS}	0.02^{NS}
Iron	E1								1	0.76**
	E2								1	0.81**
	E3								1	0.76**

Note: NS denotes non-significant and * and ** represents significant at 5 and 1% level of significance, respectively.

Appendix Table 4.2. A summary of the results of LD analyses among SNP marker pairs, including the number of significant marker pairs for each chromosome

Chr	Total number of marker pairs	Average r^2 for all pairs	D in Mbp	Total number of significant pairs*	Average r^2 for all significant pairs	D in Mbp	Number of plp(r^2>0.23)**	D in Mbp	Average r^2 for plp	Complete Ld (r^2 = 1)
	50753	0.25	1.22	22458 (44)	0.55	0.72	16791 (33)	0.47	0.7	5056 (10)
2A	40126	0.31	1.69	17775 (44)	0.62	0.9	13546 (34)	0.46	0.77	3556 (9)
3A	40328	0.22	0.16	15594 (39)	0.54	0.83	10987 (27)	0.83	0.71	3024 (7)
4A	33011	0.25	1.37	14782 (45)	0.53	0.7	10717 (32)	0.45	0.68	2763 (8)
5A	71131	0.42	1.01	41487 (58)	0.71	0.38	35887 (50)	0.27	0.8	13357 (19)
6A	33297	0.33	1.81	18931 (57)	0.57	1.15	13396 (40)	0.76	0.75	4339 (13)
7A	58308	0.42	0.88	34712(60)	0.7	0.39	29822 (51)	0.28	0.79	12817 (22)
8A	56940	0.59	0.92	42549 (75)	0.79	0.52	38575 (68)	0.41	0.86	25297 (44)
9A	96234	0.47	0.54	72592 (75)	0.61	0.37	54464 (57)	0.27	0.78	20911 (22)
T/M^A	**480128**	**0.36**	**1.07**	**280880 (59)**	**0.62**	**0.66**	**24909 (47)**	**0.47**	**0.76**	**91120 (19)**
1B	134563	0.61	0.62	96189 (71)	0.85	0.4	89436 (66)	0.38	0.9	54505 (40)
2B	34717	0.25	2.09	17249 (50)	0.48	1.6	10016 (29)	1.4	0.75	4010 (12)
3B	47759	0.29	1.39	19988 (42)	0.67	0.86	16112 (34)	0.86	0.8	8298 (17)
4B	47247	0.25	1.16	21307 (45)	0.54	0.84	15525 (33)	0.76	0.7	5451 (11)
5B	62968	0.3	1.29	35170 (56)	0.53	0.89	24434 (39)	0.7	0.71	9268 (15)
6B	55014	0.33	1.42	28671 (52)	0.62	0.78	21647 (39)	0.52	0.78	9456 (17)
7B	39904	0.26	1.53	22046 (55)	0.46	1.4	11805 (30)	1.3	0.77	3234 (8)
8B	56520	0.26	1.07	21434 (38)	0.67	0.97	16159 (29)	0.94	0.84	8431 (15)
9B	150061	0.91	0.17	143904 (96)	0.94	0.17	141529 (94)	0.17	0.94	105781(70)
T/M^B	**628753**	**0.38**	**1.19**	**405958 (65)**	**0.64**	**0.88**	**346663 (55)**	**0.78**	**0.8**	**208434 (33)**
T/M	**1108881**	**0.37**	**1.13**	**76315 (62)**	**0.63**	**0.77**	**570848 (51)**	**0.62**	**0.78**	**299554 (27)**

Chr, Chromosome; D, Physical distance, Mbp, Mega base pairs; PLP, Physically linked pairs;; Significant marker pairs, $p \leq 1.5E\text{-}6$; * Numbers in the brackets are the percentage of the total number of marker-pairs; ** Numbers in the brackets are the percentage of the number of significant marker pairs; T/MA, T/MB, and T/M, Total/Mean for A-subgenome, B-subgenome and the whole genome, respectively, LD, linkage disequilibrium

Appendix Table 4.3. Origin of genotypes clustered under various sub-populations generated from DAPC analysis presented in Fig. 3

SNP Category	Region	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Whole genome SNPs	Oromia	29	12	2	28
	Tigray	37	2	105	-
	SNNP	6	-	1	8
	Amhara	69	56	5	2
	Benishangul Gumuz	1	3	2	1
	Released varieties	**3**	**2**	**1**	**16**
	Total	**145**	**75**	**116**	**55**
Sub-genome A SNPs	Oromia	15	2	28	26
	Tigray	41	100	3	-
	SNNP	4	1	1	9
	Amhara	46	2	84	-
	Benishangul Gumuz	3	2	1	1
	Released varieties	**5**	**-**	**2**	**15**
	Total	**114**	**107**	**119**	**51**
Sub-genome B SNPs	Oromia	2	16	41	12
	Tigray	108	2	33	1
	SNNP	1	-	14	-
	Amhara	23	13	46	50
	Benishangul Gumuz	2	-	2	3
	Released varieties	**1**	**1**	**15**	**5**
	Total	**137**	**32**	**151**	**71**

Chapter 5. Hybrid Performance in Finger Millet (Eleusine Coracana) for Grain Yield and Component Traits

Abstract

Finger millet (*Eleusine coracana*) is a high-potential, climate-resilient and nutrient-rich small cereal crop for diverse product development such as food, animal feed, and value-added beverage and industrial raw materials. Finger millet has been under-researched, and better-performing varieties are yet to be bred for various market segments. Therefore, the objective of this study was to determine the combining ability, heterosis, and gene action of selected finger millet parents for economic traits in hybrid combinations to guide the selection of best families and new breeding populations. A 7 × 10 line × tester mating design was used, and the resultant 70 F_1 hybrids and 17 parents were evaluated under well-watered (NST) and drought-stress (ST) conditions across greenhouse and field environments. Genotypes were profiled for major agronomic traits: plant height (PTH), days to 50% flowering (DTF), days to maturity (DTM), number of productive tillers per plant (NT), primary finger length (FL), ear length (EL), number of fingers per ear (NF), grain yield (GY), harvest index (HI), and thousand seed weight (TSW). Significant variations ($p < 0.001$) were observed among lines, testers and their interactions for the assessed traits, indicating both additive and non-additive gene action underlying inheritance of the assessed traits. Additive genetic effect predominantly conditioned the inheritance of DTF, EL, DTM under ST conditions, whereas non-additive effects affected NT and DTM under NST conditions. Broad-sense heritability for GY was higher under ST (0.51) than NST (0.13) conditions, necessitating multiple testing environments for drought tolerance evaluation and selection. Lines such as 235700, 234187 and Addis-01 and testers such as Gute, 24394, Bako-09, Mereb-1, and 215982 exhibited higher general combining ability effects for GY in a desirable trend. Crosses Wama/Kako-1, 234187/24394, Wama/215982, 235700/213835, Addis-01/213835, Addis-01/Gute, Necho/Gute, and Necho/Kako-1 exhibited higher specific combining ability effects and heterosis for GY under ST conditions. The selected parents and the top crosses are recommended for breeding and selection of new generation and drought-adapted finger millet genotypes.

Keywords: gene action, combining ability analysis, drought tolerance, Ethiopia, finger millet, line x tester

5.1 Introduction

Finger millet (*Eleusine coracana* [L.] Gaertn.) is a high-potential, climate-smart and nutrient-rich small cereal crop. Africa is the centre of origin and genetic diversity of the crop, where it is used as food, livestock feed and for household and industrial products. Finger millet is gluten-free and rich in calcium, iron, zinc, dietary fibre, essential amino acids, and bioactive compounds such as phenolics, tannins, flavonoids and antioxidants (Gaikwad et al., 2024; Sirin, 2023; Gebreyohannes et al., 2024a,b; Shimelis et al., 2026). The nutritional value of finger millet makes it a functional food with human health benefits against diabetes, anaemia, osteoporosis, and obesity (Puranik et al., 2020; Maharajan et al., 2022; Backiyalakshmi et al., 2023). Finger millet grain is processed into specialty alcoholic and non-alcoholic beverages such as distilled spirits or domestic drinks (Lule et al., 2012; Mukisa et al. 2012). Hence, it enhances livelihoods and drives market diversification.

Finger millet is drought-tolerant and possess a C4 photosynthesis system with efficient photo-assimilation and biomass production (Yogeesh et al., 2016; Brhane et al., 2017). The grain is resilient to storage pests, enabling long-term preservation under traditional storage conditions with minimal damage. Also, the genetic plasticity and adaptation to grow under harsh environmental conditions make it a crop of choice in marginal agro-ecologies in sub-Saharan Africa and South Asia (Mbinda and Mukami, 2021; Mbinda et al., 2021). Globally, finger millet accounts for about 20% of the total millet production with an estimated area of ~2.1 million ha and 26% of total production (~3.7 million tons) annually (FAOSTAT, 2022; Indiastat, 2022; Gebreyohannes et al., 2024b). India and Ethiopia are the major contributors of finger millet production in the world. In Ethiopia, finger millet is cultivated on approximately 480,511 hectares of land with a total annual yield output of 1,218,582 tons (CSA, 2020). Ethiopia accounts for 22% of global finger millet cultivation area and 33% of total production, indicating the value of finger millet in the agricultural sector (Gebreyohannes et al., 2024b).

Despite its economic importance, finger millet productivity remains considerably low (< 2.5 t/ha) in the major producing regions such as Ethiopia, far below its attainable yield potential of 6 to 8 t/ha (CSA, 2017; Gebreyohannes et al., 2021, 2024b). The yield gap is attributed to a range of biotic, abiotic, and socio-economic constraints, as well as limited genetic improvement (Mulualem and Melak, 2013; Owere et al., 2014; Mbinda et al., 2021; Tarekegn et al., 2021).

Among abiotic constraints, recurrent drought associated with climate change is the leading constraint on millet production, causing estimated yield losses ranging from 50 to 100% (Maqsood and Ali, 2007; Gebreyohannes et al., 2025a). In Ethiopia, there are few drought-tolerant finger millet varieties available to growers for sustained, profitable production. Consequently, developing high-yielding and drought-tolerant varieties remains a key objective of Ethiopian finger millet breeding programs. However, breeding progress has been constrained by a limited understanding of the genetic architecture of key agronomic and physiological traits

In this context, the line × tester (L × T) mating design provides a robust framework for dissecting the genetic basis of traits and evaluating the breeding potential of parental lines and their crosses (Acquaah, 2012). This approach enables partitioning of genetic variance into general combining ability (GCA) and specific combining ability (SCA), thereby facilitating the dissection of additive and non-additive gene effects (Mapako and Maphosa, 2025). GCA represents the heritable component of genetic variance that can be accumulated through selection. Conversely, non-additive genetic effects are associated with SCA attributable to dominance and epistatic genes and their interactions. The SCA effects contribute to heterosis or hybrid vigour (Li et al., 2008; Liang et al., 2015; Viana, 2023).

Understanding the relative importance of additive and non-additive gene-action is critical in drought-prone production systems, where the choice of breeding methods, whether selection-based or hybrid-oriented. Integrating L × T analysis with multi-environment evaluation under both non-stressed and drought-stressed conditions enhances the accuracy of genotype performance assessment and facilitates the identification of stable, high-performing genotypes. This approach has been successfully applied in several crops, including finger millet, pearl millet, and foxtail millet, to elucidate the genetic architecture of traits related to yield, maturity, and nutrient composition (Priyadharshini et al., 2015; Thribhuvan et al., 2023; Mapako and Maphosa, 2025). Agronomic traits including, flowering and maturation times, plant height, panicle length and width, seed weight, and physiological traits (i.e., stay-green trait, and chlorophyl content) are associated with drought adaptation and yield potential. However, limited information exists on combining ability, gene action, and heterosis in Ethiopian finger millet germplasm for these economic traits under contrasting non-stressed environments. Therefore, the objective of this study was to determine the combining ability, heterosis, and the nature of gene action of selected finger millet parents for economic traits in hybrid combinations to guide the selection of the best families and new breeding populations. We hypothesise that Ethiopian finger millet accessions

possess significant combining ability and heterosis for agronomic and physiological traits under contrasting environmental conditions.

5.2 Materials and methods

5.2.1 Plant materials

Seventeen finger millet genotypes, comprising seven lines and ten testers, were used in the study. The 17 parents were selected after rigorous phenotyping and genotyping (Gebreyohannes et al., 2025a,b). These 17 parental genotypes were selected from a larger core collection of 448 Ethiopian finger millet landraces previously profiled across diverse moisture regimes in Chapter 3. Hierarchical cluster analysis was conducted based on their agronomic performance, drought response, and nutrient compositions. Consequently, the selected lines and testers represent contrasting genetic clusters, ensuring a composition of genetically divergent parents with complementary traits, including distinct maturity groups, varying grain yield potentials, and unique micronutrient stability profiles based on Mieso (MI) data. The parents have contrasting agronomic performance and unique nutritional profiles (Table 5.1). The lines have complementary traits, including early flowering and maturity, as well as high nutritional composition, like high iron, zinc, starch, and amylose contents. The four popular and widely cultivated late-maturing varieties (i.e., Addis-01, Wama, Necho, and Tessema), were used as lines due to their wide adaptability to various agro-ecologies of the country, while the three early-maturing lines were selected possessing short plant stature, longer retention of green foliage (i.e., stay-green), and lodging resistance. The 10 complementary testers were selected, possessing desirable attributes such as early maturity, seed quality, and disease resistance.

Table 5.1. Names and descriptions of the finger millet parental genotypes used in the cross.

Entry code	Name of parents	Role in the cross	Clusters (C) of parents based on MI data	Agronomic traits	Nutritional attributes
G1	227974	Line	C2	Late-maturing and susceptible to *Striga*	High iron and zinc contents
G2	234187	Line	C2	Early maturing, stay-green foliage, and stem lodge resistance	High amylose content
G3	235700	Line	C4	Early maturing and short plant stature	High iron and zinc contents
G4	Addis-01	Line	C3	Late maturing, high-yielding	High amylose and starch contents
G5	Necho	Line	C3	White seeded, lodging resistant, late maturing, susceptible to blast	High amylose, and starch contents
G6	Tessema	Line	C2	Lodging resistance and late maturing	High amylose, and starch
G7	Wama	Line	*C2*	*Striga* resistant and late maturing	High starch content
G8	24394	Tester	C2	Stay green trait, disease resistance, lodging resistance, and anthocyanin pigmentation on stem	High starch content
G9	213835	Tester	C2	Stay green trait, disease resistance, lodging resistance, and anthocyanin pigmentation on stem	High starch content
G10	215982	Tester	C1	High number of fingers	High iron and zinc contents
G11	238335	Tester	C2	Early maturing	High starch content
G12	AxumColl 21	Tester	C1	*Striga* resistant	High amylose and starch contents
G13	Bako-09	Tester	C3	Stay-green trait, anthocyanin pigmentation	High amylose
G14	Gute	Tester	C2	Stay-green trait, and lodging resistance	High amylose, and starch contents
G15	Kako-1	Tester	C2	Stay green trait, short plant stature, lodging resistance, and anthocyanin pigmentation	High amylose and starch contents
G16	Meba	Tester	C2	Stay-green trait, disease resistance, anthocyanin pigmentation	High amylose contents
G17	Mereb-1	Tester	C2	Stay-green trait, early maturing, anthocyanin pigmentation	High amylose and starch contents

5.2.2 Hybrid development

The 7 lines and 10 testers were stagger-planted in a two-week interval at Melkassa Agricultural Research Centre in Ethiopia in 2021. The stagger-planting allowed the synchronisation of flowering time for hot water emasculation and controlled pollination. At anthesis, panicles were covered with glassine paper bags. Sampled panicles were prepared by treating them in 52°C hot water in a plastic jug for two minutes to sterilise the pollen grains in the florets. Treated panicles were bagged with glassine paper to prevent foreign pollens. After 3-4 days, when the stigma appeared fluffy, controlled pollination were done using plants with freshly dehisced pollen from the designated tester. Controlled pollination was carried out by carefully intertwining the fingers of the tester panicle with the fingers of the emasculated florets of the line's panicle. After

pollination, the panicle of the female or the line was secured by covering with a labelled glassine paper bag to prevent uncontrolled cross-pollination. Crosses were made using a 7 lines × 10 testers mating design, whereby each line was crossed with all testers. Anthocyanin pigmentation is a dominant trait in millets (Renganathan et al. 2021), and thus, true hybridity in the present study was confirmed using male parental testers carrying this distinct morphological marker, enabling clear identification of F_1 progenies. Selfed or off-type genotypes were rigorously rouged out at the seedling stage, and only verified true F_1 plants were tagged and used for subsequent evaluation. This procedure resulted in the development of 70 F_1 hybrids (Appendix Table 5.1), which, together with 17 parental genotypes, constituted the 87 total genotypes used for subsequent analyses.

5.2.3 Experimental setup and trial management

The F_1 hybrids and the parents were evaluated at the Melkassa Agricultural Research Centre (39°21'E, 8°24'N, 1550m asl) in 2021 under non-stressed (NST) and drought-stressed (ST) conditions in greenhouse and field environments. A 29 x 3 row-column experimental design with a total of 87 genotypes with two replications was used in both settings. Like the field experiment, this layout was specifically chosen to control spatial variation in the greenhouse arising from differential shading and other microenvironmental effects. To control spatial variation in the greenhouse arising from differential shading and microenvironmental effects. Under the greenhouse environment, polyethene plastic pots of 20L capacity (i.e., 300 mm diameter and 280 mm height) were used. In each plastic pot > 30 seeds were sown and later, thinned to 20 vigorous plants per pot after two weeks of emergence which is equivalent number with a single plot of field experiment.

A drip irrigation system with 0.42 L h^{-1} emitters supplied water from a reservoir through regulated main and sub-lines. Soil moisture was monitored gravimetrically to maintain ~80% field capacity (FC) in non-stressed pots, while irrigation was withheld at flowering in stressed pots until moisture declined to ~30% FC, simulating post-flowering drought. In the field, stressed and non-stressed plots were separated by 10m to prevent lateral flow. Each genotype was planted in 3m rows (40 cm spacing) with 20 plants per plot. Under field conditions, furrow irrigation was applied based on discharge using a locally made and calibrated Parshall flume. Non-stressed plots were irrigated every six days to maintain ~80% FC, while stressed plots received no water after

flowering to impose controlled drought. Soil water status was monitored using tensiometers, installed at various depths across the field, and crop water requirement (CWR) was calculated. The CWR in the field experiment was estimated using the formula: CWR = KC × ETo, where KC is the crop coefficient determined at different growth and developmental stages, while ETo is the reference crop evapotranspiration. ETo was computed using a CROPWAT 8.0 application (FAO, 1998) from local meteorological data sourced from the National Meteorological Agency of Ethiopia. Standard agronomic practices were applied consistently across environments, including application of diammonium phosphate (DAP) at 100 kg/ha at planting, manual weeding, and insect pest control with recommended practices for the study areas.

5.2.4 Data collection

Data on agronomic traits, including agro-morphological and drought tolerance characteristics, were collected following modified International Board for Plant Genetic Resources (IBPGR) (1985) guidelines. Plant height (PTH, cm) was measured from the base of the plant to the tip of the head (ear) at the dough stage. Days to 50% flowering (DTF) and days to Maturity (DTM) were recorded as the number of days from sowing to when 50% of the main tillers had emerged ears and mature ears, respectively. The number of basal tillers with productive or mature ears (NT), length of the longest finger (FL, cm), and ear length (EL, cm) were measured at the dough stage on the main tiller. The number of fingers on the main ear (NF) was counted. Grain yield (GY) was computed from ~20 plants per pot per replication in the greenhouse (polyethylene pots, 300 mm diameter × 280 mm height; plot size = 0.071 m^2) and from all plants per plot per replication ~ 20 plants [total plot = 1 row × 3 m × 0.4 m). In both experiments, GY was adjusted to 12.5% moisture content and expressed in t/ha by scaling the measured yield to the corresponding pot or plot area. Harvest index in % (HI) was calculated as the ratio of grain yield to biological yield per pot (plot) multiplied by 100%. Thousand seed weight (TSW) was determined by drying 1000 randomly selected seeds to a constant moisture content of 12.5% and recording their weight. Finally, chlorophyll content at maturity (SPADM) was measured to assess the capacity of genotypes to maintain photosynthetic activity during grain filling under stress conditions. Measurements were taken from three points on mature flag leaves using a soil and plant analysis development [SPAD] meter (502 Minolta Co., Osaka, Japan), and readings were averaged for analysis following the procedure of Rad et al. (2012). The assessment was specifically intended to capture genotypic variation in chlorophyll retention associated with the

functional stay-green trait, an important physiological indicator linked to delayed senescence, drought tolerance, and grain yield stability under terminal moisture stress.

5.2.5 Data analysis

Variance components and combining ability effects

Variance components were partitioned, and combining ability effects were computed using a two-way analysis of variance (ANOVA) procedure in SAS PROC GLM (SAS, 2013). The general combining ability (GCA) and specific combining ability (SCA) variances were computed following the L × T genetic design (Kempthorne, 1957) as outlined by Singh and Chaudhary (1985). Genotypic variation among stressed and non-stressed conditions within each testing site was assessed, and homogeneity of error variances was tested using Bartlett's test (Glass, 1996). In the ANOVA model, lines, testers, and their interactions (L × T) were considered as random effects. While testing site (environment), water regimes (stress vs. non-stress), and replication were treated as fixed effects. The following linear mixed model was adopted for ANOVA:

$$Y_{ijklm}=\mu + E_k+W_m + R_{l(km)} + L_i + T_j + (LT)_{ij} + (LE)_{ik} + (LW)_{im} + (TE)_{jk} + (TW)_{jm} + (LTE)_{ijk} + (LTW)_{ijm} + (LTEW)_{ijkm}+\varepsilon_{ijklm}$$

Y_{ijklm} is the average performance of the cross between the i^{th} line and the j^{th} tester, tested at the k^{th} site, under m^{th} water regime, and in the l^{th} replication; μ is the overall mean of all observations; E_k is the fixed effect of the k^{th} testing site, and W_m is the fixed effect of water regime. $R_{l(km)}$ represents the effect of replication, which is nested within each site and water regime. L_i and i^{th} are the random effects of the line and tester, showing their general combining ability (GCA). The interaction $(LT)_{ij}$ represents the random effect of specific combining ability between lines and testers. Other interactions include line x site (LE), line × water regime (LW), tester × test site (TE), and tester × water regime (TW). Higher-order interactions are also included: SCA x test site (LTE), SCA × water regime (LTW), and the four-way interaction of line × tester × test site × water regime (LTEW). Finally, ε_{ijklm} is the residual error term, which represents random variation not explained by the model. It accounts for unexplained variations in each observation defined by the i^{th} line, j^{th} tester, k^{th} site, m^{th} water regime, l^{th} replication. This error is assumed to be independent and normally distributed with variance σ^2.

The significance of GCA for lines and testers, and SCA for crosses, was assessed using a two-tailed t-test. Error mean squares were used to estimate the standard errors associated with each parameter, enabling statistical analysis of GCA and SCA effects within each treatment as follows:

$$\text{t statistic } = \frac{Effect}{SE}$$

Where SE is the standard error of the difference.

The following formula was used for the calculation of standard errors (SE) for combining ability effects:

$$\text{SE of GCA for lines } = \sqrt{MSE/rt}, \qquad \text{SE of GCA for testers } = \sqrt{MSE/rl},$$

$$\text{SE of SCA effects } = \sqrt{MSE/r}$$

Where *MSE* = mean square error from the analysis of variance table. Where r, t, and l are the number of replications, testers, and lines, respectively.

A standard ANOVA of the line x tester mating design was conducted to estimate overall genotypic variance. In cases where genotypic effects were significant, the line x tester interaction was analysed to determine lines with superior SCA, indicated by differential performance across tester genotypes (Singh, and Chaudhary 1985). The significance of testers [GCA (T)] and lines [GCA (L)] mean squares within each site was assessed using the line x tester interaction as the error term, while the significance of the line x tester interaction (SCA) was evaluated using the error mean square. Table 5.2 outlined the ANOVA model used to analyse the line by tester design when data from all testing sites and water regimes are pooled.

