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**GENOME-WIDE ASSOCIATION STUDY OF ETHIOPIAN DURUM WHEAT (*TRITICUM TURGIDUM* SSP. *DURUM*) ACCESSIONS UNDER DROUGHT STRESS AND NON-STRESS CONDITIONS**

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VORGELEGT VON  
HERRN KEFYALEW NEGISHO BAYISSA  
GEB. AM 05.09.1973 IN OROMIA, ÄTHIOPIEN

Reviewers:

Prof. Dr. Frank Ordon, Quedlinburg

Prof. Dr. Klaus Pillen, Halle

Prof. Dr. Rod Snowdon, Giessen

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## ABBREVIATIONS

### Abbreviations

**ABA**, Abscisic acid

**AFLP**, amplified fragment length polymorphism

**AM**, Association mapping

**AMOVA**, Analysis of molecular variance

**ANOVA**, Analysis of variance

**CCDS**, Climate chamber drought stress

**CCNS**, Climate chamber non-stress

**CIMMYT**, Centro Internacional de Mejoramiento de Maíz y Trigo

**CSA**, Central statistical authority

**DArT**, Diversity arrays technology

**DGF**, Days to grain filling

**DNA**, Deoxyribonucleic acid

**DSI**, Drought susceptibility index

**DZARC**, Debre Zeit Agricultural Research Center

**EBI**, Ethiopian Biodiversity Institute

**EIAR**, Ethiopian Institute of Agricultural Research

**ETDWL**, Ethiopian durum wheat landraces

**FAO**, Food and Agriculture Organization

**FDR**, False discovery rate

**FDS**, Field drought stress

**FNS**, Field non-stress

**GMP**, Geometric mean production

**GWAS**, Genome-wide association study

**GB**, Grain biomass

**GY**, Grain yield

**HI**, Harvest index

**ICARDA**, International Center for Agricultural Research in the Dry Areas

**LD**, Linkage disequilibrium

**LOD**, Logarithm of odds

**Lsmeans**, Least squares means

**MAF**, Minor allele frequency

**MAS**, Marker assisted selection

## **ABBREVIATIONS**

**MTA**, Marker trait analysis

**p**, Probability value

**PCA**, Principal component analysis

**PVE**, Phenotypic variance explained

**QTL**, Quantitative trait locus

**r**, Pearson's correlation coefficient

**RDI**, Relative drought index

**RFLP**, Restriction fragment length polymorphism

**SNP**, Single nucleotide polymorphism

**SPAD**, Soil plant analysis development

**SPS**, Seed per spike

**SSA**, Sub Saharan Africa

**SSR**, Simple sequence repeat

**STI**, Stress tolerance index

**TKW**, Thousand kernel weight

**TOL**, Tolerance index

**YSI**, Yield stability index

## ABBREVIATIONS

### Abkürzungen

**ABA**, Abscisinsäure

**AFLP**, amplifizierter Fragmentlängen-Polymorphismus

**AM**, Assoziationskartierung

**AMOVA**, Analyse der molekularen Varianz

**ANOVA**, Varianzanalyse

**CCDS**, Klimakammer-Trockenstress

**CCNS**, Klimakammer Nicht-Stress

**CIMMYT**, Internationales Zentrum für Mais- und Getreideanbau (Centro Internacional de Mejoramiento de Maíz y Trigo)

**CSA**, Zentrale Statistikbehörde

**DArT**, Diversitäts-Array-Technologie

**DGF**, Tage bis zur Kornfüllung

**DNA**, Desoxyribonukleinsäure

**DSI**, Index der Trockenheitsanfälligkeit

**DZARC**, Landwirtschaftliches Forschungszentrum Debre Zeit

**EBI**, Äthiopisches Institut für Biodiversität

**EIAR**, Äthiopisches Institut für landwirtschaftliche Forschung

**ETDWL**, Äthiopische Hartweizen-Landrassen

**FAO**, Ernährungs- und Landwirtschaftsorganisation

**FDR**, Falsche Entdeckungsrate

**FDS**, Feld-Dürre-Stress

**FNS**, Feld-Nicht-Stress

**GMP**, Geometrisches Produktionsmittel

**GWAS**, Genomweite Assoziationsstudie

**GB**, Körner-Biomasse

**GY**, Körnerertrag

**HI**, Ernte-Index

**ICARDA**, Internationales Zentrum für Agrarforschung in den Trockengebieten

**LD**, Kopplungsungleichgewicht (Linkage disequilibrium)

**LOD**, Logarithmus der Quoten

**Lsmeans**, Mittelwerte der kleinsten Quadrate

## ABBREVIATIONS

**MAF**, Minor-Allel-Häufigkeit

**MAS**, Markerunterstützte Selektion

**MTA**, Marker-Merkmal-Analyse

**p**, Wahrscheinlichkeitswert

**PCA**, Hauptkomponentenanalyse

**PVE**, Erklärte phänotypische Varianz

**QTL**, Quantitativer Merkmalslocus

**r**, Pearsonscher Korrelationskoeffizient

**RDI**, Relativer Trockenheitsindex

**RFLP**, Restriktionsfragmentlängen-Polymorphismus

**SNP**, Einzelnukleotid-Polymorphismus

**SPAD**, Entwicklung der Boden-Pflanzen-Analyse

**SPS**, Saatgut pro Ähre

**SSA**, Afrika südlich der Sahara

**SSR**, Einfache Sequenzwiederholung

**STI**, Stresstoleranz-Index

**TKW**, Tausend-Kern-Gewicht

**TOL**, Toleranz-Index

**YSI**, Ertragsstabilitätsindex



# GENERAL INTRODUCTION

## 1 General introduction

### 1.1 Durum wheat production and importance

Durum wheat (*Triticum turgidum* ssp. *durum* (Desf.) is the 10th most important crop worldwide with an annual production of 37 million tons (Ranieri, 2015; Taylor and Koo, 2015; FAO, 2018). It was domesticated between 12,000 and 10,000 years ago in the West Levantine from wild emmer (*Triticum turgidum* ssp. *dicoccoides*). These regions include countries like Israel, Jordan, Syria, Lebanon, eastern Turkey, western Iran, and northern Iraq (Ozkan et al., 2010). Then, secondary domestication, i.e. from emmer to naked forms and durum wheat (*Triticum turgidum* ssp. *durum*) followed (Gioia et al., 2015). The allotetraploidization event took place after a cross between the two diploid species: *T. urartu* (genome AA) and an unknown close relative of *Aegilops speltoides* (genome BB) (Marcussen et al., 2014). Consequently, durum wheat has an allotetraploid genome (AABB,  $2n = 4x = 28$ , seven homoeologous groups with 12 gigabases genome size) (Borrill et al., 2015). It is predominantly a self-pollinated species and during flowering, the flower generally remains closed (cleistogamous flower), and the three anthers burst and release pollen (anthesis) (deVries, 1971). Durum wheat is the primary wheat for pasta and semolina production and the second most cultivated wheat after bread wheat (*Triticum aestivum* L.) for human consumption and commercial production (Oliveira et al., 2012). Durum wheat accounts from 5% (Haugrud et al., 2023) to 8% of the total annual wheat production (FAO, 2018). In Ethiopia, wheat (both bread and durum) is produced by around 4.62 million households with an estimated land area of 1.7 million hectares and a mean national yield of 2.7 t/ha (CSA, 2018). From this, durum accounts for 0.6 million hectares (Kabbaj et al., 2017; Alemu et al., 2019). In Ethiopia, durum wheat is not only a staple crop for food security but also is becoming a major cash crop having 10 to 20% extra prices compared to bread wheat (Sall et al., 2019). Even though there is over 10 million ha of land suitable for wheat production, wheat acreage in Ethiopia is only 1.7 million ha (CSA, 2018) and the country still imports wheat to meet the national wheat demand (for food and industry). Despite the availability of fertile soil in the lowland areas of the country, these places are prone to drought stress. Drought stress is one of the major limiting factors for the expansion of the production of wheat from the traditionally highland areas to the lowland areas. On the other hand, in Ethiopia, only less than 1% of cereal acreage is irrigated (Taffesse et al., 2011; Mann and Warner, 2017) leaving the country's agriculture very much dependent on rain. Hence, research on drought-resistant wheat varieties is vital to expand wheat production to drought stress areas and is also important to combat the recurrence of drought in the major wheat-growing highland areas in Ethiopia.

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## 1.2 Impact of drought stress on wheat production

Drought in agriculture refers to a water deficit in the root zone of plants and results in productivity reduction during the crop life cycle (Ji et al., 2010). Drought is considered the most destructive abiotic factor influencing the growth of crop plants leading to the maximum reduction in wheat productivity (Kang et al., 2009; Farooq et al., 2012). Drought affects more than 42% of the worldwide wheat production area (Kosina et al., 2007). Due to the existing climate change, it is assumed that by the year 2025, around 1.8 billion people will face absolute water shortage and 65% of the world's population will live under drought stress environments (Nezhadahmadi et al., 2013). A study based on a published meta-analysis indicated that drought stress reduces wheat yield by more than 30% (Zhang et al., 2018). Durum yield was reduced by 60% under serious drought stress compared to the yield potential (Sukumaran et al., 2018).

Ethiopia is one of the world's eight major Vavilovian centers of origin and diversity for crop plants and a major durum wheat producer in sub-Saharan Africa (SSA) (Vavilov, 1951; Kabbaj et al., 2017; Sall et al., 2019). However, its production is fully dependent on rain, which is erratic and unpredictable, particularly in the low-altitude areas of Ethiopia (Simane et al., 1994). For instance, Ethiopia currently harvests crops from 14 million out of 51.3 million hectares of potentially arable lands (Tsegaye, 2017; CSA, 2018). This is mainly due to drought stress and lack of irrigation facilities among other production constraints. Therefore, the identification of genes or genomic regions associated with drought tolerance in durum wheat landraces has paramount importance in expanding its production to the untapped drought-prone production areas. Further, this could allow using the drought-resistant genotypes in wheat improvement programs.

Genetic diversity is a base to identify drought-resistant genotypes and helps to overcome the effects of drought (Van Oosten et al., 2016). The genetic variability of wheat germplasm can be explored for drought tolerance from its centers of origin and diversity, within wild relatives, and from landraces (Nevo and Chen, 2010; Dvorak et al., 2011; Dodig et al., 2012). Drought tolerance is a complex trait, which is controlled by numerous genes mostly with minor effects (Bernardo, 2008; Gupta et al., 2017). However, the current high throughput technologies to carry out precise phenotyping and dissection of the wheat genome through transcriptomics, proteomics, metabolomics, genotyping, SNP chip assays, and bioinformatics software put optimism to identifying drought-resistant wheat genotypes (Mwadzingeni et al., 2016). Hence, the huge genetic diversity in Ethiopia durum wheat landraces identified in the current

## **GENERAL INTRODUCTION**

study (Negisho et al., 2021) and previous research reports (Mengistu et al., 2015; Mengistu et al., 2016; Alemu et al., 2020) could be a potential gene pool for national and international wheat improvements.

### **1.3 Drought tolerance mechanisms**

Drought tolerance is defined as a crop mechanism causing minimum loss of yield in a drought stress environment relative to the maximum yield in optimum moisture management (Khanna-Chopra and Singh 2015). Subsequently, drought-resistant crops have developed strategies to survive and reproduce under drought stress conditions (Fleury et al., 2010; Santana-Vieira et al., 2016). Drought avoidance and drought tolerance are the two major components, which are different but mutually unexclusive mechanisms by which crop plants achieve adaptation to drought stress (Lawlor, 2013; Blum and Tuberosa, 2018). Dehydration avoidance is focused on the maintenance of plant growth and productivity, whereas dehydration tolerance is focused on plant survival, especially during prolonged drought periods (Verslues et al., 2006). Dehydration avoidance strategies in plants are a deep rooting system to access water, solute accumulation, cell wall hardening, efficient use of available water, and matching rainfall by life cycle modification (Santana-Vieira et al., 2016). Survival due to dehydration tolerance is expressed by delayed mortality (mortality at a relatively low plant water status) and is affected by the resilience of plant metabolism (Blum and Tuberosa, 2018). Dehydration tolerance involves mechanisms to avoid cell damage caused by water loss, such as the synthesis of osmoprotectant proteins and solutes, metabolic changes, and detoxification of reactive oxygen species (ROS) (Verslues et al., 2006). Under drought stress, plants adapt to survive through the induction of various morphological, physiological, biochemical, and molecular mechanisms (Abobatta, 2019).

Morphological responses of wheat to drought stress are via above ground: grain yield, plant height, biomass, leaf (area, extension, size, number, and longevity), and below ground; root (extension, dry weight, density, and length), and root to shoot ratio displays that drought can affect vegetative and reproductive stages (Nezhadahmadi et al., 2013). Agronomic traits for improving drought tolerance include early heading, anthesis and maturity, and root system architecture. Similarly, some of the physiological parameters for drought tolerance are relative water content (RWC), canopy temperature (CT), and normalized difference vegetative index (NDVI) (Bapela et al., 2022). Hence, ideotype selection and breeding with desirable agro-morphological traits can potentially improve drought tolerance in wheat.

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Drought causes physiological and biochemical responses, and drought tolerant wheat cultivars maintain physiological functions at low plant water status and quickly recover once the stress is removed ensuring sustainable crop production under drought stress (Izanloo et al., 2008; Abid et al., 2018). Therefore, physiological and biochemical responses to drought are useful for evaluating drought-tolerant wheat genotypes (Kadam et al., 2018; Dong et al., 2018). These genotypes accumulate a higher concentration of biochemicals such as free proline, glycine, betaine, total sugars, and potassium. A higher concentration of these solutes gives an advantage to wheat plants to tolerate drought stress (Liu et al., 2015; Muhammad et al., 2016; Abid et al., 2018). Under drought stress, the photosynthesis rate shows a direct relationship with wheat grain production due to a reduction in the stomatal opening, which results in a low amount of CO<sub>2</sub> fixation, which leads to a reduction in photosynthetic amount (Mafakheri et al., 2010). The lowered photosynthetic rate is an outcome of inhibition in RuBisCO (ribulose-1, 5-bisphosphate carboxylase/oxygenase) enzyme activity under drought stress conditions (Dulai et al., 2006). The osmoregulation mechanism plays a remarkable role in preserving turgor pressure for soil water absorption and continuing to plant metabolic activities for its survival (Bilal et al., 2015). In drought-tolerant, higher cell-membrane stability protects the plant from ROS that causes a decrease in membrane stability due to the production of lipid peroxidation (Sofy et al., 2021). Therefore, physiological responses to water stress, including chlorophyll content, closure of stomata and decrease in the photosynthesis rate, development of oxidative stress, alteration in the integrity of cell wall, and production of metabolites play a crucial role in wheat drought stress adaptation.

In crop plants, significantly accumulated metabolites under drought stress are considered key metabolites and are correlated with potential biochemical pathways, enzymes, or gene locations for a better understanding of the tolerance mechanisms (Ullah et al., 2017). Plants accumulate biochemicals when exposed to various kinds of stresses, including drought stress (Khamssi, 2014). It has been associated with several osmoprotectant roles, including osmotic adjustment (Zadehbagheri et al., 2014), membrane stabilization (Hayat et al., 2012), and gene signaling to activate anti-oxidizing enzymes (Kadam et al., 2018). In the course of adaptation to stress environments, plant hormones regulate diverse processes in plants, which enable adjustment to stresses. Drought signaling gene expression is categorized into abscisic acid (ABA) dependent and ABA-independent pathways as ABA accumulation is the first step of defense against drought stress (Budak, et al., 2013). ABA is translocated from roots to leaves and is involved in the alteration of guard cell ion transport, regulates stomatal closure, reduces water loss, and inhibits plant growth (Wilkinson and Davies, 2010). Auxin is another important phytohormone, which is known as a negative regulator of drought tolerance in crop plants. In wheat leaves, drought stress tolerance is accompanied by a decrease in indole-3-acetic acid (IAA) content (Xie et al., 2003). In

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summary, wheat responds to drought stress with a wide range of modifications leading to changes at the morphological, cellular, physiological, biochemical, and molecular levels (Lopes and Reynolds, 2011; Kadam, 2015).

### 1.4 Genetic markers

A genetic marker is a polymorphism in the DNA sequence which is linked to a gene of interest. The two categories of genetic markers used in genetics and plant breeding are classical genetic markers and DNA or molecular markers (Xu, 2010). Classical markers include morphological markers, cytological markers, and biochemical markers. However, the availability of classical markers is limited, and many of these markers are not associated with important economic traits, such as grain yield and quality (Jiang, 2013). DNA markers are a small region of the DNA sequence showing polymorphisms due to deletion, insertion, and substitution between different individuals or populations (Teama, 2018). DNA markers are closely linked to the target gene and act as a sign or a flag for the respective gene (Collard et al., 2005). Owing to the invention of polymerase chain reaction (PCR), DNA markers have got a wide application (Mullis, 1990). Some of the known molecular markers are simple sequence repeats (SSRs), diversity arrays technology (DArT), and single nucleotide polymorphisms (SNP) (Jiang, 2013). Simple sequence repeats (SSRs) are co-dominant markers that have been widely used for QTL mapping (Landjeva et al., 2007). Despite their low statistical power compared to the co-dominant markers, dominant markers such as amplified fragment length polymorphisms (AFLPs) and randomly amplified polymorphic DNAs (RAPDs) have been used successfully in QTL mapping (Abdurakhmonov and Abdugarimov, 2008). In many crop species, the development of different sequencing technologies has allowed the discovery of several-fold greater numbers of SNPs than DArT markers (Poland and Rife, 2012). In wheat, despite the large genome size (17 gigabases) and hexaploid nature (AABBDD) of bread wheat and 12 gigabases and tetraploid nature (AABB) of durum wheat (Birrell et al., 2015; IWGSC, 2018) accurate and reliable methods have been developed to perform high-throughput genotyping to identify SNPs (Cavanagh et al., 2013). Several high-density wheat SNP arrays were developed from various mapping populations. For instance, a hexaploid wheat consensus genetic map with 7,504 SNP markers was generated from Wheat 9k SNP arrays (Cavanagh et al., 2013). Wang et al. (2014) mapped 46,977 SNPs from the Wheat 90K array to the hexaploid wheat genetic map using a combination of eight mapping populations. A high-density tetraploid wheat consensus genetic map with 26,626 SNPs was generated using the wheat 90K array (Maccaferri et al., 2015) by integrating 13 independent bi-parental data sets of mapping populations. A hexaploid wheat consensus map with 56,505 SNPs markers was generated using the Wheat 820K array from three independent biparental populations (Winfield et al., 2016). Most recently, a high-density wheat

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genetic map, which was based on an individual mapping population using the Affymetrix Wheat 660K SNP array has been developed for hexaploid wheat (Cui et al., 2017). This has increased the chances to identify genomic regions to explain quantitative traits in complex genomes (Poland and Rife, 2012; Sabiel et al., 2017). SNPs are generally more abundant, stable, amenable to automation, efficient, and cost-effective than other forms of genetic markers, and SNPs can be individually responsible for phenotypic expression of a trait or linked to causative SNPs (Langridge and Fleury, 2011). In general, molecular markers are segments of DNA associated with important traits and can be used by plant breeders as selection tools for genetic diversity analysis, genetic mapping, and marker-assisted breeding (Hossain et al., 2018).

Linkage disequilibrium (LD) is a non-random association of alleles at two or more loci (Slatkin, 2008). The magnitude of LD and its decay with genetic or physical distance determine the resolution of association mapping and are useful to assess the desired numbers of SNPs (Vos et al., 2017). It is assumed that, in the absence of selection, mutation, or migration, polymorphic loci stay in linkage equilibrium (Falconer and Mackay, 1996). In contrast, linkage, selection, and admixture will increase LD (Flint-Garcia, 2003). Therefore, LD has been exploited to see what has happened to a population since LD is affected by the breeding history, selection, genetic drift, and mutation (Hartl and Clark, 1997; Slatkin et al., 2008). The magnitude of LD and its decay with genetic or physical distance determines the resolution of association mapping and is useful for assessing the desired numbers of SNPs on arrays (Vos et al., 2017).

Association mapping is a powerful tool for the detection of QTL through the exploitation of the differential decay of LD between marker loci and genes of interest in natural and domesticated populations (Laidò et al., 2014). Strong LD is expected between loci in tight linkage, while recombination eliminates LD between unlinked loci (Breseghello and Sorrells, 2006). There is a difference in LD decay between self-pollinating and outcrossing plants due to differences in recombination events. In self-pollinated crop species such as durum wheat (Maccaferri et al., 2005) and barley (Kraakman et al., 2004) LD decay is at a large distance (up to 20cM). Whereas, in cross-pollinated species like maize the LD decay is at a short distance (100-1500 bp) (Remington et al., 2001). The lower number of effective recombination events in self-pollinated crops bestow to the longer distance LD decay compared to cross-pollinated crops. LD decay is determined as the intersection point of the locally weighted polynomial regression (LOESS) curve with the critical  $r^2$  value. The critical  $r^2$  for LD decay was determined by values of 0.2, which is considered the minimum threshold for a significant association between pairs of loci and to describe the maximum genetic or physical distance at which LD is significant (Voss-Fels et al., 2015).

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### 1.5 Genome wide association studies (GWAS) and QTL detection

Genome-wide association study identifies the association between hundreds of thousands of genetic variants (SNPs) and a given phenotypic trait (Challa and Neelapu, 2018; Tam et al., 2019; Uffelmann et al., 2021; Yu et al., 2006). Genetic diversity, high statistical power, low probability of Type I error, use of covariates, and high resolution are the keys to success in GWAS (Xu et al., 2017; Wang and Xu, 2019).

In the unified linear mixed model Yu et al. (2006), both population structure (Q) and family relatedness (K) are simultaneously considered as covariates. Hence, this model accommodates both fixed and random effects as:  $Y = X\beta + S\alpha + Qv + Zu + e$  Where: Y is a vector of phenotypic observations;  $\beta$  is a vector of fixed effects other than marker or population structure;  $\alpha$  is a vector of marker effects; u is a vector of random polygenic background effects; e is a vector of residuals; Q is a matrix from structure relating v to Y; and X, S, and Z are incidence matrices of 1s and 0s relating y to  $\beta$ ,  $\alpha$  and u, respectively (Yu et al., 2006). Quantitative trait loci analyses have been carried out in cereals to unravel the genetic basis of grain yield and the morphophysiological traits known to determine yield under non-stress and stress conditions. For instance, grain yield is a major goal for the improvement of durum wheat, particularly in drought-prone areas. Studies identified QTLs using SSR markers, for example, Maccaferri et al. (2008) reported that two major QTL on chromosomes 2BL and 3BS that showed significant effects on grain yield tested across a wide range of water availability. Kadam et al. (2012) identified consistent QTL with a positive effect on grain yield under drought stress in hexaploid wheat on chromosome 4B. Similarly, Tahmasebi et al. (2016) used a recombinant inbred line population to map QTLs using SRRs under well-irrigated, heat, drought, and a combination of drought and heat stress conditions.

Several GWAS studies revealed QTLs associated with different traits in wheat. For instance, in durum wheat, quantitative trait loci (QTLs) were detected under drought stress for grain yield on chromosomes 1A, 4A, 5B and 7B, and days to heading (DH), days to maturity (DM) as well as thousand-kernel weight (TKW) and for seeds per spike (SPS) on chromosome 2B (Sukumaran et al., 2018; Mengistu et al., 2016). QTLs for different biotic stresses in Ethiopian durum wheat using GWAS were revealed for yellow rust resistance (Alemu et al., 2021), septoria resistance (Kidane et al., 2017), grain shape and color (Alemu et al., 2020), strip rust resistance (Liu et al., 2017), as well as stem rust resistance (Letta et al., 2013), suggesting the potential that exists in this gene pool. Similarly, GWAS was applied to identify QTLs for drought indices that were derived from GY and agro-physiological traits as an alternative selection approach to improve drought tolerance in wheat. Sukumaran et al. (2018) detected QTLs associated with

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drought indices (SSI, TOL, STI) calculated from grain yield (GY), thousand kernel weight (TKW), and grain number in durum wheat. Likewise, Ballesta et al. (2020) identified QTLs associated with drought indices (SSI, TOL, STI, and YSI) derived from grain yield (GY), TKW, and kernels per spike in bread wheat.

Bapela et al. (2022) reported that the expression of genes such as GmDREB, HVA1, PEPC, and TaSnRK2.8 via backcrossing in wheat showed genetic improvement conferring drought tolerance as well as improved biomass and water use efficiency. Introgression of the genomic regions linked with drought tolerance traits, phenotypically showed superior performance for morpho-physiological and agronomic traits over the recurrent parent (Todkar et al., 2020). Similarly, Placido et al. (2013) reported that gene introgression from a wild wheat relatively improves drought adaptation in wheat. QTLs for drought tolerance from wild emmer wheat were introgressed through marker-assisted selection, to improve drought tolerance in elite durum (*T. turgidum* ssp.*durum*) and bread (*T. aestivum*) wheat cultivars (Merchuk-Ovnat et al., 2016). Three of the introgressed QTLs were successfully validated, two in the background of durum wheat cultivar Uzan (on chromosomes 1BL and 2BS), and one in the background of bread wheat cultivars Bar Nir and Zahir (chromosome 7AS), imposing the potential of the detected QTLs in marker-assisted breeding and selection for wheat breeding improvement.



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### 1.6. Objectives

Genome-wide association studies to investigate durum wheat study panel under drought stress and non-stress conditions for marker trait associations (MTAs), Three years of data from four field sites in Ethiopia were combined to represent moisture variants for the statistical analysis. The two moisture variants were locations Dera and Melkassa as field drought stress (FDS) and Holeta and Debre Zeit as field non-stress (FNS) variants. Similarly, a climate chamber experiment was conducted on selected accessions from the study panel under two moisture variants at the Julius Kuehn-Institute, Federal Research Centre for Cultivated Plants, in Quedlinburg, Germany.

**The objectives of this study were.**

1. To assess genetic diversity and population structure of 215 Ethiopia durum wheat landraces, 10 released durum wheat varieties, 10 advanced durum wheat lines from Ethiopia, and 50 CIMMYT durum wheat lines using highly informative SNP markers (**Publication 2.1**).
2. To assess the correlation among traits and between the same trait tested under the field and climate chamber (**Publication 2.2**).
3. To identify MTAs and quantitative trait loci (QTLs) for grain biomass and related traits under field and climate chamber drought stress and non-stress conditions (**Publication 2.2**).
4. To identify drought tolerant as well as stable accessions from the durum wheat study panel (**Publication 2.3**).
5. To detect MTAs and QTLs associated with drought indices derived from grain yield and traits that were positively and strongly associated with grain yield under drought stress and non-stress conditions (**Publication 2.3**).

## ORIGINAL PAPERS

### 2 Original papers

This dissertation comprises three original papers in which the durum wheat study panel was investigated using genome-wide association studies. **Publication 2.1** (Negisho et al., 2021) reports on the genetic diversity and population structure of the study panel. The study panel clustered into two subpopulations, with high genetic variation within a population than between populations. **Publication 2.2** (Negisho et al., 2022a) and **publication 2.3** (Negisho et al., 2022b) report on the investigation of marker-trait associations and QTLs for grain biomass and highly correlated traits under drought stress and non-stress conditions, and association mapping of drought tolerance indices, respectively. The correlation analysis for contrasting drought stresses, between the same trait and among traits was assessed. The authors, titles, publisher, volume, doi, and abstract are indicated the beginning of each original paper. The supplementary files are also attached as an index.

**Publication 2.1) Negisho, K., Shibru, S., Pillen, K., Ordon, F., & Wehner, G. (2021). Genetic diversity of Ethiopian durum wheat landraces. PLoS ONE,16(2). <https://doi.org/10.1371/journal.pone.0247016>.**

**Abstract**

Genetic diversity and population structure assessment in crops are essential for a marker-trait association, marker-assisted breeding, and crop germplasm conservation. We analyzed a set of 285 durum wheat accessions comprising 215 Ethiopian durum wheat landraces, 10 released durum wheat varieties, 10 advanced durum wheat lines from Ethiopia, and 50 durum wheat lines from CIMMYT. We investigated the genetic diversity and population structure for the complete panel as well as for the 215 landraces, separately based on 11,919 SNP markers with known physical positions. The whole panel was clustered into two populations representing on the one hand mainly the landraces, and on the other hand, mainly released, advanced, and CIMMYT lines. Further population structure analysis of the landraces uncovered 4 subgroups emphasizing the high degree of genetic diversity within Ethiopian durum landraces. Population structure-based AMOVA for both sets unveiled significant ( $p < 0.001$ ) variation between populations and within populations. Total variation within population accessions (81%, 76%) was higher than the total variation between populations (19%, 24%) for both sets. Population structure analysis based on genetic differentiation ( $F_{ST}$ ) and gene flow ( $Nm$ ) for the whole set and the Ethiopian landraces were 0.19 and 0.24, 1.04, and 0.81, respectively indicating high genetic differentiation and limited gene flow. Diversity indices verify that the landrace panel was more diverse with ( $I = 0.7$ ,  $He = 0.46$ ,  $uHe = 0.46$ ) than the advanced lines ( $I = 0.6$ ,  $He = 0.42$ ,  $uHe = 0.42$ ). Similarly, differences within the landrace clusters were observed. In summary, a high genetic diversity within Ethiopian durum wheat landraces was detected, which may be a target for national and international wheat improvement programs to exploit valuable traits for biotic and abiotic stresses.

**Keywords:** AMOVA, Gene flow, Genetic differentiation, Genetic diversity, Ethiopian durum wheat landraces, population structure.

**Veröffentlichung 2.1) Negisho, K., Shibru, S., Pillen, K., Ordon, F., & Wehner, G. (2021). Genetic diversity of Ethiopian durum wheat landraces. PLoS ONE,16(2). <https://doi.org/10.1371/journal.pone.0247016>.**

### **Abstrakt**

Die Bewertung der genetischen Vielfalt und der Populationsstruktur von Nutzpflanzen ist für die Assoziation von Markern und Merkmalen, die markergestützte Selektion und die Erhaltung des pflanzlichen genetischen Ressourcen unerlässlich. Wir analysierten ein Sortiment von 285 Hartweizen-Akzessionen, darunter 215 äthiopische Hartweizen-Landrassen, 10 freigegebene Hartweizen-Sorten, 10 fortgeschrittene Hartweizen-Linien aus Äthiopien und 50 Hartweizen-Linien von CIMMYT. Untersucht wurden die genetische Vielfalt und die Populationsstruktur für das gesamte Sortiment sowie getrennt für die 215 Landrassen, auf der Grundlage von 11.919 SNP-Markern mit bekannten physischen Positionen. Das gesamte Sortiment wurde in zwei Populationen gruppiert, die einerseits hauptsächlich die Landrassen und andererseits hauptsächlich die freigegebenen, fortgeschrittenen und CIMMYT-Linien repräsentieren. Eine weitere Analyse der Populationsstruktur der Landrassen ergab vier Untergruppen, die das hohe Maß an genetischer Vielfalt innerhalb der äthiopischen Hartweizen-Landrassen unterstreichen. Die auf der Populationsstruktur basierende AMOVA für beide Gruppen ergab eine signifikante ( $p < 0,001$ ) Variation zwischen den Populationen und innerhalb der Populationen. Die Gesamtvariation innerhalb der Populationen (81%, 76%) war bei beiden Sets höher als die Gesamtvariation zwischen den Populationen (19%, 24%). Die Analyse der Populationsstruktur auf der Grundlage der genetischen Differenzierung ( $F_{ST}$ ) und des Genflusses ( $N_m$ ) für das gesamten Sortiment und die äthiopischen Landrassen betrug 0,19 und 0,24, 1,04 bzw. 0,81, was auf eine hohe genetische Differenzierung und einen begrenzten Genfluss hinweist. Die Diversitätsindizes belegen, dass das Landrassen-Panel mit ( $I = 0,7$ ;  $He = 0,46$ ;  $uHe = 0,46$ ) vielfältiger war als die fortgeschrittenen Linien ( $I = 0,6$ ;  $He = 0,42$ ;  $uHe = 0,42$ ). Auch innerhalb der Landrassen-Cluster wurden Unterschiede festgestellt. Zusammenfassend wurde eine hohe genetische Vielfalt innerhalb der äthiopischen Hartweizen-Landrassen festgestellt, die eine Grundlage für nationale und internationale Weizenzuchtprogramme sein könnte, um wertvolle Eigenschaften zur verbesserten Resistenz und Toleranz gegenüber biotischen und abiotischen Stressfaktoren zu nutzen.

**Stichworte:** AMOVA, Genfluss, genetische Differenzierung, Genetische Vielfalt, äthiopische Hartweizen-Landrassen, Populationsstruktur.

### Introduction

Durum wheat [*Triticum turgidum* ssp. *durum* (Desf.) Husn.] was domesticated from wild emmer (*Triticum turgidum* ssp. *dicoccoides*) to emmer (*Triticum turgidum* ssp. *dicoccum*) followed by secondary domestication, i.e. from emmer to naked forms and durum wheat (*Triticum turgidum* ssp. *durum*) (Gioia et al., 2015). The allotetraploidization event was involved after a cross between the two diploid species: *T. urartu* (genome AA) (Konarev et al., 1976; Dvorak et al., 1988) and an unknown close relative of *Aegilops speltoides* (genome BB) (Gill and Chen 1987; Kerby and Kuspira, 1987). Thus, durum wheat has an allotetraploid genome (AABB genome,  $2n = 4x = 28$ , seven homoeologous groups—13,000 M bp) (Salamini et al., 2002). A high-density gene-associated SNP array was developed for the characterization of polyploid wheat (Wang et al., 2014) and complemented with fully annotated high-confident genes (IWGSC and Borrill, 2018). Maccaferri et al. (2014) developed the high-density tetraploid wheat consensus map from data sets of durum wheat cultivars (*Triticum turgidum* ssp. *durum*), cultivated emmer (*T. Turgidum* ssp. *dicoccum*) and their ancestor (wild emmer, *T. Turgidum* ssp. *dicoccoides*). Recently, the reference sequence of the genome of cv. Svevo led to the identification of 66,559 high confidence (HC) genes enabling genome-wide genetic diversity analyses in tetraploid durum wheat (Maccaferri et al., 2019).

Durum wheat is one of the ten most important crops worldwide with an annual production of 37 million tons (Kabbaj et al., 2017;) and Ethiopia is the major durum wheat producer in sub-Saharan Africa (SSA), with a durum acreage of 0.6 million ha (FAO, 2015; Kabbaj et al., 2017; Sall et al., 2019). Durum wheat is primarily used for pasta production, but in addition, it is used to make flour for leavened biscuits, cookies, bio-fuel, and for fermentation to make alcoholic beverages such as beer and liquors (Tsegaye and Berg, 2007). In the country, durum wheat nearly accounts for 15-20% of wheat production and 30% of the whole acreage (Negassa et al., 2013; Alemu et al., 2019). Hence, it contributes about 18 to 20% to the national wheat production (Tessema and Bechere, 1998; Teklu and Hammer, 2008). In Ethiopia, wheat (both bread and durum) is produced by around 4.62 million households with an estimated land area of 1.7 million ha and a mean national yield of 2.7 t/ha (CSA, 2018). Traditionally, in Ethiopia wheat straw is used as animal feed and as roof thatching material. This makes wheat biomass highly valuable in rural communities. Thus, on top of high grain yield and environmental tolerance, in wheat-growing areas, farmers also take into account those traits when selecting landraces.

The Ethiopian Biodiversity Institute (EBI) hosts more than 7000 landraces collected from durum wheat growers for genetic conservation and the exploitation of genetic diversity (IBC, 2013; Mengistu et al., 2016). Based on the genetic diversity analysis, Mengistu et al. (2016) reported high genetic variability in Ethiopian durum wheat landraces. Kabbaj et al. (2017) have demonstrated that Ethiopian durum wheat

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landraces cluster separately from the durum of the International Center for Agricultural Research in the Dry Areas (ICARDA), Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), and durum wheat derived from other countries. Genetic diversity can be described as the degree of differentiation between or within species. Existing intra and inter-specific differences are the base of all crop improvement programs (Mengistu et al., 2015). Hence, genetic variation is an essential source of novel and useful alleles to be selected by breeders for abiotic and biotic tolerance / resistance (Acosta-Gallegos et al., 2007; Bhandari et al., 2017). It is supposed that allelic variation of genes originally found in wild species, is gradually lost through domestication and breeding (Fu, 2017). Therefore, the narrowed or lost allelic variation can be recovered by exploring e.g. landraces (Fu, 2017). Landraces are genetically dynamic and are in equilibrium with biotic and abiotic stresses in the environments where they evolved (Lopes et al., 2015; Mohammadi et al., 2015). Therefore, landraces that have adapted to their natural environment over time (Brown, 2000; Reynolds et al., 2007; Acquah, 2012) and can contribute to favorable genomic regions for tolerance against abiotic stresses like drought.

Analysis of genetic diversity in populations is an important topic for breeding as well as conservation and evolutionary genetics studies (Caballero and Toro, 2002; Jost et al., 2018). Expected heterozygosity ( $H_e$ ) or the genetic diversity index, which is derived from gene frequency data, is used to determine the genetic variation within populations (Peakall and Smouse, 2006; 2012). Wright (1969), used the fixation index ( $F_{ST}$ ) to estimate genetic differentiation among populations. Leinonen et al (2008) reported that  $F_{ST}$  estimated from DNA markers provides a starting point to assess the strength of divergent selection on quantitative traits. Gene flow ( $Nm$ ), which is estimated through  $F_{ST}$  is used to estimate the gene exchange within a population and among populations (Hartl and Clark, 1997). Additionally, genetic diversity indices provide useful information on genetic diversity. Genetic analyses, such as estimation of genetic diversity and population structure, as well as genome-wide association studies and marker-assisted selection procedures, are broadly undertaken by molecular markers (Eltaher et al., 2018). Single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs) are the most common molecular markers in genetic studies (Rafalski, 2002; Kumar et al., 2012). Out of these, SNP markers provide an increased resolution due to their high abundance (Acosta-Gallegos et al., 2007; Hyten et al., 2006; Govindaraj et al., 2015). Additionally, the power of SNP markers in wheat recently elevated 100-fold from 9K (Cavanagh et al., 2013) to 820 K (Winfield et al., 2016). In this study, we used a hybridization array that includes about 90K SNPs, which was developed for genetic analyses in allohexaploid and allotetraploid wheat populations (Wang et al., 2014; Maccaferri et al., 2019).

Up to now only a small part of the huge collection of durum wheat landraces hosted at EBI was characterized using SSR (Haile et al., 2013; Teklu and Hammer, 2006; Asmamaw et al., 2019) and SNP markers (Mengistu et al., 2016; Alemu et al., 2020). Therefore, our study aimed to assess the population

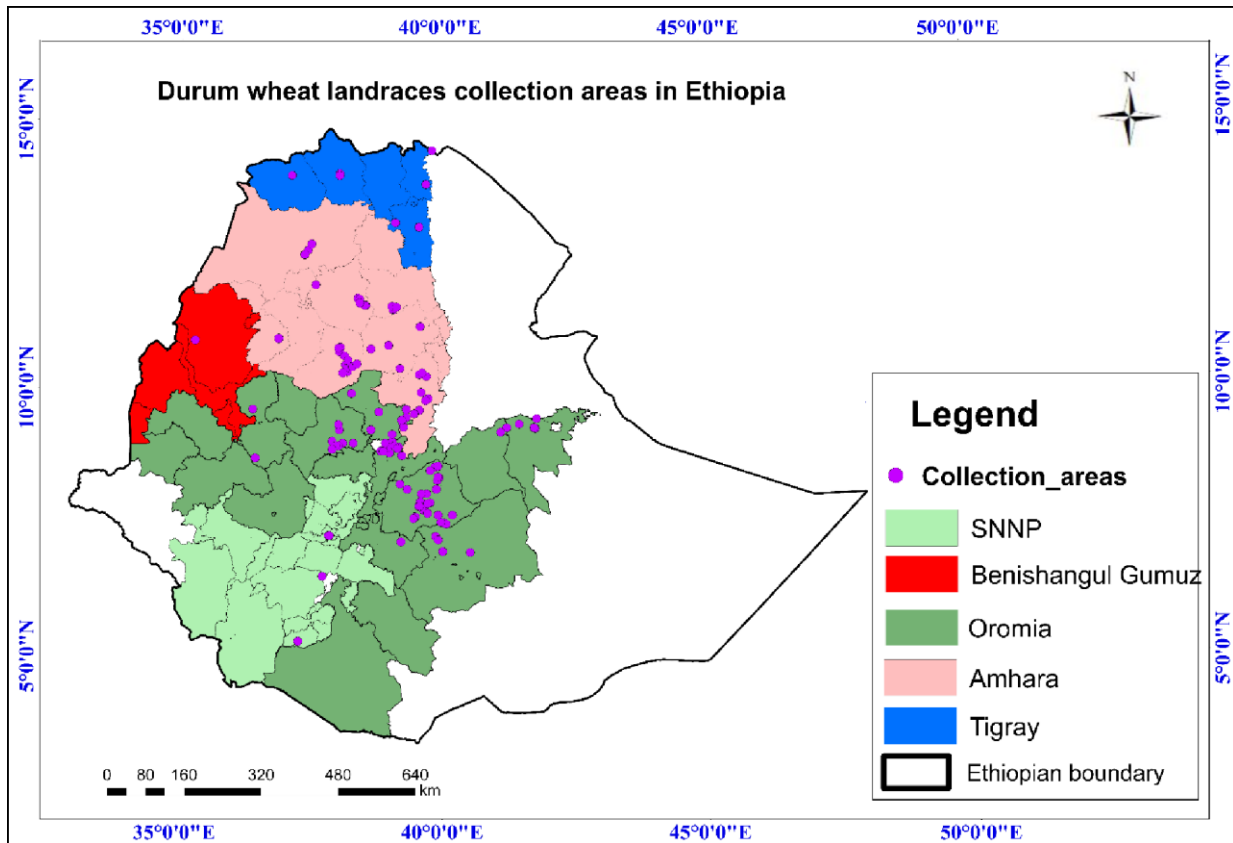
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structure and genetic diversity of 215 Ethiopia durum wheat landraces, 10 released durum wheat varieties, 10 advanced durum wheat lines from Ethiopia, and 50 CIMMYT durum wheat lines using highly informative SNP markers.

### **Material and methods**

#### **Plant material**

A total of 285 durum wheat accessions, hereafter designated as study panel (SP) were used for the analysis of genetic diversity. The SP included 215 Ethiopian durum wheat landraces assigned as ETDWL, 10 released durum wheat varieties, 10 advanced durum wheat lines from Ethiopia, and 50 durum wheat lines from CIMMYT (**Table S1**). The ETDWL was obtained from the Ethiopian Biodiversity Institute (EBI, <http://www.ebi.gov.et/>). Landraces were selected based on the acreage in each seed source region (origin). Thus, more samples were taken from major growing regions (Oromia and Amhara) and some samples from minor growing regions. 105 ETDWL were sampled from Oromia, 88 from Amhara, 1 from Benishangul Gumuz, 16 from Tigray, and 5 from South Nation Nationalities and Peoples (SNNP), representing different seed sources (origin), seed collection zones, and geographic regions (**Table S1**). Online ArcGIS software was used to map the landraces collection areas in Ethiopia, <https://www.arcgis.com/home/webmap/viewer.html>, released version 10.8.1 July 2020 (**Figure 1**). For the Ethiopian durum wheat landraces, GPS passport data were obtained from EBI and are provided in **Table S2**. A self-created layer was used to map positional data.



**Figure 1. Durum wheat landraces collection areas in Ethiopia.** GPS: Geographic position system, Regions of seed origin: South Nation Nationalities and Peoples (SNNP, Light green), Benishangul Gumuz (red), Oromia (green), Amhara (pink), Tigray (blue), Ethiopian boundary and geo-positions were indicated. The mapping was performed using the online ArcGIS software suite vs. 10.8.1.

### SNP genotyping

The durum wheat SP was grown in the greenhouse at Quedlinburg, Germany for 15 days under standard growing conditions, i.e. 20 to 22°C during daytime and 17 to 19°C at night (Wehner et al., 2016) with an automatic water supply. Genomic DNA was extracted from single plant fresh leaves following the mini-prep DNA extraction protocol (Stein et al., 2008). Genomic DNA quality was checked by 1% gel electrophoresis and DNA concentration measurement was conducted by NanoDrop® ND-1000 Spectrophotometer (Saveen Warner, Sweden). 50 ng of DNA per sample was used for SNP analysis using the 90K iSelect chip (Illumina Inc., San Diego, USA). Genotyping was conducted by Trait Genetics, Gatersleben (Germany). SNPs with a low minor allele frequency (MAF) are generally considered as rare alleles with less power in detecting marker-trait associations (MTAs) and are prone to genotyping error (Marees et al., 2017). Thus, SNPs with minor allele frequency (MAF) of < 5%, missing data > 10% and heterozygosity > 12.5% were excluded from further analyses. Additionally, imputation was conducted



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using the software Beagle (Browning, 2008). Physical SNP positions were taken from the reference sequence of durum wheat (IWGSC and Borrill, 2018) to construct a hapmap file for further analyses.

### **Population structure and genetic diversity analyses**

Genotypic data were used to describe the genetic diversity within the durum wheat study panel. We analyzed the population structure and genetic diversity of the ETDWL separately and compared this with the population structure and genetic diversity of the SP. The underlying genetic population structure was estimated with STRUCTURE 2.3.4 software (Evanno et al., 2005). SNP markers having high polymorphic information content ( $PIC \geq 0.35$ ) were selected across all durum wheat chromosomes (**Table S3**). Hence, 10,000 burn-in periods followed by 100,000 Markov Chain Monte Carlo (MCMC) iterations for  $K = 1$  to 10 clusters were used to identify the optimal range of  $K$  with five replications per cluster for the SP as well as for ETDWL. The optimal  $K$ -value was determined using the  $\Delta K$  method (Pritchard et al., 2000). DARwin 6.0.17 (Perrier et al., 2003) was used for molecular diversity analysis to get information on genetic dissimilarity among populations and within populations. The neighbor-Joining (NJ) algorithm of the genetic distances was determined according to Saitou and Nei (1987) and used to create a phylogenetic tree.

### **Analysis of molecular variance (AMOVA) and genetic diversity indices**

Genetic distance between populations was determined using Nei's Genetic Distance (Nei, 1978) based on the number of populations  $k$ . We run AMOVA, which allowed hierarchical partitioning of genetic diversity among populations and within populations (Meirmans and Liu, 2018). Thus, AMOVA was performed using GeneAIEx 6.503 (Peakall and Smouse, 2012). Additionally, the genetic differentiation ( $F_{ST}$ ), which is defined as a standardized measure of the genetic variance among populations was calculated to provide a measure of total genetic divergence between populations (Hartl and Clark, 1997). Gene flow ( $Nm$ ) among populations was calculated based on  $F_{ST}$  as:

$$Nm = \left[ \left( \frac{1}{F_{ST}} \right) - 1 \right] / 4$$

In addition, Shannon's Information Index ( $I$ ) (Brown and Weir, 1983), expected heterozygosity ( $He$ ), unbiased heterozygosity ( $uHe$ ), and the percentage of polymorphic loci (PPL) were calculated as follows:

$$I = -1 * \sum [Pi * Ln(Pi)],$$

$$He = 1 - \sum Pi^2, \quad uHe = \left[ \frac{N}{N-1} \right] * He.$$

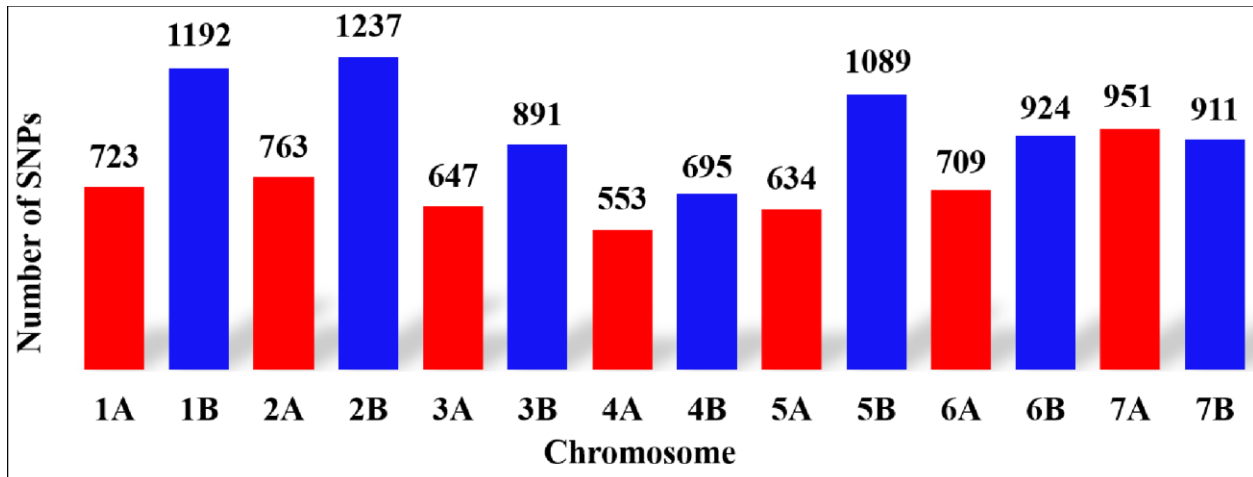
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Where  $P_i$  is the frequency of its alleles for the population and  $\sum P_i^2$  is the sum of squared population allele frequencies and,  $PPL = \sum P_i/N$ , where  $P_i$  is the proportion of loci polymorphic in a population and  $N$  the number of populations.

## Results

### SNP analyses

After filtering, 11,919 SNPs were used for genetic analysis. These were continuously distributed across the A and B genomes of durum wheat for the SP (**Figure 2**). In all cases, the B genome showed a higher number of SNPs except for chromosome 7, for which 951 SNPs were detected on chromosome 7A and 911 SNPs on chromosome 7B. The lowest number of SNPs were detected on chromosome 4A (553) and the highest SNP number was obtained for chromosome 2B (1237). Generally, in the current study, 58% of the SNPs were located on the B genome and 42% on the A genome.

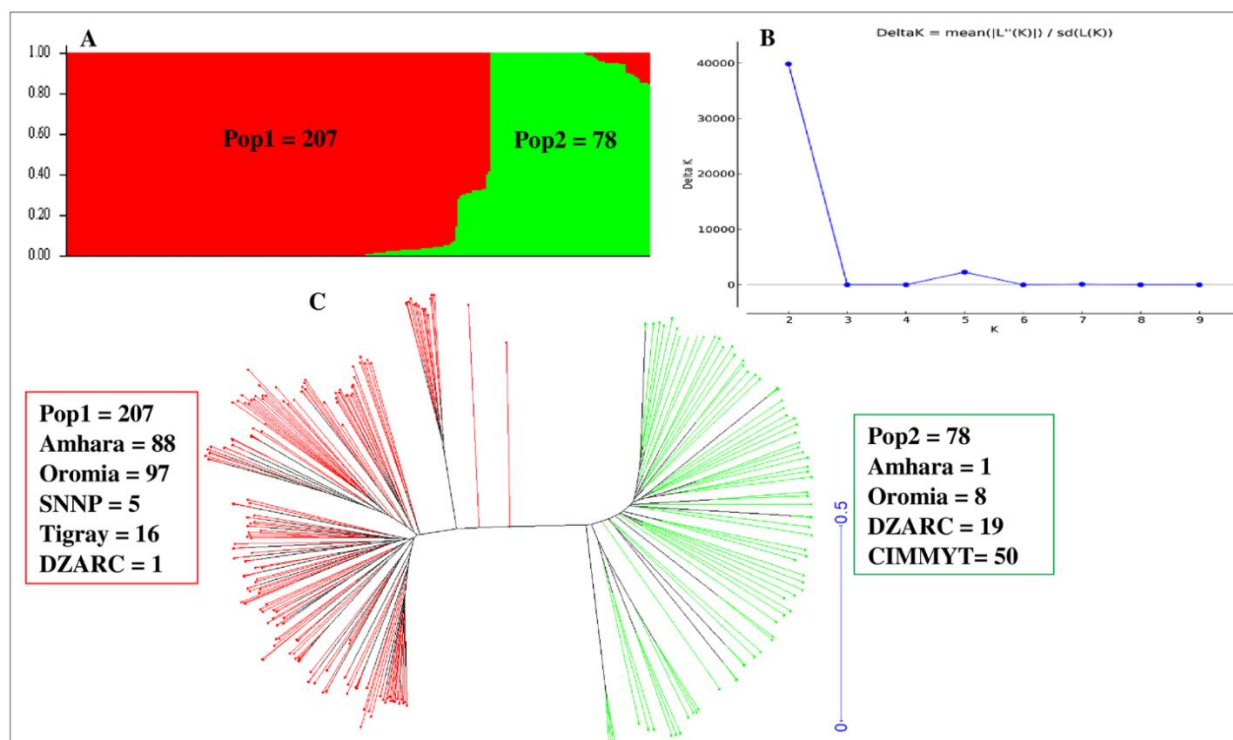


**Figure 2.** Distribution of 11,919 filtered single nucleotide polymorphisms (SNPs) across the durum wheat genome. Genome A and B are marked with red and blue colors, respectively.

### Population structure

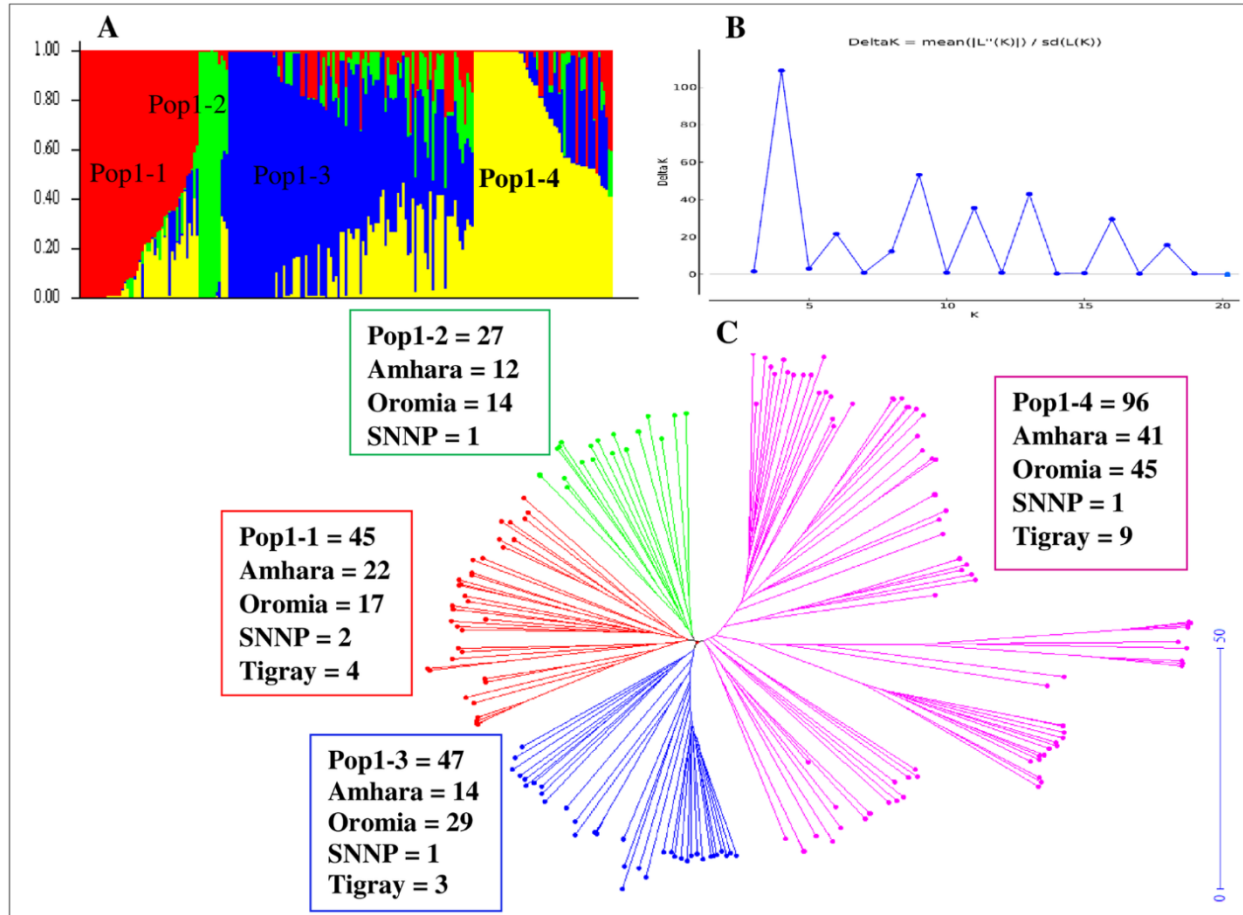
Population structure analysis for the durum wheat SP revealed  $\Delta K$  at  $K = 2$  i.e two populations hereafter considered as Pop1 and Pop2 (**Figure 3ABC, Table S1**). Pop1 comprised 207 accessions. Of these, 206 accessions were from ETDWL and 1 from the durum wheat lines of Ethiopia. Regarding seed origin, the number of accessions in Pop1 originated from Amhara (88), Oromia (97), SNNP(5), Tigray(16), and Debre Zeit Agricultural Research Center (DZAR, 1) (**Figure 3C**). Pop2 constituted 78 accessions. Fifty of the accessions in Pop2 were from CIMMYT, 19 from the group of the released and advanced durum wheat lines of Ethiopia, and 9 were landraces. The landraces clustered in Pop2 were DW006, DW007,

DW008, DW020, DW039, DW143, DW185, and DW188 from Oromia, as well as DW050 from Amhara (Figure 3C, Table S1). Thus, the SP is mainly split into the ETDWL and advanced varieties.