The proportional contribution of the genetic effects of lines, testers and interactions with lines, testers and sites was computed as follows:

$$\textbf{Contribution of lines}(\%) = \textbf{sum of square of}(\textbf{Lines/Crosses})\textbf{x100}$$

$$\textbf{Contribution of testers}(\%) = \textbf{sum of square of}(\textbf{testers/crosses})\textbf{x100}$$

Table 5.2. Structure of combined analysis of variance and expected mean squares for line × tester mating design across testing sites and water regimes

Source of variations	Degree of freedom	Mean squares (MS)	Expected mean squares (EMS)
Replications	r-1		
Testing sites (E)	e-1		
Water regimes (W)	w-1		
Lines (L)	l-1	MS_L	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rew\sigma^2_{LT} + rtw\sigma^2_{LE} + rte\sigma^2_{LW} + rtew\sigma^2_{L}$
Tester (T)	t-1	MS_T	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rew\sigma^2_{LT} + rlw\sigma^2_{TE} + rle\sigma^2_{TW} + rlew\sigma^2_{T}$
L/T	(l-1) (t-1)	MS_{LT}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rew\sigma^2_{LT}$
L/E	(l-1) (e-1)	MS_{LE}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rtw\sigma^2_{LE}$
L/W	(l-1) (w-1)	MS_{LW}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rte\sigma^2_{LW}$
T/E	(t-1) (e-1)	MS_{TE}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rlw\sigma^2_{TE}$
T/W	(t-1) (w-1)	MS_{TW}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW} + rw\sigma^2_{LTE} + rle\sigma^2_{TW}$
L × T × E	(l-1) (t-1) (e-1)	MS_{LTE}	$\sigma^2 + r\sigma^2_{LTEW} + rw\sigma^2_{LTE}$
L/T/W	(l-1) (t-1) (w-1)	MS_{LTW}	$\sigma^2 + r\sigma^2_{LTEW} + re\sigma^2_{LTW}$
L/T/E/W	(l-1) (t-1) (e-1) (w-1)	MS_{LTEW}	$\sigma^2 + r\sigma^2_{LTEW}$
Error	ew(rlt-l-t-1) + l + t - lt	MS_E	σ^2

Note: r, e, w, l, and t are the number of replications, testing sites, water regimes, lines and testers, respectively

Estimates of genetic variance components for various parameters were derived by equating the observed mean squares with the expected mean squares associated with each variable in the ANOVA model across testing sites and water regimes, as defined below:

$$\sigma^2_L = \frac{MS_L - MS_{LT} - MS_{LE} - MS_{LW} + 2xMS_{LTE} + 2xMS_{LTW} - 2xMS_{LTEW}}{rtew} = \sigma^2_{GCAL}$$

$$\sigma^2_T = \frac{MS_T - MS_{LT} - MS_{TE} - MS_{TW} + 2xMS_{LTE} + 2xMS_{LTW} - 2xMS_{LTEW}}{rlew} = \sigma^2_{GCAT}$$

$$\sigma^2_{LT} = \frac{MS_{LT} - MS_{LTW} - MS_{LTE} + MS_{LTEW}}{rew} = \sigma^2_{SCA}$$

$$\frac{(\sigma^2_L + \sigma^2_T)}{2} = \text{CovHS}_{ave} = \sigma^2_{GCA}$$

$$\sigma^2_{GCA} = Cov\ HS_{ave} = (\frac{1+F}{4})\sigma^2_A\ ;\ \ \sigma^2_{SCA} = \left(\frac{1+F}{2}\right)\sigma^2_D$$

Where $\sigma^2_L, \sigma^2_T, \sigma^2_A, \sigma^2_D, \sigma^2_{GCAL}, \sigma^2_{GCAT}, \sigma^2_{SCA}$, and σ^2_{LT}, are variances due to lines, testers, additive effects, dominance effects, GCA of lines, GCA of testers, SCA, and lines x testers interaction, respectively.

$MS_L, MS_T, MS_E, MS_{LT}, MS_{LE}, MS_{LW}, MS_{TE}, MS_{TW}, MS_{LTE}, MS_{LTW}$, and MS_{LTEW} are mean square due to lines, testes, error, interactions of lines × testers, lines × testing sites, lines ×water regimes, testers × testing sites, testers × water regimes, lines × testers × testing sites, lines × testers × water regimes, and lines × testers × testing sites × water regimes and r, t, l, e, w are the number of replications, testers, lines, testing sites, and water regimes, respectively, in that order. Assuming complete homozygosity (F = 1) for both lines and testers, additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D) were estimated using the full observed phenotypic variation.

Genetic parameters

Baker's ratio measures the comparative importance of additive (general combining ability, GCA) against non-additive (specific combining ability, SCA) genetic effects in a breeding population. It was computed from variance components of GCA and SCA, as defined by Baker (1978) as follows:

$$\text{Baker's ratio} = \frac{2x\sigma^2_{gca}}{2x\sigma^2_{gca} + \sigma^2_{sca}}$$

Where $\sigma^2_{gca}, and\ \sigma^2_{sca}$, are variances due to GCA, and SCA, respectively.

Broad-sense heritability (H^2) of traits was computed based on the combined analysis of variance according to Gowda et al. (2012) as follows:

$$H^2 = \frac{2\sigma^2_{gca} + \sigma^2_{sca}}{2\sigma^2_{gca} + \sigma^2_{sca} + 2(\sigma^2_{gcaE}/e) + 2(\sigma^2_{gcaW}/w) + (\sigma^2_{scaE}/e) + (\sigma^2_{scaW}/w) + (\sigma^2_{scaEW}/ew) + \left(\frac{\sigma^2}{rew}\right)}$$

Where $\sigma^2, \sigma^2_{gca}, \sigma^2_{sca}, \sigma^2_{gcaW}, \sigma^2_{gcaE}, \sigma^2_{scaE}, \sigma^2_{scaW}, \sigma^2_{scaEW}$, are variances due to error, GCA, SCA, interaction of water regimes with GCA, interaction of test sites with GCA, interaction of test sites with SCA, interaction of water regimes with SCA, and interaction of water regimes and test sites with SCA, in the same order.

Mid-parent (MP) and better-parent (BP) Heterosis

Heterosis was quantified as the percentage deviation from both mid-parent (MP) and better-parent (BP) values, following Falconer and Mackay (1996). The significance of heterosis of crosses was assessed using a two-tailed t-test with degrees of freedom reflecting the number of crosses. Error mean squares were utilised to estimate the standard errors associated with each parameter, enabling statistical analysis of the effects for heterosis as follows: $\text{t statistic} = \frac{Effect}{SE}$ Where SE is the standard error. The SE for heterosis effects was calculated as follows: $\text{SE of heteross of crosses} = \sqrt{MSE/r}$, where MSE = mean square error of crosses from the analysis of variance table and r is the number of replications.

5.3 Results

5.3.1 Combined analysis of variance

Combined analysis of variance revealed significant variation ($p < 0.001$) among finger millet progenies and parents for the assessed traits (Table 5.3). The main effects of test sites and water regimes were also significant for most traits. The interaction effects between crosses and water regimes significantly affected PTH, NT, GY, HI, and TSW. Highly significant variation was also noted among GCA due to lines (L), and testers (T), and SCA due to L × T interactions for most traits under stressed and non-stressed conditions (Table 5.3). Also, lines × test sites interactions and lines × water regimes interactions were significant for most traits. Testers × test sites interactions were significant, whereas testers × water regimes interactions were non-significant for most assessed traits. In contrast, the lines × testers × test sites interaction effects revealed significant effect on most traits under stressed and non-stressed conditions, and for combined analyses (Table 5.3; Appendix Tables 5.2 and 5.3).

The variance due to additive genetic effects was the highest for PTH at 85.11, but the lowest for TSW (0.04) (Table 5.3). DTF, EL, FL, NF, DTM, and chlorophyll content recorded higher additive variance, whereas GY, HI, and NT displayed low additive variance compared to their corresponding dominance variance among the F1 families. Variance due to dominance genetic effects varied from 0.01 for TSW to 10.03 for DTF (Table 5.3). Under stressed conditions across environments, additive variance ranged between 0.06 for TSW and 40.60 for DTF, whereas dominance variance varied from 0.05 for TSW to 29.55 for PTH. DTF, PTH, EL, FL, NF, DTM, HI, TSW, and chlorophyll content displayed high additive variance, while NT and GY showed

low additive variance relative to dominance variance. Under non-stressed condition across test environments, additive variance varied from 0.03 for TSW to 120.24 for PTH, whereas dominance variance varied from 0.00 for TSW to 20.62 for DTM. Variance attributed to additive gene effects was high compared to variance attributed to dominance gene effects for DTF, EL, FL, NF, GY, HI, TSW, and chlorophyll content, and low for NT and DTM. Baker's ratio varied from 0.21 (GY) to 0.99 (PTH, & DTM) across drought conditions (Table 5.3), while it ranged from 0.32 (NT) to 0.98 (DTF) under stress conditions, and from 0.25 (GY) to 0.99 (TSW) under non-stressed conditions. Thus, under drought stress conditions, additive gene action predominantly controls DTF, EL, and DTM while non-additive effects influence NT, GY, and TSW, whereas under non-stress conditions, additive effects govern most traits, including PTH, DTF, EL, FL, NF, GY, HI, TSW, and chlorophyll content, with non-additive action remaining important only for NT and DTM.

Broad-sense heritability (H^2) estimates varied from 0.13 for GY to 0.65 for NT under non-stress conditions, from 0.30 for NF to 0.74 for TSW under stress conditions, and from 0.19 for DTM to 0.57 for FL across drought conditions (Appendix Tables 5.2 and 5.3). TSW recorded a high H^2 value at 0.74 under stress conditions, whereas FL and NT had values of 0.62 and 0.65 under non-stressed conditions, respectively. Moderate H^2 values (varying from 0.3 to 0.6) were recorded for PTH, DTF, EL, FL, NT, HI, and TSW across drought conditions. Under stressed conditions, H^2 was higher for TSW (0.74) and moderate (0.3 to 0.6) for other traits. Under non-stressed conditions, the traits PTH, DTF, EL, and HI recorded moderate heritability values (0.3 to 0.6), whereas NF, DTM, GY, TSW, and chlorophyll content recorded low heritability (H^2 <0.3). For most assessed traits, the proportion of the total sum of squares attributed to general combining ability surpassed that of specific combining ability (Figure 5.1). Notably, GCA effects were higher for EL, FL, and DTF. Conversely, traits such as GY, NT, and NF exhibited greater SCA contributions.

Table 5.3. Combined analysis of variance showing mean square and genetic components for agronomic and physiological traits in finger millet genotypes evaluated under non-stress and drought-stressed conditions in glasshouse and field environments.

Sources of variation	df	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
		Mean squares and significant tests										
Progenies (F_1)	69	835.6**	426.1**	45.1**	34.7**	8.1**	10.3**	420.2**	6.5**	77.9**	0.7**	142.2**
Test sites (E)	1	8904.1**	196537.6**	29.3*	9.7^{NS}	12.0**	27.4**	107476.0**	1790.0**	16275.7**	0.2^{NS}	9577.2**
Water regimes (WR)	1	9381.1**	67.3^{NS}	48.9**	51.3**	979.1**	2.4^{NS}	24032.6**	1130.1**	3759.7**	74.9**	8333.6**
F_1/E	69	451.7**	262.1^{NS}	11.7**	7.7*	2.1**	6.0**	283.8**	4.9**	42.6**	0.3**	101.2**
F_1/WR	69	144.6**	34.3*	9.3*	6.1^{NS}	2.2**	4.6*	197.8^{NS}	2.6**	21.5**	0.3**	23.3^{NS}
F_1/E/WR	70	115.9^{NS}	68.4**	9.0^{NS}	6.6^{NS}	0.8^{NS}	4.9**	174.5^{NS}	9.9**	57.5**	0.2**	36.5**
Columns/Rep	2	88.0^{NS}	23.4^{NS}	8.7^{NS}	10.3^{NS}	3.8*	4.2^{NS}	123.3^{NS}	1.9^{NS}	17.2^{NS}	0.0^{NS}	7.8^{NS}
Rows	28	111.1^{NS}	26.5^{NS}	5.9^{NS}	4.1^{NS}	1.4^{NS}	2.8^{NS}	137.3^{NS}	1.1^{NS}	69.0**	0.1^{NS}	24.9^{NS}
Replications/E	1	742.9**	82.5^{NS}	103.3**	49.0**	0.1^{NS}	13.8*	544.1^{NS}	32.0**	4.2^{NS}	0.2^{NS}	99.8*
Replications/WR	1	287.3^{NS}	52.6^{NS}	1.8^{NS}	1.1^{NS}	0.1^{NS}	0.4^{NS}	616.0^{NS}	31.6**	7.6^{NS}	0.1^{NS}	0.3^{NS}
Parents	16	1192.0**	512**	67.1**	39.1**	5.7**	11.5**	516.4**	6.0**	125.2**	0.9**	147.2**
GCA_L	6	5070.5**	3301.1**	363.3**	283.5**	33.3**	55.2**	2332.8**	24.5**	513.2**	3.7**	779.5**
GCA_T	9	1455.1**	325.9**	33.1**	25.6**	11.0**	8.4*	376.9**	4.5**	51.8**	0.7**	76.2**
$SCA_{L\times T}$	54	497.9**	267.1**	21.4**	16.3**	8.3**	8.3**	269.4**	6.0**	57.8**	0.4**	115.3**
GCA_L × WR	6	485.2**	76.5**	14.9^{NS}	14.3*	3.6*	3.7^{NS}	205.1^{NS}	2.7^{NS}	22.6*	0.6**	28.1^{NS}
GCA_L × E	6	492.8**	878.8**	6.1^{NS}	7.3^{NS}	2.3^{NS}	3.7^{NS}	720.6**	9.4**	79.6**	0.4**	239.2**
GCA_T × E	9	309.6**	96.5**	13.7*	10.3^{NS}	1.0^{NS}	5.4^{NS}	190.3^{NS}	5.1**	58.7**	0.4**	56.2**
GCA_T × WR	9	108.5^{NS}	20.8^{NS}	8.6^{NS}	5.8^{NS}	2.4^{NS}	2.4^{NS}	188.3^{NS}	3.8*	24.4**	0.2**	47.2**
$SCA_{L\times T}$ × WR	54	147.8**	34.1^{NS}	9.2^{NS}	5.6^{NS}	1.7^{NS}	5.2**	192.5^{NS}	2.9**	24.9**	0.2**	23.6^{NS}
$SCA_{L\times T}$ × E	54	470.8**	221.2**	12.0^{NS}	7.4^{NS}	2.3**	6.4**	250.8*	4.4**	35.8**	0.3**	93.3**
$SCA_{L\times T}$ × WR x E	70	115.9^{NS}	68.4**	9.0^{NS}	6.6^{NS}	0.8^{NS}	4.9**	174.5^{NS}	9.9**	57.5**	0.2**	36.5**
Residuals	229	93.2	25.4	7.1	5.5	1.4	3.2	166.6	1.6	8.1	0.1	19
Genetic parameters												
δ^2_A		85.11	36.29	4.56	3.34	0.42	0.76	25.7	0.26	5.97	0.04	7.3
δ^2_D		0.72	10.03	1.15	1.24	0.64	0.2	0.06	1.08	6.83	0.01	4.36
Baker's ratio		0.99	0.78	0.80	0.73	0.40	0.79	0.99	0.21	0.47	0.77	0.63
Broad-sense heritability		0.43	0.44	0.55	0.57	0.47	0.29	0.19	0.27	0.4	0.38	0.31

Note: * and **= significant at p<0.05 and 0.001, respectively, df= degree of freedom, plant height, cm (PTH), days to flowering (DTF), ear length, cm (EL), length of the longest finger, cm (FL), number of productive basal tillers per main plant (NT), the number of fingers on the main ear (NF), days to maturity (DTM), grain yield, t/ha (GY), harvest index (%) (HI), thousand seed weight (g) (TSW), and chlorophyll content at maturity (SPADM, chlorophyll content), δ^2_A and δ^2_D are variances due to additive and dominance genetic effects, respectively.

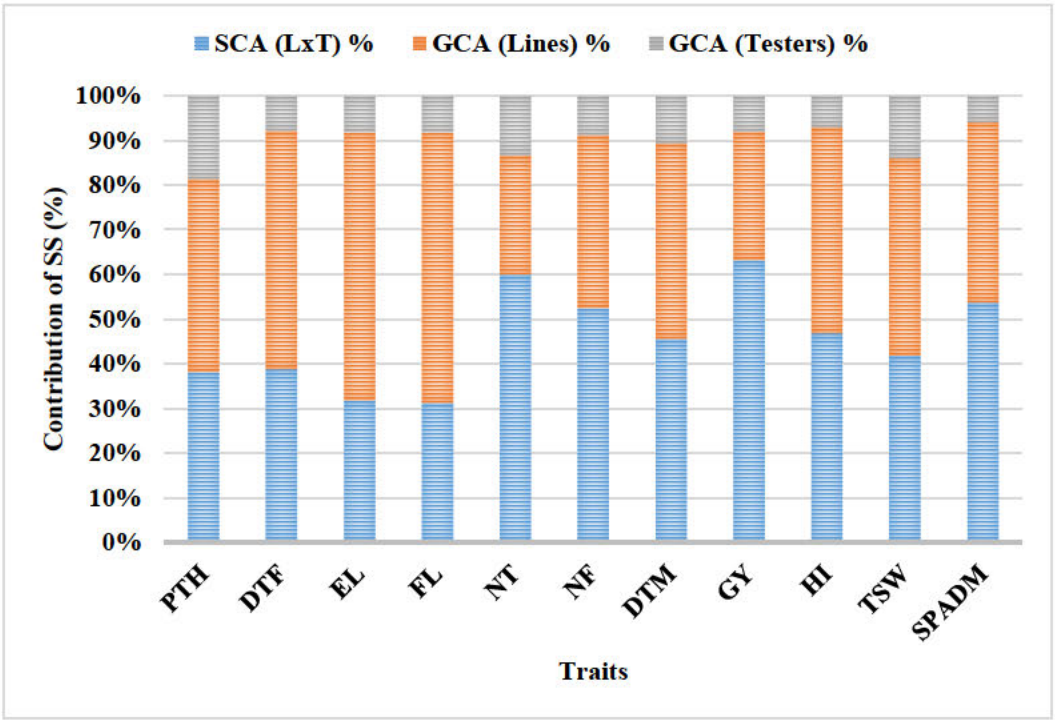


Figure 5.1. Relative contribution of the sum squares % (SS) for general combing ability (GCA) (lines or testers) and specific combining ability (SCA) (lines × testers) to the total sum of squares for plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm, FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and chlorophyll content at maturity (SPADM).

5.3.2 Performance of genotypes for agronomic and physiological traits

The performance of finger millet parental lines and testers revealed considerable variation for assessed agronomic and physiological traits under NST and ST conditions across glasshouse and field environments (Tables 5.4 and 5.5, and Appendix Tables 5.4 and 5.5). Under ST conditions, PTH varied from 88.0 cm for genotype Bako-09 to 127.0 cm for 227974, whereas it varied from 88.0 cm for cross Addis-01/Bako-09 to 140.3 cm for 227974/Meba. Under ST conditions, EL for AxumColl21 attained a maximum value of 14.5 cm and Addis-01, a minimum of 6.8 cm. Additionally, EL varied from 6.3 for cross 235700/Mereb-1 to 14.3 cm for 227974/213835. FL reached a maximum of 12.3 cm for Necho and AxumColl21, and 13.0 cm for cross 235700/Bako-09 under ST conditions. Among parents, NT ranged from 0.5 for 238335 to 3.0 for 234187, and from 0.3 for Tessema/Meba to 4.8 for 235700/Mereb-1. The NF was the highest at 10.5 for AxumColl21 and 10.3 for 235700, whereas the lowest value of 6.8 was recorded for Wama and Gute. Cross 227974/Kako-1 produced the highest number of fingers per plant at 14, followed by Necho/213835 at 12.5 and 227974/213835 at 12.3, whereas Wama/213835 recorded a mean of

7.3 fingers. DTF varied from 67.8 days for parent Mereb-1 to 100.5 days for 213835. DTF ranged from 59.8 days for cross 235700/24394 to 102.3 days for Wama/213835. The mean DTM was 125.8 days for parent 215982 and 129.5 days for cross Wama/AxumColl21, while early maturity was observed at 97.8 and 89.8 days for Mereb-1 and 235700/24394, respectively.

Drought stress caused a pronounced loss in grain yield, with parents yielding a mean of 4.8 t/ha under NST to 1.9 t/ha under ST conditions, corresponding to a 60% yield loss (Table 5.4). However, a few genotypes sustained relatively better performance for GY, including 235700, 234187, and Bako-09, which recorded GY of 3.5, 2.6, and 2.6 t/ha, whereas the testers AxumColl21 and Mereb-1 recorded GY of 2.1 and 2.4 t/ha, respectively. Consistent with this parental difference, several crosses also demonstrated superior performance under the ST conditions. For instance, GY among the top 15 crosses varied from 2.7 t/ha in several cross combinations (e.g., Tessema/AxumColl21, 234187/Kako-1, 234187/Gute, and 235700/Mereb-1) to 4.0 t/ha for 235700/238335. Other outstanding crosses with high GY were identified, namely: G38 (235700/213835, 3.4 t/ha), G23 (227974/Bako-09, 3.4 t/ha), G48 (Addis-01/213835, 3.2 t/ha), and G43 (235700/Bako-09, 3.1 t/ha). Overall, crosses recorded an average GY varying from 4.7 t/ha (NST) to 1.8 t/ha (ST), corresponding to a 62% yield loss. Contrastingly, a 51% mean GY loss was recorded for the top 15 crosses under stressed conditions compared with non-stressed conditions. The bottom five crosses showed GY values between 0.7 t/ha for Necho/215982 and 1.1 t/ha for Tessema/213835 (Table 5.5), with the bottom five crosses showing a marked decrease in productivity, at 71% yield loss with respect to their equivalent performance under NST conditions.

Under the ST conditions, harvest index showed a wide range of variation among parental genotypes, ranging from 1.6% for Necho to 23.4% for Wama, while the crosses varied from 0.5% for Necho/AxumColl21 to 18.9% for 235700/215982. Thousand seed weight among parents varied from 0.8g for 227974 to 1.9 g for 235700, accounting for an average reduction of 39% compared to the NST conditions. Likewise, crosses exhibited a TSW ranging from 0.6 for Necho/Bako-09 to 2.3 g for Tessema/215982, with an overall decline of 36% under ST. Seven crosses maintained relatively higher seed mass, recording TSW of ≥ 2.0 g. Chlorophyll content at maturity varied from 18.9 for Addis-01 to 32.6 for Mereb-1, with Bako-09 also maintaining a relatively high value of 30.4, whereas among the crosses, the lowest chlorophyll content at maturity was observed for Addis-01/215982 (16.9) and the highest 40.7 for 235700/Mereb-1.

Under NST conditions, the tallest plants were recorded for Tessema at 141.0 cm, followed by 227974 at 138.0 cm and Necho (i.e., 137.8 cm), whereas the shortest plant stature was recorded for 235700 at 94.0 cm. For crosses, PTH varied from 84.0 cm for 235700/215982 to 152.0 cm for Wama/238335. EL was highest in parent AxumColl21 (18.0 cm) and Necho (16.3 cm), and cross 227974/Gute at 16.9 cm, and shortest for parent 235700 at 5.5 cm and cross 235700/Mereb-1 at 5.0 cm. FL reached 12.5 cm in AxumColl21, 12.3 cm in Necho, and 11.8 cm in 215982 compared with the shortest FL of 4.6 cm recorded for 235700. Among crosses, 227974/Gute recorded FL of 14.5 cm, whereas 235700/Mereb-1 recorded the shortest FL at 4.8 cm. NT was noticeably higher at 6.8 in parents 234187 and 235700, and 10.8 in cross 235700/Mereb-1, compared with the lowest NT values of 2.8 in 24394, and 2.3 in Tessema/215982. NF of parents was highest at 12.3 for Necho and 11.0 for 227974, whereas the lowest value of 6.3 was recorded for Wama and Gute. Likewise, crosses 235700 produced 13.3 fingers and 235700/Mereb-1 13.0, while Wama/Kako-1 had only 6.0 fingers.

DTF for parents varied from 74.5 days in Mereb-1 to 104.8 days in Necho under NST conditions. Regarding crosses, 235700/24394 was early flowering at 65.5 days; Wama/24394 was late flowering at in 103.3 days. For parents, DTM varied from 104.5 days in Mereb-1 to 159.5 days in Necho. Late maturity was recorded in cross Addis-01/Gute at 147.5 days, whereas earliness was recorded for cross 235700/215982 at 105.3 days. GY varied from 1.8 t/ha in parent 213835 to 7.0 t/ha in 238335. Among crosses, the highest GY was recorded for Necho/Gute at 7.3 t/ha, whereas the lowest value was recorded for Necho/213835 at 1.3 t/ha. For HI, values varying from 6.6% (i.e., 213835) to 18.6% (i.e., 235700) were observed. Tremendous variation for HI was observed among crosses, with the highest value recorded for 235700/213835 at 23.5% and the lowest value for Necho/213835 at 4.4%. The highest TSW was recorded in Wama at 3.2 g followed by Tessema (3.0 g), Kako-1 and 24394 (i.e., 2.7 g), while the smallest value was recorded for 227974 and Gute, both at 1.6 g. For crosses, TSW varied from 1.6 g in Necho/238335 and Addis-01/24394 to 3.1 g in Tessema/Mereb-1. Under NST conditions, considerable variability was observed among genotypes for chlorophyll content, varying from 23.8 in parents Addis-01 to 40.6 in 234187, with the top performing 15 crosses consistently recording higher values (36.5-46.2) compared with the lowest yielding groups (22.9-27.8).

Table 5.4. Mean performance of 7 lines and 10 testers for agronomic and physiological traits under stress and non-stress growing conditions across glasshouse and field environments.

Stress condition	Traits	Lines							Testers										Mean	LSD (0.05)
		G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13	G14	G15	G16	G17		
ST	PTH	127.0	114.5	98.3	105.0	121.3	122.0	118.5	118.5	109.0	124.3	103.3	114.8	83.8	113.5	101.8	97.8	112.8	110.9	12.4
NST		138.0	118.8	94.0	105.3	137.8	141.0	118.8	126.5	127.8	134.3	116.0	134.3	98.8	120.0	109.0	116.5	108.3	120.3	10.0
ST	DTF	88.8	86.5	75.8	91.0	94.5	92.5	98.5	81.0	100.5	97.3	94.5	89.0	86.0	96.5	87.3	94.5	67.8	89.5	5.3
NST		94.0	95.0	78.8	90.5	104.8	92.8	94.3	81.3	94.3	101.0	96.5	84.5	88.3	101.3	87.8	93.3	74.5	91.3	7.5
ST	EL	12.8	11.9	8.5	6.8	13.0	10.5	9.9	7.5	7.5	11.3	6.8	14.5	8.0	9.5	8.0	6.9	8.6	9.5	3.5
NST		14.1	14.0	5.5	7.5	16.3	10.3	11.8	7.8	10.8	14.1	7.4	18.0	10.3	10.5	9.3	8.0	7.4	10.8	3.4
ST	FL	10.8	10.0	7.4	6.3	12.3	8.3	8.0	7.8	6.6	10.3	5.5	12.3	7.6	8.0	6.5	6.1	8.0	8.3	3.5
NST		10.9	11.3	4.6	5.5	12.3	8.8	9.5	6.0	8.8	11.8	6.0	12.5	9.3	8.5	7.5	6.3	6.8	8.6	2.5
ST	NT	1.5	3.0	2.5	1.5	1.5	1.5	1.0	0.8	1.0	1.3	0.5	1.8	1.0	1.3	2.0	1.8	1.8	1.5	1.1
NST		4.0	6.8	6.8	3.0	3.3	4.8	4.0	2.8	4.0	3.5	3.5	3.5	3.8	3.3	4.8	3.3	4.5	4.1	1.5
ST	NF	9.3	8.8	10.3	7.8	7.8	8.0	6.8	7.0	7.3	9.5	9.0	10.5	8.3	6.8	7.3	8.0	8.8	8.3	NS
NST		11.0	10.0	9.0	8.8	12.3	9.3	6.3	7.3	8.3	10.5	8.8	9.5	9.5	6.3	9.0	7.3	8.0	8.9	2.6
ST	DTM	117.3	114.8	105.8	119.5	120.8	121.5	122.5	111.0	123.5	125.8	123.0	117.5	114.5	118.5	115.8	123.0	97.8	117.2	7.6
NST		132.3	136.3	136.0	129.5	159.5	122.8	124.3	124.5	124.3	138.5	126.5	141.5	128.0	131.3	129.5	143.8	104.5	131.3	17.0
ST	GY	1.8	2.6	3.5	1.9	0.4	2.6	2.1	2.9	0.8	1.2	1.7	2.1	2.6	0.8	0.9	1.9	2.4	1.9	0.6
NST		4.3	4.4	5.9	6.2	3.4	4.3	5.5	4.4	1.8	5.3	7.0	6.1	4.9	6.1	4.0	3.8	3.2	4.8	2.4
ST	HI	6.8	11.1	17.2	8.9	1.6	10.3	23.4	12.8	3.1	4.2	6.8	9.4	13.8	2.7	3.3	7.0	10.1	9.0	3.6
NST		11.5	14.8	18.6	14.8	9.8	11.4	15.9	13.8	6.6	12.1	17.8	15.8	16.9	13.6	12.5	12.7	11.2	13.5	5.0
ST	TSW	0.8	1.5	1.9	1.5	1.5	1.4	1.7	1.7	0.9	1.4	1.2	1.7	1.5	1.1	1.1	0.9	1.7	1.4	0.3
NST		1.6	2.1	2.2	2.1	2.1	3.0	3.2	2.7	1.7	1.8	2.6	2.4	2.5	1.6	2.7	2.5	1.8	2.3	0.4
ST	SPADM	24.2	27.3	29.3	18.9	21.0	20.3	22.2	29.7	23.5	19.2	22.1	24.8	30.4	22.7	22.6	22.7	32.6	24.3	6.1
NST		27.8	40.6	39.4	23.8	28.8	27.8	30.3	36.5	31.6	31.9	34.4	37.6	39.9	28.5	29.4	31.8	36.2	32.7	8.4

Note: ST: stress, and NST: non stress growing conditions, LSD (0.05): least significance difference at 5%; NS: non-significant, G1: 227974, G2: 234187, G3: 235700, G4: Addis-01, G5: Necho, G6: Tessema, G7: Wama, G8: 24394, G9: 213835, G10: 215982, G11: 238335, G12: AxumColl21, G13: Bako-09, G14: Gute, G15: Kako-1, G16: Meba, and G17: Mereb-1; plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm,FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity).

Table 5.5. Agronomic and physiological trait performance for the top 15 and bottom five finger millet crosses ranked according to their grain yield (t/ha) under stress growing conditions across glasshouse and field environments.

Stress condition	Traits	Top fifteen															Bottom five					Mean*	LSD* (0.05)
		G40	G38	G23	G48	G43	G44	G83	G27	G56	G39	G57	G72	G35	G34	G47	G68	G75	G76	G78	G59		
ST	PTH	106.5	116.8	108.8	110.8	123.3	111.5	111.5	106.0	102.5	107.3	105.3	107.3	122.5	124.5	101.8	114.5	116.8	107.0	106.0	107.5	112.5	18.29
NST		95.8	123.5	111.8	105.0	124.3	129.0	129.0	121.3	116.5	124.5	99.8	120.3	122.0	132.0	108.5	121.0	135.8	112.3	116.0	114.5	121.3	19.1
ST	DTF	84.8	80.3	79.8	70.5	80.5	75.3	92.0	82.8	86.8	83.0	79.5	83.5	83.8	92.0	81.3	95.5	84.3	94.5	92.8	92.8	90.0	30.81
NST		77.3	82.3	80.0	75.5	79.3	76.0	93.3	83.3	92.0	81.3	82.3	86.5	82.8	80.3	80.5	97.0	71.3	91.3	88.5	94.0	90.8	33.5
ST	EL	10.3	10.1	8.8	13.0	14.9	7.6	10.8	11.8	11.0	8.4	8.1	7.8	9.3	11.4	7.6	8.9	11.5	9.8	7.9	12.3	10.1	3.86
NST		6.8	9.4	7.5	11.0	13.3	9.8	11.8	12.8	10.0	10.8	7.0	9.5	9.8	12.0	7.8	11.3	12.1	10.8	10.5	12.8	10.8	4.0
ST	FL	9.1	8.5	7.1	12.0	13.0	6.6	9.1	10.8	9.4	7.0	6.5	6.8	10.0	9.0	4.8	8.3	10.9	7.5	7.5	10.3	8.6	3.5
NST		5.3	8.6	6.3	8.5	10.5	8.0	8.5	10.3	9.0	8.8	5.5	9.3	8.8	10.5	6.5	10.0	11.1	10.3	9.5	10.5	9.1	3.3
ST	NT	2.0	1.5	1.8	1.8	2.3	1.0	1.5	1.8	2.3	1.3	1.5	2.8	2.0	1.5	1.5	1.8	1.8	2.0	2.3	2.3	1.9	1.23
NST		4.0	5.5	3.8	3.5	4.8	3.8	4.8	4.0	5.0	5.5	6.5	5.5	5.0	4.0	5.0	5.0	5.3	4.8	4.5	3.8	4.6	1.9
ST	NF	11.5	9.3	9.5	8.5	10.0	7.8	9.3	8.5	10.3	9.0	9.8	10.8	9.0	7.5	8.3	7.8	11.5	11.3	8.0	10.5	9.2	2.64
NST		7.8	10.3	8.8	8.8	11.0	8.3	10.3	9.8	11.5	9.3	11.3	11.3	9.5	7.0	10.0	7.8	9.5	9.3	12.3	13.8	9.4	3.0
ST	DTM	110.0	105.8	109.0	100.5	109.0	105.3	119.0	112.0	108.5	109.8	109.5	113.3	110.3	121.8	110.5	121.3	112.8	117.8	123.5	114.8	116.9	26.89
NST		129.0	134.8	148.0	123.8	130.5	118.3	131.8	123.0	131.8	118.3	121.5	133.5	112.8	110.3	144.3	128.8	101.3	131.8	128.5	143.8	130.4	30.89
ST	GY	4.0	3.4	3.4	3.2	3.1	3.1	3.0	3.0	2.9	2.8	2.7	2.7	2.7	2.7	2.7	1.1	1.0	0.8	0.7	0.7	1.8	1.79
NST		6.5	6.2	6.8	5.5	5.6	7.0	6.9	6.4	4.9	5.2	5.3	5.5	5.3	6.6	7.2	5.9	2.6	3.0	4.6	1.7	4.7	5.01
ST	HI	13.6	13.8	15.1	14.4	13.1	14.2	12.3	14.3	13.0	12.3	11.5	12.5	12.7	17.8	11.8	4.6	5.2	2.5	3.8	3.5	8.2	8.22
NST		19.2	18.8	17.8	18.0	23.5	20.7	16.3	17.7	11.0	17.2	15.5	16.3	13.8	18.1	19.0	16.2	7.1	7.8	12.4	5.6	13.5	13.15
ST	TSW	1.5	1.4	1.6	1.6	1.4	1.6	1.4	1.1	1.2	1.8	1.5	1.8	1.3	1.7	1.4	1.3	1.5	1.6	1.5	1.6	1.4	0.36
NST		2.2	2.3	2.1	1.9	2.4	2.1	2.2	2.2	1.8	2.4	2.3	2.8	2.1	2.5	2.1	2.4	2.0	2.2	2.3	1.7	2.2	0.6
ST	SPADM	24.9	20.1	19.8	27.0	25.0	22.9	27.0	23.4	23.6	25.2	26.6	24.3	24.0	23.5	26.4	25.1	21.0	24.6	27.6	21.2	24.7	8.69
NST		30.9	27.4	30.1	34.4	30.9	29.0	31.0	28.3	31.7	35.1	40.2	38.7	32.6	28.2	33.6	32.9	27.7	31.1	32.8	27.0	32.7	12.52

Note: *=the statistics for the whole crosses, ST: stress, and NST: non stress growing conditions; LSD(0.05): least significance difference at 5%; plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm,FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity). G40: 235700/238335, G38: 235700/213835, G23: 227974/Bako-09, G48: Addis-01/213835, G43: 235700/Bako-09, G44: 235700/Gute, G83: Wama/Bako-09, G27: 227974/Mereb-1, G56: Addis-01/Meba, G39: 235700/215982, G57: Addis-01/Mereb-1, G72: Tessema/AxumColl21, G35: 234187/Kako-1, G34: 234187/Gute, G47: 235700/Mereb-1, G68: Tessema/213835, G75: Tessema/Kako-1, G76: Tessema/Meba, G78: Wama/213835, and G59: Necho/215982

5.3.3 General combining ability effects of parents

The general combining ability (GCA) effects of the 17 finger millet parents for agronomic and physiological traits under drought-stress (ST) and non-stress (NST) conditions across greenhouse and field environments are presented in Table 5.6. Under ST conditions, the GCA effects of parents for PTH ranged from -10.79 for Addis-01 to 7.19 for 227974. Under the NST conditions, GCA values for PTH varied from -11.16 for Addis-01 to 10.88 for Wama. Under the ST conditions, significant and desirable positive GCA effects for EL were recorded for parent 227974 (2.17) and 234187 (1.72). Positive significant GCA effects for EL varying from 1.77 in 234187 to 3.01 were noted for 227974, under the NST conditions. For FL, positive desirable GCA effects were recorded for 227974 at 2.17 and for 234187 at 1.71 under ST conditions. Likewise, 227974 exhibited a desirable GCA effect of 3.01, followed by 234187 at 1.81 under NST conditions for the same trait. For the NT, 235700 recorded a positive and desirable GCA effect of 1.0 under NST conditions. Under the ST conditions, GCA effects for the NF varied from -0.67 for Addis-01 to 0.9 for 227974. Under NST conditions, the range for GCA effects for NF varied from -0.86 for Addis-01 to 0.97 for 235700.

For DTF, parent 235700 recorded a high and negative GCA effect of -11.91 under ST conditions, in a desirable direction. Under the NST conditions, 235700 recorded a desirable and strong negative GCA of -17.23 for DTF, followed by 234187 with a negative GCA of -0.78. For DTM, parent 235700 recorded a negative and high GCA of -7.99, in a desirable direction, while Wama recorded a positive GCA of 4.24 under ST conditions. For the same trait under the NST conditions, desirable negative GCA was recorded for 235700 (-16.34, $p<0.05$), whereas Necho recorded a high and positive GCA effect of 8.5 ($p<0.05$).

The GCA estimate for GY, HI and TSW in the assessed finger millet parents under ST and NST conditions showed contrasting effects. Under the ST conditions, line 235700 recorded highly significant and positive GCA effects for GY (1.33, $p<0.001$), HI (5.74, $p<0.001$), and TSW (0.31, $p<0.05$). Parent 234187 also recorded desirable GCA for GY at 0.12, HI (1.80), whereas Addis-01 displayed a favourable effect for HI (0.72). Likewise, Tessema and Wama displayed positive effects of 0.17 and 0.11 for TSW under the ST condition, respectively. Under NST conditions, positive GCA effects were recorded for 235700 for GY at 0.22, HI (2.04) and TSW (0.09), whereas Tessema recorded a positive and desirable GCA effect for TSW (0.52, $p<0.001$). Similarly, 234187 displayed desirable GCA effect for GY (0.17) and HI (1.55), and Addis-01 recorded GCA of 1.31 for HI. Under ST conditions, the GCA effect of parents for chlorophyll

content varied from -4.70 for 235700 to 27.70 for Necho. The parents Wama, Mereb-1, and 234187 displayed substantial positive GCA values of 2.54, 1.37, and 1.30 for chlorophyll content under ST conditions, respectively. Under the NST conditions, 234187 recorded a GCA value of 2.61, and Wama with a GCA value of 1.49 for chlorophyll content.

Table 5.6. General combining ability effects for agronomic and physiological traits of 7 lines and 10 testers of finger millets under stressed (ST) and non-stressed (NST) conditions across glasshouse and field environments.

ENV	Parents	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
	Lines											
NST	227974	7.59	0.36	3.01**	2.84**	-0.06	0.83	0.41	-0.12	-0.59	-0.29	-1.62
ST		7.19	0.57	2.17**	1.28*	0.36	0.90*	0.37	-0.27	-1.32	-0.21	0.91
NST	234187	-3.15	-0.78	1.77*	1.81*	0.69	-0.24	0.01	0.17	1.55	-0.04	2.61*
ST		-2.59	0.41	1.72*	1.71*	0.29	-0.10	-2.70	0.21	1.80	0	1.30
NST	235700	-11.12*	-17.23**	-2.12*	-1.88*	1.00*	0.97*	-16.34*	0.22	2.04	0.09	0.91
ST		-5.19	-11.91**	-1.34	-1.23	0.29	0.53	-7.99**	1.33**	5.74**	0.31*	6.30*
NST	Addis-01	-11.16*	3.97	-2.99**	-2.77**	-0.16	-0.86	1.87	0.03	1.31	-0.21	-1.33
ST		-10.79*	2.17	-2.17**	-2.05**	0.01	-0.67	0.9	-0.01	0.72	-0.14	-3.01
NST	Necho	-0.22	8.99*	1.89*	1.25	-0.52	0.55	8.57*	-0.38	-3.38*	-0.19	-1.66
ST		0.09	3.39	0.78	1.76*	-0.20	-0.03	2.86	-0.96*	-4.64*	-0.24*	-4.70*
NST	Tessema	7.18	5.86	-0.69	-0.38	-0.73	-0.42	4.49	0.11	-0.69	0.52**	-0.40
ST		6.10	3.43	-1.11	-0.96	-0.63*	-0.23	2.32	-0.12	-1.36	0.17	-3.34
NST	Wama	10.88*	-1.18	-0.87	-0.88	-0.22	-0.82	0.99	-0.03	-0.23	0.12	1.49
ST		5.20	1.94	-0.06	-0.51	-0.13	-0.40	4.24*	-0.19	-0.94	0.11	2.54
NST	SE_L	3.11	3.13	0.71	0.58	0.38	0.38	2.79	0.32	1.06	0.14	1.08
ST		2.93	2.92	0.58	0.6	0.22	0.33	2.08	0.25	1.18	0.09	1.64
	Testers											
NST	24394	3.01	0.04	0.25	0.23	0.04	-0.26	0.18	0.14	0.30	-0.01	0.46
ST		2.10	-0.29	0.36	0.18	-0.24	-0.06	-1.15	-0.02	-0.07	-0.02	0.05
NST	213835	-2.12	0.05	-0.12	-0.03	-0.25	-0.07	-0.18	0.02	0.11	0	-0.13
ST		-2.71	0.51	0.05	0.09	-0.16	0.09	1.32	-0.03	0.10	0.06	-0.44
NST	215982	-4.90	0	0	-0.08	-0.29	0.19	-0.22	-0.06	0.11	0.02	-0.10
ST		-0.05	0.16	-0.31	-0.16	-0.08	-0.04	0.73	0.04	0.32	0.05	-0.78
NST	238335	1.42	-0.08	0	0.05	-0.06	-0.05	-0.17	-0.01	-0.16	-0.02	0.20
ST		1.51	-0.75	0.29	0.15	-0.33	-0.05	-0.86	0.01	-0.19	-0.08	-0.46
NST	AxumColl21	3.28	-0.03	0.33	0.29	0.17	0.06	0.39	-0.19	-0.56	0.01	0.59
ST		1.08	-0.01	0.32	0.26	0.08	0.03	1.30	-0.13	-1.23	0.06	-0.56
NST	Bako-09	-8.16*	-0.12	-0.17	-0.25	0.03	0.13	-0.10	-0.11	-0.05	-0.03	0.87
ST		-7.36	-0.77	-0.23	-0.16	-0.16	0.05	-2.32	0.12	1.60	-0.08	0.97
NST	Gute	4.28	-0.05	0	0.08	0.13	-0.36	-0.12	0.22	0.47	-0.01	-0.51
ST		6.01	-0.03	0.16	-0.02	-0.08	-0.05	-0.03	-0.03	-0.58	0.08	0.15
NST	Kako-1	2.13	0.04	-0.05	0	-0.18	0.04	0.46	-0.07	-0.43	0.08	-0.40
ST		-0.29	0.25	-0.18	-0.20	0.16	0.03	-0.67	-0.01	-0.36	0.06	-0.09
NST	Meba	0.03	0.02	-0.05	-0.07	0.13	-0.22	-0.18	0	0.03	-0.05	-0.11
ST		-1.15	0.06	-0.24	-0.03	0.08	0	-0.81	0.02	0.12	-0.09	-0.21
NST	Mereb-1	1.05	0.14	-0.20	-0.22	0.29	-0.11	-0.06	0.05	0.18	0	0.42
ST		0.85	0.88	-0.22	-0.10	0.08	0	2.48	0.04	0.30	-0.04	1.37
NST	SE_T	3.06	0	0.39	0.36	0.29	0	1.18	0	0	0.07	0.01
ST		2.18	1.02	0.58	0.60	0.06	0.15	1.60	0.16	1.07	0.08	1.17

Note: ENV: growing conditions, ST: stress, and NST: non stress growing conditions, * and ** denotes significant at 5 and 1% level of significance, respectively. SE_L and SE_T are standard error of lines and testers, respectively, plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm, FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity).

5.3.4 Specific combining ability effects of the crosses

Specific combining ability effects for the assessed crosses and traits under ST and NST conditions in the greenhouse and field environments are presented in Table 5.7. For PTH, crosses 235700/Merab-1 and 235700/Kako-1 recorded SCA effects of -0.7 and -0.9, respectively, in the desiarble direction. Under NST conditions, desirable SCA values were recorded for PTH for Necho/Bako-09 (-1.0) and Tessema/213835 (0.6). The SCA effects of EL was higher (2.3) for 235700/24394, in a desirable trend under ST condition. Under the NST condition, the SCA effects for EL were positive for Tessema/24394 (5.5), Necho/Kako-1 (4.7), Wama/215982 (4.1), and 227974/Gute (3.9). Cross 235700/24394 also recorded positive and significant ($p<0.001$) SCA effect for FL (2.3), under ST condition, whereas under the NST condition, significant ($p<0.05$) SCA effects were recorded for crosses 235700/24394 (2.3), 234187/AxumColl21 (1.0), and Wama/Gute (1.2). For the NTs, the following crosses exhibited positive and significant SCA effects under the ST condition: Necho/Mereb-1 (1.9), 235700/Mereb-1 (1.6), 227974/Mereb-1 (1.2), and 234187/Bako-09 (1.4). For the same trait under the NST conditions, highly significant and positive SCA values were recorded for 235700/Mereb-1 (3.6), 234187/Bako-09 (2.2), Addis-01/24394 (1.8), 235700/Meba (1.7), and 227974/Gute (1.7). The SCA effects for NF were positive for 227974/Kako-1 (2.5), Wama/AxumColl21 (2.5), Necho/Meba (1.7), and 227974/213835(1.9) under ST conditions, making them ideal crosses. Under the NST conditions, crosses Necho/24394 and Tessema/AxumColl21 recorded positive SCA values of 3.1 and 2.4 for NF.

Highly significant and negative SCA effects were noted for DTF, in several crosses including 235700/24394 (-29.1), Wama/Gute (-23.3), Tessema/AxumColl21 (-22.1), 227974/215982 (-20.1), Addis-01/Bako-09 (-19.9), 227974/Bako-09 (-18.6), Necho/213835 (-15.1), Necho/AxumColl21 (-13.2), Wama/238335 (-13.1), Necho/213835 (-9.5), and 227974/215982 (-9.1) under the ST conditions. Under the NST conditions, several crosses recorded higher SCA and negative effects including 235700/24394 (-32.2), 227974/Bako-09 (-21.1), Tessema/AxumColl21 (-21.1), Addis-01/Bako-09 (-19.4), Wama/Gute (-19.2), 227974/215982 (-16.5); all at $p<0.001$, and Wama/238335 (-10.4), 235700/Bako-09 (-9.4), and Necho/Kako-1 (-8.2) for DTF. Some crosses recorded significant and negative SCA effects for DTM, including 235700/24394 (-16.8, $p<0.001$), Necho/213835 (-9.5; $p<0.05$), and 227974/215982 (-9.1; $p<0.05$) under the ST conditions. Additionally, highly significant and negative SCA values were noted for DTM in crosses 235700/24394 (-19.4; $p <0.001$), Addis-01/Bako-09 (-16.2; $p <0.001$), 227974/215982 (-15.5; $p <0.001$) and and Wama/Gute (-9.5, $p<0.05$) under NST condition.

The SCA effects for GY and related traits varied considerably among crosses under ST and NST conditions. Under the ST conditions, positive and desirable SCA effects for grain yield were recorded in several crosses. The following crosses were selected for displaying high and significant SCA effect for GY: Wama/215982 (1.4), Tessema/238335 (1.3), 235700/213835 (1.1), Addis-01/213835 (0.9), Tessema/AxumColl21 (0.9), Wama/Gute (0.9), 235700/215982 (0.8), Wama/Bako-09 (0.8), Necho/Gute (0.8), 234187/AxumColl21 (0.7), 234187/Mereb-1 (0.7), and 235700/24394 (0.7). Under the NST conditions, a highly significant ($p<0.001$) and desirable SCA effects for GY were also recorded for the following crosses: Wama/Kako-1 (2.4), Wama/238335 (2.3), 234187/24394 (2.3), Wama/215982 (2.1), Wama/Gute (2.0), Addis-01/Meba (2.0), 234187/AxumColl21 (1.7), 235700/213835 (1.5), Necho/Bako-09 (1.4), Tessema/238335 (1.4), and Necho/Gute (1.3). Positive and significant SCA effects ($p<0.001$) were recorded for HI for the following crosses: 235700/213835 (9.5), Tessema/238335 (8.1), 235700/215982 (7.9), Addis-01/213835 (5.7), 234187/AxumColl21 (4.0), Addis-01/Gute (4.0), Necho/Bako-09 (3.8) and Addis-01/AxumColl21 (3.6) under the ST conditions.