**Figure 3.** Population structure analysis of the durum wheat SP. (A) Bayesian structure analysis, (B) Structure harvester Evanno's test  $\Delta K$  at  $K = 2$ . (C) Neighbor Joining (NJ). Populations identified in STRUCTURE based on Bayesian structure analysis are shown in red and green for Pop1 and Pop2, respectively.

Ethiopian durum wheat landraces (ETDWL) comprise accessions collected from major wheat-producing regions of the country (Oromia, Amhara, Tigray, and SNNP) (Figure 1, Table S1). Population structure analysis of the ETDWL uncovers populations with  $\Delta K$  at  $K = 4$  (Figure 4ABC, Table S1). The populations in ETDWL comprised 45, 27, 47, and 96 accessions, respectively for Pop1-1, Pop1-2, Pop1-3, and Pop1-4 (Figure 4C). Pop1-1 comprises 45 accessions of which 22 originated from Amhara, 17 from Oromia, 2 from SNNP, and 4 from Tigray. In the second cluster (Pop1-2) which comprises 27 accessions, 12 accessions were from Amhara, 14 from Oromia, and 1 from SNNP. Pop1-3 consisted of 47 accessions, i.e. 14 from Amhara, 29 from Oromia, 1 from SNNP, and 3 from Tigray. Pop1-4 comprises 96 accessions of which 41 are derived from Amhara, 45 from Oromia, 1 from SNNP, and 9 from Tigray. The number of accessions per cluster in ETDWL ranged from a minimum of 27 to a maximum of 96 for Pop1-2 and Pop1-4, respectively.



**Figure 4.** Population structure analysis of ETDWL. (A) Bayesian structure analysis, (B) Structure harvester  $\Delta K$  at  $K = 4$ . (C) Neighbor-Joining (NJ). Populations identified in STRUCTURE based on Bayesian structure analysis are shown in red, green, blue and yellow/pink, for Pop1-1 to Pop1-4, respectively.

ETDWL was conducted by taking the respective population structure clusters ( $\Delta K$ ) into account (**Table 1**). In both cases, AMOVA indicated significant ( $p < 0.001$ ) effects for variation between populations and within populations. The AMOVA of the SP revealed that 19% of the total variation is between populations, while 81% of the total variation is present within populations. Fixation index ( $F_{ST}$ ) and gene flow ( $N_m$ ) for the SP were calculated at  $F_{ST} = 0.19$  and  $N_m = 1.04$ , respectively. Similarly, AMOVA for ETDWL revealed 24% of the total variation between populations and 76% variation within populations. Fixation index ( $F_{ST}$ ) and gene flow ( $N_m$ ) for the ETDWL were  $F_{ST} = 0.24$  and  $N_m = 0.81$ , respectively. Therefore, the AMOVA for SP and ETDWL showed a higher percentage of variation within populations than between populations (**Table 1**).

**Table 1. AMOVA for the SP and ETDWL based on structure analysis results.**

Source of variation	Df	Sum of squares	Variance components	Percentage of variation	Fixation index (FST)	Gene flow (Nm)
<b>Variance partition of the SP, k = 2</b>						
Between populations	1	5323.9***	22.7	19	0.19	1.04
Within populations	283	53223.7***	94.0	81		
<b>Variance partition of the ETDWL, k = 4</b>						
Between Populations	3	7069.6***	23.0	24	0.24	0.81
Within populations	211	31572.1***	74.8	76		

df: degree of freedom, \*\*\*: P-value at  $p < 0.001$ , SP: Study panel, ETDWL: Ethiopian durum wheat landraces.

### Genetic indices

We investigated the genetic diversity of the SP and ETDWL based on population structure analysis results of  $\Delta K$  at  $k = 2$  and  $k = 4$ , respectively (**Table 2**). The genetic indices for the SP such as  $I$ ,  $H_e$ , and  $uH_e$  showed higher values for Pop1 as compared to Pop2. Hence, Pop1 that comprised 99.5% accessions from ETDWL was more diverse ( $I = 0.7$ ,  $H_e = 0.46$ ,  $uH_e = 0.46$ ) than Pop2 ( $I = 0.6$ ,  $H_e = 0.42$ ,  $uH_e = 0.42$ ), which comprised 88.5% of improved varieties (advanced, released and CIMMYT durum wheat). Pop1-3 of the ETDWL was the most diverse ( $I = 0.62$ ,  $H_e = 0.39$ ,  $uH_e = 0.39$ ) with 100% PPL followed by Pop1-2 ( $I = 0.52$ ,  $H_e = 0.33$ ,  $uH_e = 0.34$ ) with 89.8% PPL. Pop1-1 and Pop1-4 showed similar genetic diversities ( $I = 0.5$ ,  $H_e = 0.32$ ,  $uH_e = 0.32$ ) with 93.1% and 97.6% PPL, respectively (**Table 2**).

**Table 2. Mean of different genetic indices parameters in each population.**

Pop	N	I	He	uHe	PPL
<b>Population of the SP, K = 2</b>					
Pop1	207	0.7	0.46	0.46	100
Pop2	78	0.61	0.42	0.42	100
<b>Population of the ETDWL, k = 4</b>					
Pop1-1	45	0.5	0.32	0.32	93.1
Pop1-2	27	0.52	0.33	0.34	89.8
Pop1-3	46	0.62	0.39	0.39	100
Pop1-4	96	0.5	0.32	0.32	97.6

Number of accessions (N), Shannon's information index (I):  $I = -1 * \sum [Pi * Ln(Pi)]$ , expected heterozygosity (He) or genetic diversity:  $He = 1 - \sum Pi^2$ , Unbiased heterozygosity  $uHe = \left[ \frac{N}{N-1} \right] * He$ , and percentage of polymorphic loci:  $PPL = \sum Pi/N$ ; SP: Study panel, ETDWL: Ethiopian durum wheat landraces.

## Discussion

Hybridization arrays are believed to represent a significant fraction of SNPs distributed across genomes. In wheat, they represent SNPs between populations of diverse geographical origins (Cavanagh et al., 2013; Wang et al., 2014; Winfield et al., 2016). Hence, in this study, we used the hybridization array that includes about 90K SNPs, which was developed to analyze genetic variation in allohexaploid and allotetraploid wheat populations (Wang et al., 2014; Maccaferri et al., 2019). Studies indicated a higher number of SNPs in the B than in the A genome of wheat (Poland et al., 2012; Alipour et al., 2017). Likewise, a higher number of SNPs was also identified in this study on the B genome (58%) than on the A genome (42%) (**Figure 2**). However, we detected a higher number of SNPs on chromosome 7A (951) than on chromosome 7B (911). Similarly, studies by Naz et al. (2019) and Desta et al. (2014) on bread wheat indicated the highest numbers of SNP markers on the B genome followed by the A genome, and less across the D genome. In this study, population structure and Neighbor-Joining (NJ) analysis showed two populations (Pop1 and Pop2) for the study panel (SP). Concerning Pop1, 206 (99.5%) accessions were from ETDWL and only 1, DZ005 (0.5%) from the advanced durum wheat lines (**Figure 3**). This durum wheat line most probably was selected from landraces by Ethiopian durum wheat breeders. This elucidates that only little effort was spent to include landraces in durum wheat improvement programs in the country. Pop2 of the SP constituted 69 (88.5%) accessions from CIMMYT and others that originate from international sources like ICARDA which are released durum wheat varieties and advanced durum wheat lines. The remaining 9 (11.5%) accessions are landraces. The landraces clustered in Pop2 were

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most probably incorrect renamings of the released durum wheat varieties as landraces during germplasm collection or they may be an admixture. In Ethiopia from 1970 until recently, CIMMYT is the major source for most of the improved durum wheat materials (Mengistu et al., 2015). In support of this, this study clearly showed that 19 out of 20 Ethiopian accessions plus advanced durum lines are clustered in Pop2 with durum wheat lines from CIMMYT. This is possible under the scenario that most improved durum wheat materials were introduced from international breeding programs to the country (Sall et al., 2019). Additionally, it shows that only a little attention was given to exploring the genetic diversity in ETDWL as pointed out by (Mengistu et al., 2016). Therefore, in Ethiopia to exploit the existing genetic diversity more focus should be given to conserving and using the landraces in durum wheat breeding programs.

It has been reported that Ethiopian durum wheat landraces are distinct and have no kinship with the Middle East, which is the primary region of origin of durum wheat (Kabbaj et al., 2017). Therefore, the separate clustering of Ethiopian durum landraces from international varieties may illustrate a long-time separation of Ethiopian durum wheat landraces from primary durum origin and international germplasm. This is attributed to the uniqueness of Ethiopian durum wheat landraces (Haile et al., 2013; Mengistu et al., 2016; Kabbaj et al., 2017; Sall et al., 2019). This is in agreement with reports that designated Ethiopian durum wheat landraces as separate sub-species under the name *T. durum subs. abyssinicum* or *T. aethiopicum* (Mengistu et al., 2015; Mengistu et al., 2016). Additionally, separate clustering of Ethiopian durum wheat from improved durum wheat in Ethiopia indicated that little or no improved varieties were generated from landraces either through selection or via crossing with international durum wheat materials. Nevertheless, germplasm originating from international organizations such as CIMMYT and ICARDA remain the main source for advanced durum lines and released durum varieties in Ethiopia (Sall et al., 2019).

Population structure analysis of ETDWL alone uncovers four populations (Pop1-1, Pop1-2, Pop1-3, and Pop1-4), which is in agreement with NJ analysis (**Figure 4**). Mengistu et al. (2016) have identified many populations ( $k = 10$ ) in Ethiopian durum wheat landraces by removing improved durum wheat varieties from the population analysis. Our study also signifies the presence of a higher admixture of accessions between different populations of landraces (**Figure 4**). This is a common phenomenon for most cereal crops grown in Ethiopia because of informal seed exchange systems involving regional and countrywide farming communities. In Ethiopia, farmers exchange seeds of cereals in various traditional forms such as gifts, barter, labor exchange, or social obligations (Hailye et al. 1998; Bishaw, 2004). Therefore, the main source of seed for planting wheat and barley landraces in Ethiopian smallholder communities is via the informal farmer to the farmer seed exchange. Once farmers obtain seed with the required quality that genotype will get a bigger chance to spread across local communities. This was demonstrated by genetic

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clustering based on seed collection regions where seeds originated from one region relatively closely clustered in the same population. For instance, 9 out of 16 accessions collected from Tigray were clustered in Pop1-4, on the other hand, no accession from this region was grouped in Pop1-3 (**Figure 4**). The geographic isolation and latitudinal variation, i.e. 1540-3190 meters above sea level from which accessions were collected, confirmed the variability and genetic dynamics in Ethiopian durum wheat landraces to adapt to wide-ranging conditions (**Figure 1, Table S1**). Subsequently, the high level of genetic diversity can be exploited in wheat breeding and improvement programs to overcome the biotic and abiotic stresses across latitudinal ranges.

Durum wheat is one of the important cereal crops grown in Ethiopia and the country is endowed with a wealth of genetic diversity for tetraploid wheat. Phenotypic and morphological analysis (Eticha et al., 2005; Eticha et al., 2006; Geleta and Grausgruber, 2013; Mengistu et al., 2015) and genotypic analysis elucidated the existence of huge genetic diversity in Ethiopian tetraploid wheat (Teklu et al., 2006; Mengistu et al., 2016; Badaeva et al., 2018). Consequently, the country is considered as the center of diversity and/or secondary center of origin for durum wheat (Vavilov, 1951; Mengistu et al., 2016; Kabbaj et al., 2017). In our study, genetic diversity within population accessions was higher than genetic diversity between populations (**Table 1**) illustrating that more attention should be given to individual accessions within populations to explore the existing genetic diversity as a basis for genomic analysis, and genetic material conservation.

Fixation index (differentiation =  $F_{ST}$ ) measures population differentiation due to genetic structure (Luo et al., 2019) and  $F_{ST}$  can be considered important in differentiating populations when its value is greater than 0.15 (Frankham et al., 2002). Hence,  $F_{ST}$  values were calculated at  $F_{ST} = 0.19$  and  $F_{ST} = 0.24$  for the SP and ETDWL, respectively indicating significant differentiation between the populations. Eventually, in our study, the higher genetic differentiation led to limited gene flow ( $Nm$ ) values of  $Nm = 1.04$  and  $Nm = 0.81$  for the SP and ETDWL, respectively (**Table 1**).  $Nm$  value less than one is an indication of limited gene exchange as it was suggested by (Hartl and Clark, 1997; Frankham et al., 2002). Therefore, the  $Nm < 1$  in ETDWL (0.81) clearly shows the high degree of genetic differentiation that exists among the ETDWL populations ( $F_{ST} = 0.24$ ) as compared to SP ( $F_{ST} = 0.19$ ) (Wright, 1965; Leinonen et al., 2008). In agreement with this, (Eltaher et al., 2018) reported that a high genetic exchange leads to low genetic differentiation between populations. Similarly, (Mengistu et al., 2016) reported high genetic diversity in Ethiopian durum wheat landrace collections. Apparently, in the present study, population structure analysis of ETDWL alone revealed more populations suggesting the huge genetic diversity that exists within Ethiopian durum wheat landraces (**Figure 4**). Information on the genetic diversity of each population can be assessed using genetic diversity indices (Eltaher et al., 2018). Likewise, in this study, diversity analysis was further supported by the genetic diversity indices such as  $I$ ,  $He$ , and  $uHe$  (**Table 2**).



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Genetic diversity indices for the SP illustrated higher genetic diversity in Pop1, which constituted 99.5% of the ETDWL in comparison to Pop2, which comprised only 11.5% of ETDWL. Genetic diversity indices for the ETDWL indicated that Pop1-3 was the most diverse followed by Pop1-2, whereas, Pop1-1 and Pop1-4 showed similar genetic diversity (**Table 2**). This marked that landraces showed huge genetic diversities that can broaden the genetic base for wheat improvement. In agreement with this, biotic and abiotic resistance/tolerance genes or genomic regions were identified in Ethiopian durum wheat landraces, e.g. resistance to biotic factors such as stripe rust resistance (Alemu et al., 2019), adult plant resistance to leaf rust, and stem rust (Klindworth et al., 2007; Haile et al., 2013; Habtamu, 2019), abiotic stress resistance such as aluminum tolerance (Wayima et al. 2019) and terminal drought tolerance (Mengistu et al., 2015). Therefore, Ethiopian durum wheat landraces may increase the rate of genetic gain if strategically included in wheat breeding programs. Most important, exploiting the landraces' genetic diversity in Ethiopian durum wheat may help to mitigate abiotic stress factors that are apparent due to adverse effects of climate change. Furthermore, these landraces may help to uncover unknown genomic regions or genes associated with economically important traits.

### **Conclusion**

We employed high quality SNP markers to analyze the population structure and genetic diversity of a durum wheat study panel comprising 285 accessions of which 215 accessions were ETDWL. AMOVA ( $P < 0.001$ ) unveiled that genetic variation within population accessions was higher than genetic variation between populations for the SP and ETDWL. Structure analysis of SP revealed two distinct populations (Pop1 and Pop2). Genetic diversity indices for the SP illustrated higher genetic diversity in Pop1, which constituted 99.5% of the ETDWL in comparison to Pop2, which comprised only 11.5% ETDWL. Further population structure analysis of the ETDWL alone uncovered four populations emphasizing the high degree of genetic diversity that exists in ETDWL. Genetic diversity indices for the ETDWL indicated Pop1-3 was the most diverse followed by Pop1-2. Therefore, the high genetic diversity detected in ETDWL showed the existence of plentiful variability that could be utilized for future wheat breeding programs.

**Publication 2.2) Negisho, K., Shibru, S., Matros, A., Pillen, K., Ordon, F., & Wehner, G. (2022a). Genomic dissection reveals QTLs for grain biomass and correlated traits under drought stress in Ethiopian durum wheat (*Triticum turgidum* ssp. *durum*). *Plant Breeding*, 141(3), 338–354. <https://doi.org/10.1111/pbr.13010>.**

### **Abstract**

Drought stress seriously challenges wheat production and productivity. Grain biomass (GB) and related traits were assessed under drought stress and non-stress for 285 and 185 durum wheat genotypes, respectively, in field and climate chamber experiments to identify quantitative trait loci (QTL). Significant correlations between traits estimated in field and climate chamber trials were observed ( $p < 0.001$ ). Genotyping with the wheat 90K iSelect single nucleotide polymorphism (SNP) array revealed 11,919 polymorphic SNP markers distributed across the durum wheat genome. The FarmCPU (Fixed and random model Circulating Probability Unification) method was used for genome-wide association studies (GWAS). A total of 191 significant ( $-\log_{10}p \geq 4$ ) marker-trait associations (MTAs) were detected at a linkage disequilibrium (LD,  $r^2 \geq 0.2$ ) at 4.78 Mb and were clustered into 70 QTLs. A total of 69 (36%) of the MTAs passed a false discovery rate (FDR) of 5%. The numbers of QTLs detected were 21, 31, 9 and 9 under field drought stress (FDS), field non-stress (FNS), climate chamber drought stress (CCDS) and climate chamber non-stress (CCNS) conditions, respectively. About 43% and 57% of the QTLs were located on the A and B genomes, respectively. Some of the detected QTLs were in agreement with previously reported QTLs, while others are novel ones for the traits investigated. QTLs on 1A between 495694477 and 501944537bp, on 3B between 416256124 and 430507900 bp, on 3B between 745357158 and 759608934 bp, on 4B between 593416763 and 605142497 bp and on 4B between 658785890 and 670511624 bp were selected for validation and may be used to increase grain yield under drought stress in marker-assisted selection (MAS) schemes.

**Keywords:** Quantitative trait loci, Polymorphism, FarmCPU, Genome-wide association study, linkage disequilibrium, Marker-assisted selection.

**Veröffentlichung 2.2) Negisho, K., Shibru, S., Matros, A., Pillen, K., Ordon, F., & Wehner, G. (2022a). Genomic dissection reveals QTLs for grain biomass and correlated traits under drought stress in Ethiopian durum wheat (*Triticum turgidum* ssp.durum). Plant Breeding, 141(3), 338-354. <https://doi.org/10.1111/pbr.13010>.**

### **Abstrakt**

Trockenstress stellt eine ernsthafte Herausforderung für die Produktion und Produktivität von Weizen dar. Die Kornbiomasse (GB) und verwandte Merkmale wurden für 285 bzw. 185 Hartweizen-Genotypen in Feld- und Klimakammerversuchen unter Trockenstress bzw. Nichtstress untersucht, um quantitative Merkmalsloci (QTL) zu identifizieren. Es wurden signifikante Korrelationen zwischen den in Feld- und Klimakammerversuchen geschätzten Merkmalen festgestellt ( $p < 0,001$ ). Die Genotypisierung mit dem Weizen 90K iSelect Single Nucleotide Polymorphism (SNP) Array ergab 11.919 polymorphe SNP-Marker, die über das Hartweizen-Genom verteilt sind. Die FarmCPU-Methode (Fixed and random model Circulating Probability Unification) wurde für genomweite Assoziationsstudien (GWAS) verwendet. Insgesamt wurden 191 signifikante ( $-\log_{10}p \geq 4$ ) Marker-Trait-Assoziationen (MTAs) in einem Kopplungsungleichgewicht (LD,  $r^2 \geq 0,2$ ) auf 4,78 Mb identifiziert und in 70 QTLs gruppiert. Insgesamt 69 (36 %) der MTAs bestanden eine Falschentdeckungsrate (FDR) von 5 %. Die Anzahl der identifizierten QTLs betrug 21, 31, 9 bzw. 9 unter Feld-Trockenstress (FDS), Feld-Nichtstress (FNS), Klimakammer-Trockenstress (CCDS) und Klimakammer-Nichtstress (CCNS). Etwa 43 % bzw. 57 % der QTLs wurden auf dem A- bzw. B-Genom detektiert. Einige der identifizierten QTLs stimmten mit bereits früher entdeckten QTLs überein, während viele andere neuartige QTLs für die untersuchten Merkmale sind. QTLs auf 1A zwischen 495694477 und 501944537 bp, auf 3B zwischen 416256124 und 430507900 bp, auf 3B zwischen 745357158 und 759608934 bp, auf 4B zwischen 593416763 und 605142497 bp und auf 4B zwischen 658785890 und 670511624 bp wurden zur Validierung ausgewählt und können zur Steigerung des Kornertrags unter Trockenstress in markergestützten Selektionsprogrammen (MAS) eingesetzt werden.

**Stichworte:** Quantitative Merkmalsloci, Polymorphismus, FarmCPU, Genomweite Assoziationsstudie, Kopplungsungleichgewicht, Marker-unterstützte Selektion.

### Introduction

Drought is one of the most serious abiotic factors challenging wheat production and quality internationally and especially in sub-Saharan Africa (Mwadzingeni et al., 2017; Zampieri et al., 2017). In the worst scenario, it leads to plant death which results in a total yield loss (Nakashima et al., 2014). Grain yield reduction due to drought at 40% water reduction has been reported to be 20.6% in wheat and 39.3% in maize (Daryanto et al., 2016). On the other hand, it has been published that due to high population pressure by 2050, the demand for wheat is estimated to increase by 60% (FAO, 2013). Furthermore, in the developing world, more than 50% of wheat (50 million ha) is produced under a rain-fed system where rainfall is highly erratic (Gupta et al., 2017). Additionally, drought in combination with inherently low-fertile soils aggravates the impact of drought stress resulting in higher wheat yield losses (Mapfumo et al., 2017; Nezhadahmadi et al., 2013).

In Ethiopia, durum wheat nearly accounts for 15%–20% of the wheat production and covers 30% of the acreage grown with wheat (Alemu et al., 2019; Negassa et al., 2012). It is of prime importance for agricultural production in Ethiopia, as durum wheat is not only a staple crop for food security but also is becoming a major cash crop having 10% to 20% higher prices than bread wheat (Sall et al., 2019). This is accounted for the unique characteristics of durum wheat for making food products such as pasta, burghul, and couscous. Nevertheless, despite the presence of over 10 million ha of land potential for wheat production, Ethiopia still imports wheat to meet the national wheat requirements (<https://www.indexmundi.com/agriculture/?coun-try=et&commodity=wheat&graph=imports>). Water availability is the major limiting factor for the expansion of the production of wheat from the traditionally known growing areas in the highland to the lowland. Despite the availability of fertile soil in the lowland, this region, in general, has a moisture deficit and is prone to drought. In Ethiopia, only less than 1% of the cereal acreage has access to irrigation (Mann & Warner, 2015; Taffesse et al., 2011). Hence, the production of important crops like wheat is limited to the highland areas, only. One way of overcoming this problem is developing drought-tolerant wheat varieties that are used not only to expand wheat production to drought-prone areas but also are important to combat the recurrence of drought in the major wheat-growing regions. Ethiopia is considered the center of diversity or secondary origin for durum wheat (Kabbajet al., 2017), which offers the great potential to identify landraces that are tolerant to various stresses as evidenced by pathogens such as stem rust (Klindworth et al., 2007). This may also hold for drought.

Phenotyping of quantitative traits in the field, representing realistic environmental conditions and in growth chambers, which is better to control, has paramount importance in crop breeding. Phenotyping

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and genotyping of populations or landrace collections are crucial to further define and understand traits of interest concerning complex abiotic stresses like drought via genetic mapping (Lopes et al., 2015). The two common genetic mapping methods are (1) linkage mapping and (2) association mapping or linkage disequilibrium (LD) mapping (Xu et al., 2017). Association mapping has the advantages of high resolution, high allelic richness, no need for developing mapping populations, and is used as a powerful tool to detect natural variation underlying complex traits in several crop species (Wehner et al., 2015; Xu et al., 2017; Zhu et al., 2008). The magnitude of LD and its decay with genetic or physical distance determines the resolution of association mapping and is useful for assessing the desired numbers of SNPs on arrays (Vos et al., 2017). With the advent of rapid genotyping and next-generation sequencing technologies, GWAS has become a routine strategy for mapping genotype-phenotype associations in many species (Liu & Yan, 2019). For instance, in durum wheat, quantitative trait loci (QTLs) were detected under drought stress for grain yield on chromosomes 1A, 4A, 5B, and 7B and days to heading (DH), days to maturity (DM), and thousand-kernel weight (TKW) on chromosome 2B (Sukumaran et al., 2018) and for seeds per spike (SPS) on chromosome 2B (Mengistu et al., 2016). In this study, we used a wheat 90K iSelect SNP array facilitating the analyses (Wang et al., 2014) with a high-density SNP-based consensus map and a physical reference sequence of tetraploid wheat (Maccaferri et al., 2015, 2019). The objectives of this study were (i) to identify marker-trait association (MTAs) and QTLs for yield and related traits under field and climate chamber conditions for drought stress and non-stress conditions and (ii) to assess the correlation between respective traits under field and climate chamber conditions.

### Materials and methods

#### Study panel (SP)

An SP of 285 durum wheat accessions was used for the analyses of drought stress tolerance in field experiments in Ethiopia (**supporting information Table S1**). The genetic diversity and population structure were described in Negisho et al. (2021). From the SP, a set of 185 durum wheat accessions was selected for phenotyping in climate chamber experiments conducted at the Julius Kühn Institute (JKI), Germany (**supporting information Table S1**), based on the drought susceptibility index (DSI) calculated from the least-squares means (lsmeans) of field data as described by Fischer and Maurer (1978). Accordingly, based on the DSI results, a 1:2:1 ratio was used to select drought-tolerant, medium, and susceptible accessions, respectively. A selection was needed to represent the varying genotypes in the size-limited climate chambers and was based on choosing characteristic genotypes from each group.

### Field experiments

Field phenotyping experiments were conducted at four sites for three seasons (2016–2018) in Ethiopia (**Table 1**). Biplot analysis for the relationship among environments explained 74.40% of the variation by PCA1 and PCA2. Drought stress sites and high-potential sites were clustered separately (**Figure S1**). The three years of data from the four sites were combined into two representing the two drought-stress scenarios. Dera and Melkassa are sites for field drought stress (FDS), and Holeta and Debre Zeit are sites for non-drought stress (FNS) conditions. The FDS sites are located in the rift valley and were selected for screening genotypes for drought stress tolerance by the Ethiopian Institute of Agricultural Research (EIAR) (personal communication). Accessions were randomized in an incomplete block alpha lattice design with three replications per location and accession. Plots were arranged in rows of 1 m (**Figure 1**). The spacing between rows was 0.2 m, and sowing density was calculated based on a seeding rate of 395 seeds/m<sup>2</sup>.

### Climate chamber experiments

A total of 185 accessions were planted in two replications for two scenarios. The climate chamber drought stress (CCDS) variant was 20% of the maximum soil water capacity (SWC), and the non-stress (CCNS) variant was 70% SWC. Pots with 15 cm x 15 cm x 20 cm capacity filled with 1500 g of ED73 soil containing 70% white soil and 30% clay with pH around 6 (H. Nitsch and Sohn GmbH and Co.KG, Germany) were used for the climate chamber experiments. Five seeds of durum wheat per accession were planted in each pot. Subsequently, germinated plants were thinned to three plants per pot. Watering was performed by weighing each pot every other day to maintain 70% SWC for both soil moisture variants until flowering time. At the time of flowering (BBCH 65), the CCDS treatment abstained from water supply until it reached 20% SWC. Then, CCNS and CCDS treatments were maintained at 70% and 20% SWC until maturity. The climate chamber temperature was set to 24<sup>0</sup>C during the daytime and 18<sup>0</sup>C during the night at the time of planting, with 13/11light/dark hours, respectively. Then, to simulate the field conditions, from the time of flowering until harvest, it was readjusted to 26<sup>0</sup>C during day time and 20<sup>0</sup>C at night (**Figure 1**).

### Phenotyping

The durum wheat panel was evaluated for 10 agro-physiological traits under drought stress and non-stress for field and climate chamber experiments (**Table 2**). Hence, grain biomass (GB), DH, Days to grain filling (DGF), DM, plant height (PH), SPAD, spike length (SL), SPS, harvest index (HI), and TKW were investigated under field and climate chamber conditions.