Under NST the conditions, desirable SCA values for HI were registered for 235700/213835 (7.2), 234187/24394 (6.7), Tessema/Gute (6.1), 234187/AxumColl21 (5.4), Wama/Gute (5.0), Addis-01/Gute (4.8), Necho/Bako-09 (4.3), Tessema/238335 (4.3), 227974/Meba (3.5), Addis-01/Meba (3.4), and Wama/215982 (3.4) at $p<0.001$. Highly significant ($p<0.001$) and higher SCA effects were noted for TSW for Tessema/AxumColl21 (0.5), 235700/Meba (0.5) and 234187/Mereb-1 (0.4) under ST conditions. Under the NST conditions, desirable and higher SCA effects for TSW were recorded in the crosses 235700/Gute (0.6), 235700/Meba (0.6), Necho/Bako-09 (0.6), Necho/213835 (0.5), Necho/24394 (0.5) and 234187/Gute (0.5). Under the ST conditions, desirable and high SCA values were recorded for chlorophyl content at maturity (chlorophyll content) by crosses 235700/Mereb-1 (15.7, $p<0.001$), 227974/Bako-09 (12.9, $p<0.001$), Addis-01/24394 (7.4, $p<0.05$), Tessema/Kako-1 (6.3, $p<0.05$), and 235700/213835 (6.2, $p<0.05$), making them drought tolerant combinations with significant potential. Under the NST conditions, a higher SCA effect of 1.0 was recorded in the cross 227974/Bako-09 for chlorophyll content.

Table 5.7. Specific combining ability effects for agronomic and physiological traits of 70 finger millet crosses under stressed and non-stressed growing conditions in greenhouse and field environments.

ENV	Crosses	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
ST	227974/213835	2.5	3.6	0.9	0.8	-0.3	1.9*	3.1	-0.2	-1.0	0.2	1.5
NST	227974/213835	-3.2	3.5	1.9	0.8	0.0	0.7	3.3	0.0	-0.1	0.0	0.2
ST	227974/215982	0.7	-20.1**	0.0	-0.2	-0.3	-0.5	-9.1*	-0.3	-1.9	-0.1	-8.2**
NST	227974/215982	1.4	-16.5**	-1.5	-0.3	-0.5	0.3	-15.5**	-0.1	-0.2	-0.3	0.1
ST	227974/238335	-11.3	-10.9**	0.3	0.5	-0.6	-0.9	-4.6	0.0	-0.3	-0.2	3.7
NST	227974/238335	-8.5	-1.1	2.7	0.8	-1.2	0.3	-3.1	0.0	-0.3	0.0	0.1
ST	227974/24394	3.5	4.6	0.1	0.3	-0.3	-0.5	4.2	-0.2	-1.2	0.2	-1.2
NST	227974/24394	9.2	0.3	-1.4	0.4	0.5	-0.6	5.9	0.0	0.0	-0.5**	-0.2
ST	227974/AxumColl21	-1.9	7.0*	0.4	0.2	-0.3	1.6	3.7	0.1	2.0	-0.3*	-2.2
NST	227974/AxumColl21	-3.9	0.3	-0.8	-0.9	-0.3	0.1	-2.0	-0.1	-0.3	-0.1	-0.5
ST	227974/Bako-09	-4.0	-18.6**	-1.7	-1.8*	0.3	1.0	-8.2	-0.3	-0.2	0.0	12.9**
NST	227974/Bako-09	-7.3	-21.1**	-5.4**	-2.4*	0.4	-0.1	-8.4	0.0	3.3**	-0.2	1.0**
ST	227974/Gute	11.3	-1.7	0.3	0.5	-0.3	-1.2	0.0	-0.2	0.1	0.1	-2.2
NST	227974/Gute	15.2*	-3.0	3.9*	0.8	1.7*	0.5	-4.6	0.0	0.0	0.1	0.1
ST	227974/Kako-1	-11.7	10.9**	0.6	0.1	0.6	2.5**	-6.8	-0.7**	-2.5*	0.2	0.0
NST	227974/Kako-1	-24.5**	10.1*	2.9	0.7	0.0	0.7	5.9	-1.2**	-2.8*	0.3	-0.2
ST	227974/Meba	14.5*	14.8**	-0.7	-0.6	0.0	-1.8	10.7*	0.5*	2.6*	-0.3*	-1.5
NST	227974/Meba	18.1*	15.6**	1.6	0.5	-0.3	0.3	11.1*	0.0	3.5**	-0.2	-0.2
ST	227974/Mereb-1	5.9	11.4**	0.4	0.6	1.2*	0.1	11.3*	-0.4*	-1.9	-0.1	-1.4
NST	227974/Mereb-1	15.0*	12.4**	-0.1	0.2	-0.6	-0.6	7.8	0.0	-0.2	-0.2	-0.3
ST	234187/213835	-10.2	3.4	-0.3	-0.1	-0.5	-0.2	-4.0	-0.3	-1.1	0.1	-1.5
NST	234187/213835	-5.2	-0.1	0.6	0.4	-0.5	1.4	2.8	-1.1**	-3.8**	-0.2	0.0
ST	234187/215982	-0.5	-3.3	-0.2	0.0	0.1	-0.5	1.4	-0.1	0.0	0.2	2.8
NST	234187/215982	-1.1	-3.3	1.0	0.0	0.1	0.3	8.8	0.0	0.3	-0.1	0.6
ST	234187/238335	7.2	-1.9	0.3	0.2	0.4	1.0	2.2	-0.3	-1.4	0.1	-2.2
NST	234187/238335	-0.2	-3.3	-0.3	0.4	0.8	-0.1	-5.4	0.1	0.1	0.2	-0.3
ST	234187/24394	0.5	-5.3	0.1	-0.1	-0.8	0.1	0.3	0.0	1.0	-0.1	-1.3
NST	234187/24394	0.0	-4.7	-0.3	-0.2	-1.3	-0.6	2.8	2.3**	6.7**	-0.1	0.6
ST	234187/AxumColl21	0.2	-8.7*	0.1	-0.2	-0.2	-0.5	-1.7	0.7**	4.0**	-0.1	5.2
NST	234187/AxumColl21	-0.5	-3.8	3.1	1.0	0.6	0.3	-5.8	1.7**	5.4**	-0.3	-0.2
ST	234187/Bako-09	-1.8	9.7**	0.8	0.4	1.4*	1.0	-5.7	-0.3	-1.4	-0.1	-0.1
NST	234187/Bako-09	-4.4	10.7**	-0.2	-0.3	2.2**	0.3	5.8	-0.1	-0.4	-0.2	0.1
ST	234187/Gute	5.7	2.5	-0.1	0.0	0.8	-0.5	4.8	-0.5*	-2.2	0.0	0.8
NST	234187/Gute	2.7	-0.1	-0.7	-0.4	0.6	-0.8	-3.6	0.0	-0.2	0.5**	0.4
ST	234187/Kako-1	-1.8	2.5	0.0	0.2	-0.8	-0.8	4.8	-0.6**	-3.0*	-0.5**	-5.0
NST	234187/Kako-1	3.3	3.2	-1.4	-0.2	-1.5*	0.5	-0.2	0.0	-0.3	-0.1	-0.2
ST	234187/Meba	-3.1	4.9	0.0	0.2	0.8	0.7	-3.4	0.1	2.9*	-0.2	0.1
NST	234187/Meba	-1.0	3.2	-0.1	-0.2	0.8	-0.3	-0.2	0.0	0.4	-0.1	-0.3
ST	234187/Mereb-1	0.4	0.5	0.0	0.1	-0.2	0.1	3.7	0.7**	1.8	0.4**	3.1
NST	234187/Mereb-1	-7.8	-2.8	0.4	0.0	-0.2	-1.7	-5.1	0.0	-0.1	-0.4*	-0.2
ST	235700/213835	-1.5	-6.8	-0.3	-0.3	0.5	1.5	-3.8	1.1**	9.5**	0.2	6.2*
NST	235700/213835	-1.7	-4.7	-2.7	-0.8	0.2	0.9	-6.7	1.5**	7.2**	-0.2	0.5
ST	235700/215982	-11.1	-5.8	-0.8	-0.7	-1.0	0.6	-3.2	0.8**	7.9**	-0.1	1.6
NST	235700/215982	-28.8**	-3.8	-1.6	-0.3	-	-0.4	-5.9	0.0	0.0	-0.1	0.3
ST	235700/238335	-2.5	3.4	-1.0	-1.0	0.2	-1.5	2.1	0.1	-0.6	-0.1	-0.8
NST	235700/238335	0.0	-5.7	-0.9	-0.7	0.6	-0.2	2.7	0.0	-0.1	0.0	0.3
ST	235700/24394	11.2	-29.1**	2.3*	2.3**	0.2	0.9	-16.8**	0.7**	0.0	-0.3*	-7.9*
NST	235700/24394	19.4**	-32.2**	2.0	2.3*	0.2	-0.9	-19.4**	0.1	-0.3	0.0	-0.7
ST	235700/AxumColl21	-3.7	4.3	-0.7	-0.9	0.9	0.6	2.7	-0.7**	-4.4**	0.2	-6.7*
NST	235700/AxumColl21	9.3	8.3*	2.9	0.7	-0.3	1.6	3.8	-1.4	-5.2	-0.2	-0.4
ST	235700/Bako-09	1.7	-4.4	-0.5	-0.4	-1.0	-0.3	-2.4	-0.2	-1.1	0.1	4.2
NST	235700/Bako-09	-4.2	-9.4*	-0.4	-0.3	-0.7	0.3	0.5	0.0	0.3	-0.2	0.3
ST	235700/Gute	-2.5	11.6**	-0.1	0.0	-0.1	0.9	5.2	-0.2	0.0	0.2	1.0
NST	235700/Gute	-7.1	8.3*	-0.4	-0.5	-0.7	0.5	3.8	0.0	0.5	0.6**	0.4
ST	235700/Kako-1	-0.9	-3.4	0.5	0.5	0.2	-0.9	-1.8	-0.1	-1.0	0.1	-1.5

NST	235700/Kako-1	-4.0	-6.6	1.2	0.0	0.1	-0.2	-8.2	0.0	-0.3	0.0	0.0
ST	235700/Meba	3.3	-4.9	0.7	0.5	0.5	0.3	-2.7	0.0	0.8	0.5**	-2.2
NST	235700/Meba	10.4	-5.2	-0.5	-0.1	1.7*	-0.6	-7.0	0.0	0.4	0.6**	-0.2
ST	235700/Mereb-1	-0.7	12.1**	-0.5	-0.5	1.8**	0.6	4.6	-0.2	-2.2	-0.3	15.7**
NST	235700/Mereb-1	-8.0	29.2**	-2.2	-0.8	3.6**	1.1	20.7**	0.0	-0.2	-0.5**	0.1
ST	Addis-01/213835	4.5	3.4	0.4	0.4	-0.3	0.5	5.9	0.9**	5.7**	0.3	-0.1
NST	Addis-01/213835	8.6	3.0	0.7	0.1	-0.7	0.1	1.8	0.0	0.3	-0.1	-0.2
ST	Addis-01/215982	3.6	4.8	-0.3	-0.4	0.6	-1.3	-0.3	0.6**	0.7	0.1	-6.5*
NST	Addis-01/215982	-6.0	2.5	-0.7	-0.2	-0.5	-0.3	1.4	0.9*	0.1	-0.4*	-0.6
ST	Addis-01/238335	-2.8	-3.4	0.8	0.6	-0.6	1.1	2.2	0.1	0.5	-0.1	-1.2
NST	Addis-01/238335	-5.5	-0.3	-0.4	-0.3	-0.5	-0.6	-0.8	0.1	2.9*	-0.5**	0.3
ST	Addis-01/24394	-11.1	5.8	-0.4	-0.3	1.6**	-1.6	-1.7	-0.3	-1.7	-0.1	7.4*
NST	Addis-01/24394	0.6	10.0*	-0.3	-0.4	1.8*	-0.1	11.2*	-1.6**	-4.4**	-0.3	0.4
ST	Addis-01/AxumColl21	-2.2	2.9	0.3	0.1	0.0	-0.1	-0.3	0.9**	3.6**	0.1	-3.1
NST	Addis-01/AxumColl21	-4.1	4.4	2.1	0.6	0.5	-0.1	2.9	0.0	-0.1	0.3	-0.1
ST	Addis-01/Bako-09	-7.4	-19.9**	0.0	-0.1	-0.6	0.2	-5.7	-0.5*	-2.0	-0.3	-4.8
NST	Addis-01/Bako-09	-11.3	-19.4**	-0.7	0.1	0.0	1.0	-16.2**	-0.1	-0.7	0.2	-0.2
ST	Addis-01/Gute	-2.2	4.8	-0.3	-0.3	-0.6	-0.7	-2.6	0.8**	4.0**	-0.2	-4.0
NST	Addis-01/Gute	-2.5	1.6	-2.0	0.0	-0.9	-1.5	0.7	0.0	4.8**	-0.5**	0.0
ST	Addis-01/Kako-1	-1.7	5.8	-0.4	-0.3	-0.6	-1.0	-5.7	-0.4	-2.8*	0.3	-1.3
NST	Addis-01/Kako-1	-2.8	2.0	-2.0	-0.3	-0.4	-1.0	1.0	1.0*	0.0	0.4*	-0.3
ST	Addis-01/Meba	1.1	-4.4	-0.5	-0.5	1.0	-0.1	1.7	-0.5*	-2.8*	-0.3	3.4
NST	Addis-01/Meba	-0.4	-4.0	-1.3	-0.3	1.0	-0.6	-3.8	2.0**	3.4**	-0.2	0.3
ST	Addis-01/Mereb-1	3.9	5.3	-0.5	0.0	-0.6	-0.1	5.4	-0.5*	-2.2	-0.1	5.6
NST	Addis-01/Mereb-1	0.2	5.3	0.2	-0.2	-0.7	0.3	3.7	0.0	0.2	0.3	-0.1
ST	Necho/213835	-8.0	-15.1**	-0.2	-0.1	-0.3	0.4	-9.5*	-0.7**	-2.6*	0.5*	-4.3
NST	Necho/213835	0.2	5.3	-3.0	-0.3	-1.0	-1.6	7.7	-2.6**	-5.8**	0.5**	-0.4
ST	Necho/215982	0.2	11.5**	-0.7	-0.7	0.0	-0.8	6.3	-0.3	-1.1	0.3	-2.9
NST	Necho/215982	-7.6	8.5*	0.7	-0.3	0.1	1.3	5.8	-0.1	-0.6	-0.1	-0.4
ST	Necho/238335	2.8	3.3	0.9	0.7	0.0	0.1	1.2	-0.4*	-1.7	-0.4*	0.0
NST	Necho/238335	4.9	-0.8	0.2	0.3	-0.6	-0.2	-2.5	-0.1	-0.3	-0.5**	-0.1
ST	Necho/24394	-0.4	2.8	0.4	0.5	-0.3	-0.8	1.5	-0.7**	-2.6*	0.2	1.5
NST	Necho/24394	-9.0	7.6	2.2	0.4	-0.9	3.1**	2.4	-1.1*	-2.9*	0.5**	0.7
ST	Necho/AxumColl21	7.0	-13.2**	0.7	0.9	-0.3	-0.5	7.4	-0.7**	-2.6	-0.2	-4.3
NST	Necho/AxumColl21	3.0	-4.0	0.8	0.3	0.6	-0.2	7.7	-1.1*	-3.0*	0.2	-0.3
ST	Necho/Bako-09	-3.0	1.3	0.6	0.7	-0.3	-0.2	2.9	0.7**	3.8**	-0.5**	3.1
NST	Necho/Bako-09	-1.0	-3.6	-0.7	0.1	-0.3	-0.2	-4.7	1.4**	4.3**	0.6**	0.0
ST	Necho/Gute	5.0	2.8	0.5	0.2	-0.3	-0.5	3.8	0.8**	1.9	0.0	-0.8
NST	Necho/Gute	14.0*	-3.6	-2.9	-0.6	0.2	-0.9	-4.7	1.3**	3.2*	-0.3	0.0
ST	Necho/Kako-1	1.8	-0.1	-0.8	-0.8	-0.3	-0.2	-3.6	0.4*	0.4	0.1	-1.2
NST	Necho/Kako-1	11.0	-8.2*	4.7*	0.6	0.0	0.6	-8.5	-2.7**	-6.0**	-0.4*	-0.2
ST	Necho/Meba	-7.8	6.2	-0.7	-0.8	-0.3	1.7*	-8.4	-0.6**	-2.0	-0.3	1.7
NST	Necho/Meba	-11.6	8.5*	1.7	0.1	-1.2	1.1	5.8	0.0	0.2	0.4*	0.0
ST	Necho/Mereb-1	2.6	6.2	-0.1	0.1	1.9**	0.1	2.9	-0.7**	-2.1	-0.1	0.0
NST	Necho/Mereb-1	-3.9	1.6	-0.9	-0.3	1.8*	-0.5	-0.6	-1.0*	0.1	-0.1	0.2
ST	Tessema/213835	6.0	1.6	0.1	-0.2	-0.1	1.0	7.0	-0.3	-1.4	-0.5**	-5.4
NST	Tessema/213835	0.6	2.6	-0.8	0.1	-0.7	-0.5	1.0	0.0	0.0	0.2	-0.6
ST	Tessema/215982	8.2	-0.4	0.4	0.3	-0.4	-0.9	2.1	0.0	-1.1	0.1	-4.4
NST	Tessema/215982	11.4	7.3	-2.7	-0.5	-1.0	-1.2	4.7	0.1	0.2	-0.2	-0.5
ST	Tessema/238335	-0.1	2.5	0.3	0.4	-0.4	-0.6	3.8	1.3**	8.1**	-0.1	-1.2
NST	Tessema/238335	-3.5	-0.2	-1.1	0.0	0.2	-0.1	-1.3	1.4**	4.3**	-0.1	-0.2
ST	Tessema/24394	1.8	3.0	-1.0	-0.7	0.2	-1.2	-4.1	-0.1	-0.7	0.2	-0.2
NST	Tessema/24394	6.2	-1.6	5.5**	0.2	-0.2	1.0	-2.4	0.0	0.3	0.2	-0.3
ST	Tessema/AxumColl21	5.3	-22.1**	0.0	0.1	-0.1	0.1	-8.9	0.9**	2.5*	0.5**	2.8
NST	Tessema/AxumColl21	13.2	-21.1**	0.4	0.4	1.1	2.4*	-8.4	0.0	0.1	0.4*	0.4
ST	Tessema/Bako-09	1.8	-0.4	-0.2	-0.1	-0.1	-0.6	2.1	-0.6**	-3.6**	0.0	-6.1
NST	Tessema/Bako-09	12.2	1.7	1.8	0.9	-0.2	-0.1	0.2	-0.1	-0.7	-0.1	-0.1
ST	Tessema/Gute	-1.0	4.0	0.2	-0.1	0.2	1.0	0.4	0.4*	2.8*	0.2	3.6
NST	Tessema/Gute	-4.0	4.0	-1.6	0.1	0.1	-0.5	2.1	0.1	6.1**	0.0	0.5

ST	Tessema/Kako-1	0.3	4.5	-0.4	-0.3	-0.1	1.0	3.3	0.6**	2.6*	-0.2	6.3*
NST	Tessema/Kako-1	12.1	4.9	-2.8	-0.6	0.5	-0.5	2.8	-0.1	-6.0**	0.0	0.6
ST	Tessema/Meba	-3.7	8.8*	0.3	0.2	-0.7	0.7	-0.8	-0.9**	-4.4**	0.1	-0.6
NST	Tessema/Meba	-14.2*	7.3	1.3	-0.1	-1.0	-1.2	4.7	-1.4**	-3.7**	0.2	-0.1
ST	Tessema/Mereb-1	-10.6	5.0	0.0	0.2	-0.4	-0.3	0.0	-0.4	-2.5*	-0.1	0.1
NST	Tessema/Mereb-1	-12.8	2.6	-0.6	-0.5	-0.8	-0.5	1.0	0.1	0.3	0.4*	-0.4
ST	Wama/213835	-2.3	14.5**	-0.4	-0.4	-0.5	-0.6	6.7	-0.6**	-2.3	-0.1	-3.1
NST	Wama/213835	-4.6	2.6	-1.7	-0.6	-0.3	-0.2	3.2	0.0	0.2	-0.2	-0.6
ST	Wama/215982	-1.3	3.4	0.1	0.3	0.1	0.3	2.7	1.4**	4.4	-0.2	5.6
NST	Wama/215982	-0.1	0.8	4.1*	0.9	0.5	0.7	-3.2	2.1**	3.4**	0.4*	0.5
ST	Wama/238335	11.9	-13.1**	-0.1	-0.1	-0.2	-0.9	-4.3	0.2	-0.7	0.0	-5.4
NST	Wama/238335	32.8**	-10.4*	0.1	-0.1	-0.1	0.0	-2.0	2.3**	0.1	0.0	-0.4
ST	Wama/24394	1.5	15.5**	0.4	0.2	0.7	-0.3	7.6	-0.9**	-3.6	0.0	2.6
NST	Wama/24394	4.3	18.0**	-4.2*	-1.0	0.2	0.0	13.0**	-2.3**	-6.0**	-0.2	0.0
ST	Wama/AxumColl21	-1.1	7.7*	0.7	1.0	0.1	2.5**	5.0	0.1	0.3	0.2	-0.3
NST	Wama/AxumColl21	-6.5	6.4	1.7	0.3	-0.6	0.2	1.3	-3.4**	-9.8**	0.2	0.4
ST	Wama/Bako-09	-11.7	6.8	-0.3	-0.4	-0.8	-0.6	-5.7	0.8**	2.8*	0.0	5.6
NST	Wama/Bako-09	-27.5**	3.6	1.2	-0.1	-1.1	0.2	-0.9	0.1	0.3	0.3	0.3
ST	Wama/Gute	3.5	-23.3**	0.4	0.5	-0.2	1.0	-10.3	0.9**	1.4	0.3	3.8
NST	Wama/Gute	1.6	-19.2**	4.0*	1.2	0.5	1.5	-9.5*	2.0**	5.0**	0.0	0.1
ST	Wama/Kako-1	13.2*	3.8	-0.5	-0.3	-0.2	-1.5	3.9	0.2	-0.5	0.2	1.3
NST	Wama/Kako-1	14.3*	5.0	-2.4	-0.2	-0.5	-1.8	0.2	2.4**	0.3	0.3	0.4
ST	Wama/Meba	-8.1	-9.7**	-0.3	-0.3	0.1	-0.9	-3.2	-0.9**	-3.6**	-0.4*	-4.2
NST	Wama/Meba	-20.7**	-5.3	-3.0	-0.5	0.7	-0.2	-8.0	-1.4**	-3.8**	0.4*	-0.1
ST	Wama/Mereb-1	1.3	-5.4	-0.4	-0.6	0.1	-0.9	-1.5	-0.1	-0.4	0.2	-2.1
NST	Wama/Mereb-1	25.9**	-2.9	-0.7	-0.2	0.0	-2.0	7.0	0.0	0.0	0.0	0.0
ST	Standard error of crosses	6.1	3.5	0.9	0.8	0.4	0.8	5.1	0.1	1.2	0.1	3.0
NST	Standard error of crosses	6.9	2.9	1.8	0.9	0.7	1.1	4.6	0.3	1.2	0.2	1.2

ENV: growing conditions, ST: stress, and NST: non stress growing conditions, * and ** denotes significant at 5 and 1% level of significance, respectively, plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm,FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity.

5.3.5 Heterosis in finger millet hybrids for agronomic and physiological traits

Heterosis for the assessed traits for finger millet crosses evaluated under drought stress and non-stress conditions across greenhouse and field environments are presented in Tables 5.8 and 5.9. Agronomic traits had higher heterosis for several crosses under ST and NST conditions. For instance, crosses 235700/Kako-1 and Addis-01/238335 recorded desirable and negative better parent heterosis (BPH) of -2.1 and -1.9% for PTH, in that order under the NST conditions. In addition, crosses such as Addis-01/Mereb-1-1, and Wama/Kako-1 recorded negative BPH with values -0.9 and -2.1 under ST conditions for PTH. For EL, positive mid-parent heterosis (MPH) was noticeable in crosses, namely: Addis-01/Gute (MPH= 63.1% and BPH= 39.5%), Addis-01/Mereb-1 (MPH = 75.6% and BPH = 56.5%), and Wama/238335 (MPH= 54.9% and BPH= 30.4%) under ST condition, which were desirable selections. Under the NST conditions, the following crosses recorded desirable positive and significant ($p<0.001$) heterosis for EL, including 227974/Gute (MPH = 36.85 and BPH=19.29) and 235700/Kako-1 (MPH=40.0 and BPH=11.62). For FL, high and positive MPH and BPH were recorded for crosses Addis-01/Gute

(MPH = 50.9%, BPH = 34.4%), Addis-01/Mereb-1 (MPH = 64.9%, BPH = 46.9%), and Wama/238335 (MPH = 63.3%, BPH = 37.9%) under the ST conditions. Under NST conditions, crosses such as 227974/Gute, 227974/213835 and Wama/Gute showed marked heterosis for FL as follows: MPH at 49.7, 45.2, and 30.6%, and BPH at 33.3, 31.0, and 23.7%, in that order. For the NT, higher and positive heterosis were recorded in crosses, namely: Addis-01/24394 (MPH= 211.1%, and BPH = 133.3%), Addis-01/Gute (MPH= 154.5%, and BPH = 133.3%), and Wama/238335 (MPH = 233.3%, BPH = 150%) under ST condition. Under NST condition, 227974/Gute, 227974/24394, and Wama/Gute recorded MPH of 100.0, 63.0 and 44.8%, and BPH at 81.2, 37.5, and 31.2%; in that order. For the number of NF, the following crosses recorded significant and desirable positive heterosis: Addis-01/Gute (MPH= 44.8%, BPH= 35.5%), Addis-01/24394 (MPH= 42.4%, BPH= 35.5%), and Wama/Kako-1 (MPH= 35.7%, BPH= 31%) under the ST conditions. On the other hand, under the NST conditions, cross Wama/Gute recorded better and positive heterosis for NF with MPH and BPH values of 72%.

Under the ST conditions, highly significant ($p<0.01$) and negative MPH for DTF and DTM were recorded for cross 227974/215982 at -35.8% and -26.1%, respectively. Best crosses that recorded high MPH and BPH for agronomic traits included Tessema/Meba (MPH of -23.0% for DTF, MPH of -16.6% for DTM) and BPH -23.8% for DTF and -17.1% for DTM, while Tessema/213835 had MPH of -22.0% for DTF and -14.1% for DTM and BPH of DTF -25.1% for DTF and -14.8% for DTM under ST conditions. Further, under the ST conditions, notable crosses were 234187/Gute, 227974/Mereb-1, 235700/238335, Addis-01/Kako-1, and Necho/Meba achieving significant and desirable negative BPH values ranging from -25.4% to -18.0%, and MPH varying from -21.5% to -9.5% for DTF, and BPH ranging from -14.9% to 12.6% and MPH varying from -13.5% to -6.4% for DTM. Under the NST conditions, significant negative BPH was recorded for cross 235700/215982 for DTF (-25.5%) and DTM (-24.0%); and MPH of-16.3% and -23.3% for DTF and DTM, respectively. Also, 235700/Meba recorded desirable BPH for DTF (-18.8%) and DTM (-26.43%); and desirable MPH for DTF (-11.9%) and DTM (-24.4%).

For GY, several crosses such as 227974/213835, 227974/Mereb-1, Addis-01/238335, Addis-01/Kako-1, Necho/AxumColl21, and Necho/Kako-1 presented significant and positive MPH and BPH, with MPH varying from 69.7% in 227974/213835 to 172.5% for Necho/Kako-1 and BPH varying from 20.3 to 99.2% in the same crosses under the ST conditions. Under the NST conditions, crosses such as 234187/215982, 227974/213835, and Tessema/Mereb-1 recorded

desirable MPH and BPH for GY with MPH values varying from 21.4% in 234187/215982 to 69.3% in Tessema/Mereb-1 and BPH ranging from 11.2% in 234187/215982 to 48.2% in Tessema/Mereb-1. For HI, crosses with high heterosis for GY also demonstrated remarkably high and substantial MPH ranging from 65.4% in Addis-01/238335 to 223.8% in Necho/Kako-1 and BPH ranging from 34.5% to 143.1%, under ST conditions. Under the NST conditions, 234187/215982, 227974/213835 and Tessema/Mereb-1 displayed higher MPH and BPH for HI, with MPH varying from 28.7% in 234187/215982 to 31.4% in 227974/213835 and BPH ranging from 3.5% in 227974/213835 to 30.2% in Tessema/Mereb-1. MPH was positive and significant for TSW, ranging from 18.8% in Necho/AxumColl21 to 65.6% in 227974/213835, and BPH values ranging from 7.1% in Addis-01/Kako-1 to 54.1% in 227974/213835 under the ST conditions. Under the NST conditions, crosses such as 227974/213835, 227974/215982, and Tessema/Mereb-1 showed remarkable positive MPH for TSW from 13.5 to 28.2% and BPH from 2.2 to 14.4%. For chlorophyll content, several crosses recorded higher heterosis as follows: MPH varying from 7.0% in Addis-01/215982 to 44.7% in Tessema/Meba and BPH varying from 5.7% in Wama/215982 to 37.0% in Tessema/Meba under ST conditions. Under NST conditions, cross Wama/215982 showed significant ($p< 0.001$) MPH and BPH for chlorophyll content at 32.5 and 29.1%, respectively. The cross Tessema/Gute also recorded positive MPH and BPH for chlorophyll content at 28.6 and 27.0%, under NST conditions, in that order.

Table 5.8. Mid-parent heterosis (MPH, %) for agronomic and physiological traits of 70 finger millet crosses under stressed and non-stressed growing conditions in greenhouse and field environments.

ENV	Codes of crosses	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
ST	G18	-5.9**	-10.2**	11.1**	12.2**	0	3.0**	-5.7	69.7**	107.5**	65.6**	16.8**
NST	G18	-9.1	-1.5	32.7**	45.2**	6.2**	19.5**	2.3	64.7**	31.4**	14.8**	18.8**
ST	G19	5.3**	-35.8**	8.3**	16.7**	136.4**	9.3**	-26.1**	88.3**	129.2**	24.6**	-7.6**
NST	G19	-5.6	-13.3**	-0.9	-0.5	0	-7.0**	-7.1	-32.9**	-0.4	-1.8**	15.5**
ST	G20	-21.0**	7.8*	-32.1**	-29.2**	300.0**	-20.5**	-0.9	-54.3**	-43.3**	24.3**	28.3**
NST	G20	-1.4	-2.6	46.5**	68.9**	-26.7**	3.8**	2.0	-32.4**	-25.8**	-12.4**	11.8**
ST	G21	4.3**	8.4*	35.8**	18.9**	77.8**	26.2**	6.0	-18.1**	-24.4**	32.3**	-27.1**
NST	G21	4.0	7.0	37.1**	63.0**	63.0**	-1.4	7.9	-3.4**	1.5	-2.6**	-3.7
ST	G22	-14.4**	3.2	-33.9**	-21.7**	-23.1**	-24.1**	0.7	-72.2**	-78.1**	1.7**	-9.5**
NST	G22	-6.5	2.0	-22.2**	-12.3**	13.3**	9.7**	-6.5	-40.8**	-24.1**	-8.4**	-14.6**
ST	G23	10.3**	9.6**	-25.3**	-23.8**	40.0**	-5.7**	1,0	-38.0**	-40.8**	26.5**	-19.7**
NST	G23	-11.9*	-18.8**	-46.7**	-47.8**	35.5**	2.4*	-3.2	4.5**	14.1**	3.6**	36.5**
ST	G24	5.8**	5.3	-1.1	-4.0**	100.0**	25.0**	4.6	23.9**	84.2**	48.2**	25.2**
NST	G24	7.9	-4.7	36.8**	49.7**	100.0**	21.7**	0.6	-25.2**	3.5	3.5**	20.8**
ST	G25	7.5**	4.3	37.3**	47.8**	14.3**	48.5**	3.2	28.0**	45.4**	63.9**	15.5**
NST	G25	5.7	6.5	15.5**	52.4**	2.9**	15.0**	10.8	-8.8**	0.3	-10.3**	9.0**
ST	G26	-3.9**	4.0	35.0**	30.4**	7.7**	27.5**	-3.9	-19.8**	20.6**	88.8**	19.5**
NST	G26	11.8*	9.0*	44.6**	54.7**	17.2**	20.5**	2.4	34.3**	33.2**	-3.3**	6.1
ST	G27	-11.4**	-10.9**	-19.3**	-25.3**	53.8**	16.7**	-7.2	75.2**	111.7**	63.8**	18.7**
NST	G27	15.3**	14.2**	32.6**	39.0**	-5.9**	7.9**	17.0	14.0**	0.3	6.9**	-6.4
ST	G28	-15.4**	3.2	-4.5*	8.3**	-37.5**	56.3**	1.6	-76.4**	-70.2**	41.0**	-32.1**
NST	G28	-2.6	-1.7	1.0	20.0**	-16.3**	20.5**	-2.1	33.6**	25.0**	8.7**	-1.6
ST	G29	3.7**	5.0	-25.4**	-35.8**	-52.9**	-1.4	6.7	-28.8**	-18.6**	-33.1**	-25.3**
NST	G29	-7.7	-8.7*	-4.0*	-4.3**	2.4*	-7.3**	1.5	21.34*	28.7**	13.5**	14.8**
ST	G30	-6.3**	13.0**	-18.1**	-6.5**	-14.3**	-18.3**	7.5	-64.6**	-58.8**	9.8**	-2.9
NST	G30	0.1	-5.2	8.3**	42.0**	26.8**	9.3**	-0.7	7.5**	-4.9*	1.9**	-14.3**
ST	G31	-11.4**	14.3**	18.7**	15.5**	-33.3**	23.8**	9.9	-10.1**	30.2**	-1.4	-20.2**
NST	G31	-5.0	-2.1	24.1**	27.5**	-26.3**	-4.3**	11.6	28.9**	44.4**	-3.1**	9.7**
ST	G32	9.9**	-2.3	2.4	-1.1	-36.8**	1.3	-1.0	-48.2**	-49.6**	-36.3**	-33.2**
NST	G32	3.0	3.1	4.7**	20.0**	26.8**	-7.7**	-6.7	10.7**	12.1**	-16.2**	-15.5**
ST	G33	13.7**	4.1	5.7**	2.1*	25.0**	-2.9**	3.2	-22.1**	-25.6**	2.4**	-3.3
NST	G33	-0.2	9.4**	-5.1**	-3.7**	61.9**	2.6**	6.7	-22.0**	-25.4**	-28.1**	-9.5**
ST	G34	-15.8**	-21.3**	-36.8**	-36.1**	-52.9**	32.3**	-12.5*	101.9**	172.3**	7.8**	26.6**
NST	G34	4.5	-7.0	-8.2**	2.5	25.0**	-7.7**	-9.7	4.4**	-6.3**	24.5**	16.5**
ST	G35	2.7**	10.2**	-34.6**	-33.3**	-20.0**	-9.4**	2.2	37.6**	41.6**	14.0**	-32.5**
NST	G35	6.5	2.6	3.2**	12.0**	-47.8**	7.9**	1.8	19.2**	-8.9**	-8.8**	-7.8*
ST	G36	-1.5	12.7**	1.3	-0.8	-26.3**	4.5**	7.9	-78.7**	-82.6**	22.3**	-26.4**
NST	G36	-3.7	-2.5	15.9**	20.0**	30.0**	13.0**	-13.0	31.5**	30.7**	-10.7**	-14.2**
ST	G37	2.1*	24.5**	-7.3**	-13.9**	-57.9**	5.7**	17.2**	7.8**	1.6	42.5**	-40.3**
NST	G37	-2.4	5.6	14.6**	16.7**	-2.2*	-22.2**	7.4	4.7**	10.8**	-12.5**	-16.1**
ST	G38	5.4**	-7.8*	62.5**	64.3**	0.0	0.0	-3.6	-41.2**	-40.9**	-33.7**	4.0
NST	G38	-9.4	-14.4**	-32.3**	-23.1**	7.0**	44.9**	-9.1	57.0**	86.8**	9.9**	14.8**
ST	G39	4.3**	0.9	21.5**	6.4**	33.3**	-8.9**	0.0	-67.8**	-70.2**	-17.1**	3.5
NST	G39	-26.4**	-16.3**	-28.7**	-20.4**	-514**	-15.4**	-23.3	-18.6**	4.4	-9.6**	6.3
ST	G40	7.2**	-9.5**	-1.6	-8.7**	33.3**	-9.1**	-6.4	69.4**	26.2**	6.8**	6.3*
NST	G40	1.9	-15.0**	8.7**	4.0**	26.8**	7.0**	-8.4	-8.6**	-15.5**	-8.9**	1.8
ST	G41	3.6**	20.9**	46.9**	38.8**	38.5**	13.0**	13.0*	-20.7**	-41.1**	-26.9**	12.5**
NST	G41	25.8**	-18.1**	134.0**	167.1**	26.3**	20.0**	-16.3	21.4**	-14.4**	-19.6**	-30.2**

ST	G42	2.1*	9.6**	-2.2	-13.4**	-29.4**	-3.6**	6.4	-48.4**	-46.3**	-34.7**	-25.4**
NST	G42	13.03	2.6	4.3**	14.2**	7.3**	24.3**	-1.3	-51.4**	-48.6**	-2.2**	-23.6**
ST	G43	34.6**	14.4**	68.2**	58.3**	14.3**	-2.7*	7.6	-77.1**	-80.6**	-57.9**	-26.6**
NST	G43	4.5	-14.4**	-7.9**	-13.9**	-9.5**	13.5**	-7.6	3.8**	1.1	-18.6**	-4.3
ST	G44	19.0**	7.7*	13.9**	8.9**	-60.0**	-5.9**	8.1	20.2**	21.0**	-12.5**	-19.7**
NST	G44	0.7	-6.4	-9.4**	-4.4**	-5.0**	73.8**	-14.5	1.1	21.1**	40.9**	14.3**
ST	G45	18.5**	3.1	18.2**	17.1**	-22.2**	2.9*	2.9	11.4**	-1.4	-6.1**	-16.2**
NST	G45	5.2	-7.5*	40.0**	22.1**	-4.3**	13.9**	-12.4	-13.8**	-12.7**	15.7**	-1.2
ST	G46	16.3**	10.4**	78.9**	83.3**	-29.4**	23.3**	6.0	-48.7**	-47.2**	-41.2**	-17.0**
NST	G46	11.9*	-11.9**	18.5**	29.3**	60.0**	10.8**	-24.4*	13.6**	18.3**	14.6**	-10.5**
ST	G47	10.0**	24.0**	54.7**	36.6**	17.6**	-13.2**	15.5**	-56.4**	-45.1**	-15.5**	-12.8**
NST	G47	-0.6	25.0**	-22.3**	-16.1**	91.1**	52.9**	16.0	16.9**	-2.3	-11.2**	-7.6*
ST	G48	-6.1**	-0.3	8.8**	1.0	0.0	10.0**	-2.5	82.3**	72.4**	20.0**	-8.9**
NST	G48	-5.8	7.7*	-15.1**	-5.3**	0.0	0.0	2.1	40.3**	58.0**	14.0**	1.1
ST	G49	7.3**	-5.7	41.7**	36.4**	-9.1**	7.2**	5.0	-89.3**	-92.2**	-25.9**	7.0*
NST	G49	-10.4	-1.6	-35.3**	-33.3**	7.7**	-11.7**	0.7	-16.2**	16.6**	-13.6**	-17.9**
ST	G50	16.2**	-13.2**	25.9**	23.4**	100.0**	7.5**	-8.9	78.8**	65.4**	60.0**	16.9**
NST	G50	2.8	0	4.2**	0	15.4**	-8.6**	4.7	-3.3**	6.7**	-21.6**	15.9**
ST	G51	0.2	-6.7	36.8**	16.1**	211.1**	42.4**	-4.3	-64.6**	-63.4**	21.2**	-4.9
NST	G51	-2.5	19.1**	-1.6	4.3**	143.5**	12.5**	10.2	-1.9	14.0**	-34.6**	14.1**
ST	G52	9.2**	13.3**	27.1**	27.0**	23.1**	26.0**	9.3	-53.6**	-49.1**	7.5**	33.6**
NST	G52	-4.8	10.0**	-23.5**	-2.8	61.5**	-12.3**	6.8	-30.3**	-11.0**	6.7**	-5.2
ST	G53	11.3**	-5.6	6.8**	-2.7**	120.0**	46.9**	-3.0	-27.8**	-14.7**	-24.5**	34.0**
NST	G53	-6.6	-14.1**	-9.9**	-15.2**	33.3**	15.1**	-17.1	-51.7**	-35.5**	-18.2**	-11.0**
ST	G54	-3.7**	0	63.1**	50.9**	154.5**	44.8**	-8.2	65.4**	56.6**	1.1	34.3**
NST	G54	0.3	-1.4	-25.0**	-3.6*	12.0**	-6.7**	13.1	-10.8**	20.2**	1.6**	16.6**
ST	G55	-4.2**	-19.5**	11.9**	2.0*	-28.6**	23.3**	-13.5**	82.7**	96.7**	24.5**	35.1**
NST	G55	-0.8	9.7**	-25.4**	-11.5**	-3.2**	-15.5**	7.9	6.9**	9.4**	0.8**	2.8
ST	G56	-13.2**	-16.4**	7.5**	-5.1**	-7.7**	42.9**	-11.3*	12.6**	64.9**	-23.3**	-3.2
NST	G56	0.3	-2.6	-12.9**	-6.4**	92.0**	-3.1**	-5.4	20.7**	-2.9	-12.6**	21.6**
ST	G57	2.6**	18.4**	75.6**	64.9**	-23.1**	12.1**	12.8*	7.9**	6.3**	-64.4**	-1.4
NST	G57	2.6	16.7**	0.8	-10.2**	6.7**	19.4**	15.6	19.3**	22.4**	7.7**	-4.5
ST	G58	-9.0**	-2.6	-9.8**	-13.9**	-60.0**	20.0**	-7.1	483.8**	460.6**	26.2**	40.8**
NST	G58	-10.4	-4.3	-20.4**	-7.1**	-31.0**	-17.1**	-9.2	-49.5**	-46.8**	25.0**	-15.3**
ST	G59	10.8**	-4.0	-1.0	-6.7**	63.6**	4.3**	-2.2	8.6**	37.6**	-4.1**	22.1**
NST	G59	-19.3**	-0.8	-17.7**	-20.8**	18.5**	-3.3**	-6.2	-51.3**	-51.6**	11.2**	-16.3**
ST	G60	14.5**	-5.3	24.1**	12.7**	250.0**	1.5	-3.2	74.2**	81.3**	6.3**	39.7**
NST	G60	-7.6	-9.1**	18.5**	26.0**	-3.7**	0.0	-15.0	-52.9**	-48.4**	-29.8**	-6.4
ST	G61	-10.1**	1.1	-11.0**	-22.5**	11.1**	11.9**	1.2	-21.0**	-23.2**	0.3	-18.1**
NST	G61	-18.6**	7.5*	16.7**	31.5**	0.0	30.8**	-1.2	-1.8	-49.5**	4.5**	19.4**
ST	G62	-11.2**	-8.2*	-40.0**	-41.8**	38.5**	12.3**	-5.4	87.7**	140.4**	18.8**	34.6**
NST	G62	-9.9	-2.0	-13.8**	-3.0*	55.6**	-10.3**	-5.3	-8.0**	-12.8**	-4.9**	-18.7**
ST	G63	-3.2**	5.8	-35.7**	-44.7**	-20.0**	-6.3**	-1.8	46.4**	16.0**	-23.9**	-27.1**
NST	G63	2.1	0.0	-5.7**	-4.6**	7.1**	-8.0**	-6.4	3.6**	2.1	18.1**	-12.8**
ST	G64	5.0**	-2.6	4.4*	-13.6**	63.6**	13.8**	1.6	228.0**	212.9**	7.5**	-12.6**
NST	G64	9.6	-12.1**	-27.1**	-13.2**	38.5**	-2.7**	-10.2	52.2**	26.6**	8.5**	7.7*
ST	G65	-0.2	7.6*	-10.7**	-20.0**	0.0	33.3**	3.0	172.5**	223.8**	43.0**	9.3**
NST	G65	4.6	-2.9	15.7**	24.0**	0.0	-5.9**	-8.8	-46.2**	-49.1**	-10.2**	-2.1
ST	G66	15.8**	-18.0**	8.2**	-0.7	-7.7**	14.3**	-11.8*	65.3**	39.0**	53.2**	36.6**
NST	G66	-1.1	3.3	15.5**	13.5**	-15.4**	17.9**	-6.5	16.5**	0.1	-13.5**	-0.7
ST	G67	-6.8**	15.9**	20.2**	-1.2	115.4**	69.7**	0.7	-28.0**	-38.0**	-13.9**	-2.7
NST	G67	-1.8	9.1**	-4.7**	-2.6	80.6**	-8.6**	-3.2	6.2**	-0.8	-0.3	0.1

ST	G68	-14.1**	-22.0**	-8.3**	-7.6**	80.0**	21.3**	-14.1**	45.1**	41.5**	66.4**	21.3**
NST	G68	1.0	4.5	-7.1**	2.9	-37.1**	14.3**	8.3	58.7**	45.3**	7.3**	-22.6**
ST	G69	-12.7**	-1.4	-31.0**	-36.5**	27.3**	-11.4**	-10.8*	-8.7**	-22.0**	15.6**	-3.0
NST	G69	-8.2	-0.1	-32.3**	-29.3**	-45.4**	-13.9**	-3.0	26.1**	22.2**	9.3**	-18.28**
ST	G70	4.1**	1.6	21.7**	16.4**	75.0**	14.7**	-3.1	-35.6**	-33.9**	-3.1**	7.4**
NST	G70	3.3	-8.8*	13.5**	22.0**	3.0**	5.6**	-6.7	-24.6**	-11.5**	-21.4**	-11.6**
ST	G71	-7.5**	7.2*	27.8**	31.3**	11.1**	26.7**	3.9	-24.8**	-3.1*	-47.1**	4.8
NST	G71	-0.6	5.7	44.4**	35.6**	0.0	12.1**	4.1	16.9**	15.7**	-14.1**	-16.4**
ST	G72	-2.4*	5.8	-37.0**	-35.4**	-38.5**	8.1**	2.9	-39.7**	-35.7**	25.7**	14.6**
NST	G72	-6.1	-8.3*	-15.0**	-1.2	39.4**	17.3**	6.3	6.0**	1.3	8.1**	5.3
ST	G73	31.5**	3.4	-1.4	-8.7**	-20.0**	-7.7**	2.3	-9.2**	-40.2**	17.5**	2.0
NST	G73	-0.1	1.4	21.9**	19.4**	-11.7**	1.3	-2.9	-45.2**	-44.2**	-29.0**	-13.9**
ST	G74	19.1**	4.0	26.3**	35.4**	63.6**	25.4**	6.5	41.1**	53.8**	-34.3**	4.0
NST	G74	2.5	-7.7*	-15.7**	7.2**	6.2**	6.4**	-5.9	22.8**	39.2**	23.3**	28.6**
ST	G75	0.3	4.0	29.7**	37.3**	71.4**	24.6**	-4.3	2.4**	55.1**	-6.6**	18.6**
NST	G75	12.6*	3.0	-17.9**	-10.8**	-5.3**	-4.1**	4.9	-20.5**	-34.1**	4.0**	30.9**
ST	G76	3.8**	-23.0**	20.9**	18.3**	130.8**	31.3**	-16.6**	15.0**	46.9**	74.9**	44.7**
NST	G76	-9.5	4.8	6.8**	13.3**	-31.2**	-9.1**	10.3	-9.4**	-27.7**	-11.4**	-1.0
ST	G77	-9.9**	11.4**	-33.9**	-33.8**	84.6**	-7.5**	7.4	-29.0**	-16.4**	-37.0**	-4.2
NST	G77	1.9	19.8**	-6.4**	-9.7**	-29.7**	-7.2**	14.6	69.3**	31.2**	28.2**	-23.8**
ST	G78	3.3**	0.3	15.1**	9.6**	-75.0**	50.0**	-2.0	3.6**	-68.3**	16.9**	-8.1**
NST	G78	-1.0	-2.1	-31.1**	-27.4**	-6.2**	10.3**	9.0	58.9**	28.8**	-13.3**	-9.0**
ST	G79	-8.1**	-14.2**	4.1*	12.5**	77.8**	4.6**	-8.8	-54.8**	-68.2**	-28.1**	13.4**
NST	G79	-0.4	-6.5	4.3**	1.2	33.3**	16.4**	-7.7	19.4**	22.2**	10.5**	32.5**
ST	G80	13.6**	-1.0	54.9**	63.3**	233.3**	30.2**	3.7	-9.9**	-55.1**	-32.0**	-4.7
NST	G80	29.5**	-9.8**	-0.6	6.4**	13.3**	10.0**	6.9	2.2*	-15.2**	-25.5**	-4.4
ST	G81	-9.7**	6.7	13.7**	4.9**	42.9**	45.5**	-4.3	-51.3**	-78**	-48.9**	-9.2**
NST	G81	11.3	17.7**	-20.5**	-19.3**	40.7**	11.1**	8.3	-3.6**	-15.0**	-39.3**	4.1
ST	G82	-0.5	-4.0	0.5	8.8**	45.5**	13.0**	-1.3	67.8**	-5.2**	-8.4**	33.8**
NST	G82	5.1	0.7	-21.0**	-11.4**	6.7**	46.0**	-9.7	-67.0**	-61.3**	-20.8**	15.5**
ST	G83	-0.6	-8.1*	-30.1**	-32.7**	375.0**	60.0**	-4.4	-0.1	-31.1**	-13.5**	54.8**
NST	G83	5.1	3.8	-9.1**	-20.0**	-22.6**	4.7**	5.6	23.7**	-4.6*	-5.5**	10.9**
ST	G84	-5.8**	-0.5	-35.5**	-20.2**	77.8**	22.2**	2.7	10.0**	-51.9**	-18.3**	25.3**
NST	G84	14.3*	-18.2**	32.6**	30.6**	44.8**	72.0**	-1.2	4.4**	9.3**	-10.6**	22.9**
ST	G85	5.3**	2.6	23.1**	45.1**	150.0**	35.7**	1.8	-14.8**	-66.4**	-23.8**	1.5
NST	G85	21.8**	2.7	-19.0**	-8.8**	-20.0**	-21.3**	13.3	51.4**	6.9**	-9.9**	33.1**
ST	G86	-5.2**	4.9	4.5*	-2.5*	-27.3**	18.6**	1.6	-45.3**	-73.2**	23.7**	-5.5*
NST	G86	5.6	-13.8**	-39.2**	-11.1**	51.7**	33.3**	-17.3	-54.6**	-46.9**	-23.6**	7.8*
ST	G87	0.5	16.1**	-16.2**	-20.2**	27.3**	-6.5**	12.8*	-41.3**	-72.4**	-9.0**	1.8
NST	G87	33.0**	7.6*	-11.1**	-7.7**	11.7**	-12.3**	13.2	9.9**	-3.2	-0.1	6.3
ST	MSE	109.7	24.2	8.7	6.9	0.7	2.6	60.2	0.2	4.7	0.0	15.6**
NST	MSE	68.1	26.1	5.4	4.2	2.0	3.8	279.2	2.16	10.2	0.1	22.0

Note: ENV: growing conditions, ST: stress, and NST: non stress growing conditions, * and ** denotes significant at 5 and 1% level of significance, respectively,plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm,FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity.