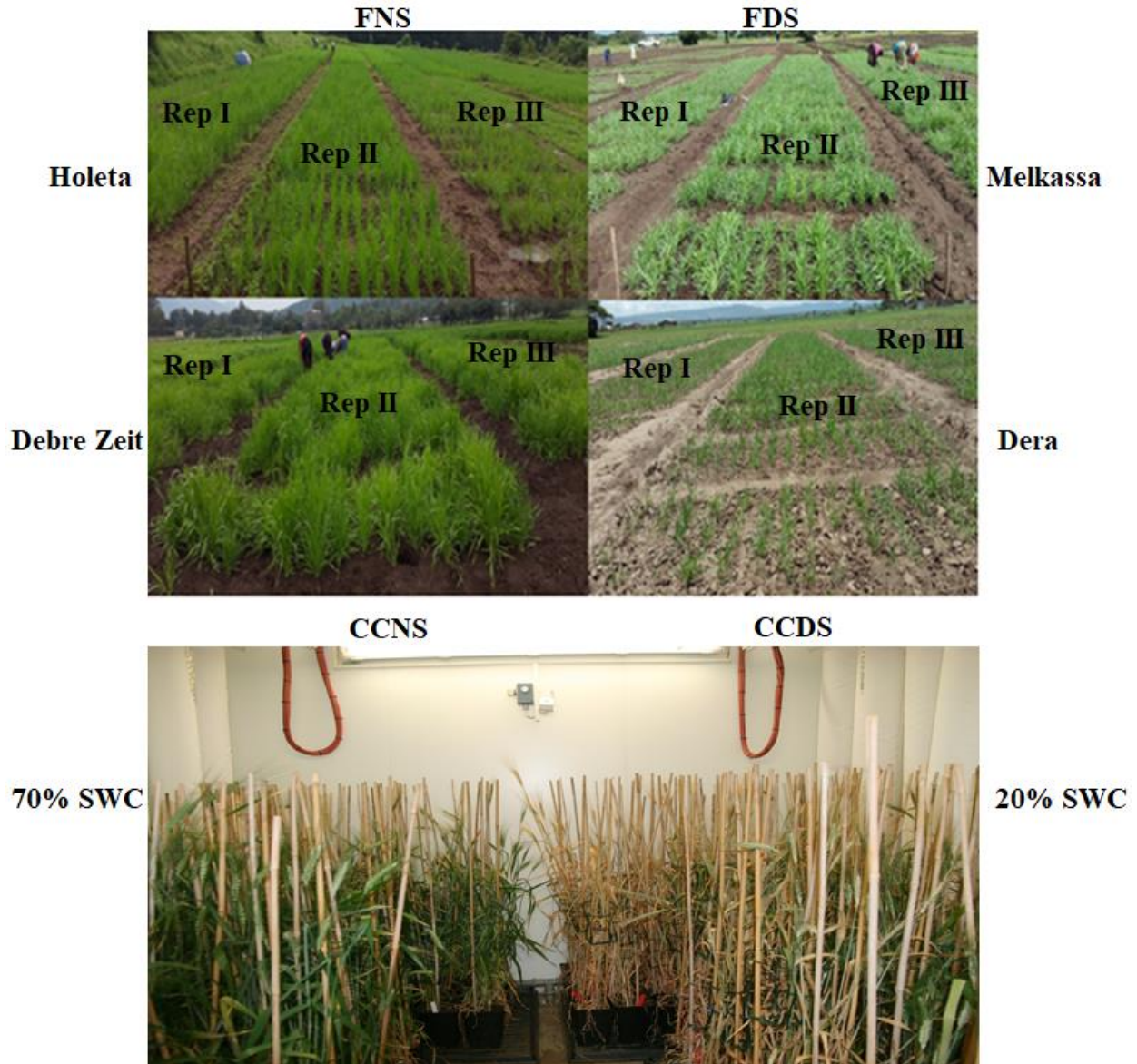
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We recorded DH per pot for the climate chamber and per plot for the field at 50% spike emergence (Zadoks stage 65), and DM when 50% of spikes turned yellow or lost green color (Zadoks stage 87) (Zadoks et al., 1974). We calculated DGF as the difference between DM and DH. At physiological maturity, PH was determined by measuring from the soil surface to the tip of the plant excluding awns, and SL was obtained by measuring the spike from its base to its tip excluding the awns. The number of SPS was recorded as an average seed count from 10 spikes per plot after harvesting spikes from ten randomly selected main culms under the field and from three spikes per pot for the climate chamber. GB in gram per plot for field and gram per pot for climate chamber was determined based on the weight of harvested grain. We measured TKW by taking the weight of 1000 grains for the field experiments and it was estimated from 100 seeds for the climate chamber experiments. HI was calculated from total GB per plot to above-ground total biomass per plot for the field experiments. Similarly, for the climate chamber experiments, HI was determined from the total GB per pot to the above-ground total biomass of three plants per pot. Leaf color was obtained indirectly with a Soil Plant Analysis Development (SPAD) chlorophyll meter after 10 to 15 days of flowering using a SPAD-502 Plus instrument (Minolta, Co. Ltd, Japan). Hence, three flag leaves were selected and five readings preselected leaf were acquired to get mean SPAD readings (Wehneret al., 2016).

**Table 1.** Summary of rainfall, minimum and maximum temperature as well as geositions of the field experimental sites in Ethiopia for the three growing seasons.

Location	Treatment <sup>a</sup>	Latitude	Longitude	Altitude	Rainfall (mm)			Temperature (°C)					
					2016	2017	2018	2016		2017		2018	
					2016	2017	2018	Min	Max	Min	Max	Min	Max
Dera	FDS	8 <sup>o</sup> 24'N	39 <sup>o</sup> 21'E	1620	467	397	422	16	27	16	26	15	27
Melkassa	FDS	8 <sup>o</sup> 20'N	39 <sup>o</sup> 19'E	1500	371	475	401	15	28	15	29	15	29
Holeta	FNS	8 <sup>o</sup> 10'N	38 <sup>o</sup> 30'E	2400	615	629	792	8	22	7	23	8	22
Debre Zeit	FNS	8 <sup>o</sup> 44'N	38 <sup>o</sup> 58'E	1900	374	368	299	12	26	13	26	13	26

Abbreviations: FDS, field drought stress; FNS, field non-stress. Treatment<sup>a</sup>: FDS and FNS.



**Figure 1.** Field and climate chamber experiments. FNS: field non-stress (Holeta and Debre Zeit), FDS: field drought stress (Melkassa and Dera), CCNS: climate chamber non-stress = 70% soil water capacity (SWC), CCDS: climate chamber drought stress = 20% SWC. The numbers of replications under field conditions were indicated.

### Statistical analysis of phenotypic data

The least-squares means (lsmeans) were calculated by the lsmeans package in R (Russell, 2016) and were used for further analyses. Genotype was fixed, and years, locations, replications, and blocks were considered random. Descriptive statistics were conducted based on the lsmeans by Rcmdr (Fox, 2017) in the R statistical computing environment (R Core Team, 2019/URL <http://www.R-project.org/>). Pearson's correlation coefficients ( $r$ ) among different traits under drought stress and non-stress conditions were



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calculated using the `corstars` function in R, and the `corrplot` package was used to visualize the results (Graffelman, 2013; R CoreTeam, 2019/URL <http://www.R-project.org/>). For the 10 agro-physiological traits, selected correlations between the same traits were also analyzed for FDS versus CCDS, as well as for FNS versus CCNS treatments.

The following linear mixed model was used for the combined analysis of variance (ANOVA) by the `lmer` function in the `lme4` package for R (Bates et al., 2015):

$$Y_{i\text{lyr}} = \mu + G_i + L_l + Y_y + R_r(L_l Y_y) + B(L_l Y_y R_r) + GLY_{i\text{ly}} + \varepsilon_{i\text{lyr}}$$

Where  $Y_{i\text{lyr}}$  is the trait of interest in the  $i$ th accession,  $l$ th location  $y$ th year,  $r$ th replication,  $\mu$  is the overall mean,  $G_i$  is the effect of the  $i$ th accession,  $L_l$  is the effect of the  $l$ th location (i.e., Dera and Melkassa for FDS) and  $Y_y$  is the effect of the  $y$ th year.  $R_r(L_l Y_y)$  is the  $r$ th replication within  $l$ th location and  $y$ th year,  $B(L_l Y_y R_r)$  is the effect of  $k$ th incomplete block within  $l$ th location,  $y$ th year and  $r$ th replication,  $GLY_{i\text{ly}}$  is the effect of the interaction among the  $i$ th accession,  $l$ th location and the  $y$ th year and  $\varepsilon_{i\text{lyr}}$  is the effect of residual. The effect of year was excluded from the climate chamber experiments. The distribution was assumed normal with mean zero and effect-specific variances.

Broad sense heritability ( $H^2$ ) of traits analyzed in field experiments was calculated from variance components of location (l), year (y), and replication (r):

$$H^2 = \sigma^2_g / [(\sigma^2_g + \sigma^2_{gl} / l + \sigma^2_{gy} / y + \sigma^2_{gly} / ly + \sigma^2_e / lyr)]$$

where  $\sigma^2_g$ ,  $\sigma^2_{gl}$ ,  $\sigma^2_{gy}$ ,  $\sigma^2_{gly}$ , and  $\sigma^2_e$  are accession variance, accession x location, accession x year, and accession x location x year interaction and error variance, respectively, and  $l$ ,  $y$ ,  $ly$ , and  $r$  refer to the number of locations, years, interaction of locations and years and replications, respectively (Falconer & Mackay, 1996; Vargas-Reeve et al., 2013).

### Genotyping

Genotyping was conducted by SGS TraitGenetics GmbH (Gatersleben, Germany) using the wheat 90K iSelect SNP array (Wanget al., 2014). The consensus linkage map of tetraploid wheat (Maccaferri et al., 2015) and the IWGSC RefSeq v1.0 genomic assembly (International Wheat Genome Sequencing Consortium, 2018) were applied to assign a genomic location to each SNP marker. SNP markers with minor allele frequency (MAF) of < 5%, missing data > 10%, and heterozygosity > 12.5% were excluded, and SNP markers were imputed by the Beagle method in R (Browning and Browning, 2007). Physical distance positions were aligned to the recent Durum Wheat (cv. 'Svevo') RefSeq Rel. 1.0 (Maccaferri et al., 2019). Finally, a total of 11,919 high confident SNP markers were used to construct HapMap files for further MTA analyses. The genetic population structure was estimated with STRUCTURE 2.3.4 software

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(Falush et al., 2003, 2007; Hubisz et al. 2009; Pritchard et al., 2000) implementing a model-based Bayesian cluster analysis as described in (Negisho et al., 2021).

LD, LD decay, and LD plots of the durum wheat genomes (A and B) were analyzed using R packages genetics, LD heatmap, and trio (R Core Team, 2014; Shin et al., 2006; Warnes, 2013). Thus, inter-marker genetic distances were assessed using the consensus physical distance position of the respective SNP markers (Maccaferri et al., 2019). LD critical value was set at  $r^2 \geq 0.2$  (Oyiga et al., 2017; Voss-Fels et al., 2015).

## GWAS

GWAS was conducted using the genome association and prediction integrated tool (GAPIT) in R (Lipka et al., 2012). A mixed linear model was employed for each trait by including lsmeans, and drought treatments-based combined analysis was done for years, locations and replications. SNP markers, kinship matrix, and q-matrix were used as cofactors for MTA analysis (Yu et al., 2006). FarmCPU method, which is iteratively using the fixed-effect model and the random effect model for powerful and efficient GWAS (Liu et al., 2016), was used. In the present study, Bonferroni–Holm correction for multiple testing was too strict to select significant MTAs (Gaetano, 2013; Holm, 1979). Therefore, in this study, the threshold for associated markers was adjusted to  $-\log_{10}p \geq 4$  (Bai et al., 2016; Bhatta et al., 2018; Ma et al., 2016). We also tested the MTA at FDR 5% as  $p = 1/\text{total number of SNP} * 0.05 = 4.19498E-06$  (LOD score = 5.4) (Benjamini & Hochberg, 1995). The phenotypic variance explained (PVE) was calculated based on sample size, MAF, effect size, and standard error of effect size for each SNP following Teslovich et al. (2010). Identified MTAs were clustered into QTL using the critical LD decay value, and MTAs not in LD was considered as independent QTL (Kidane et al., 2017; Negro et al., 2019). An MTA, which was similarly associated with a trait or several traits under the various treatments (FDS, FNS, CCDS, and CCNS) on the same chromosome and at the same position, was considered as an overlapping MTA (Ahmad et al., 2014). Likewise, a QTL detected for a trait or several traits under the various treatments (FDS, FNS, CCDS, and CCNS) on the same chromosome and within the same interval was considered as an overlapping QTL (Tricker et al., 2018). A QTL that relates to two or more traits within the same treatment was considered as a co-located QTL, while a QTL associated with a single trait was considered as an individual QTL (Ma et al., 2019; Sukumaran et al., 2018).

In the current study, the interval of the identified QTL was used as input in the *Triticum turgidum* Durum Wheat 'Svevo' (RefSeq Rel.1.0, Maccaferri et al., 2019) in the GrainGenes database to compare these with previously reported QTLs. If the detected QTL did not match with any of the reported QTLs for the

trait of interest, it is reported as likely a new QTL detected in this study. Graphical representation of linkage groups and QTLs was carried out using MapChart2.32 software (Voorrips, 2002).

### Results

#### Phenotyping

The durum wheat study panel displayed broad phenotypic differences for each of the traits under field and climate chamber drought conditions, indicating the broad genetic diversity in the panel (**supporting information Table S2, Table 2, and supporting information Figures S3 and S4, respectively**). For all studied traits, the mean values of the drought stress treatments were lower than the mean values of the non-stress treatments both under field and climate chamber conditions. In the climate chamber experiments, the mean value of GB was reduced by drought stress treatment by 52.4%, which was higher than the mean GB reduction due to drought in the field (35.79%). Similarly, a higher reduction due to drought stress was observed for SPAD and HI under climate chamber conditions (36.71%, 28.63%) as compared with the field (9.69%, 21.15%), respectively. Notably, in the current study, a higher reduction was obtained under field (24.57%) as compared with the climate chamber conditions (3.66%) for PH. Boxplots illustrate the mean value reduction for all studied traits (**Figures S2 and S3**). The dispersion of the data from the mean was expressed in percentage of standard deviation (SD%) and was comparable under field as well as climate chamber conditions for all tested traits (**Table 2**). Under field conditions, higher dispersion from the mean was observed for GB and HI as compared with the climate chamber experiment. In contrast, for SPAD and SPS, the SD% was higher under the climate chamber as compared with field conditions (**Table 2**).

Under FNS conditions, the heritability of traits analyzed varied between 48.2% for DM and 89.11% for PH. Similarly, under FDS, heritability ranged between 42% for DM and 83.37% for SL. The current study showed higher heritability for GB, PH, SPAD, HI, and TKW under FNS as compared with FDS conditions. However, heritability for DH, DGF, SL, and SPS was higher under FDS as compared with FNS conditions. The coefficient of variation (CV) was comparable for drought stress and non-stress conditions for all same traits, except for SL, HI, and SPS under CCDS as compared with CCNS conditions. ANOVA revealed significant ( $p < 0.0001$ ) effects for genotype and treatment and accession by treatment interactions for GB, DH, DGF, DM, PH, SL, SPS, and TKW under field conditions (**supporting information Table S2**). Similarly, significant ( $p < 0.0001$ ) effects were observed among accessions and between treatments for GB, SPAD, PH, HI, and SPS for the climate chamber experiment. These results indicate high genetic variability in the SP. However, under field conditions, no significant

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difference was observed for HI between treatments and accession by treatment interactions. Likewise, accession by treatment interactions was non-significant for PH, SPAD, SPS, and HI for the climate chamber experiment (**supporting information Table S2**).

**Table 2.** Descriptive statistics, heritability, and the number of significant ( $-\log_{10}p \geq 4$ ) MTA for traits analysed under drought stress and non-stress conditions for field and climate chamber experiments.

Trait	Unit	Trt	Mean	Min	Max	SD (%)	CV (%)	LSD	H <sup>2</sup> (%)	% Reduction = (Yns-Ys/Yns)*100	MTA
GB	g/plot	FNS	77.10	33.00	115.00	15.60	20.25	6.62	69.60	35.79	4
		FDS	49.50	24.00	80.00	11.50	23.21	4.60	61.57		6
	g/pot	CCNS	2.91	0.00	5.00	1.04	35.77	0.21	NA	52.41	3
		CCDS	1.39	0.00	5.00	0.50	36.01	0.09	NA		8
DH	days	FNS	72.20	62.00	88.00	3.98	5.51	0.90	80.33	9.58	4
		FDS	65.30	57.00	77.00	4.27	6.55	0.96	80.37		5
		CCNS	73.00	64.00	85.00	4.58	6.28	0.72	NA	1.37	10
		CCDS	72.00	57.00	96.00	6.07	8.41	0.93	NA		5
DGF	days	FNS	47.70	39.00	57.00	3.17	6.65	1.29	56.58	35.56	10
		FDS	30.70	23.00	40.00	2.99	9.72	1.23	59.36		6
		CCNS	43.58	24.00	58.00	5.88	13.50	1.05	NA	44.10	0
		CCDS	24.36	12.00	40.00	5.55	22.80	1.04	NA		0
DM	days	FNS	120.00	113.00	129.00	3.00	2.51	1.34	48.20	19.91	7
		FDS	96.00	90.00	105.00	2.56	2.67	0.99	42.00		6
		CCNS	116.57	98.00	130.00	5.20	4.46	0.94	NA	17.35	1
		CCDS	96.34	84.00	109.00	6.29	6.23	0.97	NA		0
SPAD	free	FNS	40.40	31.00	53.00	4.84	11.98	1.55	72.79	9.69	12
		FDS	36.50	27.00	50.00	4.94	13.53	1.51	70.82		4
		CCNS	36.90	3.00	57.00	13.40	36.37	2.78	NA	36.71	6
		CCDS	23.40	4.00	58.00	12.40	52.96	2.48	NA		5
PH	cm	FNS	101.60	40.70	160.00	21.60	21.30	1.92	89.11	24.57	5
		FDS	76.60	35.00	125.00	15.70	20.40	2.13	75.72		6

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Trait	Unit	Trt	Mean	Min	Max	SD (%)	CV (%)	LSD	H <sup>2</sup> (%)	% Reduction = (Yns-Ys/Yns)*100	MTA
		CCNS	85.30	48.00	113.00	11.70	13.74	1.73	NA	3.66	0
		CCDS	82.10	46.00	120.00	11.10	13.46	1.64	NA		0
		FNS	7.90	5.00	12.00	1.15	14.57	0.19	72.32	28.62	7
SL	cm	FDS	5.64	4.00	8.00	0.85	14.99	0.20	83.37		5
		CCNS	7.16	4.00	11.00	1.46	20.45	0.15	NA	1.47	5
		CCDS	7.06	4.00	11.00	1.30	18.47	0.18	NA		4
		FNS	50.00	35.00	70.00	6.47	12.95	2.69	52.25	21.15	9
HI	%	FDS	39.40	24.00	59.00	6.29	15.95	3.29	51.40		9
		CCNS	0.31	0.00	0.47	0.07	22.96	0.01	NA	28.63	6
		CCDS	0.22	0.00	0.08	0.08	37.88	0.00	NA		3
		FNS	28.40	20.00	42.00	4.60	16.19	1.48	74.91	27.72	7
SPS	count	FDS	20.60	14.00	31.00	3.96	19.26	1.19	77.56		5
		CCNS	18.10	2.00	32.00	5.82	32.16	1.19	NA	13.29	0
		CCDS	15.70	1.00	31.00	5.28	33.64	0.97	NA		5
		FNS	38.20	29.00	49.00	4.24	11.10	1.25	70.49	22.75	3
TKW	g/1000	FDS	29.50	20.00	41.00	3.34	11.31	1.22	64.70		6
		CCNS	23.39	6.00	53.00	7.90	33.80	1.15	NA	29.07	3
		CCDS	16.59	5.00	49.00	7.58	45.20	1.13	NA		1
Total											191

Abbreviations: CCDS, climate chamber drought stress; CCNS, climate chamber non-stress; CV, coefficient of variation (standard deviation divided by mean)\*100; DGF, days to grain filling; DH, days to heading; DM, days to maturity; FDS, field drought stress; FNS, field non-stress; GB, grain biomass; H<sup>2</sup>, heritability; HI, harvest index; LSD, least significant difference; mean, minimum, maximum; MTA, marker-trait association; NA, not applicable (heritability was not calculated for the climate chamber experiments since it was conducted only once with two replications for each drought variant); PH, plant height; SD, standard deviation; SL, spike length; SPAD, Soil Plant Analysis Development; SPS, seed per spike; TKW, thousand-kernel weight. Trt, treatment.

### Correlation analysis

Correlations between traits investigated under FDS and CCDS conditions (above diagonal) and FNS and CCNS conditions (below diagonal) are shown in **Table 3A,B**. Under FDS and FNS conditions, GB was positively and significantly ( $p < 0.001$ ) correlated with DGF ( $r = 0.46, 0.21$ ), SPAD ( $r = 0.29, 0.31$ ), SPS ( $r = 0.47, 0.39$ ), HI ( $r = 0.54, 0.44$ ) and TKW ( $r = 0.47, 0.55$ ), respectively (**Table 3A**). Similarly, under CCDS and CCNS conditions, GB was positively and significantly ( $p < 0.001$ ) correlated with PH ( $r = 0.48, 0.60$ ), SL ( $r = 0.32, 0.40$ ), SPS ( $r = 0.50, 0.52$ ) and HI ( $r = 0.39, 0.66$ ), respectively (**Table 3B**). However, under FDS conditions, GB was negatively and significantly ( $p < 0.001$ ) associated with DH ( $r = -0.48$ ), DM ( $r = -0.27$ ) and SL ( $r = -0.24$ ) (**Table 3A**). In the current study, TKW was significantly ( $p < 0.05$ ) correlated with GB under all the experimental conditions except under CCDS condition (**Table 3A, B**).

**Table 3.** Pearson's correlation coefficients ( $r$ ) between traits under FDS and FNS conditions (A) and CCDS and CCNS conditions (B).

FDS/FNS		DH	DM	DGF	PH	SL	SPAD	SPS	HI	TKW	GB
A	DH		0.73	-0.81	0.23	0.37	-0.18	-0.51	-0.60	-0.37	-0.48
	DM	0.62		-0.20	-0.06	-0.07	0.26	-0.12	-0.27	-0.07	-0.27
	DGF	-0.66	0.17		-0.37	-0.59	0.48	0.62	0.63	0.48	0.46
	PH	0.47	-0.05	-0.63		0.63	-0.57	-0.46	-0.49	0.06	-0.04
	SL	0.52	-0.03	-0.69	0.75		-0.71	-0.62	-0.61	-0.38	-0.24
	SPAD	-0.21	0.32	0.58	-0.62	-0.64		0.71	0.53	0.38	0.29
	SPS	-0.31	0.18	0.57	-0.54	-0.57	0.69		0.68	0.38	0.47
	HI	-0.47	0.00	0.59	-0.63	-0.58	0.64	0.73		0.40	0.54
	TKW	-0.19	0.17	0.41	-0.11	-0.37	0.55	0.43	0.46		0.47
	GB	-0.14	0.04	0.21	0.10	-0.01	0.31	0.39	0.44	0.55	
CCDS/CCNS		DH	DM	DGF	PH	SL	SPAD	SPS	HI	TKW	GB
B	DH		0.61	-0.28	0.00	0.10	-0.21	0.07	-0.04	0.06	0.00
	DM	0.33		0.54	-0.11	-0.10	-0.10	0.08	0.19	0.31	0.10
	DGF	-0.59	0.57		-0.15	-0.24	0.14	0.05	0.27	0.30	0.11
	PH	0.10	-0.03	-0.11		0.48	-0.01	0.59	0.00	-0.33	0.48
	SL	0.15	-0.23	-0.33	0.43		-0.05	0.39	-0.09	-0.35	0.32
	SPAD	-0.17	0.16	0.28	0.18	0.07		0.14	0.14	-0.06	-0.04
	SPS	0.00	-0.06	-0.05	0.59	0.36	0.06		0.25	-0.54	0.50
	HI	-0.34	-0.11	0.21	0.39	0.14	0.30	0.53		0.09	0.39
	TKW	-0.20	0.02	0.19	0.00	-0.06	0.40	-0.38	0.14		0.01
	GB	-0.14	-0.12	0.02	0.60	0.40	0.40	0.52	0.66	0.35	

*Note:* Above diagonal indicates the correlation between traits under drought stress treatments and below diagonal shows correlation between traits under non-stress treatments. Correlations  $\geq 0.15$  were significant at  $p < 0.05$  and highlighted. Abbreviations: CCDS, climate chamber drought stress; CCNS, climate chamber non-stress; DGF, days to grain filling; DH, days to heading; DM, days to maturity; FDS, field drought stress; FNS, field non-stress; GB, grain biomass; HI, harvest index; PH, plant height, SL, spike length SPAD, Soil Plant Analysis Development; SPS, seeds per spike; TKW, thousand-kernel weight. Colors indicate the degree of correlation between the trait.

Under FDS and FNS conditions, SPAD was positively and significantly ( $p < 0.001$ ) correlated with GB, DM, DGF, SPS, HI, and TKW and negatively and significantly ( $p < 0.01$ ) correlated with DH, PH, and SL (Table 3A). Likewise, under CCNS conditions, SPAD was positively and significantly ( $p < 0.001$ )

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correlated with GB, DGF, HI, and TKW. But under CCDS and CCNS conditions, SPAD was negatively and significantly ( $p < 0.05$ ) correlated with DH (**Table 3B**).

DH and DM were positively and significantly ( $p < 0.001$ ) correlated under all conditions (**Table 3A, B**). Under FDS and FNS conditions, DH was negatively and significantly ( $p < 0.001$ ) correlated with DGF, SPAD, SPS, HI, and TKW. Under CCDS and CCNS conditions, DH was negatively correlated with DGF and SPAD, while under CCNS conditions DH, was negatively and significantly ( $p < 0.01$ ) correlated with HI and TKW. Correlation between the same traits was positive for field versus climate chamber ranging from non-significant to significant ( $p < 0.001$ ) (**Table 4A, B**). Accordingly, the correlations between GB for FDS versus CCDS and FNS versus CCNS were positive and significant with  $r = 0.17$  and  $0.32$ , respectively. Similarly, the correlations between the same traits, namely DH, DM, DGF, PH, and SL, were positive and significant ( $p < 0.001$ ) for FDS versus CCDS and FNS versus CCNS. Positive and significant ( $p < 0.01$ ) correlation was also observed for SPAD with  $r = 0.19$  between FDS and CCDS, but it was non-significant for FNS versus CCNS. Positive and significant ( $p < 0.001$ ) correlation was detected between SPS for FNS versus CCNS with  $r = 0.26$ , but the correlation was non-significant for FDS versus CCDS. Correlations between TKW for FDS versus CCDS and FNS versus CCNS were positive and significant with  $r = 0.18$  and  $0.45$ , respectively. In this study, HI showed a non-significant correlation between FDS versus CCDS and FNS versus CCNS conditions. Generally, ANOVA, descriptive analysis, boxplots, and correlations between the same traits tested under similar drought treatment for field versus climate chamber indicate a similar trend.

**Table 4.** Pearson's correlation coefficients ( $r$ ) for the same traits tested under FDS versus CCDS conditions (**A**) and under FNS versus CCNS conditions (**B**) for those traits which MTAs were analysed.

<b>A</b>		<b>B</b>	
<b>Drought stress treatments</b>	<b><math>r</math> (<math>p</math> value)</b>	<b>Non-stress treatments</b>	<b><math>r</math> (<math>p</math> value)</b>
DH_FDS vs DH_CCDS	0.47***	DH_FNS vs DH_CCNS	0.56***
DM_FDS vs DM_CCDS	0.29***	DM_FNS vs DM_CCNS	0.35***
DGF_FDS vs DGF_CCDS	0.31***	DGF_FNS vs DGF_CCNS	0.32***
PH_FDS vs PH_CCDS	0.53***	PH_FNS vs PH_CCNS	0.66***
SL_FDS vs SL_CCDS	0.56***	SL_FNS vs SL_CCNS	0.48***
SPAD_FDS vs SPAD_CCDS	0.19**	SPAD_FNS vs SPAD_CCNS	0.12



A		B	
Drought stress treatments	<i>r</i> ( <i>p</i> value)	Non-stress treatments	<i>r</i> ( <i>p</i> value)
SPS_FDS vs SPS_CCDS	0.07	SPS_FNS vs SPS_CCNS	0.26***
HI_FDS vs HI_CCDS	0.12	HI_FNS vs HI_CCNS	0.03
TKW_FDS vs TKW_CCDS	0.18*	TKW_FNS vs TKW_CCNS	0.45***
GB_FDS vs GB_CCDS	0.17*	GB_FNS vs GB_CCNS	0.32***

Abbreviations: CCDS, climate chamber drought stress; CCNS, climate chamber non-stress; DH, days to heading; DM, days to maturity; DGF, days to grain filling; FDS, field drought stress; FNS, field non-stress; GB, grain biomass; HI, harvest index; PH, plant height; SL, spike length; SPAD, Soil Plant Analysis Development; SPS, seed per spike, TKW, thousand-kernel weight; vs, versus.