Table 5.9. Better-parent heterosis (BPH, %) for agronomic and physiological traits of 70 finger millet crosses evaluated under stressed and non-stressed growing conditions in greenhouse and field environments.

ENV	Codes of	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
ST	G18	-12.6	-15.4**	-11.8**	-9.3**	-16.7**	-8.1**	-8.1	20.3**	50.5**	54.1**	15.2**
NST	G18	-12.5*	-1.6	16.8**	31.0**	6.2**	4.5**	-0.7	17.4**	3.5	14.4**	11.7**
ST	G19	4.1	-38.6**	2.0*	14.0**	116.7**	7.9**	-28.6**	55.7**	85.0**	-3.3**	-17.1**
NST	G19	-6.9	-16.3**	-0.9	-4.3**	-6.2**	-9.1**	-9.2	-38.9**	-3.0	-6.2**	8.1*
ST	G20	-28.3**	4.5	-48.0**	-46.5**	166.7**	-21.6**	-3.3	-56.4**	-43.4**	1.8	22.7**
NST	G20	-9.2	-3.9	11.5**	31.0**	-31.2**	-6.8**	-0.2	-45.5**	-39.0**	-28.5**	1.1
ST	G21	0.8	3.7	7.8**	2.3*	33.3**	10.8**	3.2	-33.3**	-42.0**	-5.0**	-33.9**
NST	G21	-0.4	-0.3	6.2**	26.4**	37.5**	-18.2**	4.7	-4.3**	-7.0**	-21.7**	-15.2**
ST	G22	-18.5**	3.1	-37.9**	-26.5**	-28.6**	-28.6**	0.6	-74.0**	-81.0**	-27.1**	-10.6**
NST	G22	-7.8	-3.2	-30.6**	-18.0**	6.2**	2.3*	-9.5	-49.5**	-34.5**	-22.9**	-25.7**
ST	G23	-8.5	7.9*	-39.2**	-34.9**	16.7**	-10.8**	-0.2	-47.4**	-55.7**	-5.6**	-27.9**
NST	G23	-24.5**	-21.3**	-54.0**	-51.7**	31.2**	-4.5**	-4.7	-1.8	-4.3	-14.4**	15.9**
ST	G24	0.2	1.0	-13.7**	-16.3**	83.3**	8.1**	4.0	-9.5**	29.0**	26.5**	21.4**
NST	G24	0.9	-8.1*	19.3**	33.3**	81.2**	-4.5**	0.2	-36.2**	-4.5	1.5**	19.4**
ST	G25	-3.1	3.4	11.8**	18.6**	0.0	32.4**	2.6	-4.7**	7.3**	38.5**	11.6**
NST	G25	-5.4	2.9	-4.4**	28.7**	-5.3**	4.5**	9.6	-11.9**	-3.7	-28.3**	6.0
ST	G26	-15.0*	0.8	3.9**	2.3*	0.0	18.9**	-6.1	-21.7**	19.1**	71.2**	15.8**
NST	G26	3.1	8.5*	13.3**	21.8**	6.2**	0.0	-1.7	26.9**	26.8**	-19.7**	-0.6
ST	G27	-16.3*	-21.4**	-32.4**	-34.9**	42.9**	13.5**	-14.9**	54.8**	77.9**	19.3**	3.3
NST	G27	2.9	2.4	0.9	12.6**	-11.1**	-6.8**	4.7	-0.5	-0.7	2.7**	-17.3**
ST	G28	-17.5*	-4.0	-22.1**	-10.0**	-58.3**	42.9**	-2.0	-84.8**	-80.9**	10.7**	-36.8**
NST	G28	-6.1	-2.1	-10.7**	6.7**	-33.3**	10.0**	-6.4	-5.2**	-9.7**	-2.4**	-12.5**
ST	G29	-0.4	-0.8	-27.4**	-36.6**	-66.7**	-5.3**	2.0	-48.4**	-43.9**	-36.8**	-36.4**
NST	G29	-13.0*	-11.4**	-4.4**	-6.4**	-22.2**	-9.5**	0.7	11.2**	16.8**	6.0**	2.5
ST	G30	-10.9	8.2*	-35.8**	-27.5**	-50.0**	-19.4**	3.9	-71.2**	-66.8**	-2.8**	-12.2**
NST	G30	-1.0	-6.0	-17.3**	8.9**	-3.7**	2.5*	-4.2	-12.8**	-12.7**	-8.2**	-21.0**
ST	G31	-12.9	10.7**	-3.2	2.5*	-58.3**	11.4**	8.1	-14.0**	21.6**	-7.0**	-23.4**
NST	G31	-7.9	-9.2**	-3.6*	-2.2*	-48.1**	-17.5**	6.8	28.6**	39.3**	-14.3**	4.2
ST	G32	9.8	-3.7	-6.9**	-10.2**	-50.0**	-7.1**	-2.1	-53.7**	-53.6**	-40.0**	-36.2**
NST	G32	-3.0	-2.6	-6.9**	14.0**	-3.7**	-10.0**	-8.5	-5.1**	8.6**	-21.9**	-18.6**
ST	G33	-1.5	3.8	-11.6**	-10**	-16.7**	-5.7**	3.1	-22.8**	-32.8**	2.3*	-8.2**
NST	G33	-8.6	5.5	-17.9**	-12.2**	25.9**	0.0	3.5	-26.2**	-30.1**	-34.3**	-10.4**
ST	G34	-16.2*	-25.4**	-43.2**	-42.5**	-66.7**	17.1**	-13.9**	32.9**	69.7**	-8.6**	15.9**
NST	G34	4.0	-9.9**	-19.6**	-10.0**	-7.4**	-25.0**	-11.4	-10.5**	-10.4**	9.5**	-1.0
ST	G35	-3.1	9.7**	-45.3**	-45**	-33.3**	-17.1**	1.7	-8**	-8.4**	-2.5*	-38.3**
NST	G35	2.1	-1.3	-14.3**	-6.7**	-55.6**	2.5*	-0.7	14.3**	-16.2**	-19.8**	-20.5**
ST	G36	-8.7	7.9*	-20.0**	-20.0**	-41.7**	0.0	4.3	-81.6**	-85.8**	-1.9	-32.6**
NST	G36	-4.6	-3.4	-8.9**	-6.7**	-3.7**	-2.5	-15.3	23.5**	21.2**	-17.9**	-23.5**
ST	G37	1.3	11.0**	-20.0**	-22.5**	-66.7**	5.7**	8.5	2.3*	-3.3*	37.5**	-45.1**
NST	G37	-6.7	-5.8	-12.5**	-6.7**	-18.5**	-30.0**	-5.1	-9.1**	-2.7	-18.7**	-20.6**
ST	G38	0.2	-19.2**	52.9**	55.9**	-30.0**	-14.6**	-10.5	-64.2**	-65.1**	-51.7**	-6.2*
NST	G38	-21.3**	-21.5**	-48.8**	-41.4**	-14.8**	38.9**	-13.0	2.9**	26.6**	-2.9**	3.5
ST	G39	-6.6	-10.3**	6.7**	-8.5**	0.0	-12.2**	-8.0	-78.4**	-81.5**	-29.1**	-14.4**
NST	G39	-37.4**	-25.5**	-50.4**	-44.7**	-63.0**	-21.4**	-24.0*	-23.0**	-13.7**	-16.9**	-3.8
ST	G40	4.6	-18.5**	-11.8**	-20.3**	-20.0**	-14.6**	-13.0*	24.7**	-11.8**	-13.7**	-6.7*
NST	G40	-7.7	-22.8**	-5.1**	-8.3**	-3.7**	5.6**	-11.6	-16.0**	-17.4**	-16.6**	-4.8
ST	G41	-5.3	17.0**	38.2**	35.5**	-10.0**	-4.9**	10.4	-27.6**	-48.5**	-30.6**	11.6**
NST	G41	9.7	-19.4**	100.0**	135.4**	-11.1**	8.3**	-19.8	6.0**	-25.4**	-27.8**	-32.7**

ST	G42	-5.2	1.4	-22.4**	-30.6**	-40.0**	-4.8**	1.1	-58.8**	-58.5**	-37.8**	-31.0**
NST	G42	-3.9	-0.9	-31.9**	-22.0**	-18.5**	21.0**	-3.2	-52.3**	-52.4**	-7.3**	-25.3**
ST	G43	24.7**	7.6*	63.2**	55.7**	-20.0**	-12.2**	3.5	-80.1**	-82.5**	-62.2**	-28.0**
NST	G43	2.0	-19.0**	-29.3**	-35.7**	-29.6**	10.5**	-10.3	-4.8**	-3.3	-24.4**	-4.8
ST	G44	11.0	-3.9	7.9**	4.7**	-70.0**	-22.0**	2.3	-25.5**	-29.8**	-31.9**	-28.6**
NST	G44	-10.2	-16.8**	-30.9**	-26.5**	-29.6**	47.2**	-16.0	-0.7	4.8	22.1**	-1.5
ST	G45	16.5*	-3.7	14.7**	10.2**	-30.0**	-12.2**	-1.5	-30.1**	-41.3**	-26.4**	-25.8**
NST	G45	-2.1	-12.2**	11.6**	-1.7	-18.5**	13.9**	-14.5	-27.5**	-27.1**	3.3**	-13.7**
ST	G46	16.0*	-0.5	61.8**	67.8**	-40**	9.8**	-1.4	-60.3**	-62.8**	-56.4**	-26.3**
NST	G46	1.1	-18.8**	0.0	12.0**	18.5**	0.0	-26.4*	-6.2**	-0.5	7.1**	-19.1**
ST	G47	2.9	17.5**	53.6**	31.3**	0.0	-19.5**	11.1*	-63.4**	-56.5**	-21.5**	-17.3**
NST	G47	-7.2	21.6**	-32.2**	-29.6**	59.3**	44.4**	2.6	-9.6**	-21.6**	-18.9**	-11.3**
ST	G48	-7.8	-5.0	3.3**	-1.9	-16.7**	6.5**	-4.0	27.5**	16.2**	-5.3**	-17.9**
NST	G48	-14.1*	5.6	-27.9**	-22.9**	-12.5**	-2.9*	0.0	-9.1**	14.2**	1.8**	-11.4**
ST	G49	-1	-8.7**	13.3**	9.8**	-16.7**	-2.6**	2.4	-91.3**	-94.2**	-29.6**	6.1*
NST	G49	-20.1**	-6.7	-50.4**	-51.1**	0.0	-19.0**	-2.5	-22.6**	5.9**	-19.7**	-28.3**
ST	G50	15.2*	-14.8**	25.9**	16.0**	33.3**	0.0	-10.2	67.0**	46.3**	42.4**	8.3**
NST	G50	-1.9	-3.1	3.3*	-4.2**	7.1**	-8.6**	3.5	-9.0**	-2.1	-29.0**	-1.9
ST	G51	-5.5	-11.8**	30.0**	4.8**	133.3**	35.5**	-7.7	-70.7**	-69.0**	13.8**	-22.3**
NST	G51	-10.7	13.0**	-3.2	0.0	133.3**	2.9**	8.1	-16.1**	10.1**	-41.8**	-5.8
ST	G52	4.6	12.1**	-6.9**	-4.1**	14.3**	9.5**	8.4	-55.5**	-50.3**	0.6	17.5**
NST	G52	-15.1**	6.3	-45.8**	-30.0**	50.0**	-15.8**	2.3	-30.7**	-13.8**	0.0	-22.6**
ST	G53	0.0	-8.2*	-1.6	-11.5**	83.3**	42.4**	-5.0	-37.4**	-29.9**	-24.9**	8.6**
NST	G53	-9.5	-15.2**	-21.9**	-32.4**	20.0**	10.5**	-17.6	-56.7**	-39.5**	-24.9**	-28.9**
ST	G54	-7.3	-2.8	39.5**	34.4**	133.3**	35.5**	-8.6	19.0**	2.5	-13.9**	22.8**
NST	G54	-5.8	-6.7	-35.7**	-20.6**	7.7**	-20.0**	12.4	-11.4**	15.2**	-11.1**	7.0*
ST	G55	-5.7	-21.2**	3.1**	0.0	-37.5**	19.4**	-14.9**	34.1**	34.5**	7.1**	24**
NST	G55	-2.5	8.0*	-32.4**	-23.3**	-21.0**	-16.7**	7.9	-11.9**	0.7	-11.0**	-7.0*
ST	G56	-16.2*	-18.0**	6.5**	-6.0**	-14.3**	40.6**	-12.6*	12.4**	47.6**	-38.2**	-11.4**
NST	G56	-4.5	-4.0	-15.6**	-12.0**	84.6**	-11.4**	-10.1	-2.2*	-9.8**	-19.2**	6.2
ST	G57	-0.9	3.3	56.5**	46.9**	-28.6**	5.7**	2.5	-2.6**	0.1	-65.8**	-22.2**
NST	G57	1.1	6.3	0.0	-18.5**	-11.1**	14.3**	4.4	-9.4**	7.6**	-0.6**	-20.9**
ST	G58	-13.6	-5.5	-28.8**	-33.7**	-66.7**	16.1**	-8.1	350.2**	328.7**	-0.7	33.2**
NST	G58	-13.6*	-9.1**	-33.8**	-20.4**	-37.5**	-30.6**	-19.3	-61.2**	-55.6**	12.6**	-19.1**
ST	G59	9.5	-5.4	-7.7**	-14.3**	50.0**	-5.3**	-4.2	-26.9**	-4.4**	-9.1**	16.9**
NST	G59	-20.3**	-2.6	-23.1**	-22.4**	14.3**	-10.2**	-12.4	-59.9**	-56.1**	4.2**	-20.3**
ST	G60	6.0	-5.3	-5.8**	-18.4**	133.3**	-5.6**	-4.1	8.8**	12.3**	-5.6**	36.1**
NST	G60	-14.9**	-12.6**	-13.8**	-6.1**	-7.1**	-14.3**	-23.8	-65.0**	-59.9**	-37.0**	-13.9**
ST	G61	-11.1	-6.1	-29.8**	-36.7**	-16.7**	6.5**	-2.9	-54.9**	-56.7**	-5.6**	-30.2**
NST	G61	-22.0**	-4.5	-13.8**	-2.0*	-7.7**	4.1**	-12.1	-12.8**	-56.8**	-7.9**	6.9*
ST	G62	-13.6	-10.8**	-43.1**	-41.8**	28.6**	-2.4*	-6.6	12.5**	41.2**	11.5**	24.1**
NST	G62	-11.1	-11.5**	-18.1**	-4.0**	50.0**	-20.4**	-10.7	-28.3**	-29.3**	-11.7**	-28.2**
ST	G63	-18.1*	1.1	-48.1**	-55.1**	-33.3**	-9.1**	-4.3	-15.2**	-35.1**	-24.1**	-38.4**
NST	G63	-12.3*	-7.9*	-23.1**	-16.3**	0.0	-18.4**	-15.7	-12.2**	-19.3**	7.5**	-24.9**
ST	G64	1.6	-3.6	-9.6**	-28.6**	50.0**	6.5**	0.6	144.7**	149.6**	-8.6**	-16.1**
NST	G64	2.5	-13.6**	-40.0**	-26.5**	38.5**	-26.5**	-18.2	18.6**	9.2**	-4.3**	7.0*
ST	G65	-8.2	3.4	-27.9**	-38.8**	-12.5**	29.0**	0.8	99.2**	143.1**	22.7**	5.4
NST	G65	-6.35	-10.7**	-9.2**	0	-15.8**	-18.4**	-17.4	-50.2**	-54.4**	-21.3**	-3.1
ST	G66	4.5	-18.0**	-17.3**	-25.5**	-14.3**	12.5**	-12.6*	0.5	-14.3**	23.2**	31.4**
NST	G66	-8.7	-2.4	-13.8**	-14.3**	-15.4**	-6.1**	-11.1	10.0**	-11.1**	-20.7**	-5.4
ST	G67	-10.1	-0.5	0.0	-18.4**	100.0**	60.0**	-8.9	-57.7**	-63.9**	-17.2**	-20.1**
NST	G67	-12.3*	-6.7	-30.8**	-24.5**	55.6**	-24.5**	-19.9	3.9**	-6.9**	-7.2**	-10.2**

ST	G68	-18.6**	-25.1**	-21.4**	-16.7**	50.0**	15.6**	-14.8**	-6.0**	-7.9**	33.9**	13.0**
NST	G68	-3.7	3.7	-9.3**	2.9*	-42.1**	8.1**	7.6	13.2**	14.7**	-16.7**	-27.3**
ST	G69	-13.5	-3.9	-33.3**	-42.7**	16.7**	-18.4**	-12.3*	-33.3**	-45.0**	12.6**	-5.7*
NST	G69	-10.5	-4.2	-41.6**	-38.3**	-52.6**	-19.0**	-8.5	14.6**	18.6**	-12.4**	-23.5**
ST	G70	-3.9	0.5	0.0	-3.0**	16.7**	8.3**	-3.7	-47.1**	-45**	-11.8**	3.0
NST	G70	-5.8	-10.6**	-2.4	2.9*	-10.5**	2.7**	-8.1	-39.3**	-27.4**	-26.6**	-20.1**
ST	G71	-8.8	0.5	9.5**	27.3**	-16.7**	18.8**	-0.6	-28.9**	-12.9**	-51.5**	-11.8**
NST	G71	-5.7	-0.8	26.8**	14.3**	-21.0**	0.0	3.4	15.6**	5.6*	-18.3**	-26.4**
ST	G72	-5.3	3.8	-45.7**	-45.9**	-42.9**	-4.8**	1.2	-45.4**	-38.5**	14.9**	4.1
NST	G72	-8.3	-12.4**	-33.3**	-16.0**	21.0**	15.8**	-0.7	-9.7**	-12.8**	-2.5**	-8.5**
ST	G73	10.9	-0.3	-13.1**	-12.1**	-33.3**	-9.1**	-0.6	-9.6**	-47.8**	14.1**	-15.0**
NST	G73	-15.1**	-1.1	21.9**	16.2**	-21.0**	0.0	-4.9	-48.6**	-53.3**	-34.6**	-27.0**
ST	G74	15.0*	1.8	20.2**	33.3**	50.0**	15.6**	5.1	-6.5**	-2.5	-42.8**	-1.6
NST	G74	-5.1	-11.6**	-16.7**	5.7**	-10.5**	-10.8**	-9.0	4.6**	28.1**	-5.9**	27.0**
ST	G75	-8.0	1.1	14.3**	22.7**	50.0**	18.8**	-6.6	-31.1**	2.2	-17.9**	12.6**
NST	G75	-0.2	0.3	-21.9**	-17.1**	-5.3**	-5.4**	2.1	-23.0**	-36.9**	-0.3	27.2**
ST	G76	-6.6	-23.8**	0.0	3.0**	114.3**	31.3**	-17.1**	0.2	23.7**	43.7**	37.0**
NST	G76	-17.4**	4.6	-4.9**	-2.9**	-42.1**	-18.9**	2.3	-14.2**	-31.4**	-19.0**	-7.3*
ST	G77	-13.3	-3.5	-39.8**	-34.8**	71.4**	-11.4**	-3.1	-31.8**	-17.3**	-41.0**	-22.3**
NST	G77	-9.9	8.1*	-19.5**	-20.0**	-31.6**	-13.5**	6.1	48.2**	30.2**	2.2**	-32.7**
ST	G78	-0.8	-0.7	1.3	0.3	-75.0**	44.8**	-2.4	-29.6**	-82.1**	-11.0**	-10.7**
NST	G78	-4.5	-2.1	-34.0**	-30.3**	-6.2**	-3.0*	9.0	6.1**	-8.8**	-34.3**	-11.0**
ST	G79	-10.3	-14.7**	-2.2	0.0	60.0**	-10.5**	-9.9	-64.7**	-81.3**	-34.7**	5.7*
NST	G79	-6.1	-9.6**	-4.4**	-8.5**	25.0**	-7.1**	-12.4	17.1**	7.7**	-13.7**	29.1**
ST	G80	6.3	-3.0	30.4**	37.9**	150.0**	13.9**	3.5	-19.7**	-71.0**	-42.0**	-4.9
NST	G80	28.0**	-10.9**	-19.1**	-13.2**	6.2**	-5.7**	5.9	-9.2**	-19.7**	-32.6**	-10.1**
ST	G81	-9.7	-2.8	0.0	3.4**	25.0**	42.9**	-8.8	-57.8**	-83.0**	-49.7**	-20.8**
NST	G81	7.9	9.5**	-34.0**	-34.2**	18.7**	3.4**	8.2	-13.0**	-20.5**	-44.1**	-4.9
ST	G82	-2.1	-8.6**	-15.5**	-10.2**	14.3**	-7.1**	-3.3	66.6**	-33.6**	-10.0**	26.7**
NST	G82	-0.9	-4.5	-34.7**	-22.0**	0.0	21.0**	-15.	-68.7**	-61.4**	-30.7**	4.2
ST	G83	-15.2*	-14**	-36.7**	-34.2**	375.0**	45.5**	-7.6	-9.5**	-45.2**	-17.2**	33.9**
NST	G83	-3.79	0.53	-14.9**	-21.0**	-25**	-13.2**	4.1	17.4**	-7.67**	-15.6**	-2.5
ST	G84	-7.8	-1.5	-36.7**	-20.3**	60**	22.2**	1.0	-23.2**	-73.1**	-33.1**	23.8**
NST	G84	13.7*	-21.0**	25.5**	23.7**	31.3**	72.0**	-3.8	-1.2	1.3	-33.3**	19.3**
ST	G85	-2.1	-3.3	11.4**	31.7**	87.5**	31**	-1.0	-39.4**	-80.9**	-37.1**	0.7
NST	G85	16.8**	-0.8	-27.7**	-18.4**	-26.3**	-33.3**	11.0	31.4**	-4.6*	-16.4**	31.2**
ST	G86	-13.5	2.8	-11.4**	-13.8**	-42.9**	9.4**	1.4	-47.9**	-82.6**	-3.9**	-6.5*
NST	G86	4.6	-14.3**	-48.9**	-26.3**	37.5**	24.1**	-23.0	-61.3**	-52.3**	-32.3**	5.21
ST	G87	-1.9	-2.0	-21.5**	-20.3**	0.0	-17.1**	1.4	-44.5**	-80.3**	-9.7**	-14.5**
NST	G87	27.2**	-3.7	-27.7**	-21.1**	5.6**	-21.9**	4.23	-12.6**	-17.3**	-22.3**	-2.46
ST	MSE	109.7	24.2	8.7	6.9	0.7	2.6	60.2	0.2	4.7	0.0	15.6**
NST	MSE	68.1	26.1	5.4	4.21	1.97	3.8	279.18	2.16	10.2	0.1	22.0

Note: ENV: growing conditions, ST: stress, and NST: non stress growing conditions, * and ** denotes significant at 5 and 1% level of significance, respectively, plant height (cm, PTH), days to flowering (DTF), ear length, (cm, (EL), length of the primary finger, (cm,FL), number of productive tillers per plant (NT), the number of fingers on the primary ear (NF), days to maturity (DTM), grain yield (t/ha, GY), harvest index (%, HI), thousand seed weight (g, TSW), and SPADM, chlorophyll content at maturity

5.4 Discussions

The present study pursued a detailed genetic analysis of yield and yield-influencing traits in finger millet using a line × tester mating genetic design involving seven lines and 10 testers. A combined ANOVA revealed significant variability among the parents, F_1 hybrids, and their interactions for grain yield and associated-component traits (Table 5.3). The observed variability underscores the presence of a rich reservoir of heritable variations for key agronomic and physiological traits in the assessed finger millet genetic pool for hybrid breeding and new population development. Both additive and non-additive gene effects were deciphered, contributing to trait expression which needs strategic selection. The genetic effects are consistent with earlier findings that quantitative traits in several crop species, including finger millet (Owere et al., 2016; Mapako & Maphosa, 2025), rice (Madhusudan et al., 2025), sorghum (Mengistu et al. 2020) and barley (Yadav et al. 2022). Under non-stress conditions, additive gene action was predominant, revealed by higher GCA mean squares, large additive variance, and Baker's ratios approaching unity for PTH, DTF, EL, FL, NF, GY, HI, TSW, and chlorophyll content (Appendix Table 5.3). The predominance of additive effects under favorable moisture conditions may be attributed to the greater expression and transmission of cumulative allelic effects when environmental constrains are minimized. In such environments, genetic potential is more fully expressed, reducing the masking influence of stress-induced physiological disturbance and allowing additive gene effects to account for a larger proportion phenotypic variation. Consequently, trait performance becomes more predictable across generations, enhancing the effectiveness of selection for genetic improvement. This pattern is consistent with earlier reports that GCA contributes more of the genetic variance for PTH, DTF, EL and NT in foxtail millet (Siles et al., 2004) and that additive effects are the major drivers of trait inheritance in well-watered environments (Abrha et al., 2018; Mengistu et al., 2020).