\*\*\*  $p < .001$ . \*\*  $p < 0.01$ . \*  $p < 0.05$ .

### LD decay

The significant ( $-\log_{10}p \geq 4$ ) MTA was clustered into QTL by the critical LD decay value ( $r^2 \geq 0.2$ ) at 4.78 Mb. The highest LD decay was calculated for the A genome on chromosome 4A and the B genome on chromosome 6B. Therefore, in the sets, chromosomes 4A and 3A had the highest and the lowest decay rates, respectively. Similarly, chromosomes 6B and 2B had the highest and the lowest decay rates in the set, respectively. Chromosome 2B had a notably slower decay rate than the others (**supporting information Table S3**).

### MTAs

A total of 191 significant ( $-\log_{10}p \geq 4$ ) MTAs were detected across the whole durum wheat genome (**supporting information Table S4**). The numbers of detected significant MTAs were 58, 68, 36, and 29 for FDS, FNS, CCDS, and CCNS, respectively. The highest number of MTAs (25) was detected on chromosome 1B, and the lowest number was detected on chromosome 3A (5). Concerning the traits analyzed, the highest numbers of MTAs detected were 27 each for SPAD and HI, followed by 24 for DH. The lowest number of MTAs obtained was 11 for PH (**Table 2 and supporting information Table S4**). In the current study, no MTA was detected for PH under climate chamber conditions.

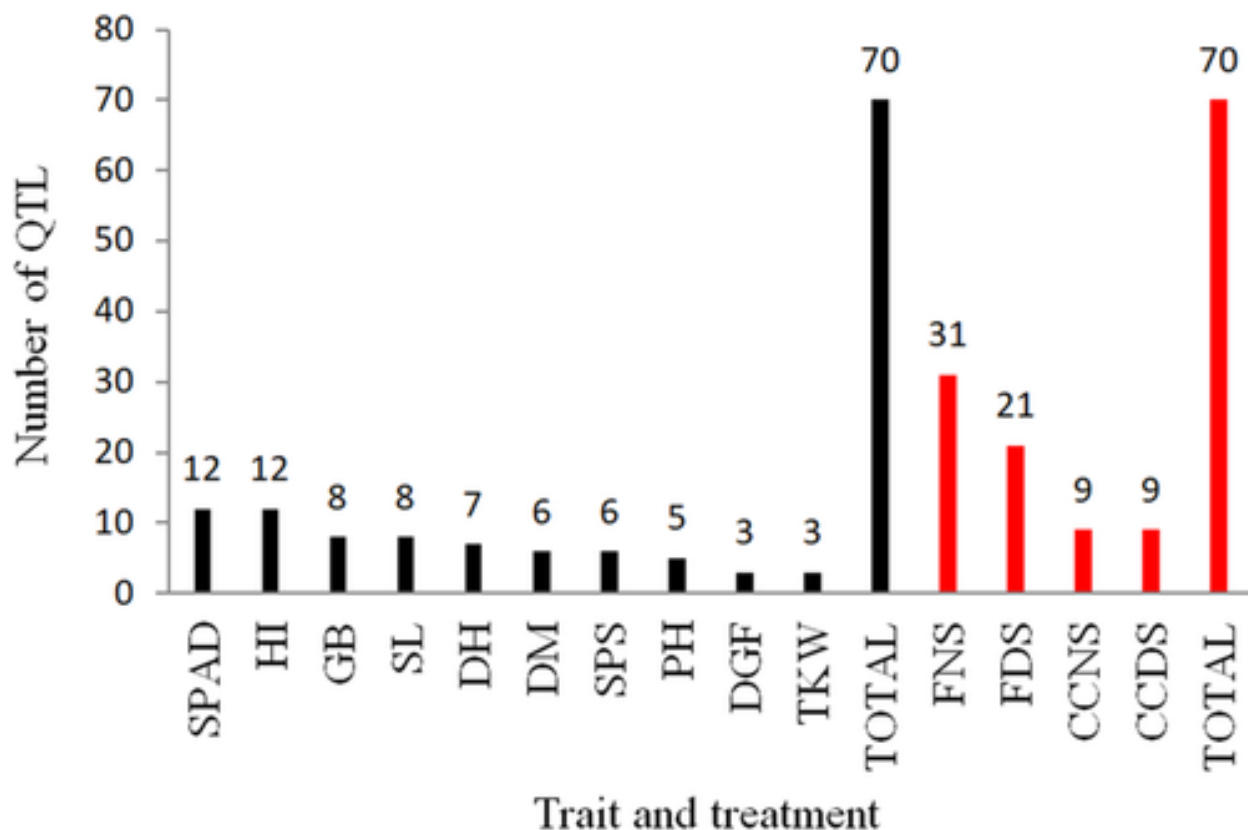
In this study, eight overlappings MTA were detected associated with multiple phenotypic traits for drought stress and non-stress conditions and highlighted in yellow color (**supporting information table S4**). Three overlapping MTAs were detected on chromosome 1B at 10778560 bp associated with DH and

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DM under FDS, at 534692879 bp for GB and DH under CCNS and at 381876470 bp associated with DH and DGF under CCNS and FDS conditions, respectively. One overlapping MTA was detected for SPS on chromosome 3B at 25269809 bp both under FDS and FNS conditions. One overlapping MTA was detected on chromosome 4B at 485705797 bp associated with DM and HI under FNS and FDS conditions, respectively. Two overlappings MTAs were detected on chromosome 5A at 112213041 bp for SL under FDS and DGF under FNS and at 110830599 bp for GB under FDS and HI under FNS. Similarly, one overlapping MTA was detected on chromosome 7A at 616616464 bp associated with DH and SL both under CCDS conditions. Therefore, from the eight overlappings MTAs associated with multiple phenotypic traits, regardless of the traits associated with, five markers (Excalibur\_c7964\_1290 on chromosome 4B at 485705797 bp, Kukri\_rep\_c116526\_98 on chromosome 5A at 112213041 bp, Ra\_c18323\_183, RAC875\_c60169\_200 on chromosome 1B at 381876470 bp and Tdurum\_contig76578\_537 on chromosome 5A at 110830599 bp) were detected under contrasting drought treatment conditions, indicating that these markers are potentially stable. One stable marker, detected for SPS (RAC875\_c60169\_200) located on chromosome 3B at 25269809 bp, was detected under FDS and FNS (**supporting information Table S4**). Notably, after clustering into QTL, just one overlapping QTL remained (see below).

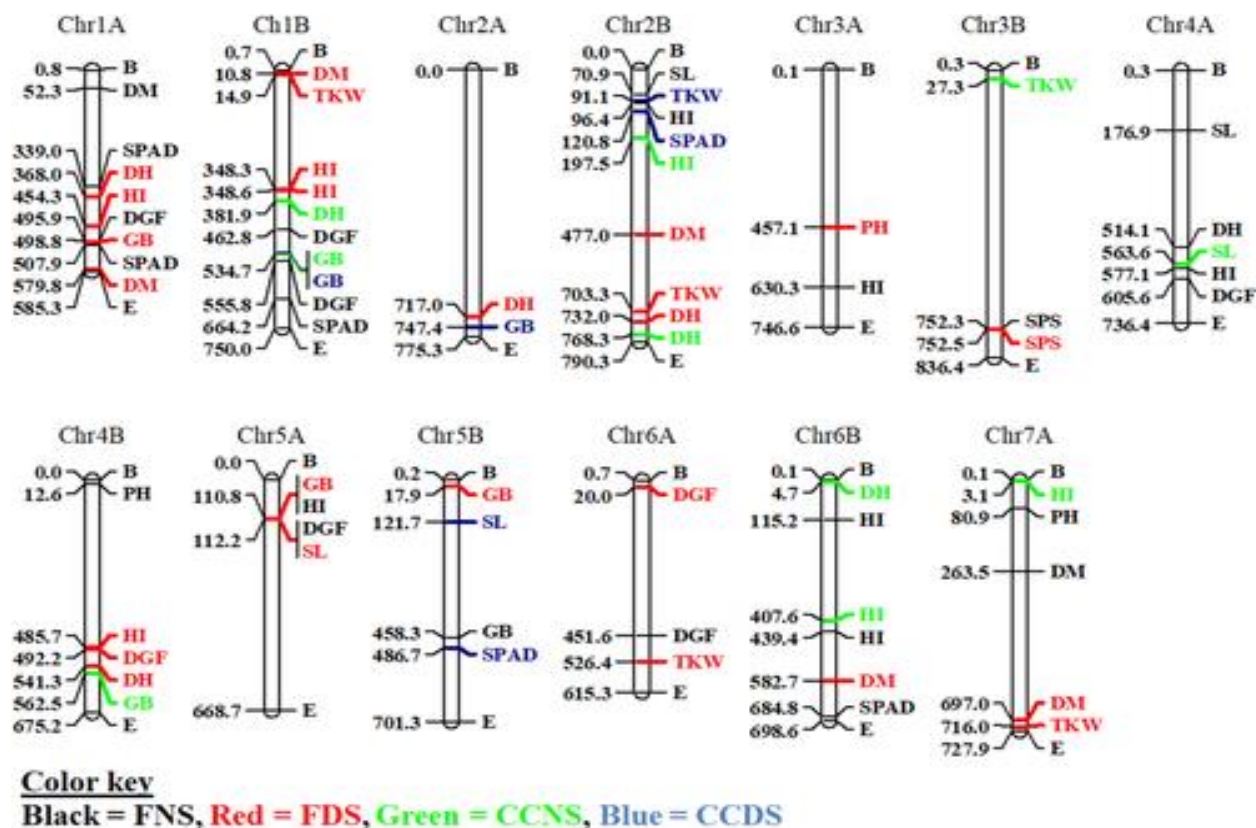
The percentage of PVE by each MTA varied from 0.03% to 11.83%. The highest PVE detected was 11.83% for SL under FNS followed by 10.61% PVE for HI under CCDS, while others showed lower than 10% PVE indicating the polygenic nature of the quantitative traits evaluated (**supporting information Table S4**). Manhattan plots for all investigated traits under FNS, FDS, CCNS, and CCDS are visualized in **Figures S5, S6, S7, and S8**, respectively. In the current study, out of 191 detected MTAs, 69 MTAs associated with GB, DH, DGF, DM, PH, SPAD, SPS, HI, and TKW were significant at FDR 5% highlighted in grey color (**supporting information Table S4**) and with black, red, green and blue colors for FNS, FDS, CCNS, and CCDS, respectively (**Figure 2**).

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**Figure 2.** Number of detected quantitative trait loci (QTLs) for the investigated traits (black bar) and under field non-stress (FNS), field drought stress (FDS), climate chamber non-stress (CCNS), and climate chamber drought stress (CCDS) treatments (red bar).

Using critical LD ( $r^2 \geq .2$ ), the detected MTAs were clustered into 70 QTLs (**Figure 2 and supporting information Table S5**). Consequently, 31, 21, 9, and 9 QTLs were identified under FNS, FDS, CCDS, and CCNS, respectively. The highest numbers of QTLs obtained were 12 each for SPAD and HI, followed by 8 QTLs each for GB and SL. The lowest number of QTLs detected was three for DGF and TKW, each (**Figure 2**). In the SP, 30 QTLs were identified on the A genome and 40 QTLs on the B genome. The largest number of QTLs was detected on chromosomes 6B (10 QTLs), followed by 1A (eight QTLs) and 2B (seven QTLs). The smallest numbers of QTL detected were one on chromosome 6A, followed by 3A (two QTLs) (**supporting information Table S5**). In this study, only one QTL overlapping between the two watering regimes was detected on chromosome 1B between 620250467–627873395 bp for HI under FDS and SPAD and HI under FNS.



**Figure 3.** Physical linkage map of the durum wheat genome in Mb by MapChart (Voorrips, 2002). A total of 69 significant marker trait association (MTAs) at false discovery rate (FDR) 5% under field non-stress (FNS), field drought stress (FDS), climate chamber non-stress (CCNS), and climate chamber drought stress (CCDS) elucidated by black, red, green, and blue colours, respectively. GB: grain biomass, DH: days to heading, DGF: days to grain filling, DM: days to maturity, PH: plant height, SL: spike length, SPAD, SPS: seed per spike, HI: harvest index, and TKW: thousand-kernel weight.

The eight detected QTLs for GB, which are independent of DH were located on chromosomes 1A between 495694477 and 501944537 bp; 3B between 416256124 and 430507900 bp and 745357158 and 759608934 bp; 4B between 561075112 and 572800846, 593416763 and 605142497 and 658785890 and 670511624 bp; 6B between 505703728 and 510449994 bp and on 7A between 637937043 and 645127159 bp with PVE ranging from 1.92% to 4.24%. These QTLs for GB were co-located with DGF, DM, SL, SPS, SPAD, and HI traits. Six out of the eight QTLs for GB were previously reported and two were likely new (**supporting information Table S5**). All the seven detected QTLs for DH were previously reported, and out of these, four QTLs turned out to be co-located with TKW, SL, SPAD, GB, and HI. Two out of the three detected QTLs for DGF are co-located with SL, SPS, SPAD, and TKW traits. One QTL detected for DGF was previously reported, and two are novel. Four out of the six detected QTLs for DM are co-located with DH, DGF, PH, SL, SPAD, HI, and SPS. From the detected QTLs for DM, four are likely new. Five previously reported QTLs were detected for PH, and out of these,

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four QTLs are co-located with SL, DH, GB, DGF, SPS, and SAPD. All the twelve QTLs detected for SPAD were previously reported, and eight QTLs are co-located with DGF, DM, SPS, HI, DH, PH, and SL traits. Six out of the eight detected QTLs for SL are co-located with DGF, PH, DM, GB, HI, SPAD, TKW, and DH traits and one QTL detected for SL is novel. Four out of the six detected QTLs for SPS are co-located with DGF, GB, HI, SPAD, PH, and TKW traits, and one QTL for SPS is likely new. Six out of the 12 detected QTLs for HI are co-located with DGF, SPS, TKW, SPAD, DH, GB, and SL, and five QTLs for HI are novel. The three detected QTLs for TKW were previously reported, and one QTL out of the three is co-located with DH and HI.

### Discussion

Drought stress alters the morphological, physiological, and molecular responses of plants. In the current study, GB reduction due to drought stress ranged from 35.79% to 52.41% for field and climate chamber experiments, respectively. Other recent reports revealed that grain yield reduction due to drought was up to 60% on durum wheat and more than 40% and 30% for bread wheat, and rice, respectively (Sukumaran et al., 2018; Zhang et al., 2018). Field experiments in our study were reliable, showing moderate to high broad-sense heritability. Higher heritability values were obtained for most of the evaluated traits under FNS compared with FDS conditions (**Table 2**). ANOVA results indicate the broad genetic diversity of the SP enabling the dissection of the embedded genetic diversity.

The negative correlation of GB with DH ( $r = -0.48$ ) and DM ( $r = -0.27$ ) under FDS condition indicates that early maturing accessions had a yield advantage. This is in agreement with the finding of Millet et al. (2016), Sukumaran et al. (2018), and Qaseem et al. (2019). GB was also negatively correlated with SL ( $r = -0.24$ ) under FDS, which is in line with results on durum wheat (Pour-Aboughadareh et al., 2020). The negative correlation of GB with SL under FDS indicated a reduced seed set due to prolonged terminal drought under field conditions. A positive and significant correlation was observed between GB and DGF under FDS and FNS conditions. However, there was no correlation between GB and DGF under CCDS treatment. A report by Sukumaran et al. (2018) also indicated no association between GB and DGF in durum wheat genotypes studied under well-watered and drought conditions. In the current study, under field conditions, GB did not show a correlation with PH but a positive and significant ( $r = 0.6$ ) correlation with GB and PH under CCDS conditions. This is in agreement with Qaseem et al. (2017) who suggested that under drought stress environments, tall genotypes accumulate and mobilize more resources to grain and thus had a higher yield than shorter genotypes. In the current study, TKW was significantly ( $p < 0.05$ ) correlated with GB except under CCDS under which the association between these traits was positive but non-significant. A recent study on durum wheat also reported a non-significant correlation between GB

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and TKW under drought stress and non-stress conditions (Sukumaran et al., 2018). However, studies revealed a significant association between GB and TKW in wheat (del Pozo et al., 2019; Mohammadi et al., 2018). This may be due to the complex nature of GB and that GB and TKW are affected by several factors under different environmental conditions.

GWAS is a powerful tool for the identification of quantitative trait loci and to exploit the differential decay of LD between marker loci and genes of interest in natural and domesticated populations (Laidò et al., 2014). The basic principle behind LD is to detect and cluster the detected MTAs during GWAS analysis. If the distance between two identified MTAs is less than the critical ( $r^2 \geq 0.2$ ) LD decay value, it shows 95% confidence that the two MTAs stay tighter and are assigned as one QTL; otherwise, they are in linkage equilibrium (Kidane et al., 2017). In crop plants, several QTLs have been reported on agronomic, physiology, and root traits using linkage mapping and genome-wide association studies (Gupta et al., 2020). In our SP, the LOESS curve crossed the critical LD ( $r^2 \geq 0.2$ ) at 4.78 Mb. Similarly, other studies reported LD decay values of 4.5 Mb (Maccaferri et al., 2019) and 5.71 Mb (Taranto et al., 2020) at the critical LD ( $r^2 = 0.2$ ) for the durum wheat SP. Hence, based on the critical LD value, the identified 191 MTAs were grouped into 70 QTLs. LD pattern of an SP is important for selecting the marker density required for GWAS and for defining identified QTLs (Siol et al., 2017). The PVE varied from 0.03% to 11.83%, and only for two MTAs, are value higher than 10% for PVE was calculated, demonstrating the polygenic control of the traits measured in this study. This is also reported in other studies on durum wheat (Wang et al., 2019) and bread wheat (Liu et al., 2018). In our study, two major MTAs were detected for traits HI under CCDS and SL under FNS with 10.6% and 11.83% PVE, respectively (**supporting information Table S4**). Interestingly, similar results were reported from GWAS analysis for the trait PH in durum wheat explaining 16% to 39% of total PVE (Wang et al., 2019) and in bread, wheat explaining 10.10% to 30.68% of the phenotypic variation (Jin et al., 2020).

In our study, QTLs were detected for yield and yield-related traits and matched with previously reported results from durum wheat in the GrainGenes database (**supporting information Table S5**). Grain yield is the main target in wheat breeding and it is a complex trait due to high GxE interaction and low to intermediate heritability (Börner et al., 2002). Identification and use of QTLs associated with valuable agronomic traits at early generation selection in wheat breeding programs enhance the development of improved cultivars (Collard and Mackill, 2008). A QTL that relates to two or more traits is considered a co-located QTL, while a QTL associated with a single trait is considered an individual QTL (Ma et al., 2019; Sukumaran et al., 2018). Thus, in this study, eight co-located QTLs were detected associated with GB (**supporting information Table S5**). QTLs for GB were found to be also linked with DGF between 495694477 and 501944537 bp; DM between 416256124 and 430507900 bp; SL and SPS between

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745357158 and 759608934 bp; SL between 561075112 and 572800846, 593416763 and 605142497 and 637937043 and 645127159 bp; with HI, DM and SPAD between 658785890 and 670511624 bp; as well as with SPAD between 505703728 and 510449994 bp under drought stress and non-stress conditions. Interestingly, in our study, QTLs detected for GB were not linked with DH, which hints at a limited effect of flowering time on grain yield as also reported in other studies for durum wheat (Zaïmet et al., 2020) and wheat (Ullah et al., 2021). The detected GB QTLs were located on chromosomes 1A, 3B (2), 4B (3), 6B, and 7A. Except for two QTLs located on chromosomes 1A and 4B, which we believe to be reported for the first time, the other six QTLs have been reported in previous studies (Maccaferri et al., 2008; Mengistu et al., 2016; Soriano et al., 2017) on chromosome 3B, (Milner et al., 2016; Patilet et al., 2013) on chromosome 4B, (Marcotuli et al., 2017) on 6B and on 7A (Mengistu et al., 2016). The current identification of QTLs within similar QTL intervals in our study and the mentioned previous studies confirms the findings and the power of GWAS (**supporting information Table S5**). Therefore, QTLs located on chromosomes 3B and 4B can be considered constitutive QTLs linked to GB whose selection may help to increase yield under drought stress. Similarly, recent findings identified QTLs for grain yield in the durum wheat genome (Arifet et al., 2020; Mangini et al., 2018, 2021; Zaïm et al., 2020). Conversely, in our study and the report by Mangini et al. (2021), no QTL associated with GB was detected on chromosome 2B, which was reported to carry QTLs for GB by Zaïm et al. (2020). More important, in our study, GB QTLs detected under drought stress including newly detected QTLs showed a positive effect on grain biomass with significant LOD values ranging between 4.11 and 7 and with up to 4.24% PVE, indicating that they could have the potential in increasing grain yield in durum.

DH provides the basis for plant adaptation and is a major trait in plant breeding (Zaïm et al., 2020). Also, under terminal drought, early flowering time and a shorter vegetative phase are important for wheat production (Shavrukov et al., 2017). In the present study, seven (four co-located and three individual) QTLs for DH were located on chromosomes 1A, 1B, 2A, 4A, 4B, and 6B. Interestingly, five of the identified QTLs were positioned within reported QTL intervals on chromosomes 1A and 1B (Milner et al., 2016), 2A (Giunta et al., 2018), 4A (Maccaferri et al., 2011; Milner et al., 2016) and on chromosome 6B (Maccaferri et al., 2011; Roncallo et al., 2018). In addition, affirming the finding of our study, QTLs on chromosomes 2A, 2B, 4B, 5B, and 7B were also reported for this phenology trait (Zaïm et al., 2020). Maccaferri et al. (2015), using durum wheat elite cultivars report QTL on chromosome 4A out of the 43 QTLs associated with DH across the durum wheat genome except for chromosome 6A. Genomic regions on chromosomes 2A and 2B were reported to be associated with the major photoperiod sensitivity loci Ppd-A1 and Ppd-B1 (Arjona et al., 2018; Maccaferri et al., 2008, 2011). Notably, our study we detected a QTL on chromosome 2A under FDS that is located very close to the position of Ppd-1A, but no QTL was detected in the vicinity of Ppd-B1. Ppd1 genes affect the time of heading and other traits and play an

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important role in modifying source-sink equilibrium, thus affecting wheat growth and development (Foulkes et al., 2004; Kamran et al., 2014; Würschum et al., 2018).

The duration between heading and maturity is an important yield component in wheat. Here, three QTLs were detected for DGF located on chromosomes 1B between 378,065,006–385,687,934 bp, on 3B between 732,882,447–747,134,223 bp, and on 7B between 543,578,199–552,021,963 bp. The three detected QTLs have not been reported before and thus represent new QTLs linked to DGF in durum wheat. QTLs for DGF on chromosome 7B cluster with two or more traits, for example, SPS, TKW, and SPAD. This may suggest the linear relationship between DGF and the traits or may be due to pleiotropic effects (Bhoite et al., 2018). A total of six (three co-located and three individuals) QTLs associated with DM were located on chromosomes 1A, 2B, 4A, 5B, and 7A. Interestingly, two QTLs on chromosomes 4A and 7A were detected in the same intervals in Ethiopian durum wheat landraces and modern varieties on chromosome 4A (Kidane et al., 2017) and Ethiopian durum wheat landraces on chromosome 7A (Mengistu et al., 2016). When compared with the GrainGenes database, the QTLs detected on chromosomes 1A, 2B, and 5B are likely to be novel QTLs associated with DM in durum wheat.

Plant height is frequently altered when water is limited to overcome the deleterious effects of drought (Arif et al., 2020). Five (co-located with other traits) QTLs were identified as associated with PH located on chromosomes 1A, 2B, 6B, 7A, and 7B. The identified QTL on chromosome 6B was previously reported associated with PH in Ethiopian durum wheat landraces (Mengistu et al., 2016). Similarly, the QTL on chromosome 7B linked with PH is located within a previously reported QTL region for PH in Mediterranean durum wheat landraces (Soriano et al., 2017) and close to a QTL region identified in Elite durum cultivars (Maccaferri et al., 2011). Similarly, Mangini et al. (2021) reported QTLs associated with PH on chromosomes which we also identified, except on chromosome 1A. However, opposite to our findings, Zaim et al. (2020) reported QTLs associated with PH on chromosomes 4A, 4B, and 5B. The Green Revolution resulted in the release of short, high-yielding cultivars, which are mainly related to genes controlling PH in wheat. The introduction of semidwarf genes into bread wheat resulted in the replacement of tall cultivars with semidwarf cultivars with high response to inputs (e.g., fertilizers) and resistance to lodging. Thereby, a significant increase in yield was achieved in many national breeding programs (Xynias et al., 2020). In agreement with our study, Chai et al. (2021) mentioned different alleles responsible for dwarfing genes in wheat located on chromosomes 2B, 7A, and 7B. In the current study, out of two QTLs for PH under FDS, the one located on chromosome 1A showed a high reducing effect with 1.47% PVE.

SPAD values serve as a valuable indicator of the photosynthetic capacity of plants (Fiorentini et al., 2019; Lopes and Reynolds, 2012). A total of 12 (eight co-located and four individuals) QTLs were identified for



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SPAD readings from flag leaves and were mapped on chromosomes 1A, 2A, 2B, 3A, 5B, 6B, and 7B. A recent study reported QTLs for flag leaf chlorophyll content for the durum wheat genome but on chromosomes 1B and 3B (Huang et al., 2018). GWAS results also indicated QTLs linked to leaf chlorophyll content under drought stress located on chromosomes 1B, 2A, 2B, 3B, 6B, and 7B in winter wheat seedlings (Maulana et al., 2020). These results highlight the potential of exploring QTLs associated with leaf chlorophyll content in durum wheat as a key factor for photosynthesis by which 80% of wheat yield is realized in canopy leaves (Ghosh et al., 2003; Hussain et al., 2015).

SL is a yield-related trait in wheat. Eight (six co-located with other traits DGF, PH, DM, GB, HI, SPAD, TKW, and HI and two individual) QTLs were detected for SL on chromosomes 2B, 4A, 5A, 5B, 7A, and 7B. All QTLs were detected under drought stress conditions except a QTL located on chromosome 7B. Similarly, Hu et al. (2015) identified eight QTLs associated with the length of the main spike in durum wheat located on chromosomes 1B, 2B, 4A, 5A, 5B, 7A, and 7B (Huet et al., 2015). The QTL detected on chromosome 7B is located in a QTL region reported by Thanh et al. (2013). There was no QTL for SL reported yet on chromosome 2B suggesting this QTL is novel. Six (five co-located with DGF, GB, HI, SPAD, and TKW and one individual) QTLs were detected associated with SPS located on chromosomes 2B, 3B, 6A, 6B, and 7A, of which five were reported earlier (Giunta et al., 2018; Mangini et al., 2018; Mengistu et al., 2016; Roncallo et al., 2018). One of the QTLs on 6B linked to SPS was reported here for the first time. Four of the six QTLs detected for SPS were detected under FDS and CCDS with a positive effect on the trait. Interestingly, these QTLs identified under drought stresses were also identified for traits such as DGF, PH, TKW, and SPAD.

HI is an important trait directly associated with yield. Twelve QTLs were detected for HI located on chromosomes 1A, 1B, 2A, 2B, 3A, 5A, 6B, and 7A. Recently, a study on association mapping of QTLs for yield and yield-related traits revealed QTLs associated with HI on chromosomes 1B, 2B, 3B, 4B, 5B, 7A, and 7B (Arif et al., 2020). Similarly, in the current study, the two detected QTLs on chromosomes 2A and 6B were close to the reported QTL interval by Roncallo et al. (2018) and within the reported QTL interval on chromosome 6A (Pelog et al., 2009). QTLs for HI obtained in this study located on chromosomes 1A, 3A, and 5A are reported for the first time in durum wheat. Three (two individual and one co-located with DH and HI) QTLs were detected associated with TKW located on chromosomes 2B, 3B, and 4A. These three QTLs were also identified in multi-locations in tetraploid wheat in segregating populations and germplasm collections for TKW (Mangini et al., 2018). The QTLs on chromosome 2B detected under CCDS and on 3B under CCNS and on 4A under FNS were found to be in close vicinity and within the already detected QTL intervals, respectively (Mangini et al., 2018). Recent, studies also

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identified QTLs for TKW on chromosomes 1A, 1B, 2A, 3A, 4B, 5A, 5B, and 6B in durum wheat (Giancaspro et al., 2019; Mangini et al., 2021), which we lack to identify in our study.

Despite the detection of significant positive correlations between climate chamber and field results for several traits, we did not observe common QTLs for any trait under the two environments (climate chamber and field). In our study, we mainly investigated polygenetic quantitative traits. This phenomenon has been explained as a quantitative trait being controlled by numerous genes, with each gene having a relatively small effect, and readily affected by environments (Zhang et al., 2020). Supported by our ANOVA results showing the strongest effects for the environment, we concluded that the missing overlap of detected associated loci for a certain trait in the two environments may be explained by the effect of the environment leading to varying regulatory scenarios for the various traits under the two watering conditions. As a result, genetic selection for drought stress has to be conducted in the target environment and ideally may include the design of ideotypes for certain growth scenarios (Senapati and Semenov, 2019).

### Conclusion

The experimental setting revealed the impact of drought on the durum wheat SP. Traits such as DGF, SPAD, SPS, HI, and TKW showed a strong and significant ( $p < 0.0001$ ) correlation with GB under FDS. Heritability of the traits analyzed varied between 48.2% for DM and 89.11% for PH under FNS. Similarly, under FDS, heritability ranged between 42% for DM and 83.37% for SL. A significant ( $p < 0.01$ ) positive correlation was detected between GB for FNS versus CCNS, as well as for FDS versus CCDS conditions. Similarly, significant ( $p < 0.001$ ) positive correlations were observed between the same traits (DH, DM, DGF, PH, and SL) for FDS versus CCDS and FNS versus CCNS conditions. However, the correlation between HI was not significant for FDS versus CCDS and FNS versus CCNS conditions. GWAS is a powerful tool to pinpoint the association between traits and markers. Critical ( $r^2 > 0.2$ ) LD decay value identified 70 QTLs, of which 50 QTLs were linked to several traits and where 20 QTLs were associated with any one of the traits under the drought treatments. Many of the QTLs were detected within or in close vicinity of previously reported QTL intervals, a fact highlighting the consistency of our study. In addition, we have identified several novel QTLs for some of the tested traits referring to the GrainGenes database for durum wheat and literature reports. QTLs with a positive effect size that was detected under drought stress conditions for GB and traits co-located with GB may have high potential in increasing grain biomass in durum wheat. These include, for example, QTL on 1A between 495694477 and 501944537 bp, on 3B between 416256124 and 430507900 bp, on 3B between 745357158 and 759608934 bp, on 4B between 593416763 and 605142497 bp and 4B between 658785890 and

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670511624 bp. We concluded that our SP is showing reasonable genetic evidence for adaptations under drought-stress environments. In the future, genomic selection markers may be developed and validated for QTL markers with relevance for yield stability and yield improvement under drought stress conditions. While the environment and selected germplasm will strongly depend on the breeding strategy, the novel QTL markers identified in our study likely represent potential candidates for MAS in wheat breeding programs for drought tolerance.

**Publication 2.3) Negisho K, Shibru S, Matros A, Pillen K, Ordon F, & Wehner G. (2022b). Association Mapping of Drought Tolerance Indices in Ethiopian Durum Wheat (*Triticum turgidum* ssp. *durum*). *Frontiers in Plant Sciences* 13:838088. <https://doi.org/10.3389/fpls.2022.838088>.**

**Abstract**

Ethiopia is a major producer of durum wheat in sub-Saharan Africa. However, its production is prone to drought stress as it is fully dependent on rain, which is erratic and unpredictable. This study aimed to detect marker-trait associations (MTAs) and quantitative trait loci (QTLs) related to indices. Six drought tolerance indices, i.e., drought susceptibility index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) were calculated from least-square means (lsmeans) of grain yield (GY) and traits significantly ( $p < 0.001$ ) correlated with grain yield (GY) under field drought stress (FDS) and field non-stress (FNS) conditions. GY, days to grain filling (DGF), soil plant analysis development (SPAD) chlorophyll meter, seeds per spike (SPS), harvest index (HI), and thousand kernel weight (TKW) were used to calculate DSI, GMP, RDI, STI, TOL, and YSI drought indices. Accessions, DW084, DW082, DZ004, C037, and DW092 were selected as the top five drought-tolerant based on DSI, RDI, TOL, and YSI combined ranking. Similarly, C010, DW033, DW080, DW124-2, and C011 were selected as stable accessions based on GMP and STI combined ranking. A total of 184 MTAs were detected linked with drought indices at  $-\log_{10}p \geq 4.0,79$  of which were significant at a false discovery rate (FDR) of 5%. Based on the linkage disequilibrium (LD,  $r^2 \geq 0.2$ ), six of the MTAs with a positive effect on GY-GMP were detected on chromosomes 2B, 3B, 4A, 5B, and 6B, explaining 14.72, 10.07, 26.61, 21.16, 21.91, and 22.21% of the phenotypic variance, respectively. The 184 MTAs were clustered into 102 QTLs. Chromosomes 1A, 2B, and 7A are QTL hotspots with 11 QTLs each. These chromosomes play a key role in drought tolerance and respective QTL may be exploited by marker-assisted selection for improving drought stress tolerance in wheat.

**Keywords:** Ethiopia, Durum wheat, Drought tolerance indices, GWAS, QTLs, Field studies.

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**Veröffentlichung 2.3) Negisho K, Shibru S, Matros A, Pillen K, Ordon F, & Wehner G. (2022b). Association Mapping of Drought Tolerance Indices in Ethiopian Durum Wheat (*Triticum turgidum* ssp. durum). *Frontiers in Plant Sciences* 13:838088. <https://doi.org/10.3389/fpls.2022.838088>.**

### **Abstrakt**

Äthiopien ist ein wichtiger Produzent von Hartweizen in Afrika südlich der Sahara. Die Hartweizen-Produktion ist jedoch anfällig für Trockenstress, da sie vollständig vom Regen abhängig ist, der unregelmäßig und unvorhersehbar ist. Ziel dieser Studie war es, Marker-Trait-Assoziationen (MTAs) und quantitative Trait-Loci (QTLs) im Zusammenhang mit Trockenstresstoleranz-Indizes zu ermitteln. Sechs Trockenstresstoleranz-Indizes, nämlich der Index der Trockenheitsanfälligkeit (DSI), die geometrische mittlere Produktivität (GMP), der relative Trockenheitsindex (RDI), der Stresstoleranzindex (STI), der Toleranzindex (TOL) und der Ertragsstabilitätsindex (YSI) wurden aus den kleinsten quadratischen Mittelwerten (lsmeans) des Kornertrags (GY) und den Merkmalen berechnet, die signifikant ( $p < 0,001$ ) mit dem Kornertrag (GY) unter Feld-Trockenstress (FDS) und Feld-Nichtstress (FNS) Bedingungen korrelierten. GY, Tage bis zur Kornfüllung (DGF), Blatt Chlorophyll-Gehalt (SPAD), Samen pro Ähre (SPS), Ernte-Index (HI) und Tausendkorngewicht (TKW) wurden zur Berechnung der Dürre-Indizes DSI, GMP, RDI, STI, TOL und YSI verwendet. Die Sorten DW084, DW082, DZ004, C037 und DW092 wurden auf der Grundlage des kombinierten Rankings von DSI, RDI, TOL und YSI als die fünf Trockenstress-tolerantesten Sorten ausgewählt. In ähnlicher Weise wurden C010, DW033, DW080, DW124-2 und C011 auf der Grundlage der kombinierten GMP- und STI-Rangliste als stabile Sorten ausgewählt. Insgesamt wurden 184 MTAs identifiziert, die mit Trockenstresstoleranz-Indizes bei  $-\log_{10} p \geq 4,0$  assoziiert waren, von denen 79 bei einer Falschentdeckungsrate (FDR) von 5% signifikant waren. Auf der Grundlage des Kopplungsungleichgewichts (LD,  $r^2 \geq 0,2$ ) wurden sechs der MTAs mit einem positiven Effekt auf GY-GMP auf den Chromosomen 2B, 3B, 4A, 5B und 6B identifiziert, die 14,72, 10,07, 26,61, 21,16, 21,91 bzw. 22,21 % der phänotypischen Varianz erklärten. Die 184 MTAs wurden anhand des LD in 102 QTLs gruppiert. Die Chromosomen 1A, 2B und 7A sind QTL-Hotspots mit jeweils 11 QTLs. Diese Chromosomen spielen eine Schlüsselrolle bei der Trockenstresstoleranz, und die entsprechenden QTL können zukünftig für die markergestützte Selektion zur Verbesserung der Trockenstresstoleranz bei Weizen genutzt werden.

**Stichworte:** Äthiopien, Hartweizen, Trockenstresstoleranzindizes, GWAS, QTLs, Feldstudien.

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### Introduction

Globally, drought is a serious abiotic factor challenging crop production, productivity, and quality. It is enhanced by climate change leading to food and livelihood crises (Lobell et al., 2011). Singh et al. (2016) reported total crop failure and death of livestock due to drought in Ethiopia affecting nearly 10 million people, especially in the northern part of the country. Hence, Ethiopia is experiencing significant climate-induced drought and water-related stresses on crop and livestock productivity (Brown et al., 2017). Durum wheat ( $2n = 28$ , AABB, *Triticum turgidum* L. ssp. *durum*) is the most commonly cultivated form of allotetraploid wheat and is grown in 8% of the world's wheat area (FAO, 2016). In Ethiopia, durum wheat nearly accounts for 15–20% of wheat production and covers 30% of wheat cultivated land areas (Negassa et al., 2013). In Ethiopia, durum wheat is not only a staple crop for food security but also it becomes a major cash crop having 10–20% higher prices than bread wheat (Sall et al., 2019).

Ethiopia is one of the world's eight major Vavilovian centers of origin of crop plants, such as durum wheat and a major durum wheat producer, in sub-Saharan Africa (Vavilov, 1951; Sall et al., 2019). However, its production is fully dependent on rain, which is erratic and unpredictable, particularly in the low altitude regions (Simane et al., 1994). Ethiopia is currently harvesting crops only from 14 million out of 51.3 million hectares of arable lands [Tsegaye, 2017; Central Statistical Agency of Ethiopia (CSA), 2018]. This is primarily due to drought stress and the lack of irrigation facilities among other production constraints. Therefore, the selection of drought-tolerant durum wheat genotypes has paramount importance in expanding its production to the untapped potential production areas and to use drought-tolerant genotypes in wheat improvement programs. The huge genetic diversity in Ethiopian durum wheat landraces could be a potential gene pool for national and international wheat improvements (Mengistu et al., 2015; Negisho et al., 2021). Thereby, the identification and use of drought-tolerant accessions from the existing genetic diversities could help to overcome the drastic effect of drought (Van Oosten et al., 2016).

Drought indices provide a mathematical measure for yield loss under drought stress conditions as compared to non-stress conditions in screening drought-tolerant genotypes (Fernandez, 1992; Mitra, 2001). They have been widely used for screening drought-tolerant genotypes in durum wheat (Patel et al., 2019), bread wheat (Abdolshahi et al., 2012; Song et al., 2017), barley (Sallam et al., 2019), and maize (Naghavi et al., 2013; Yousefi, 2015). The drought susceptibility index (DSI) is used to measure yield stability in wheat genotypes that apprehends the changes in both drought stress and non-stress environments (Fischer and Maurer, 1978). Guttieri et al. (2001) suggested genotypes with DSI values of < 1 showing tolerance to drought stress. Genotypes with high values for yield stability index (YSI)

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(Bousslama and Schapaugh, 1984) and relative drought index (RDI) (Fischer et al., 1998) are generally regarded as stable under stress and non-stress conditions. Rosielle and Hamblin (1981) also proposed drought stress tolerance (TOL) criteria based on mean yield from drought stress and non-stress conditions. Similarly, the stress tolerance index (STI) (Fernandez, 1992) and geometric mean productivity (GMP) (Ramirez-Vallejo and Kelly, 1998) are useful indices for the identification of stable genotypes, which produce high yield under drought stress and higher or optimum yield under non-stress.

Quantitative trait loci have been detected for grain yield related drought tolerance indices traits in wheat (Edae et al., 2014; Maccaferri et al., 2015; Qaseem et al., 2019) and chickpea (Kale et al., 2015). However, research on the identification of QTLs associated with drought tolerance indices for traits other than grain yield is scarce. For instance, Sukumaran et al. (2018) detected QTLs associated with drought indices (SSI, TOL, STI) calculated from grain yield (GY), thousandgrain weight (TGW), and grain number in durum wheat. Similarly, Ballesta et al. (2020) identified QTL-rich regions associated with drought indices (SSI, TOL, STI, and YSI) derived from grain yield (GY), TKW, and kernels per spike in bread wheat.

Association mapping was applied to identify QTLs for drought indices that were derived from GY and agro-physiological traits positively and strongly correlated ( $p < 0.001$ ) with GY as an alternative selection approach to improve drought tolerance in wheat. Therefore, the objectives of this study were to detect MTAs and QTLs significantly associated with drought indices and to identify drought-tolerant as well as stable genotypes from a durum wheat study panel.

## Materials and Methods

### Study panel

The study panel included 215 Ethiopian durum wheat landraces, 10 released durum wheat varieties and 10 advanced durum wheat lines from the Ethiopian Institute of Agricultural Research (EIAR), and 50 durum wheat lines from the International Wheat and Maize Improvement Centre (CIMMYT) (Negisho et al., 2021).

### Field Experiments

The field phenotyping experiments were conducted in four locations for three seasons (2016–2018) in Ethiopia. The locations were grouped into two moisture variants, field drought stress (FDS) and field non-stress (FNS). An incomplete block alpha lattice design with 3 replications per location per accession was

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used. A detailed summary of field experiments and evaluated traits was presented in the study of Negisho et al. (2022a).

### Drought Indices Analysis

Phenotypic traits with significant ( $p < 0.05$ ) ANOVA results for accessions, treatments, and accessions x treatment interaction, with moderate (52.25%) to high (74.91%) heritability for HI and SPS, respectively, were used. Also, traits with positive and significant ( $p < 0.001$ ) correlation with GY under FDS and FNS conditions were selected to calculate drought indices (Negisho et al., 2022a). These traits were GY, DGF, SPAD, SPS, HI, and TKW. Data across years and locations per FNS and FDS were combined to analyze the lsmeans. The lsmeans of these traits were estimated for each accession using the lme4 package in R (Lenth, 2016). Variance components of selected traits were computed by restricted maximum likelihood following the model of Yu et al. (2006). Then, drought indices (DSI, GMP, RDI, STI, TOL, and YSI) were calculated from lsmeans values of these traits. Pearson correlation coefficients ( $r$ ) were analyzed by cor and Corstars function in R and plotted by the R package “corrplot” (Wei et al., 2017). Principal component analysis (PCA) for the drought tolerance indices was analyzed by R package FactoMineR (Husson et al., 2010). The description of drought indices and their corresponding equation are indicated in **Table 1**.

**Table 1.** Drought indices calculated from grain yield and from traits with significant positive correlation ( $p < 0.001$ ) with grain yield (GY) under FDS and FNS conditions.

Drought indices	Formula (equation)	Reference
Drought susceptibility index (DSI)	$(1-(GY\_FDS/GY\_FNS))/(1-(\bar{Y}_{FDS}/\bar{Y}_{FNS}))$	Fischer and Maurer, 1978
Relative drought index (RDI)	$(GY\_FDS/GY\_FNS)/(\bar{Y}_{FDS}/\bar{Y}_{FNS})$	Fischer et al., 1998
Stress tolerance index (STI)	$(GY\_FDS \times GY\_FNS)/(\bar{Y}_{FNS}^2)$	Fernandez, 1992
Geometric mean productivity (GMP)	$\sqrt{GY\_FDS \times GY\_FNS}$	Ramirez and Kelly, 1998
Tolerance (TOL)	$GY\_FNS - GY\_FDS$	Rosielle and Hamblin, 1981
Yield stability index (YSI)	$GY\_FDS/GY\_FNS$	Bousslama and Schapaugh, 1984

GY\_FDS and GY\_FNS: Grain yield lsmean under FDS and FNS conditions for each genotype, respectively.  $\bar{Y}_{FDS}$  and  $\bar{Y}_{FNS}$ : Grain yield lsmean under FDS and FNS conditions for all genotypes, respectively.



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### Genotyping

Genotyping was conducted by SGS Trait Genetics, Gatersleben, Germany using the wheat 90k iSelect single-nucleotide polymorphism (SNP) array (Wang et al., 2014). The consensus linkage map of tetraploid wheat (Maccaferri et al., 2015) and the IWGSC RefSeq v1.0 genomic assembly (International Wheat Genome Sequencing Consortium, 2018) were applied to assign a genomic location to each SNP marker. SNP markers with minor allele frequency (MAF) of  $< 5\%$ , missing data  $> 10\%$ , and heterozygosity  $> 12.5\%$  were omitted, and SNP markers were imputed by the Beagle software package in R (Browning and Browning, 2007). A total of 11,919 SNPs with physical positions were taken from the reference sequence of durum wheat (Maccaferri et al., 2019). Population structure and genome-wide association study (GWAS) were taken from our previous study (Negisho et al., 2021). STRUCTURE HARVESTER (Earl and vonHoldt, 2012) was used to determine the q-matrix based on the results obtained for population structure by the STRUCTURE 2.3.4 software (Evanno et al., 2005). Linkage disequilibrium (LD), LD decay, and LD plots within and across chromosomes of durum wheat genomes (A and B) were analyzed using R packages “genetics,” “LDheatmap,” and “trio” (Shin et al., 2006; Warnes, 2013; R Development Core Team, 2014). Inter-marker genetic distances were assessed using the consensus physical position of durum wheat with 11,919 SNPs (Maccaferri et al., 2019). The critical  $r^2$  value was set at  $r^2 \geq 0.2$  (Voss-Fels et al., 2015; Oyiga et al., 2017).

### Genome-Wide Association

Study Genome-wide association study was conducted using the genome association and prediction integrated tool (GAPIT) in R (Lipka et al., 2012). FarmCPU method, which is iteratively using the fixed-effect model and the random effect model for powerful and efficient GWAS (Liu et al., 2016; de Souza et al., 2018), was used.

MTAs were analyzed using calculated drought indices  $l_{\text{means}}$  as a phenotypic trait, filtered SNP markers, kinship matrix, and qmatrix (Yu et al., 2006). In this study, the Bonferroni correction test was too stringent to detect MTAs, thus, a threshold for significant MTAs was adjusted at  $-\log_{10}p \geq 4.0$  (Bai et al., 2016; Ma et al., 2016; Bhatta et al., 2018), and MTAs at FDR 5% were assessed (Benjamini and Hochberg, 1995). The PVE was calculated following (Teslovich et al., 2010). The detected MTAs were clustered into QTLs using the critical ( $r^2 \geq 0.2$ ) LD decay value (4.78 Mb) (Negisho et al., 2022a), and MTAs not in the LD were taken as an independent QTL (Kidane et al., 2017; Negro et al., 2019).

Based on the  $l_{\text{means}}$  of the combined analysis, each SNP locus in the MTAs with a positive phenotypic effect ( $a_i > 0$ ) was identified as a favorable allele, and those with a negative phenotypic effect ( $a_i < 0$ ) were identified as an unfavorable allele for the respective drought indices (Chong et al., 2019). Even

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though it is difficult to make a comparison between the previously reported QTLs at the chromosomal position level, current and previous reports on QTLs related to drought indices in wheat were assessed and discussed (Dashti et al., 2007; Edae et al., 2014; Sukumaran et al., 2018; Qaseem et al., 2019; Arif et al., 2020; Ballesta et al., 2020).

### Candidate Gene Analysis

Significant ( $-\log_{10}p \geq 4.0$ ) MTAs for drought index traits were aligned with the annotated sequence of Durum Wheat (cv. Svevo) RefSeq Release 1.0 at GrainGenes (Maccaferri et al., 2019). In addition, detected MTAs were further assessed for their association with drought tolerance using previously published literature. Finally, in case, the annotation is not found in Durum Wheat (cv. Svevo) RefSeq Release 1.0 at GrainGenes and also not reported so far in the previously published literature, and then, the detected MTAs were considered as novel.

### Results

Mean grain yield under field non-stress (GY\_FNS) and field drought stress (GY\_FDS) conditions were 77.09 and 49.5 g/plot showing 35.79% GY reduction with 20.25 and 23.25% coefficient of variation, respectively (**Table 2**). The mean values of drought indices were 0.97, 1.01, 0.66, 61.49, 27.61, and 0.65 for DSI, RDI, STI, GMP, TOL, and YSI, respectively. Deviation of the data from the mean was expressed in percentage of standard deviation (SD%). A higher percentage of SD was observed for GY under FNS (15.61%) as compared to FDS (11.49%). Similarly, a higher percentage value of SD was detected for GMP (12.13%) and TOL (12.33%) as compared to the other drought indices. The coefficient of variation for the drought indices ranged from 19.27 (GY-STI) to 44.64% (GY-TOL) (**Table 2**).

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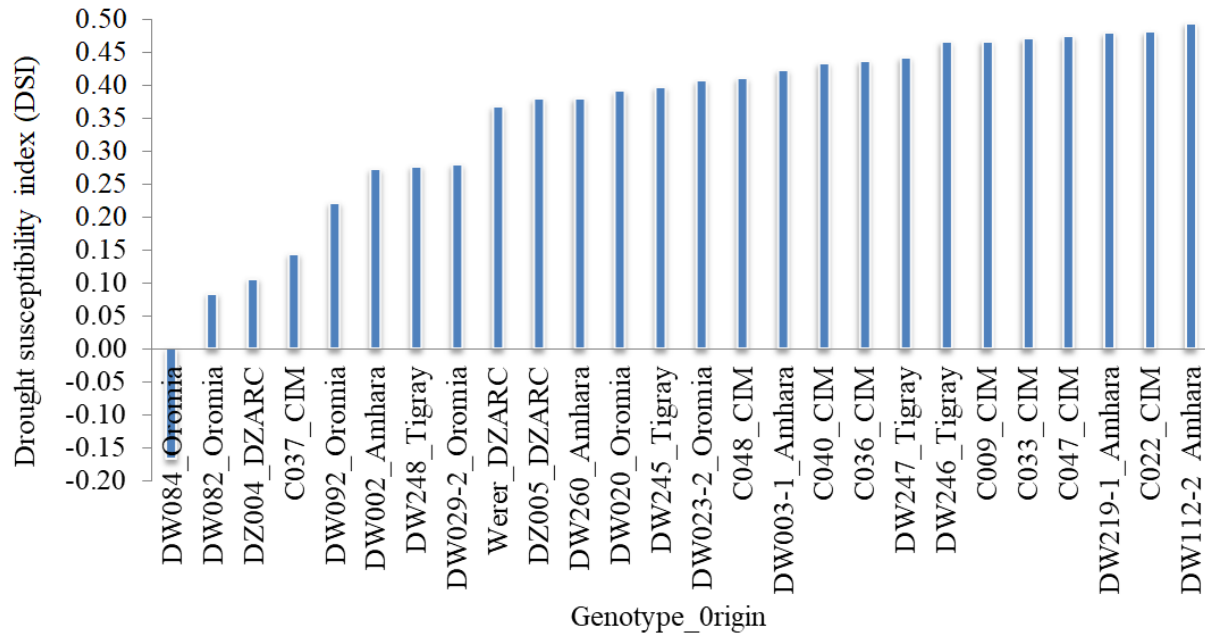
**Table 2.** Descriptive statistics for grain yield (GY) drought indices.

<b>Traits</b>	<b>Mean</b>	<b>SD%</b>	<b>Min</b>	<b>Max</b>	<b>%CV</b>
GY_FNS	77.09	15.61	32.75	114.63	20.25
GY_FDS	49.50	11.49	23.50	79.92	23.21
% GY loss	35.79	-	-	-	-
DSI	0.97	0.35	-0.17	1.86	36.05
RDI	1.01	0.20	0.52	1.65	19.33
STI	0.66	0.25	0.17	1.37	37.27
GMP	61.49	12.13	32.05	90.27	19.72
TOL	27.61	12.33	1.24	61.11	44.64
YSI	0.65	0.13	0.34	1.06	19.31

GY\_FNS, grain yield lsmeans in g/plot under FNS; GY\_FDS, grain yield lsmeans in g/plot under FDS; %GY loss, percentage of yield loss due to drought stress; DSI, drought susceptibility index; RDI, relative drought index; STI, stress tolerance index; GMP, geometric mean productivity; TOL, tolerance index; YSI, yield stability index. Mean, standard deviation (SD), minimum, maximum, and percentage of the coefficient of variation (CV), n = 285.

The 52% of the accessions (147) in the SP revealed GY-DSI values <1 that indicates the existence of drought-tolerant accessions. Out of drought-tolerant accessions, 96 were from Ethiopian durum wheat landraces, 9 from advanced lines, 7 from released varieties, and 35 were from the CIMMYT durum wheat collection and the top 26 (9%) are visualized in **Figure 1**. DW084, DW082, DZ004, C037, and DW092 were selected as the top five drought-tolerant accessions based on the combined rank of GY-DSI, GYRDI, GY-TOL, and GY-YSI (**Figure 1, Supplementary Table S1**). Additionally, accessions with high value based on the combined rank of GY-GMP and GY-STI are considered as stable genotypes under FDS and FNS. Based on GMP and STI drought indices ranking C010, DW033, DW080, DW124-2, and C011 were selected as the top five stable accessions. The remaining 138 (48%) accessions in the SP showed a GY-DSI value higher than one indicating the susceptibility of the accessions to drought.

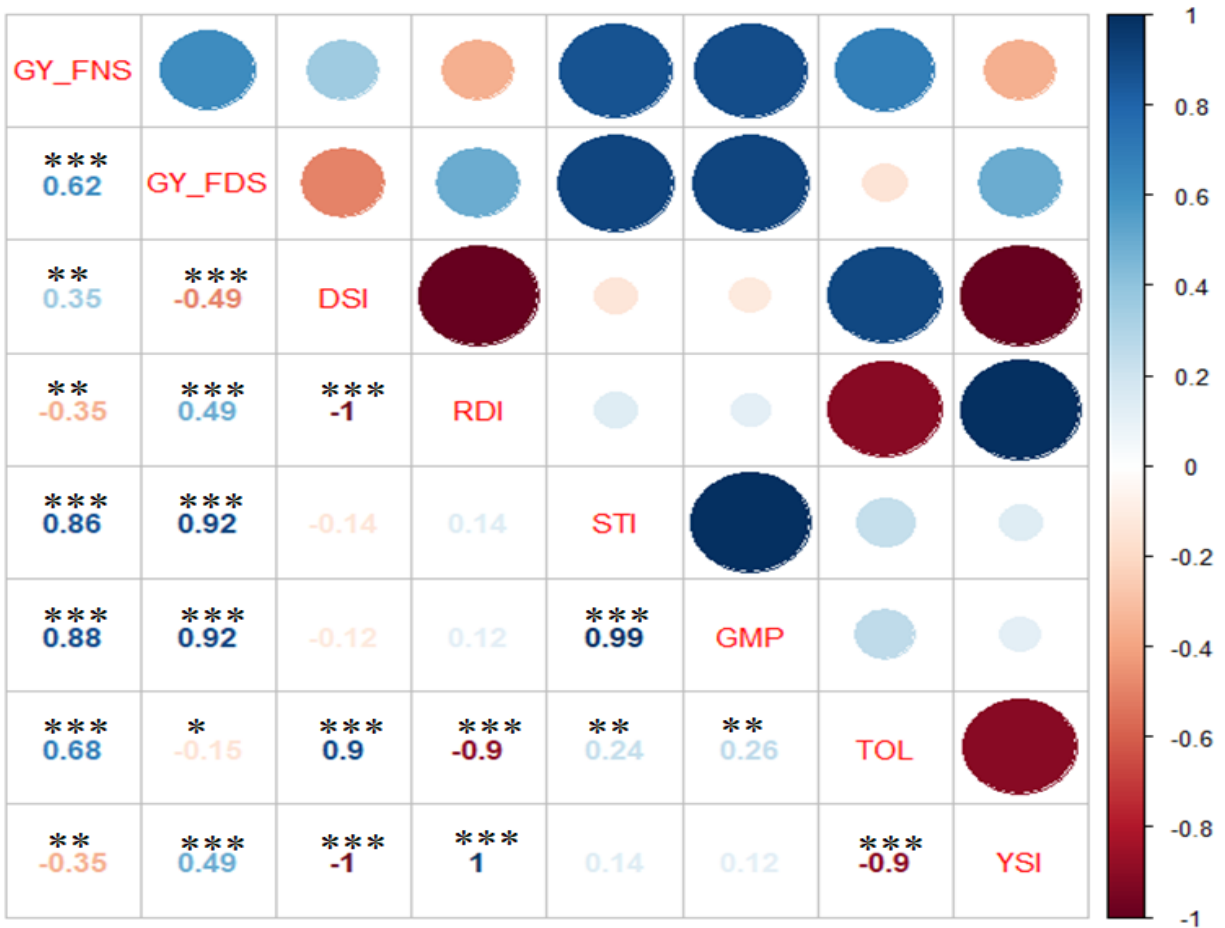
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**Figure 1.** Top 26 drought tolerant accessions identified based drought susceptibility index calculated from grain yield (GY). The x-axis indicates selected genotypes and seed origin with DSI < 0.5 and the y-axis shows DSI values.