Under drought stress conditions, dominance and epistatic gene actions were more influential, associated with larger SCA contributions, higher non-additive variance, and relatively low Baker's ratios for NT, GY, and TSW (Appendix Table 5.2). This suggests that breeding for drought tolerance in finger millet should be harnessed through heterosis-based strategies (Falconer & Markay, 1996; Acquaah, 2012). The present findings agree with previous reports that heterosis in finger millet is largely driven by dominance gene action associated with higher SCA affecting grain yield expression under stress

(Krishnappa et al. 2009; Mapako & Maphosa 2025). Reportedly, non-additive effects were greater in other cereals for yield components in stress-prone growing environments (Abraha et al., 2018; El-Aty et al., 2022; Madhusudan et al., 2025). The shift from additive genetic control under non-stress to increased dominance × environment interactions under drought aligns with earlier reports that indicated that moisture stress enhances non-additive gene expression and genotype × environment interaction effects in millets such as finger millet and pearl millet (Shailaja, et al., 2010; Owere et al., 2016; Rouamba et al., 2024). From the variable genetic effects across environments, it can be deduced that pure-line breeding is most effective for additive traits under non-stress conditions, whereas heterosis breeding is essential for exploiting dominance and epistatic genetic effects for yield improvement (Kempthorne, 1957; Mengistu et al., 2020; Thungo et al., 2022).

In the present study, the test genotypes showed a maturity period varying between 90 to 130 days. Early maturity or drought escape is a crucial proxy trait for genotype selection for drought tolerance. Earliness has been consistently linked with enhanced performance under terminal drought in finger millet (Assefa et al., 2013; Mude et al., 2020) and other millets such as foxtail millet and pearl millet (Xiao et al., 2022; Bazie et al., 2025). Early maturation and short grain filling stages are reportedly traits of choice in drought-prone agro-ecologies (Tesfaye and Mengistu, 2017; Mukami et al., 2020). In the present study, parents, such as 235700, 234187 and Addis-01 (lines) and Gute, 24394, Bako-09, Mereb-1, and 215982 (tester) showed significant and desirable GCA effect across environments (Table 5.6). Notably, line 235700 was the most promising parent with higher and positive GCA effects for grain yield, harvest index, thousand seed weight, and chlorophyll content. The line is the best candidate for future crosses to combine high yield and early maturity across drought-stressed and non-stressed conditions. A higher GCA effect is linked with additive gene effects, which have minor and cumulative genetic effects that govern the average performance of progenies. Further, lines 227974 and 234187 were identified as desirable parents for panicle-related traits such as ear and finger length, while 234187 had better grain yield and harvest index values. Parents such as Wama are superior with higher TSW and chlorophyll content, while Tesema also excelled for TSW, making both lines promising donors for enhancing seed weight and physiological vigour in finger millet breeding under drought-prone environments. Tester Bako-09 has higher GCA effects for early flowering and maturity (Table 5.6), suggesting its potential in drought tolerance breeding. Selection of parents with favourable GCA effects for early maturation and yield

stability, and physiological attributes is critical for breeding under water-limited conditions in various cereal crops, such as finger millet (Owere et al., 2016; Mapako & Maphosa, 2025), pearl millet (Rouamba et al., 2024), tef (Abraha et al., 2018), wheat (Thungo et al. 2022; Shamuyarira et al., 2023), barley (Yadav et al., 2022), and sorghum (Mengistu et al., 2020).

In this study, crosses such as 235700/238335, 235700/213835, 227974/Bako-09, Addis-01/213835, 235700/Bako-09, 235700/Gute, Wama/Bako-09, and 227974/Mereb-1 displayed superior grain yield and yield components under stressed and non-stressed conditions, owing to the desirable genetic combinations for hybrid breeding and population development through recurrent selection. The crosses involved common parents such as 235700 and Bako-09, which were elite lines with local adaptation and yield performance. The present findings corroborate with earlier reports (Parashuram et al., 2011; Savitha et al., 2013; Owere et al., 2016) who pinpointed that elite finger millet parents contribute significantly to hybrid vigour under drought. Due to drought stress, grain yield declined by approximately 60% (Table 5.4), corroborating earlier reports that indicated a yield loss of 50-60% in finger millet under drought conditions (Maqsood and Ali 2007; Gebreyohannes et al., 2025a). Hence, there is a need to develop drought-adapted and new-generation finger millet cultivars that buffer drought stress. In crosses such as 235700/Mereb-1, 235700/213835, and Wama/215982, higher chlorophyll content was recorded under drought conditions (Table 5.4), suggesting superior photosynthetic capacity and functional stay-green expression. Chlorophyll retention during the later stages of plant development is indicative of delayed leaf senescence and prolonged photosynthetic activity. This enables continued assimilation and translocation to developing grains under moisture stress, thereby enhancing drought adaptation and yield stability. These findings support previous studies that identified chlorophyll retention and stay-green traits as key physiological mechanisms contributing to drought tolerance and maintenance of productivity in cereal crops (Jordan et al. 2012; Borrell et al. 2014; Shin et al. 2020; Gebreyohannes et al. 2025a,b).

The SCA analysis in the present study identified unique crosses such as 235700/213835, Tessema/238335, Necho/Bako-09, Necho/Gute, Wama/215982, and 234187/AxumColl21 (Table 5.7) under stressed and non-stressed conditions. Higher SCA genetic effects imply non-additive gene action attributable to the deviation of a hybrid's performance from its

expected value based on GCA of parents (Singh and Chaudhary 1985; Acquaah, 2012). The afore-mentioned crosses showed highly significant positive SCA effects for grain yield and harvest index across growing conditions. These hybrids are recommended for production after stability tests and recommended for further selection and genetic advancement through pure-line or recurrent selection to develop high-yielding stable cultivars. Additionally, crosses 235700/24394, Addis-01/Bako-09, Wama/Gute, and 227974/215982 had low SCA values in an acceptable trend for early flowering and maturity, suggesting their potential for moisture-limited agro-ecologies. Crosses 227974/24394, Tessema/Kako-1, 235700/Mereb-1, Wama/215982, and 227974/Bako-09 had higher SCA effects for chlorophyll content, which could enhance efficient photosynthesis under stress conditions. Previous reports in finger millet (Owere et al., 2016; Mapako & Maphosa, 2025) and other cereals such as pearl millet (Kumawat et al., 2019), wheat (Mwadzingeni et al., 2018; Semahegn et al., 2021), and barley (Zhang et al., 2015) indicated non-additive gene action for yield stability and drought adaptive traits.

Heterosis is a measure of the superiority of hybrid performance relative to its parental lines. Heterosis arises from gene interaction due to dominance, overdominance, and epistatic gene actions (Shull 1908; Falconer and Marckay, 1996; Acquaah, 2012). In the present study, crosses 227974/213835, Addis-01/Gute and Wama/215982 had higher BPH for grain yield, earliness, and chlorophyll content (Table 5.9). These values are consistent with the SCA effects (Table 5.7). Crosses with higher heterosis buffer drought stress and yield better. Crosses 227974/215982 and 227974/213835 had high heterosis for early flowering and maturity, and better grain yield, harvest index, and chlorophyll content. Therefore, there is a possibility of developing short-duration, drought-tolerant and high-yielding finger millet genotypes. The crosses Addis-01/215982, and Wama/215982 showed high heterosis for days to flowering, maturity and chlorophyll content (Tables 5.8 and 5.9), indicating the contribution of hybrid vigour to improve both productivity and stress adaptation. Earlier reports found significant and better heterosis for grain yield and drought-related traits in finger millet (Parashuram et al., 2011; Krishna et al., 2020). Higher heterosis values for chlorophyll content in some crosses, such as 227974/213835, 227974/Gute, Addis-01/Gute, Tessema/Kako-1, Wama/215982, and Wama/Gute, supports the role of delayed senescence and sustained photosynthetic activity in buffering drought impacts, an important adaptation mechanism in millets, including sorghum and pearl millet (Abebe et al., 2021; Sehgal et al., 2015). The heterotic gains for early maturity and

enhanced harvest index highlight a crucial breeding pathway for climate-smart finger millet hybrids. This aligns with other small millets such as foxtail millet and proso millet, where hybridization improved earliness and resource-use efficiency (Siles, et al., 2004; Shi et al., 2021). Some unique crosses (i.e., 227974/213835, 227974/215982, 227974/Kako-1, and 234187/Mereb-1) were selected with high heterotic performance for earliness, high chlorophyll content and better grain yield. These crosses are promising genetic resources for selection and the advancement of the derived progenies to fix desirable alleles as elite pure lines.

5.6 Conclusion and recommendations

The current study appraised the potential of hybrid breeding and new population development in finger millet to enhance yield gains and improve drought resilience. The line × tester genetic design discovered variable genetic effects including general combining ability due to lines, and testers and specific combining ability of line × tester in finger millet for agronomic and physiological traits. Additive genetic effect predominantly conditioned the inheritance of days to flowering, ear length, and days to maturity under drought stressed conditions, whereas non-additive effects affected number of productive basal tillers per main plant and days to maturity under non-stressed conditions. Broad-sense heritability for grain yield was higher under stressed (H^2=0.51) than non-stressed (0.13) conditions, necessitating multiple testing environments for drought tolerance evaluation and genotype selection. The study identified lines such as 235700, 234187 and Addis-01 and testers such as Gute, 24394, Bako-09, Mereb-1, and 215982 exhibited higher general combining ability effects for grain yield in a desirable trend. Crosses Wama/Kako-1, 234187/24394, Wama/215982, 235700/213835, Addis-01/213835, Addis-01/Gute, Necho/Gute, and Necho/Kako-1 were identified and exhibited higher specific combining ability effects and heterosis for grain yield under drought stressed conditions. The selected parents and the top crosses are recommended for breeding and selection of new generation and drought-adapted finger millet genotypes.

5.6 References

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Appendix Table 5.1: List of F1 families of finger millet used in the study

Cross/family	Code for family	Cross/family	Code for family
227974/213835	G18	Addis-01/Bako-09	G53
227974/215982	G19	Addis-01/Gute	G54
227974/238335	G20	Addis-01/Kako-1	G55
227974/24394	G21	Addis-01/Meba	G56
227974/AxumColl21	G22	Addis-01/Mereb-1	G57
227974/Bako-09	G23	Necho/213835	G58
227974/Gute	G24	Necho/215982	G59
227974/Kako-1	G25	Necho/238335	G60
227974/Meba	G26	Necho/24394	G61
227974/Mereb-1	G27	Necho/AxumColl21	G62
234187/213835	G28	Necho/Bako-09	G63
234187/215982	G29	Necho/Gute	G64
234187/238335	G30	Necho/Kako-1	G65
234187/24394	G31	Necho/Meba	G66
234187/AxumColl21	G32	Necho/Mereb-1	G67
234187/Bako-09	G33	Tessema/213835	G68
234187/Gute	G34	Tessema/215982	G69
234187/Kako-1	G35	Tessema/238335	G70
234187/Meba	G36	Tessema/24394	G71
234187/Mereb-1	G37	Tessema/AxumColl21	G72
235700/213835	G38	Tessema/Bako-09	G73
235700/215982	G39	Tessema/Gute	G74
235700/238335	G40	Tessema/Kako-1	G75
235700/24394	G41	Tessema/Meba	G76
235700/AxumColl21	G42	Tessema/Mereb-1	G77
235700/Bako-09	G43	Wama/213835	G78
235700/Gute	G44	Wama/215982	G79
235700/Kako-1	G45	Wama/238335	G80
235700/Meba	G46	Wama/24394	G81
235700/Mereb-1	G47	Wama/AxumColl21	G82
Addis-01/213835	G48	Wama / Bako-09	G83
Addis-01/215982	G49	Wama/Gute	G84
Addis-01/238335	G50	Wama/Kako-1	G85
Addis-01/24394	G51	Wama/Meba	G86
Addis-01/AxumColl21	G52	Wama/Mereb-1	G87

Appendix Table 5.2. Mean square and variance components for line x tester mating design for agronomic and physiological traits in finger millet under drought-stressed conditions.

Sources of variation	df	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
		Mean square										
Progenies (F1)	69	414.2**	191.7**	17.0**	13.3**	2.2**	5.9**	180.7**	2.1**	45.5**	0.4**	66.5**
Test sites (E)	1	5263.6**	88253.0**	14.7^{NS}	2.9^{NS}	2.1^{NS}	0.8^{NS}	60182.2**	207.6**	3235.8**	0.2^{NS}	2562.8**
F1 x E	69	212.7**	160.1**	6.6^{NS}	5.5^{NS}	1.0*	4.5**	127.8**	1.6**	32.3**	0.1**	49.9**
Columns (Rep)	2	133.8^{NS}	5.2^{NS}	2.4^{NS}	4.3^{NS}	1.0^{NS}	1.3^{NS}	58.7^{NS}	0.3^{NS}	12.9^{NS}	0.0^{NS}	17.0^{NS}
Rows	28	116.6^{NS}	23.3^{NS}	5.7^{NS}	4.2^{NS}	0.8^{NS}	2.2^{NS}	70.9^{NS}	0.2^{NS}	5.7^{NS}	0.1^{NS}	10.6^{NS}
Replications (E)	1	237.7^{NS}	10.0^{NS}	56.2*	39.0*	0.7^{NS}	13.3*	0.6^{NS}	0.0^{NS}	9.5^{NS}	0.0^{NS}	36.0^{NS}
Parents	16	518.0**	289.7**	23.5**	17.1**	1.5*	5.3^{NS}	202.4**	2.9**	129.0**	0.5**	67.9**
GCA_L	6	1657.1**	1938.5**	135.1**	105.2**	9.5**	22.1**	1341.3**	10.4**	298.8**	2.2**	450.9**
GCA_T	9	548.0**	173.3**	11.25^{NS}	9.2^{NS}	2.7**	6.6**	235.9**	1.5**	35.2**	0.6**	54.3**
$SCA_{L\ x\ T}$	54	314.8**	137.5**	10.8^{NS}	8.7^{NS}	2.6**	6.0**	112.6**	2.3**	42.5**	0.3**	59.8**
GCA_L x E	6	333.1**	434.6**	11.7^{NS}	13.9^{NS}	1.2^{NS}	3.8^{NS}	176.3*	5.0**	58.0**	0.1**	137.6**
GCA_T x E	9	229.0*	94.4**	8.0^{NS}	9.7^{NS}	0.5^{NS}	3.5^{NS}	45.7^{NS}	2.3**	52.7**	0.1*	47.9**
SCA x E	54	196.6**	140.6**	5.9^{NS}	3.9^{NS}	1.1*	4.7**	136.0**	1.1**	26.1**	0.1**	40.5**
Residuals	139	112.2	23.8	8.4	6.5	0.7	2.5	62.2	0.2	4.9	0.1	14.6
		Genetic parameters										
δ^2_A		37.32	40.6	3.02	2.35	0.20	0.49	37.34	0.18	6.82	0.06	7.81
δ^2_D		29.55	0.77	1.23	1.20	0.38	0.33	5.85	0.30	4.10	0.05	4.83
Baker's ratio		0.50	0.98	0.72	0.67	0.32	0.61	0.82	0.41	0.65	0.44	0.65
Broad sense heritability		0.45	0.47	0.46	0.45	0.55	0.3	0.45	0.51	0.53	0.74	0.43

Note: * and **= significant at p<0.05 and 0.01, respectively, GCA_L, and GCA_T, are general combining abilities due to lines and testers, respectively, and $SCA_{L\ x\ T}$ is the specific combining ability due to line x tester interaction, df= degree of freedom, plant height, cm (PTH), days to flowering (DTF), ear length, cm (EL), length of the longest finger, cm (FL), number of productive basal tillers per main plant (NT), the number of fingers on the main ear (NF), days to maturity (DTM), grain yield, t/ha (GY), harvest index (%) (HI), thousand seed weight (g) (TSW), and chlorophyll content at maturity (SPADM, chlorophyll content), δ^2_A and δ^2 are variances due to additive and dominance genetic effects, respectively.

Appendix Table 5.3. Mean square and genetic components for line x tester mating design for agronomic and physiological traits in finger millet under non-stressed conditions

Sources of variation	df	PTH	DTF	EL	FL	NT	NF	DTM	GY	HI	TSW	SPADM
		Mean square										
Progenies (F_1)	69	501.3**	173.6**	31.8**	22.5**	7.3**	8.7**	403.0*	6.5**	43.6**	0.3**	66.8**
Test sites (E)	1	1479.4**	70774.1**	2.1^{NS}	1.7^{NS}	10.3*	10.8^{NS}	30565.8**	1276.6**	9419.8**	1.0**	4982.9**
F_1 x E	69	357.9**	147.0**	14.0**	9.4**	1.8^{NS}	6.4**	311.7^{NS}	6.6**	37.8**	0.4**	77.4**
Columns (Rep)	2	91.5^{NS}	78.6*	8.3^{NS}	10.9*	2.4^{NS}	6.3^{NS}	273.0^{NS}	6.8*	29.4*	0.1^{NS}	16.3^{NS}
Rows	28	62.3^{NS}	31.9^{NS}	5.8^{NS}	4.1^{NS}	2.4^{NS}	3.6^{NS}	200.9^{NS}	1.7^{NS}	6.8^{NS}	0.1^{NS}	27.9^{NS}
Replications (E)	1	542.0**	163.8*	31.4*	10.8^{NS}	0.6^{NS}	1.1^{NS}	834.4^{NS}	53.2**	72.9**	0.6**	50.0^{NS}
Parents	16	805.7**	141.5**	49.4**	25.3**	5.4**	10.2**	741.1**	7.0*	37.2**	1.0**	98.4**
GCA_L	6	3898.6**	1439.1**	243.1**	192.6**	27.4**	36.8**	1196.6**	16.9**	237.0**	2.1**	356.7**
GCA_T	9	1015.6**	173.4**	30.4**	22.3**	10.7**	4.1^{NS}	329.4^{NS}	6.8*	41.0**	0.4**	69.1**
$SCA_{L\,x\,T}$	54	330.0**	163.7**	19.8**	13.2**	7.5**	7.5**	349.3^{NS}	6.6**	40.2**	0.4**	79.0**
GCA_L x E	6	335.4**	634.5**	4.0^{NS}	3.3^{NS}	1.2^{NS}	3.1^{NS}	923.9^{NS}	6.3*	55.0**	0.7**	150.7**
GCA_T x E	9	226.9**	55.0*	19.0**	13.1**	1.2^{NS}	6.5^{NS}	295.8^{NS}	6.9**	31.2**	0.5**	37.3^{NS}
SCA x E	54	379.3**	129.4**	14.6**	8.9**	2.1^{NS}	6.7**	266.8^{NS}	6.3**	35.2**	0.4**	77.1**
Residuals	139	71.4	26.7	5.9	4.5	2.1	3.8	267	2.7	10.8	0.1	23.6
		Genetic parameters										
δ^2_A		120.24	22.26	6.07	4.8	0.67	0.94	6.5	0.27	4.6	0.03	6.17
δ^2_D		12.33	8.58	1.30	1.08	1.35	0.2	20.62	0.08	1.25	0	0.48
Baker's ratio		0.85	0.70	0.82	0.82	0.25	0.85	0.42	0.86	0.81	0.99	0.93
Broad sense heritability		0.53	0.36	0.57	0.62	0.65	0.29	0.15	0.13	0.33	0.17	0.19

Note: * and **= significant at p<0.05 and 0.001, respectively, GCA_L, and GCA_T, are general combining abilities due to lines and testers, respectively, and $SCA_{L\,x\,T}$ is the specific combining ability due to line x tester interaction, df= degree of freedom, plant height, cm (PTH), days to flowering (DTF), ear length, cm (EL), length of the longest finger, cm (FL), number of productive basal tillers per main plant (NT), the number of fingers on the main ear (NF), days to maturity (DTM), grain yield, t/ha (GY), harvest index (%) (HI), thousand seed weight (g) (TSW), and chlorophyll content at maturity (SPADM, chlorophyll content), δ^2_A and δ^2_D are variances due to additive and dominance genetic effects, respectively.

Appendix Table 5.4. Mean performance of F_1 families of finger millet under drought-stressed conditions for agronomic and physiological traits

Cross/family	PTH	DTF	EL	FL	NF	NT	DTM	GY	HI (%)	TSW	SPADM
227974/213835	123.0	91.8	14.3	12.8	12.3	2.0	120.3	1.7	7.3	1.5	27.0
227974/215982	126.0	85.8	13.5	11.0	9.8	1.5	115.0	1.2	5.2	1.0	17.4
227974/238335	109.3	81.3	13.0	11.5	8.8	1.8	110.5	1.3	6.0	0.9	27.4
227974/24394	128.0	92.0	13.8	11.0	10.3	2.0	121.0	1.9	7.4	1.7	19.7
227974/AxumColl21	114.0	94.0	13.8	12.4	11.3	1.5	121.3	1.4	6.4	0.8	21.6
227974/Bako-09	105.0	83.5	7.9	6.8	11.8	2.8	113.5	1.6	9.7	1.2	33.0
227974/Gute	136.0	92.0	12.0	10.5	9.0	2.3	120.5	0.9	4.0	1.4	24.5
227974/Kako-1	109.0	94.0	13.0	10.0	14.0	3.5	110.0	1.0	3.6	1.4	26.1
227974/Meba	140.3	98.3	12.6	11.0	9.3	2.3	127.8	2.4	10.0	0.8	22.4
227974/Mereb-1-1	126.0	95.5	12.9	11.0	10.3	2.5	127.3	1.7	6.8	1.0	21.1
234187/213835	108.0	95.3	13.3	11.0	11.0	1.8	115.5	1.5	8.4	1.6	28.0
234187/215982	112.8	89.8	10.5	9.0	8.3	2.5	118.3	2.0	9.3	1.6	27.9
234187/238335	116.0	87.3	12.0	9.4	9.0	2.5	115.8	0.8	3.2	1.4	25.1
234187/24394	111.0	85.0	11.3	9.8	8.5	1.3	113.5	2.2	10.3	1.4	27.9
234187/AxumColl21	116.0	89.0	13.3	10.5	8.3	2.5	117.5	1.3	7.5	1.5	27.0
234187/Bako-09	105.3	93.8	13.3	10.8	10.5	3.5	109.3	2.3	9.1	1.3	27.9
234187/Gute	128.5	89.5	12.3	10.0	8.5	3.5	118.0	1.8	7.7	1.4	30.1
234187/Kako-1	111.3	93.0	11.5	10.5	9.5	1.3	120.8	2.1	11.2	0.8	26.2
234187/Meba	112.3	93.5	12.0	10.1	9.5	3.0	113.5	1.8	10.5	1.2	25.4
234187/Mereb-1-1	116.0	90.0	12.3	11.0	9.8	2.0	118.5	3.5	15.5	1.6	31.5
235700/213835	106.3	69.8	8.6	7.0	10.5	2.5	99.8	3.7	17.9	2.0	33.7
235700/215982	96.0	72.0	6.8	5.8	10.3	1.0	102.0	3.5	18.9	1.4	31.7
235700/238335	108.0	77.0	7.5	5.9	8.8	2.0	107.0	4.4	15.1	1.7	27.3
235700/24394	132.3	59.8	13.0	12.3	10.3	3.3	89.8	2.8	12.7	1.3	20.1
235700/AxumColl21	112.0	80.3	9.8	8.1	10.5	3.5	110.3	0.8	4.0	2.0	23.1
235700/Bako-09	99.0	71.8	8.3	6.5	9.3	1.3	101.8	2.6	11.9	1.6	28.0
235700/Gute	104.8	84.3	8.3	7.1	10.3	2.3	112.8	2.3	13.2	2.0	30.8
235700/Kako-1	99.3	75.3	8.3	6.9	9.3	2.3	105.3	2.4	9.4	1.9	26.6
235700/Meba	114.0	72.0	10.5	8.5	10.5	3.8	102.0	2.6	12.7	2.1	31.1
235700/Mereb-1-1	100.5	84.8	6.3	5.3	12.0	4.8	113.3	2.4	12.8	1.4	40.7
Addis-01/213835	103.3	95.8	11.5	10.3	9.8	1.3	124.0	2.5	15.6	1.6	22.8
Addis-01/215982	111.0	95.8	6.5	5.5	7.3	2.0	117.8	2.4	10.2	1.5	16.9
Addis-01/238335	108.8	90.3	11.3	8.5	10.0	1.5	118.8	1.4	7.1	1.2	20.2
Addis-01/24394	91.0	98.8	6.6	5.8	7.3	4.0	119.0	0.8	3.9	1.2	29.7
Addis-01/AxumColl21	100.5	95.5	7.8	6.5	8.3	1.3	118.5	2.4	10.3	1.4	19.3
Addis-01/Bako-09	88.0	77.5	7.3	5.9	11.3	1.5	107.5	2.2	13.1	0.9	20.1
Addis-01/Gute	99.3	95.5	6.8	5.5	7.5	1.0	115.5	2.2	8.9	1.2	18.7
Addis-01/Kako-1	107.5	93.5	7.5	5.9	7.8	1.8	110.3	1.7	5.6	1.6	19.1
Addis-01/Meba	105.8	89.3	6.3	5.4	7.8	3.0	117.8	1.8	8.5	1.0	25.4
Addis-01/Mereb-1-1	109.3	97.0	6.3	6.4	8.3	2.0	123.8	1.6	6.3	1.1	28.1
Necho/213835	94.5	96.5	9.3	9.0	12.5	1.3	121.0	0.4	2.1	1.7	17.3
Necho/215982	104.5	102.0	9.5	8.0	8.8	1.8	128.3	0.5	1.6	1.5	18.4
Necho/238335	122.5	92.5	13.9	11.9	9.0	2.0	118.5	0.7	3.0	0.7	21.9
Necho/24394	103.5	91.8	9.0	9.0	7.5	1.3	118.3	0.5	1.8	1.3	22.2
Necho/AxumColl21	123.0	88.8	12.8	11.3	9.3	1.3	128.8	0.2	0.5	1.1	20.3
Necho/Bako-09	111.8	94.0	13.5	11.8	9.3	1.3	122.5	2.3	10.1	0.6	25.4
Necho/Gute	123.3	93.0	11.8	8.8	8.3	2.3	121.5	2.0	6.9	1.4	19.1
Necho/Kako-1	117.3	95.0	10.5	8.0	9.8	1.8	118.5	1.4	5.6	1.3	22.8
Necho/Meba	107.0	95.8	9.9	8.3	10.0	1.3	111.8	1.2	4.0	0.9	23.6
Necho/Mereb-1-1	116.0	95.3	11.0	10.5	9.5	3.8	121.3	1.3	4.5	1.1	22.7
Tessema/213835	123.8	96.5	8.6	6.5	9.0	1.0	128.3	1.4	6.2	1.0	17.4
Tessema/215982	116.0	96.0	9.5	7.8	9.3	1.0	124.5	2.7	10.8	2.3	17.9
Tessema/238335	126.0	92.8	10.3	8.4	8.0	0.8	121.3	2.6	12.0	1.3	20.9
Tessema/24394	116.3	95.8	7.8	7.0	8.3	1.8	117.0	1.4	6.1	1.5	21.9
Tessema/AxumColl21	121.0	80.5	8.5	7.3	9.0	2.0	110.5	3.2	13.0	2.2	23.9
Tessema/Bako-09	107.8	88.8	9.1	7.8	8.3	1.3	117.3	1.3	5.6	1.6	20.8