### Correlation Analysis

A significant positive correlation was observed between GY\_FNS and GY\_FDS ( $r = 0.62$ ) (**Figure 2**). Likewise, GY\_FNS and GY\_FDS were significantly and positively correlated with GMP ( $r = 0.88$  and  $0.92$ ) and STI ( $r = 0.86$  and  $0.92$ ), respectively. GY\_FNS was significantly and positively correlated with DSI ( $r = 0.35$ ) and TOL ( $r = 0.68$ ), but a significant ( $r = -0.35$ ) negative correlation was observed with RDI and YSI. GY\_FDS was significantly ( $r = 0.49$ ) and positively correlated with RDI and YSI but significantly and negatively correlated with DSI ( $r = -0.49$ ) and TOL ( $r = -0.15$ ). There was a significant positive correlation between DSI and TOL ( $r = 0.9$ ). A highly significant ( $r = -1.0$ ) negative correlation was observed between RDI and YSI. RDI was significantly and positively correlated with YSI ( $r = 1.0$ ) but showed a strong significant negative correlation with TOL ( $r = -0.9$ ). STI and GMP showed a significant ( $r = 0.99$ ) positive correlation. STI and GMP revealed a significant positive correlation with TOL ( $0.24$  and  $0.26$ ), respectively. Finally, there was a strong significant negative ( $r = -0.9$ ) correlation between TOL and YSI.



**Figure 2.** Pearson correlation between the drought indices traits. GY\_FNS: Ismeans from FNS at (Holeta and Debre Zeit), GY\_FDS: Ismeans from FDS at (Dera and Melkassa), DSI: Drought susceptibility index, RDI: Relative drought index, STI: Stress tolerance index, GMP: Geometric mean productivity, TOL: Tolerance index and YSI: Yield stability index. \*, \*\*, and \*\*\* significance at  $p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively.

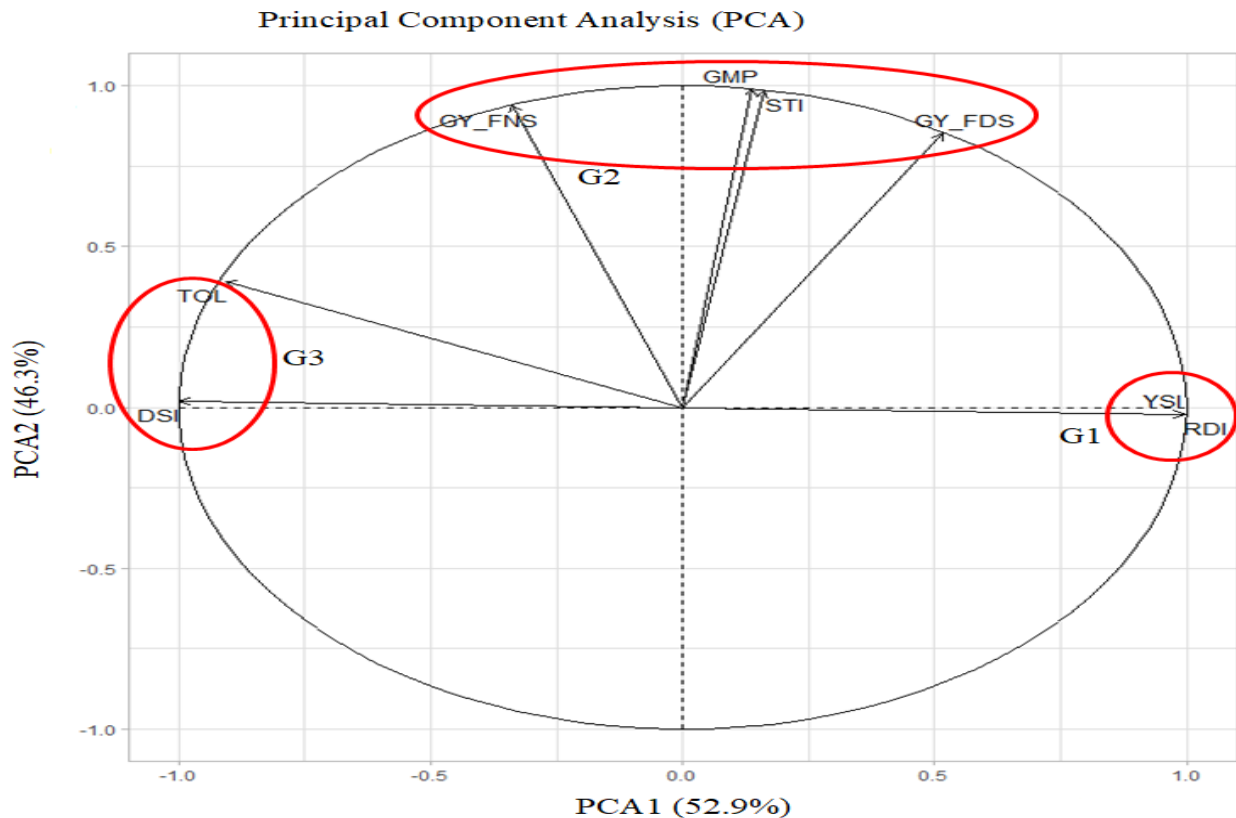
### PCA

PCA1 and PCA2 explained 52.9 and 46.3% of the variation among drought indices, respectively (**Figure 3**). PCA clustered the drought indices into three groups (G1, G2, and G3). G1 indicated drought-tolerant accessions with higher values of YSI and RDI, G2 indicated stable accessions with higher values of GY\_FNS, GY\_FDS, GMP, and STI, and G3 showed drought-tolerant accessions with lower values of DSI and TOL.

A narrow angle ( $<90^\circ$ ) shows a positive correlation within each group, whereas a wide angle ( $>90^\circ$ ) indicates a negative correlation, e.g., between G1 and G3. Hence, GY\_FNS was positively correlated with

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GY\_FDS, STI, GMP, TOL, and DSI, but negatively correlated with YSI and RDI. Similarly, GY\_FDS was positively correlated with GY\_FNS, YSI, RDI, STI, and GMP but negatively correlated with DSI and TOL as was revealed by Pearson correlation analysis (**Figure 2; Supplementary Figure S1**).



**Figure 3.** PCA showing the contribution of drought indices. PCA1 and PCA2 accounted for 99.2% of total variations among drought indices.

### Marker-Trait Association Analysis for Drought Indices

A total of 184 MTAs were detected across the durum wheat genome for the analyzed drought indices at  $-\log_{10}p \geq 4.0$  (**Table 3**) explaining up to 26.61% of the total phenotypic variation. The Manhattan plots for MTAs were indicated in **Supplementary Figures S2–S7**. A total of 41 (22.28%) of the significant MTAs detected were associated with two or more drought indices highlighted in blue color (**Supplementary Table S2**). Predominantly, 16 (39.02%) of these stable MTAs were associated with GMP and STI drought indices.

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**Table 3.** Significant ( $-\log_{10}p \geq 4.0$ ) marker-trait associations (MTAs) and quantitative trait loci (QTL) that were detected for the drought indices traits calculated from grain yield and traits significantly ( $p < 0.001$ ) positively correlated with grain yield under FNS and FDS.

Trait	MTA	MTAs per Chromosomes	QTL
GY-DSI	0	-	0
GY-GMP	10	2A, 2B, 3B, 4A, 5A, 5B, 6B, 7A (2), 7B	6
GY-RDI	6	1A (2), 1B, 4A, 7A, 7B	4
GY-STI	8	1A, 2A, 3B, 4B, 5A (2), 5B, 6B	4
GY-TOL	0	-	0
GY-YSI	0	-	0
DGF-DSI	3	1A, 3B, 4B	1
DGF-GMP	2	1A, 4B	0
DGF-RDI	7	1A, 1B, 3B,4B, 5B, 6B (2)	5
DGF-STI	5	1B, 2A, 2B, 3B, 7B	4
DGF-TOL	6	3B, 4A, 4B, 5B, 6B, 7A	4
DGF-YSI	6	2B, 3B, 4B, 5B, 6B (2)	2
SPAD-DSI	2	1A, 2B	1
SPAD-GMP	11	1A (2), 3A, 3B, 4A, 4B (2), 5A, 6B (2), 7A	8
SPAD-RDI	2	1A , 5A	2
SPAD-STI	7	1A, 1B, 2B (2), 4B, 6B (2)	6
SPAD-TOL	0	-	0
SPAD-YSI	4	1A (2), 2B, 3A	2
SPS-DSI	2	1B, 2B	1
SPS-GMP	10	1A, 2A (3), 2B, 3A, 5A, 5B, 6A, 7A	6
SPS-RDI	2	1B, 2B	0
SPS-STI	9	1A (2), 2A, 3A, 3B, 4B, 5A 7A (2)	8
SPS-TOL	0	-	0
SPS-YSI	2	1B, 2B	0
HI-DSI	8	1A, 1B, 2A (2), 4B, 6A, 6B, 7A	6
HI-GMP	11	1A (2), 1B, 2B, 4A, 4B, 5A (2), 7A (2), 7B	3
HI-RDI	6	2A (2), 4B, 6B, 7A, 7B	1
HI-STI	7	1B, 4A, 4B, 5A, 7A, 7B (2)	5
HI-TOL	4	2A (2), 4B, 6B	2

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Trait	MTA	MTAs per Chromosomes	QTL
HI-YSI	6	2A (2), 4B, 6B, 7A, 7B	3
TKW-DSI	8	2B (2), 4A (2), 4B (2), 6B, 7A,	4
TKW-GMP	6	1A, 2B (2), 4A, 4B, 6A	4
TKW-RDI	8	2B (2), 4A (2), 4B, 7A, 7B (2)	1
TKW-STI	4	2B, 4A, 6A, 7A	1
TKW-TOL	5	2A, 2B, 5A, 5B, 7B	5
TKW-YSI	7	2B, 4A (2), 4B, 6B, 7A (2)	3
Total	184	-	102

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Detected MTAs: A = 89 (48%) and B = 95 (52%)

Genome	Detected QTLs: A = 48 (47%) and B = 54 (53%)
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Brackets enclose the number of MTAs detected per chromosome only if it is more than one.

In this study, SNP alleles with positive effects that led to increased drought index traits were defined as “favorable alleles.” Accordingly, five major MTAs were detected associated with GY-GMP as favorable SNP alleles (>10% PVE): RFL\_Contig2569\_2187 on chromosome 3B at 752,249,328 bp, Kukri\_c22602\_704 on chromosome 4A at 733,371,835, IAAV2346 on chromosome 5B at 17,863,862 bp, wsnp\_Ex\_c3940\_7144946 on chromosome 6B at 508,076,861 bp, and Tdurum\_contig4658\_346 on chromosome 7B at 663,797,774 bp. On the other hand, four major MTAs were detected associated with GY-GMP as unfavorable SNP alleles: Tdurum\_contig10785\_2433 on chromosome 2A at 12,102,513 bp, Kukri\_rep\_c116526\_98 on chromosome 5A at 112,213,041 bp, BobWhite\_C21378\_234 on chromosome 7A at 693,389,984 bp, and wsnp\_Ex\_c5839\_10246915 on chromosome 7A at 709,145,347 bp. From these, three major MTAs with favorable SNP alleles located on chromosomes 2B, 5B, and 7B, and two major MTAs with unfavorable SNP alleles located on chromosomes 7A were novel MTAs. Generally, in this study, the phenotypic effect size on drought indices ranged from -5 to 5 (**Supplementary Table S2**).

### Candidate Genes

Candidate genes for MTAs linked with drought tolerance were calculated from grain yield with identified positive phenotypic effect size, particularly U-box domain-containing protein on chromosome 4A associated with GY-GMP, potassium transporter on chromosome 3B associated with GY-GMP, MODIFIER OF SNC1 1 G on chromosome 5A associated with GY-GMP, and cytochrome P450 family protein on chromosome 7A associated with GY-RDI. As regards the MTAs associated with drought indices calculated from DGF, the genes identified were methyltransferase on chromosome 4A and

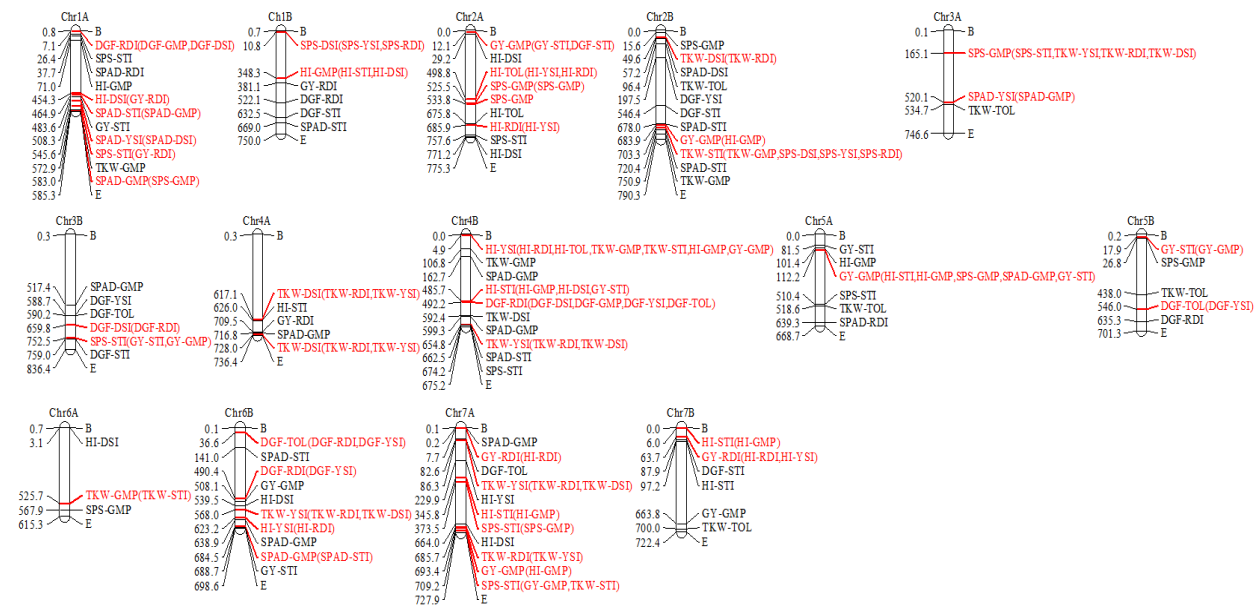


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leucine-rich repeat receptor-like kinase (LRK2) on chromosome 6B associated with DGF-TOL. In this study, other important MTAs identified associated with drought tolerance were as follows: UNC93-like protein on chromosome 5A associated with SPAD-GMP, ribosomal protein on chromosome 4B associated with HI-TOL, HI-RDI, HI-YSI, Acyl-CoA dehydrogenase-related family protein on chromosome 2B associated with TKW-TOL, and RNA-binding protein on chromosome 1A associated with HI-DSI.

### MTA Cluster into QTL

The detected MTAs for drought tolerance indices were clustered into 102 QTLs (**Supplementary Table S3**). The numbers of QTLs detected from the highest to the lowest were 28, 27, 13, 13, 11, and 10 for STI, GMP, DSI, RDI, TOL, and YSI drought indices, respectively (**Supplementary Table S3; Figure 4**). Out of which, 43 stable QTLs harbor more than one drought tolerance index (up to four drought indices), for instance, four drought indices QTLs were co-located on chromosome 4B between 487,222,406–497,250,660 and 4,927,519–9,941,646 bp shown in red color. In contrast, some detected QTLs like those located on chromosome 1A between 478,563,347–488,591,601 and 66,026,146–76,054,400 bp are examples of individual QTLs for STI and GMP, respectively, as indicated by black color (**Figure 4**).



**Figure 4.** Linkage map showing number of QTLs detected for drought indices. Co-clustered QTLs were marked in red color and in parenthesis and individual QTLs were marked in black color.

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A total of twenty-eight detected QTLs for STI were calculated from SPS, SPAD, GY, DGF, TKW, and HI traits, out of which, ten stable QTLs are co-located with QTL for GMP, DSI, RDI, and YSI located on chromosomes 1A, 2B, 3B, 4B, 5A, 7A, and 7B. The remaining 18 were individual QTLs for STI. Out of 28 selected QTLs for STI located on chromosomes 1A (3 QTLs), 2B (3 QTLs), 3B (2 QTLs), 4B (3 QTLs), 5A, 6B, and 7B (3 QTLs), 16 were not reported so far and are likely to be novel. A total of twenty-seven QTLs were detected for GMP calculated from HI, TKW, SPAD, GY, SPS, and DGF traits, out of which, ten stable QTLs were co-located with QTL for STI, DSI, YSI, and RDI on chromosomes 1A, 1B, 2A, 2B, 3A, 5A,6A, 6B, and 7A, whereas the other 17 detected QTLs were individual QTLs for GMP. Out of the 27 detected QTLs for GMP, 26 could be novel.

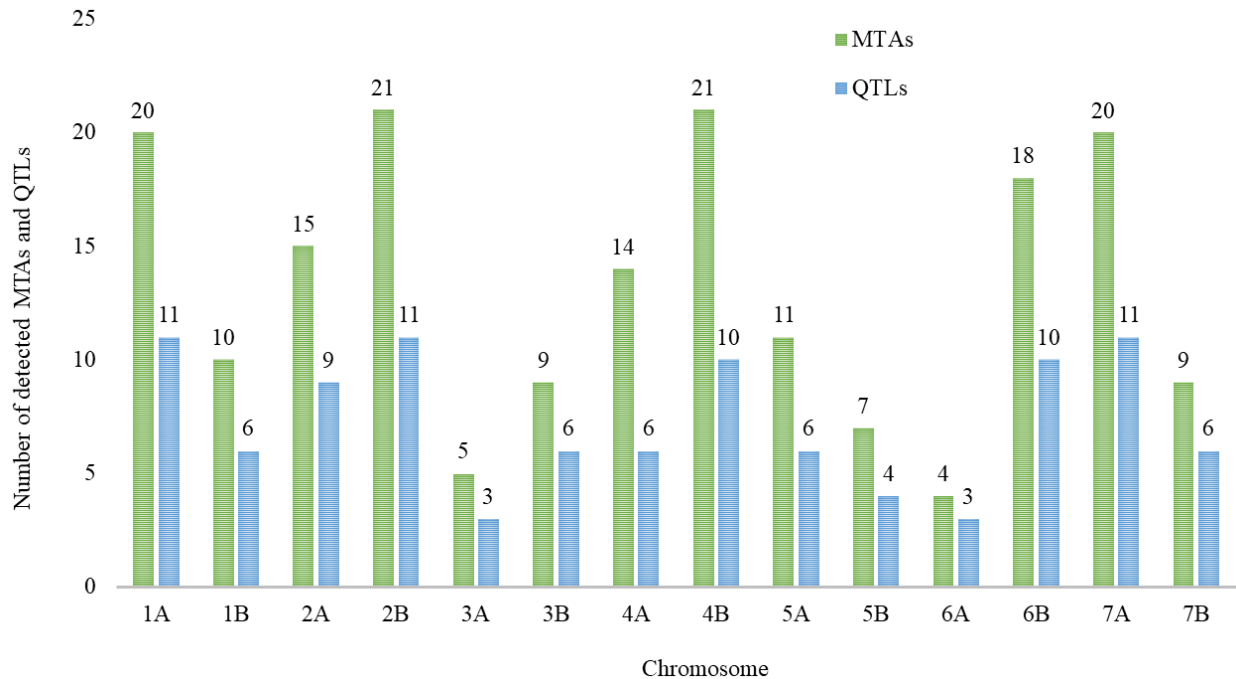
As regarded the 13 detected QTLs for DSI were calculated from HI, SPS, TKW, SPAD, DGF, and GY traits, of which six stable QTLs are co-located with QTL for RDI and YSI on chromosomes 1A, 1B, 2B, 3B, and 4A. The remaining seven were individual QTLs for DSI. From the six co-located QTLs for DSI, three QTLs were associated with RDI located on chromosomes 1A, 2B, and 3B between 449,301,491–459,329,745, 44,634,623–54,662,877, and 654,733,402–664,761,656 bp, respectively. Similarly, DSI QTLs were co-located with RDI and YSI located on chromosomes 1B between 5,764,433–15,792,687 bp and on 4A between 722,943,476–732,971,730 and 612,075,413–622,103,667 bp. Seven QTLs detected for DSI located on chromosomes 1A, 1B, 2A (2 QTLs), 2B, 3B, and 6A were not reported so far and are novel putatively QTLs.

The 13 detected QTLs for RDI were calculated from DGF, SPAD, GY, HI, and TKW traits, of which seven stable QTLs included were co-located with GMP, DSI, YSI, and STI on chromosomes 1A, 2A, 4B, 6B, 7A, and 7B, whereas the others six detected were individual QTLs. The ten QTLs detected for RDI, located on chromosomes 1A (2 QTLs), 1B (2 QTLs), 2A, 5A, 6B, 7A (2 QTLs), and 7B, were could be new.

The 11 detected QTLs for TOL were calculated from HI, TKW, and DGF. Three QTLs are co-located with QTL for YSI and RDI on chromosomes 2A, 5B, and 6B, and the remaining eight are individual QTLs for TOL. In particular, five QTLs for TOL that were located on chromosomes 2A (2 QTLs), 4A, 6B, and 7A, were putatively novel. The 10 detected QTLs for YSI were calculated from SPAD, DGF, HI, and GY, of which seven QTLs located on chromosomes 1A, 3A, 4B, 6B, and 7A were co-located with QTLs for DSI, GMP, RDI, TOL, and STI. The remaining eight QTLs for YSI were likely to be new.

The distribution of single MTA/QTL on genomes A and B was 48%/47% and 52%/53%, respectively (**Table 3**). Chromosomes 1A, 2B, and 7A each harbor eleven QTLs, which is the highest number of QTLs detected per chromosome followed by ten QTLs each were detected on chromosomes 4B and 6B, and nine QTLs were detected on chromosome 2A (**Figure 5**).

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**Figure 5.** The Number of detected marker-trait associations (MTAs) and quantitative trait loci (QTLs) that were detected for drought indices across the durum wheat genome.

In our study, these chromosomal regions were considered as QTL hotspots for drought tolerance in durum wheat. The lowest numbers of QTLs (3) each were detected on chromosomes 3A and 6A. Six (5.88%) of the detected QTLs were major QTLs and all of them were associated with GY-GMP drought index between 658,783,647–668,811,901, 503,062,734–513,090,988, 107,198,914–117,227,168, 678,867,539–688,895,793, 7,088,386–17,116,640, and 688,375,857–698,404,111 bp and located on chromosomes 7B, 6B, 5A, 2B, 2A, and 7A with 22.21, 21.91, 17.00, 14.72, 14.59, and 13.59% PVE, respectively (**Supplementary Table S3**).

## Discussion

Drought tolerance is a complex quantitative trait, which is affected by the timing and severity of drought stress relative to plant development and growth. In this study, 35.79% GY reduction was observed under field conditions in durum wheat due to drought stress. In agreement with this, depending on plant growth stage and severity of drought, 60% in durum wheat (Sukumaran et al., 2018) and 10–76% grain yield reduction in bread wheat have been reported (Grzesiak et al., 2019). Nevertheless, studies revealed that in wheat, the effect of drought stress is more pronounced during the reproductive stage (Nezhadahmadi et

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al., 2013). In our study, 147 (52%) accessions from the study panel revealed a GY-DSI value of  $< 1$ , indicating drought tolerance, whereas 138 (48%) showed a GY-DSI higher than 1, implying that these genotypes are drought susceptible. This suggests that in this study, drought stress was moderate but enough to facilitate the selection of drought-tolerant accessions. Moderate drought stress was reported as recommended to select drought-tolerant wheat lines (Ali and El-Sadek, 2016; Patel et al., 2019).

From our previous experimental procedures under FDS and FNS conditions, traits from which drought indices were calculated showed significant ( $p < 0.05$ ) differences among durum wheat accessions, between treatments, and for accession x treatment interaction. This illustrates the broad genetic diversity present in the panel herein used for drought tolerance in general and in Ethiopian durum wheat landraces in particular (Negisho et al., 2021). Also, moderate to high heritability values and a significant ( $p < 0.001$ ) correlation with GY under FDS and FNS conditions have been found in this study. This relation provides the basis for utilizing drought tolerance indices as a means to explain the phenotypic variation. It has been also reported that drought tolerance indices can be derived from GY and traits that are strongly and positively correlated with GY as a measure for selecting the best genotypes (Farshadfar et al., 2012; Patel et al., 2019; Ayed et al., 2021).

The significant ( $r = 0.62$ ) positive correlation between GY\_FNS and GY\_FDS suggests that high GY performance under the FNS condition is generally closely connected with stable and high GY under FDS conditions. Similarly, studies depicted a positive and significant correlation between GY under favorable and drought stress conditions in durum wheat (Patel et al., 2019), bread wheat (Ali and El-Sadek, 2016), and rice (Mau et al., 2019). The strong and positive correlation of GY\_FNS and GY\_FDS: GMP ( $r = 0.88$  and  $0.92$ ) and STI ( $r = 0.86$  and  $0.92$ ), respectively, suggests that GMP and STI may be potential drought indices to select stable and relatively higher-yielding accessions under drought stress conditions. Respectively, GMP and STI were reported as convenient drought indices parameter to select stable and high-yielding durum wheat genotypes under drought stress and non-stress conditions (Patel et al., 2019; Ayed et al., 2021). Interestingly, in this study, three out of the top five accessions selected based on the combined rank of drought indices were from Ethiopian durum wheat landraces and could be recommended as parents for wheat drought-tolerant improvement breeding with other cultivars.

The first two PCAs explained 99.2% of the total variation among drought indices and clustered the drought indices into three groups, G1 indicating drought-tolerant accessions with high values of RDI and YSI, G2 indicating yield stable and drought-tolerant accessions with high values of GY\_FNS, GY\_FDS, GMP, and STI, and G3 indicating drought tolerant accessions with lower values for DSI and TOL. The PCA angles in our study also allowed us to interpret the interrelationships among the drought indices and were confirmed with correlation analysis and scatter plot results (**Figure 3; Supplementary Figure S1**).

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In this study, a total of 102 QTLs were detected at  $-\log_{10}p \geq 4.0$ . The number of QTLs on A and B genomes was (48%) and (52%), respectively. In accordance, research results showed a larger number of QTLs on the B genome as compared to the A genome in durum wheat (Soriano et al., 2017; Desiderio et al., 2019; Alemu et al., 2020; Ballesta et al., 2020). Similarly, using simple sequence repeat (SSR) and diversity array technology (DArT) markers, Maccaferri et al. (2014) mapped a higher number of markers on the B genome as compared to the A genome. Our result showed at the chromosomal level, a higher number of QTLs (11.78%) each were located on chromosomes 1A, 2B, and 7A, suggesting that these genome regions are QTL hotspots and play a pivotal role in drought tolerance in wheat. In this study, a considerable number of QTLs, namely, 6 (5.88%), were detected for drought indices on chromosome 4A, which is in agreement with the result reported by Ballesta et al. (2020). In our study, six of the 13 QTLs detected for DSI were on chromosomes 2B, 4A (2 QTLs), 4B, 6B, and 7A between 44,634,623–54,662,877, 612,075,413–622,103,667, 722,943,476–732,971,730, 587,392,128–597,420,382, 534,453,653–544,481,907, and 658,941,965–668,970,219 bp, respectively (**Supplementary Table S3**). Accordingly, studies reported QTLs for DSI located on chromosomes 2B, 4A (2 QTLs), 4B, 6B, and 7A (Dashti et al., 2007; Edae et al., 2014; Sukumaran et al., 2018; Ballesta et al., 2020). To the best of our knowledge, seven QTLs detected for DSI located on chromosomes 1A, 1B, 2A (2 QTLs), 2B, 3B, and 6A between 449,301,491–459,329,745, 5,764,433–15,792,687, 24,208,804–34,237,058, 766,212,336–776,240,590, 52,165,550–62,193,804, 654,733,402–664,761,656, and 3,084,526–80,98,653 bp were not reported so far and could be novel.

Edae et al. (2014) detected QTLs for SPS-DSI located on chromosomes 7A and 7B using DArT markers. However, we did not find QTL for SPS-DSI on these chromosomes. In this study, QTLs for SPS-STI were detected on chromosomes 1A, 2A, 3B, 4B, 5A, and 7A. Edae et al. (2014) also detected QTL GY-DSI located on chromosome 4A, but no QTL was detected for GY-DSI on this chromosome.