Tessema/Gute	111.3	97.8	9.4	7.5	10.0	1.8	121.8	1.8	7.9	1.9	23.8
Tessema/Kako-1	115.5	96.0	7.9	6.6	10.0	1.0	123.0	1.4	6.3	2.0	25.9
Tessema/Meba	117.5	99.8	10.0	8.0	10.5	0.3	120.5	1.5	4.2	1.5	21.0
Tessema/Mereb-1-1	102.5	101.3	8.8	6.9	8.8	1.0	124.8	1.1	4.1	1.6	21.2
Wama/213835	102.0	102.3	7.6	7.3	7.3	1.5	127.8	0.8	3.7	1.5	24.0
Wama/215982	112.3	94.8	11.8	10.5	9.8	2.3	122.5	2.5	8.8	1.3	33.2
Wama/238335	118.5	84.0	9.8	8.1	9.0	1.8	114.0	2.4	10.1	1.4	21.7
Wama/24394	127.3	97.5	11.0	9.0	10.0	2.8	123.3	1.6	8.8	1.4	29.4
Wama/AxumColl21	120.0	102.0	13.5	11.8	11.5	2.0	129.5	0.9	4.6	1.8	29.2
Wama/Bako-09	104.8	95.0	9.3	8.1	9.0	0.5	113.5	3.4	13.2	1.5	31.3
Wama/Gute	126.8	77.5	10.8	9.1	9.0	1.5	107.5	1.9	6.0	1.9	29.8
Wama/Kako-1	135.3	92.3	9.1	7.3	7.5	1.0	120.8	2.3	7.2	1.8	25.8
Wama/Meba	111.5	84.0	11.0	10.3	8.5	2.0	113.3	0.7	4.4	1.1	23.5
Wama/Mereb-1-1	116.3	96.5	7.8	6.4	7.3	1.8	124.3	1.3	4.6	1.5	27.9
Mean	112.9	90.1	10.2	8.7	9.4	2.0	116.8	1.8	8.1	1.4	24.8
Minimum	88.0	59.8	6.3	5.3	7.3	0.3	89.8	0.2	0.5	0.6	16.9
Maximum	140.3	102.3	14.3	12.8	14.0	4.8	129.5	4.4	18.9	2.3	40.7

Note: Plant height, cm (PTH), days to flowering (DTF), ear length, cm (EL), length of the longest finger, cm (FL), number of productive basal tillers per main plant (NT), the number of fingers on the main ear (NF), days to maturity (DTM), grain yield, t/ha (GY), harvest index (%) (HI), thousand seed weight (g) (TSW), and chlorophyll content at maturity (SPADM, chlorophyll content).

Appendix Table 5.5. Mean performance of crossed under non- stressed conditions for agronomic and physiological traits

Cross/family	PTH	DTF	EL	FL	NF	NT	DTM	GY	HI(%)	TSW	SPADM
227974/213835	120.8	92.8	16.5	14.3	11.5	4.3	131.3	5.1	11.9	1.9	35.3
227974/215982	128.5	84.5	14.0	11.3	10.0	3.8	125.8	3.2	11.7	1.7	34.5
227974/238335	125.3	92.8	15.8	14.3	10.3	2.8	132.0	3.8	10.8	1.9	34.7
227974/24394	137.5	93.8	15.0	13.8	9.0	5.5	138.5	4.2	12.8	2.1	31.0
227974/AxumColl21	127.3	91.0	12.5	10.3	11.3	4.3	128.0	3.1	10.3	1.9	27.9
227974/Bako-09	104.3	74.0	6.5	5.3	10.5	5.3	126.0	4.8	16.2	2.2	46.2
227974/Gute	139.3	93.0	16.9	14.5	10.5	7.3	132.5	3.9	13.0	1.7	34.0
227974/Kako-1	130.5	96.8	13.5	14.0	11.5	4.5	145.0	3.8	12.0	2.0	31.2
227974/Meba	142.3	102.0	16.0	13.3	11.0	4.3	141.3	5.5	16.1	2.0	31.6
227974/Mereb-1	142.0	96.3	14.3	12.3	10.3	4.0	138.5	4.3	11.4	1.8	30.0
234187/213835	120.0	93.0	12.5	12.0	11.0	4.5	127.5	4.2	13.4	2.0	35.6
234187/215982	116.8	89.5	13.5	11.0	9.5	5.3	139.5	5.8	17.3	2.2	41.6
234187/238335	117.5	90.8	11.6	12.3	10.3	6.5	130.5	6.1	15.5	2.4	32.1
234187/24394	116.5	86.3	13.5	11.0	8.3	3.5	145.5	5.7	20.7	2.3	42.3
234187/AxumColl21	130.3	92.5	16.8	14.3	9.0	6.5	129.5	5.8	17.2	1.9	33.1
234187/Bako-09	108.5	100.3	11.5	9.9	10.0	8.5	141.0	3.6	11.8	1.7	36.4
234187/Gute	124.8	91.3	11.3	10.1	7.5	6.3	120.8	5.5	13.3	2.3	40.3
234187/Kako-1	121.3	93.8	12.0	10.5	10.3	3.0	135.3	5.0	12.4	2.2	32.3
234187/Meba	113.3	91.8	12.8	10.5	9.8	6.5	121.8	5.4	18.0	2.0	31.1
234187/Mereb-1	110.8	89.5	12.3	10.5	7.0	5.5	129.3	4.0	14.4	1.7	32.3
235700/213835	100.5	74.0	5.5	5.1	12.5	5.8	118.3	6.1	23.5	2.1	40.8
235700/215982	84.0	75.3	7.0	6.5	8.3	2.5	105.3	4.5	16.0	1.8	37.9
235700/238335	107.0	74.5	7.0	5.5	9.5	6.5	120.3	5.9	15.3	2.2	37.5
235700/24394	138.8	65.5	15.5	14.1	9.8	6.0	109.0	6.3	13.8	2.0	26.5
235700/AxumColl21	129.0	83.8	12.3	9.8	11.5	5.5	137.0	2.9	8.8	2.2	29.5
235700/Bako-09	100.8	71.5	7.3	6.0	10.5	4.8	122.0	5.6	18.0	1.9	38.0
235700/Gute	107.8	84.3	7.3	6.3	13.3	4.8	114.3	6.1	19.5	2.6	38.8
235700/Kako-1	106.8	77.0	10.3	7.4	10.3	5.5	116.3	4.3	13.5	2.8	34.0
235700/Meba	117.8	75.8	8.0	7.0	9.0	8.0	105.8	5.5	18.5	2.7	31.9
235700/Mereb-1	100.5	95.8	5.0	4.8	13.0	10.8	139.5	5.3	14.6	1.7	35.0
Addis-01/213835	109.8	99.5	7.8	6.8	8.5	3.5	129.5	5.6	16.9	2.1	28.0
Addis-01/215982	107.3	94.3	7.0	5.8	8.5	3.5	135.0	4.8	15.7	1.7	22.9
Addis-01/238335	113.8	93.5	7.8	5.8	8.0	3.8	134.0	6.4	17.4	1.8	33.7
Addis-01/24394	113.0	102.3	7.5	6.0	9.0	7.0	140.0	5.2	16.3	1.6	34.4
Addis-01/AxumColl21	114.0	96.3	9.8	8.8	8.0	5.3	144.8	4.3	13.6	2.4	29.1

Addis-01/Bako-09	95.3	76.8	8.0	6.3	10.5	4.5	106.8	2.7	10.2	1.9	28.3
Addis-01/Gute	113.0	94.5	6.8	6.8	7.0	3.5	147.5	5.5	17.1	1.9	30.5
Addis-01/Kako-1	106.3	97.8	6.3	5.8	7.5	3.8	139.8	5.5	14.9	2.4	27.4
Addis-01/Meba	111.3	89.5	6.8	5.5	7.8	6.0	129.3	6.1	13.4	2.0	33.8
Addis-01/Mereb-1	109.5	96.3	7.5	5.5	10.0	4.0	135.3	5.6	15.9	2.1	28.7
Necho/213835	119.0	95.3	10.8	9.8	8.5	2.5	128.8	1.3	4.4	2.3	25.6
Necho/215982	109.8	102.0	12.5	9.5	11.0	4.0	139.8	2.1	5.3	2.1	25.4
Necho/238335	117.3	91.5	14.0	11.5	10.5	3.3	121.5	2.5	7.1	1.6	29.6
Necho/24394	107.5	100.0	14.0	12.0	12.8	3.0	140.3	3.8	6.0	2.5	39.0
Necho/AxumColl21	122.5	92.8	14.8	12.0	9.8	5.3	142.5	4.4	11.2	2.1	27.0
Necho/Bako-09	120.8	96.5	12.5	10.3	10.0	3.8	134.5	4.3	13.7	2.7	30.0
Necho/Gute	141.3	90.5	9.8	9.0	9.0	4.5	130.5	7.3	14.8	2.0	30.9
Necho/Kako-1	129.0	93.5	14.8	12.3	10.0	4.0	131.8	2.0	5.7	2.2	28.5
Necho/Meba	125.8	102.3	14.0	10.5	11.5	2.8	141.8	4.2	11.3	2.0	30.1
Necho/Mereb-1	120.8	97.8	11.3	9.3	9.3	7.0	127.8	3.6	10.4	1.9	32.6
Tessema/213835	135.8	97.8	9.8	9.0	10.0	2.8	133.8	4.9	13.1	2.5	23.0
Tessema/215982	126.3	96.8	8.3	7.3	8.5	2.3	126.8	6.0	14.3	2.6	24.4
Tessema/238335	132.8	86.3	10.0	9.0	9.5	4.3	116.3	4.3	12.9	2.2	27.5
Tessema/24394	133.0	92.0	13.0	10.0	9.3	3.8	128.8	5.1	14.6	2.4	26.9
Tessema/AxumColl21	129.3	81.3	12.0	10.5	11.0	5.8	140.5	5.5	13.8	2.9	34.4
Tessema/Bako-09	119.8	91.8	12.5	10.8	9.5	3.8	121.8	2.5	7.9	2.0	29.1
Tessema/Gute	133.8	89.5	8.8	9.3	8.3	4.3	119.5	6.4	17.4	2.8	36.2
Tessema/Kako-1	140.8	93.0	8.0	7.3	8.8	4.5	132.3	3.3	7.9	3.0	37.4
Tessema/Meba	116.5	97.5	9.8	8.5	7.5	2.8	147.0	3.7	8.7	2.4	29.5
Tessema/Mereb-1	127.0	100.3	8.3	7.0	8.0	3.3	130.3	6.4	14.8	3.1	24.4
Wama/213835	122.0	92.3	7.8	6.6	8.0	3.8	135.5	5.8	14.5	2.1	28.1
Wama/215982	126.0	91.3	13.5	10.8	9.8	5.0	121.3	6.4	17.1	2.8	41.2
Wama/238335	152.0	86.0	9.5	8.3	8.3	4.3	134.0	6.4	14.3	2.2	30.9
Wama/24394	136.5	103.3	7.8	6.3	7.5	4.8	134.8	4.8	12.6	1.8	34.7
Wama/AxumColl21	133.0	90.0	11.8	9.8	11.5	4.0	120.0	1.9	6.1	2.2	39.2
Wama/Bako-09	114.3	94.8	10.0	7.5	8.3	3.0	133.3	6.4	15.6	2.7	38.9
Wama/Gute	136.5	80.0	14.8	11.8	10.8	5.3	126.3	6.0	16.1	2.1	36.1
Wama/Kako-1	138.8	93.5	8.5	7.8	6.0	3.5	143.8	7.2	15.1	2.7	39.7
Wama/Meba	124.3	80.8	6.0	7.0	9.0	5.5	110.8	2.1	7.6	2.2	33.5
Wama/Mereb-1	151.0	90.8	8.5	7.5	6.3	4.8	129.5	4.8	13.1	2.5	35.4
Mean	121.5	90.6	10.8	9.3	9.5	4.7	130.2	4.7	13.4	2.2	32.7
Minimum	84.0	65.5	5.0	4.8	6.0	2.3	105.3	1.3	4.4	1.6	22.9
Maximum	152.0	103.3	16.9	14.5	13.3	10.8	147.5	7.3	23.5	3.1	46.2

Note: Plant height, cm (PTH), days to flowering (DTF), ear length, cm (EL), length of the longest finger, cm (FL), number of productive basal tillers per main plant (NT), the number of fingers on the main ear (NF), days to maturity (DTM), grain yield, t/ha (GY), harvest index (%) (HI), thousand seed weight (g) (TSW), and chlorophyll content at maturity (SPADM, chlorophyll content).

Chapter 6: An overview of research findings and implications for breeding

6.1 Introduction and objectives of the study

Finger millet is a high-potential, climate-resilient, and nutrient-rich small grain cereal crop suitable for diverse product development, including food, feed, and value-added industrial raw materials. The nutritional profile and human health benefits of finger millet make it a superfood to combat malnutrition and other ailments. However, finger millet productivity in Ethiopia is low, <2.5 t/ha, compared to the attainable grain yields of 6-8 t/ha. The yield gap is attributed to several production constraints, such as biotic and abiotic stresses, and various socio-economic factors, including poor access to improved seeds and production inputs, and use of traditional agronomic management practices. Drought stress is the leading constraint affecting finger millet production and other main crops in Ethiopia. Ethiopia is the centre of genetic diversity of finger millet, providing unique genetic resources and genes for current and future breeding programmes. Hence, this study aimed to develop high-yielding, nutritious and drought-resilient finger millet genotypes for marginal agro-ecologies in Ethiopia by integrating farmer-centred trait priorities with high-throughput phenotyping, genomic analysis and crosses using genetically complementary germplasm. This section of the study summarised the research objectives and highlighted the core findings and their implications for finger millet breeding, emphasising high-yield potential, nutritionally rich and drought-tolerant genotypes.

The overall objectives of this study were:

1. To systematically assess finger millet production systems in Ethiopia by identifying key production constraints, opportunities, and farmer-preferred traits and to inform ideotype and variety design for targeted breeding programs.

2. To evaluate and characterise genetically diverse Ethiopian finger millet accessions for agronomic performance, drought response, and grain nutritional compositions under contrasting moisture regimes, and to identify superior genotypes for use in breeding and/or production.
3. To analyse the population structure of the Ethiopian finger millet landraces and to identify robust marker-trait associations and quantitative trait nucleotides (QTNs) and haplotypes linked to key agronomic and nutritional traits, and
4. To determine the combining ability, heterosis, and gene action of selected finger millet parents for economic traits in hybrid combinations to guide the selection of the best families and new breeding populations.

6.2 Research findings in brief

6.2.1 Finger millet production in Ethiopia: opportunities, problem diagnosis, key challenges, and recommendations for breeding.

A participatory rural appraisal (PRA) study was undertaken in six selected districts of the Southern Nation Nationalities People Region (SNNPR) and Oromia Region in Ethiopia. The PRA study was conducted using 240 and 180 participant farmers through a semi-structured questionnaire and focus group discussion, respectively. The core findings of this study were:

- Finger millet was the most important crop in the study areas grown mainly for a combination of uses, including for food, feed and cash (reported by 38.8% of respondent farmers), food and feed (14.5%), food and cash (13.7%), food (11.5%) and food, cash, feed and construction material (9.7%).
- The main constraints to finger millet production in the study areas were drought stress (reported by 41.3% respondents), lack of improved varieties (12.9%), lack of financial resources (11.3%), small land holdings (10.8%), limited access to seed (10.0%), a shortage of fertilizers (5.4%), poor soil fertility (4.6%), shortage of draught power (1.3%), labour shortages (1.3%) and high labour costs (1.3%).
- The most important farmer-preferred traits in a finger millet variety were high grain yield, compact head shape, ‘enjera’-making quality, high marketability and early maturity, resolved through principal component analysis.

- The above-mentioned production constraints and farmer-preferred traits are strategic drivers to enhance finger millet productivity and need to be incorporated into Ethiopia's finger millet breeding and technology development.

6.2.2 Profiling Ethiopian finger millet (*Eleusine coracana*) accessions for major agronomic traits and nutrient composition under varying growing conditions.

A total of 448 Ethiopian finger millet accessions (landraces and improved varieties) were evaluated under field conditions for agronomic performance, drought response and nutrient composition. The study was conducted across three moisture regimes: non-stressed (Arsinegelle: denoted as AN), moderately drought-prone (Maitsebri: SH), and severely drought-stressed (Meiso: MI). The major findings of the study were:

- Significant variations were recorded among genotype, environment, and genotype × environment interaction for all assessed traits. Grain yield (GY) declined by ~60% at the MI site.
- The test genotypes varied considerably at MI for days to 50% flowering (DTF) (78.5–107.5 days), days to maturity (DTM) (101.0–149.5 days), GY (0.5-3.2 t/ha), iron (Fe) (53.6 – 81.0 ppm) and zinc (Zn) (67.8-83.1 ppm) contents suggesting considerable genetic variation for selection.
- Black-seeded genotypes maintained higher GY and Fe/Zn under drought, while red-seeded types flowered and matured earlier and produced larger seed size.
- Broad-sense heritability was > 60% for drought tolerance (Drt) score, DTF, and DTM, but <30% for plant height, starch content and GY.
- GY was negatively correlated with DTF, DTM, Drt and stay green traits, but positively correlated with seed weight across environments.
- Principal component analysis explained >67% of the variance for some traits across test sites, and hierarchical clustering grouped genotypes into four genetic clusters.
- Eight accessions, G141 (219819), G423 (AxumColl37), G297 (238326), G247 (237449), G171 (229726), G204 (234176), G294 (238323), and G46 (211473) were identified as promising candidates for breeding and further validation through multi-environment testing and variety evaluation procedures prior to potential release.

6.2.3 Genetic structure of Ethiopian finger millet landraces and genome-wide association mapping for agronomic and nutritional traits.

A total of 448 finger millet accessions were evaluated across three contrasting environments to characterise for their agronomic performance, drought response, and grain micronutrient compositions. A subset of 391 genotypes from this panel was skim-sequenced, generating 24,112 high-quality Single Nucleotide Polymorphisms (SNPs) that were employed for population structure, association mapping and haplotype analysis. This study found that:

- Genome-wide association study (GWAS) resolved 70 marker-trait associations, including 15 major QTNs with more than 30% phenotypic variance explained (PVE) for all assessed traits except stay-green score and grain yield.
- Pleiotropic major QTNs were identified for 50% days to flowering/days to maturity and high Fe/Zn contents on chromosomes 9B and 2B, respectively.
- Haplotype analysis of major QTNs identified 54 significant haplotype blocks and 2 additional haplotypes, many of which originated from landraces collected in Tigray and Amhara regions.
- The genetic profiles provide invaluable insights for targeted breeding to enhance finger millet resilience, nutritional profile, and grain yield.

6.2.4 Hybrid performance in finger millet (*Eleusine coracana*) for grain yield and component traits.

This study appraised hybrid performance in finger millet for grain yield and component traits. A 7 × 10 line × tester mating design was used, and the resultant 70 F_1 hybrids and 17 parents were evaluated under well-watered (NST) and drought-stress (ST) conditions across greenhouse and field environments. The major findings of the study were:

- Significant variations ($p < 0.001$) were observed among lines, testers and their interactions for the assessed traits.
- Additive genetic effect predominantly conditioned the inheritance of DTF, ear length (EL), DTM under ST conditions, whereas non-additive genes affected the number of tillers (NT) and DTM under NST conditions.

- Broad-sense heritability for GY was higher under ST (H^2=0.51) than NST (0.13) conditions, necessitating multiple testing environments for drought tolerance evaluation and selection.
- Lines such as 235700, 234187 and Addis-01 and testers such as Gute, 24394, Bako-09, Mereb-1, and 215982 exhibited higher general combining ability effects for GY in a desirable trend.
- Crosses Wama/Kako-1, 234187/24394, Wama/215982, 235700/213835, Addis-01/213835, Addis-01/Gute, Necho/Gute, and Necho/Kako-1 exhibited higher specific combining ability effects and heterosis for GY under ST conditions.
- The selected parents and the top crosses are recommended for breeding and selection of new generation and drought-adapted finger millet genotypes.

6.3 Implications of the research findings to breeding finger millet for drought tolerance

The following implications for breeding were noted:

- The participatory rural appraisal identified drought stress as the major production constraint and highlighted farmers' strong preference for high-yielding, early-maturing, compact-headed, and high-quality enjera-making varieties, underscoring the need for a demand-led breeding approach that integrates farmers' priorities into drought-tolerance improvement. These findings provide a strategic framework for designing end-user-oriented breeding that combines yield, drought-adaptation, and market traits to enhance the adoption and impact of newly developed varieties in marginal environments.

- The significant genotype, environment, genotype x environment interactions for agronomic and nutrition traits revealed a rich reservoir of genetic diversity for drought tolerance within Ethiopian finger millet germplasms. High heritability for key drought-responsive traits (DTF, DTM, and Drt) and significant trait associations among several agronomic and drought-response traits under low-moisture growing conditions provide opportunities for indirect selection. The identification of superior genotypes resilient to moisture deficit provides parental sources for breeding programs targeting water-limited environments.

- The genome-wide association analysis identified several quantitative trait nucleotides (QTNs) and haplotypes linked with yield, phenology, and micronutrient traits, confirming the genetic basis of drought adaptation and nutritional quality in finger millet. The distinct population structure and region-specific haplotype diversity emphasize the potential of Ethiopian landraces as reservoirs of adaptive alleles and provide molecular markers-assisted and genomic selection, thereby accelerating the efficiency and precision of drought-tolerance breeding.

- The research highlights that both additive and non-additive gene actions govern key agronomic traits under drought stress, implying that breeding for drought-tolerant finger millet should integrate recurrent selection using high general combiner parents with hybridization among superior specific combiners to develop high-yielding and drought-resilient genotypes adapted to water-limited environments.

- In sum, the present study identified the major production constraints, traits of economic value of finger millet, identified unique genetic resources and genes and developed new breeding populations with better agronomic performance, nutrient compositions and drought tolerance. New breeding populations were developed integrating farmers' preferred traits and will be evaluated across representative growing sites for selection and release in the marginal production areas in Ethiopia and similar agro-ecologies.