In this study, three out of the 13 QTLs for RDI were detected on chromosomes 4A, 4B, and 5B between 704,477,416–714,505,670, 487,222,406–497,250,660, and 630,323,029–64,0351,283 bp, respectively. Similarly, studies reported QTLs for RDI on chromosomes 4A (Arif et al., 2020) and 4B (Ballesta et al., 2020) and chromosome 5B (Arif et al., 2020). The other QTLs detected for RDI could be new. A QTL was detected associated with GMP on chromosome 3B between 512,345,933–522,374,187 bp. In agreement with, Dashti et al. (2007) reported a QTL on chromosome 3B using SSR marker in doubled haploid bread wheat associated with GMP. In our study, 12 of the 28 detected QTLs for STI were on chromosomes 1A, 2B (2 QTLs), 2A, 2B, 4A, 5A, 5B, 6B, and 7A (2 QTLs) between 478,563,347–488,591,601, 627,518,169–637,546,423, 663,977,245–674,005,499, 752607375–762,635,629, 698,319,457–708,347,711, 621,025,922–631,054,176, 76,490,700–86,518,954, 12,849,735–22,877,989, 683,730,386–693,758,640, 340,762,156–350,790,410, 368,439,457–378,467,711, and 704,181,285–

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714,209,539 bp, in that order. In agreement with this, studies in wheat QTLs were reported for STI on chromosomes 1A, 1B, 2A, 2B, 4A, 5A, 5B, 6B, and 7A (Dashti et al., 2007; Sukumaran et al., 2018; Qaseem et al., 2019; Arif et al., 2020; Ballesta et al., 2020). The remaining 18 detected QTLs for STI were likely to be novel QTLs.

Moreover, six out of the 11 QTLs identified for TOL were detected on chromosomes 2B, 3A, 5A, 5B (2 QTLs), and 7B between 91,393,993–101,422,247, 529,677,366–539,705,620, 513,570,349–523,598,603, 433,014,029–443,042,283, 540,970,848–550,999,102, and 695,007,223–705,035,477 bp, respectively. Consistent with this result, studies revealed QTLs for TOL located on chromosomes 2B, 3A, 5A, 5B, and 7B (Dashti et al., 2007; Sukumaran et al., 2018; Arif et al., 2020; Ballesta et al., 2020). However, five of the 11 detected QTLs for TOL located on chromosomes 2A (2 QTLs), 4A, 6B, and 7A were not reported so far and could be novel. Out of the detected 10 QTLs for YSI, two were located on chromosomes 4B and 6B between 649,804,818–659,833,072 and 563,024,848–573,053,102 bp, correspondingly. Similarly, Ballesta et al. (2020) reported QTLs for YSI on chromosomes 4B and 6B, whereas the remaining eight are likely new QTLs.

In general, 30 out of the 102 detected QTLs for drought indices were previously reported (Dashti et al., 2007; Sukumaran et al., 2018; Qaseem et al., 2019; Arif et al., 2020; Ballesta et al., 2020), whereas 72 QTLs reported in this study are likely novel QTLs.

In this study, MTAs that were previously reported associated with drought stress tolerance and/or their annotation show associations with drought stress tolerance are considered as candidate genes. Accordingly, one MTA was identified associated with GY-GMP on chromosome 4A (Kukri\_c22602\_704) at 733,371,835 bp, annotated as a U-box domain-containing protein. In agreement, studies indicated the involvement of these proteins in drought stress in barley (Ryu et al., 2019) and in drought and salinity stresses in *Arabidopsis* (Cho et al., 2006). Another MTA was detected associated with GY-GMP on chromosome 6B (wsnp\_Ex\_c3940\_7144946) at 508,076,861 bp, annotated as a DNA topoisomerase 2. Similarly, studies showed the upregulation of DNA topoisomerase 2 under abiotic stresses, such as cold and salinity in tobacco and pea (John et al., 2016; Tammamo et al., 2016). An MTA was detected associated with GY-GMP on chromosome 3B (RFL\_Contig2569\_2187) at 752,249,328 bp, annotated as a potassium transporter. Congruent to this, Ouyang et al. (2010) and Cheng et al. (2018) reported overexpression of a potassium transporter (OsHAK1) in rice enhanced drought tolerance at both vegetative and reproductive stages via decreasing the levels of lipid peroxidation, increasing proline accumulation, and improving the activities of antioxidant enzymes. One MTA was detected on chromosome 5A (Kukri\_rep\_c116526\_98) associated with GY-GMP at 112,213,041 bp, annotated as a Protein MODIFIER OF SNC1 1 G. In line with this, the research report showed the involvement of MOS14 (protein modifier of snc1-1, 14) in drought tolerance in *Arabidopsis* (Xu et al., 2016). As regards,

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the MTA was detected associated with GY-GMP and GY-STI on chromosome 2A (Tdurum\_contig10785\_2433) at 12,102,513 bp, annotated as an NBS-LRR-like resistance protein. It is known that NBS-LRR-like resistance protein is particularly involved in resistance to various diseases (Shao et al., 2014; Dubey and Singh, 2018), as well as in drought stress tolerance (Chini et al., 2004; Rampino et al., 2017).

An MTA was identified associated with GY-RDI and HI-DSI on chromosome 1A (Ra\_c2895\_591) at 454,315,618 bp, annotated as an RNA-binding protein (RBP). Similarly, Maroundedze et al. (2019) reported that RBPs operate as a posttranscriptional modulator in drought stress in Arabidopsis by controlling the stability of metabolic processes for short and longterm stress adaptations. The other MTA was detected associated with GY-STI, HI-GMP, HI-STI, SPAD-GMP, and SPS-GMP on chromosome 5A (Tdurum\_contig76578\_537) at 110,830,599 bp, annotated as UNC93-like protein. Likewise, a study indicated that UNC93 functions as a positive regulator of drought stress tolerance via ABA-dependent signal transduction pathways (Xiang et al., 2018). An MTA was detected associated with GY-RDI on chromosome 7A (Excalibur\_c24593\_1217) at 7,721,495 bp, annotated as cytochrome P450 family protein. In agreement, research reports elucidated that cytochrome P450 family protein involves in drought and salinity stresses (Narusaka et al., 2004; Ehltng et al., 2008; Jun et al., 2015). Particularly, Melloul et al. (2014) showed the upregulation of cytochrome P450 proteins in durum wheat leaves under drought stress. Another MTA was identified associated with DGF-TOL on chromosome 4A (IAAV1775) at 590,188,609 bp, annotated as a methyltransferase. Respectively, Lu et al. (2020) indicated that this protein enhances drought tolerance in poplar plants by leading to a higher density of trichomes and a better-developed root system.

Marker-trait association was detected associated with DGF-RDI, DGF-TOL, and DGF-YSI on chromosome 6B (Tdurum\_contig61383\_627) at 36,557,072 bp, annotated as a leucine-rich repeat receptor-like protein kinase family protein. Similarly, a study on rice revealed that this family protein increases drought tolerance via promoting root growth while reducing plant height (Kang et al., 2017). Another MTA was detected associated with HI-RDI, HI-TOL, and HI-YSI, on chromosome 4B (tplb0050b23\_546) at 4,927,519 bp, annotated as a Ribosomal protein. In agreement, research results indicated the upregulation of ribosomal proteins under drought stress in the root of drought tolerant bread wheat cultivar (Arg) (Ma et al., 2016). MTA was identified associated with TKW-TOL on chromosome 2B (Kukri\_c36879\_83) at 96,408,120 bp, annotated as acyl-CoA dehydrogenase-related family protein. Similarly, a study revealed that this protein is one of the drought-responsive protein species in leaves and is altered under dehydration (Wang et al., 2016).

Chromosomes 1A, 2B, and 7A are identified as QTL hotspots each encompassing 11 QTLs between 2,116,602– 577,966,934, 10,629,564–745,910,537, and 172,269–704,181,285 bp, respectively

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(**Supplementary Table S3**). Despite the identification of several QTLs that were associated with drought indices in our study, further validations and investigations are needed to understand the molecular functions of the associated genes in drought stress-response mechanisms in wheat. Major QTLs with favorable SNP alleles identified in this study could be used to develop polymerase chain reaction (PCR)-based markers, such as cleaved amplified polymorphic sequence (CAPS) and competitive allele-specific polymerase chain reaction (KASP) markers, to facilitate future marker-assisted breeding in wheat.

### Conclusion

Durum wheat *Triticum turgidum ssp. durum* accessions used in our study showed large natural variation ( $p < 0.0001$ ) for drought tolerance as assessed based on six agro-physiological traits, including GY. Among the investigated drought indices, significant correlations were observed and criteria defining drought-tolerant accessions could be defined. Based on the combined rank of GY-DSI, GY-RDI, GY-TOL, and GY-YSI, DW084, DW082, DZ004, C037, and DW092 were identified as the most drought-tolerant accessions. Similarly, based on the combined rank of GY-GMP and GY-STI, C010, DW033, DW080, DW124-2, and C011 were selected as the best stable accessions both under FDS and FNS conditions. Major MTAs with favorable SNP alleles identified in this study may be used to develop DNA markers, such as CAPS and KASP markers, for marker-assisted breeding for drought stress tolerance in wheat. The detected MTAs were further clustered into 102 QTLs. Chromosomes 1A, 2B, and 7A are QTL hotspots with 11 QTLs each. A higher number of QTLs (52%) linked to drought indices were detected on the B genome. Six (5.88%) of the identified QTLs represent major QTLs with higher than 10% PVE. The detected major QTLs were particularly associated with GY-GMP and located on chromosomes 4A, 7B, 6B, 5B, and 2B, with 22.21, 21.91, and 14.72% PVE, respectively. Our study successfully elucidated the significance and alternative means of identifying genetic loci for drought tolerance via drought indices using the GWAS technique.



## GENERAL DISCUSSION

### 3 General discussion

#### 3.1 Durum wheat and drought

Ethiopia is a major durum wheat producer in sub-Saharan Africa (SSA) (Vavilov, 1951; Kabbaj et al., 2017; Sall et al., 2019). However, its production in Ethiopia is significantly affected by drought stress, which is to some extent due to global climate changes (Shah et al., 2017). In support of this, in this study, descriptive statistics and the box plots indicated a reduction in quantitative traits due to drought stress that ranged from 1.37% for spike length (SL) to 52.41% for grain biomass (GB) under climate chamber and from 9.58% for days to heading (DH) to 35.79% for GB under field conditions. Hence, GB reduction due to drought stress ranged between 35.79 to 52.41% for field and climate chamber experiments, respectively (see **publication 2.2, table 2**). This is in agreement with several studies that indicated grain yield reduction due to drought up to 60% in durum wheat (Sukumaran et al. 2018) and 10-76% in bread wheat (Daryanto et al. 2016; Qaseem et al., 2019 Grzesiak et al., 2019). Furthermore, it is stated that globally, 42% of the wheat production areas are affected by drought (Kosina et al., 2007), underlining the importance of drought in wheat production.

GMP and STI were reported as drought indices suited to select stable and high-yielding durum wheat genotypes under drought stress and non-stress conditions (Patel et al., 2019; Ayed et al., 2021). Interestingly, in the current study, out of the top five (C010, DW033, DW080, DW124-2, and C011), three (DW033, DW080, and DW124-2) genotypes selected by the combined rank of GMP and STI as drought tolerant and stable were Ethiopian durum wheat landraces. Also, accessions DW084, DW082, DZ004, C037, and DW092 were selected as the top five drought-tolerant accessions based on DSI, RDI, TOL, and YSI combined ranking (see **publication 2.3, Table S1**). Hence, these genotypes may be recommended as parents in wheat drought stress breeding programs. In this thesis, 147 accessions from the study panel revealed a GY-DSI value of less than 1, indicating the differences among the genotypes that could be exploited for drought tolerance. Whereas, 138 showed a GY-DSI higher than 1, implying these genotypes are susceptible to drought. This shows that in the current study, drought stress was moderate but high enough to facilitate the selection of drought-tolerant accessions. This is in agreement with the theory that moderate drought stress is best to select drought-tolerant wheat lines (Ali and El-Sadek, 2016; Patel et al., 2019).

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### 3.2 Population structure of the durum wheat panel

The statistical power of GWAS is strongly dependent on the extent of population structure, the sample size, and the minor allele frequency (MAF) of SNPs (Xu et al., 2017). Moreover, deployment of population structure and kinship as a covariate reduces Type I error (false positives) (Yu et al., 2006). 11,919 SNP markers with a known physical position and  $PIC \geq 0.35$  were employed for population structure and genetic diversity analysis in the durum wheat study panel comprising 285 accessions, of which 215 accessions were Ethiopian durum wheat landraces (ETDWL). The study panel was clustered into two populations ( $\Delta K$  at  $K = 2$ ), clustering mainly the landraces on the one hand, and mainly released, advanced, and CIMMYT lines on the other hand (see **publication 2.1, Figure 3**). This also strongly supports the designation given to the Ethiopian durum wheat landraces as separate sub-species under the name *Triticum durum* subs. *Abyssinicum* or *Triticum aethiopicum* (Mengistu et al., 2015; Mengistu et al., 2016; Kabbaj et al., 2017). Further population structure analysis of the ETDWL alone revealed 4 populations ( $\Delta K$  at  $K = 4$ ) (see **publication 2.1, Figure 4**). Correspondingly, Mengistu et al. (2016) uncovered more populations in another set of ETDWL after removing improved durum wheat ( $\Delta K$  at  $K = 10$ ), stressing the high degree of genetic diversity within Ethiopian durum landraces. Hence, this is in agreement with the theory that Ethiopia is endowed with a wealth of genetic diversity for tetraploid wheat, and is considered the center of diversity and/or secondary center of origin (Vavilov, 1951; Mengistu et al., 2016; IBC, 2013; Kabbaj et al., 2017). On the other hand, the separate clustering of ETDWL from improved durum wheat in Ethiopia elucidated that little or no improved varieties were generated from landraces either through selection or via crossing with international durum wheat materials. Nevertheless, germplasm originating from international organizations such as CIMMYT and ICARDA remains the main source for advanced and released durum wheat in Ethiopia (Sall et al., 2019). AMOVA for the genetic diversity analysis showed significant ( $p < 0.001$ ) effects among and within the identified populations (see, **publication 2.1, Table 1**). High genetic diversity was observed within a population (81%, 76%) compared between populations (19%, 24%) for the SP and ETDWL, respectively, which may be a target for national and international wheat improvement programs to exploit valuable traits for drought stress. Remarkably, this supports the idea that genetic variability from the centers of origin, within wild relatives, and from landraces could be vital to discovering drought tolerance (Nevo and Chen, 2010; Dvorak et al., 2011; Dodig et al., 2012; Van Oosten et al., 2016). In the frame of this thesis, the diversity indices verify that the Ethiopian durum wheat landraces (ETDWL) were more diverse with ( $I = 0.7$ ,  $He = 0.46$ ,  $uHe = 0.46$ ) than the advanced lines ( $I = 0.6$ ,  $He = 0.42$ ,  $uHe = 0.42$ ) (see, **publication 2.1, Table 2**), showing the existence of plentiful variability in the ETDWL. Hence, the data suggest that the study panel used in this thesis is an essential source of novel and useful alleles for abiotic

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and biotic tolerance / resistance , as described by studies by Acosta-Gallegos et al.(2007), Bhandari et al., (2017). This is also in line with the idea that allelic variation could be recovered by exploring landraces (Fu, 2017). Besides, it is in agreement with the theory that landraces adapted to their natural environment over time may contribute to favorable genomic regions for tolerance against abiotic stress like drought (Brown, 2000; Reynolds et al., 2007; Acquaaah, 2012). Furthermore, ANOVA revealed a highly significant ( $P < 0.001$ ) difference for accessions and accession by treatment interaction for most of the traits evaluated, highlighting the existence of high genetic diversity in the study panel (**see publication 2.2, Table S2**). Consequently, the experimental setting applied facilitated the dissection of the embedded genetic diversity, which is in agreement with Bhatta et al. (2018). Correspondingly, in the present study, moderate to high broad-sense heritability ( $H^2$ ) (**see publication 2.2, Table 2**) was obtained for the traits under field conditions showing the reliability of the phenotypic data for marker-trait association analysis (Sukumaran et al., 2018; Bhatta et al., 2018).

### 3.3 Comparison of field and climate chamber experiments

The correlation between the same trait tested under field and climate chamber was analyzed (**see publication 2.2, Table 3**). Significant correlations were observed between traits estimated in the field and climate chamber trials ( $p < 0.001$ ). In this study, the significant ( $p < 0.001$ ) and positive correlation between GB and HI under FDS, FNS, CCDS, and CCNS conditions suggests the strong relationships between the traits under contrasting environmental conditions, as was reported by Pour-Aboughadareh et al. (2020). Significant ( $p < 0.001$ ) negative correlation of GB with DH and DM under FDS conditions indicates that early maturing accessions had a yield advantage under drought stress conditions, which is in agreement with Sukumaran et al. (2018) on durum wheat, Qaseem et al. (2019) on bread wheat, and Millet et al. (2016) on maize. Similarly, the negative correlation of GB with SL ( $p < 0.01$ ) under FDS indicated a reduced seed set that may be due to pollen abortion because of prolonged terminal drought and the associated heat effect under field conditions which is in line with another study on durum wheat (Pour-Aboughadareh et al., 2020). In this thesis, under field conditions, GB did not show a significant correlation with PH but a positive and significant ( $p < 0.001$ ) correlation between GB and PH was observed under CCDS conditions. This may be in line with Qaseem et al. (2017) who suggested that under drought stress environments tall genotypes accumulate and mobilize more resources to grain resulting in a yield advantage over shorter genotypes.

The significant ( $p < 0.001$ ) positive correlation observed between seed per spike (SPS) and GB under all drought stress and non-stress conditions are in agreement with results on winter wheat (Philipp et al.,

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2018). TKW was significantly ( $p < 0.05$ ) and positively correlated with GB except under CCDS which showed a positive but non-significant association. Similarly, a recent study on durum wheat indicated a non-significant correlation between GB and TKW under drought stress and non-stress conditions (Sukumaran et al., 2018). In contrast, a significant correlation between GB and TKW in bread wheat was observed (del Pozo et al., 2019; Mohammadi et al., 2018). These contrasting reports may show the complex nature of GB and/or maybe due to several environmental factors that affect GB and TKW.

The significant ( $p < 0.001$ ) positive correlation between GY\_FNS and GY\_FDS suggests that high GY performance under the FNS condition is closely related to stable and high GY under FDS conditions (see **publication 2.1, Table 4**). Similarly, studies depicted a positive and significant correlation between GY under favorable and drought stress conditions in durum wheat (Patel et al., 2019), bread wheat (Ali and El-Sadek, 2016), and rice (Mau et al., 2019). The significant ( $p < 0.001$ ) and positive correlation of GY\_FNS and GY\_FDS with GMP and STI, suggests that GMP and STI may be potential drought indices to select stable and relatively higher-yielding accessions under drought stress conditions.

### 3.4 QTL for drought stress tolerance in durum wheat

Gupta et al. (2020) reviewed several QTLs associated with agronomic, and root traits as well as physiological traits of wheat using genome-wide association studies. Hence, based on the critical LD value, in the current study, the identified 191 MTAs at  $\text{LOD} \geq 4$  for the ten investigated traits under field and climate chamber conditions were grouped into 70 QTLs (see **publication 2.2, Table S4 and S5, respectively**). Likewise, the detected 184 MTAs associated with the drought indices were clustered into 102 QTLs (see **publication 2.3, Table 3**). In general, in this study panel, more QTLs were identified on the B genome (57%, 52%) than on the A genome (43%, 48%) for morpho-physiological traits and drought indices, respectively, which is in agreement with results in durum wheat (Soriano et al., 2017; Desiderio et al., 2019; Alemu et al., 2020; Ballesta et al., 2020), implying the high number of polymorphic loci that exist in the B genome. Similarly, using SSR (simple sequence repeat) and DArT (Diversity Arrays Technology) markers Maccaferri et al. (2015) mapped a higher number of markers on the B genome as compared to the A genome. Furthermore, in this study, chromosomes 6B, 1A, 2B, and 7A were identified as QTL hotspots for morpho-physiological traits harboring 10, 8, 7, and 7 QTLs, respectively (see **publication 2.2, Table S5**). Correspondingly, for the drought indices at the chromosomal level, a higher number of QTLs, i.e. 11 each was identified on chromosomes 1A, 2B, and 7A, suggesting these genome regions are also QTL hotspots and play a pivotal role in drought tolerance in wheat (see **publication 2.2, Table S3**). In the current study, 6 QTLs detected for drought indices were on

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chromosome 4A, which is a substantial number and in agreement with the results of Ballesta et al. (2020) that indicated chromosome 4A as a hotspot for QTLs for drought indices in wheat.

Some of the detected QTLs were in agreement with previously reported QTLs, while others are novel QTLs. In our study, QTLs were detected for grain biomass and related traits that matched with previously reported results and with durum wheat in the GrainGenes database. The identification and use of QTLs associated with valuable agronomic traits at early generation selection in wheat breeding programs enhance the development of improved cultivars (Collard and Mackill, 2008). In this thesis, some of the discovered QTLs are associated with more than one trait (co-located) (**see publication 2.2, Table S5 and publication 2.3, Table S3**), while others are individual QTLs linked to a single trait of interest (Ma et al., 2019; Sukumaran et al., 2018). The co-located QTLs entail the existence of physiological and/or genetic relationships between these traits which may lead to the possible simultaneous improvement of multiple quantitative traits (Bhoite et al., 2018; Shariatipour et al., 2021).

Thus, in this thesis, the QTLs detected associated with GB that are located on chromosomes 1A, 3B (2), 4B (3), 6B, and 7A co-localize with DGF, DM, SPAD, SPS, and HI. Interestingly, these QTLs were not co-located with DH, which hints at the limited confounding effect of flowering time on grain yield, as was reported in other studies on durum wheat (Zaïm et al., 2020) and wheat (Ullah et al., 2021). Except for two QTLs associated with GB located on chromosomes 1A and 4B, which are putatively novel, the other six QTLs were reported in previous studies (Maccaferri et al., 2008; Mengistu et al., 2016; Soriano et al., 2017) on chromosome 3B, (Milner et al., 2016; Patil et al., 2013) on chromosome 4B, (Marcotuli et al., 2017) 6B, and 7A (Mengistu et al., 2016). Above all, the current identification of QTLs within similar QTL intervals to the previous studies confirms the findings and also shows the power of GWAS for QTL detection. Therefore, QTLs located on chromosomes 3B at 423,382,012 bp and 4B at 566,937,979 bp can be considered stable QTLs for GB whose selection may help to increase yield under FDS and FNS, respectively. Interestingly, in this thesis, QTLs detected under drought stress including newly detected QTLs for GB showed a positive effect on grain biomass with significant LOD values ranging between 4.11 and 7.0 and with up to 4.24% PVE, underlining the potential of these QTLs in increasing grain yield in durum wheat (**see publication 2.2, Table S5**). Most importantly, we identified QTLs under FDS with a positive effect on GB that is located on chromosome 1A between 495694477 and 501944537 bp, on 3B between 416256124 and 430507900 bp, on 3B between 745357158 and 759608934 bp, on 4B between 593416763 and 605142497 bp and 4B between 658785890 and 670511624 bp. Therefore, these QTLs could be validated and may be used to increase grain yield under drought stress via marker-assisted selection (MAS) schemes.

DH provides the basis for plant adaptation and is a major trait in plant breeding (Zaïm et al., 2020). Also, under terminal drought, early flowering time and a shorter vegetative phase are important for wheat

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production (Shavrukov et al., 2017). In the present study, the seven (four co-located) QTLs for DH were located on chromosomes 1A, 1B, 2A, 4A, 4B, and 6B (see **publication 2.2, Table S5**). Interestingly, five of the identified QTLs were positioned within previously reported QTL intervals on chromosomes 1A and 1B (Milner et al., 2016), 2A (Giunta et al., 2018), 4A (Maccaferri et al., 2011; Milner et al., 2016), and on chromosome 6B (Maccaferri et al., 2011; Roncallo et al., 2018). Supporting our findings, QTLs on chromosomes 2A, 2B, 4B, 5B, and 7B were also reported for this phenological trait (Zaïm et al., 2020). Similarly, in previous studies, genomic regions on chromosomes 2A and 2B were reported to be associated with the major photoperiod sensitivity loci *Ppd-A1* and *Ppd-B1* (Arjona et al., 2018; Maccaferri et al., 2008, 2011). Results obtained in our study suggest that the detected QTL for DH on chromosome 2A is located very close to the position of *Ppd-1A* but no QTL was detected associated with *Ppd-B1*. Particularly, *Ppd1* genes affect the time of heading and other traits and play an important role in modifying source-sink equilibrium affecting wheat growth and development under drought stress (Foulkes et al., 2004; Kamran et al., 2014; Würschum et al., 2018). The duration between days to heading and days to maturity is an important yield component in wheat, whereas drought stress may reduce DGF up to 71% in drought-sensitive wheat genotypes (Ihsan et al., 2016). In the current study, the three detected QTLs for DGF on chromosomes 1B, 3B, and 7B were not reported before. Therefore, they are putatively new QTLs in durum wheat. QTLs for DGF on chromosome 7B were clustered with two or more traits, for example, with SPS, TKW, and SPAD. Thus, the data suggests the linear relationship between DGF and these traits may be due to pleiotropic effects (Bhoite et al., 2018).

The six (three co-located) QTLs associated with DM were located on chromosomes 1A, 2B, 4A, 5B, and 7A. Interestingly, two QTLs on chromosomes 4A and 7A were detected in the same intervals in Ethiopian durum wheat landraces and modern varieties on chromosome 4A (Kidane et al., 2017) and Ethiopian durum wheat landraces on chromosome 7A (Mengistu et al., 2016). When compared with the GrainGenes database, the QTLs detected for DM on chromosomes 1A, 2B, and 5B are likely to be novel in durum wheat. Plant height is frequently altered when water is limited to overcome the deleterious effects of drought (Arif et al., 2020). The five (co-located) detected QTLs associated with PH were located on chromosomes 1A, 2B, 6B, 7A, and 7B. The identified QTL on chromosome 6B was previously reported associated with PH in Ethiopian durum wheat landraces (Mengistu et al., 2016). Similarly, the QTL on chromosome 7B linked with PH is located within a previously reported QTL region for PH in Mediterranean durum wheat landraces (Soriano et al., 2017) and close to a QTL region identified in elite durum cultivars (Maccaferri et al., 2011), suggesting the importance and stability of the QTL. Likewise, Mangini et al. (2021) reported QTLs associated with PH on these chromosomes which we also identified, except on chromosome 1A. Zaïm et al. (2020) also reported QTLs for PH on chromosomes 4A, 4B, and 5B, which are not detected in this study. The introduction of semidwarf genes into bread wheat resulted in

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the replacement of tall cultivars with semidwarf cultivars with high response to inputs (e.g., fertilizers) and resistance to lodging. Thereby, a significant increase in yield was achieved in many national breeding programs (Xynias et al., 2020). In agreement with our study, Chai et al. (2021) mentioned different alleles responsible for dwarfing genes in wheat that are located on chromosomes 2B, 7A, and 7B. In the current study, QTL for PH under FDS located on chromosome 1A showed a height-reducing effect with 1.47% PVE, which implies the importance of this QTL.

SPAD values serve as a valuable indicator of the photosynthetic capacity of wheat (Fiorentini et al., 2019; Lopes and Reynolds, 2012). A total of 12 (eight co-located) QTLs were identified for SPAD readings from flag leaves and were mapped on chromosomes 1A, 2A, 2B, 3A, 5B, 6B, and 7B. A recent study reported QTLs for flag leaf chlorophyll content for the durum wheat genome but on chromosomes 1B and 3B (Huang et al., 2018). GWAS results also indicated QTLs linked to leaf chlorophyll content under drought stress located on chromosomes 1B, 2A, 2B, 3B, 6B, and 7B in winter wheat (Maulana et al., 2020). These results highlight the potential of exploring QTLs associated with leaf chlorophyll content in durum wheat as a key factor for photosynthesis by which 80% of wheat yield is realized (Ghosh et al., 2003; Hussain et al., 2015). Grain yield can be increased through the manipulation of yield-related traits like spike length (SL) (Gaju et al., 2009). The eight (six co-located) QTLs for SL were identified on chromosomes 2B, 4A, 5A, 5B, 7A, and 7B. Remarkably, all the QTLs were detected under drought stress conditions except a QTL located on chromosome 7B. Similarly, Hu et al. (2015) identified eight QTLs associated with the length of the main spike in durum wheat on chromosomes 2B, 4A, 5A, 5B, 7A, and 7B. Correspondingly, Thanh et al. (2013) reported a QTL on chromosome 7B in emmer wheat, which is located in a QTL region detected in our study showing that these QTLs may be responsible for SL in durum wheat. Furthermore, a QTL detected on chromosome 2B was not reported yet.

Six (five co-located) QTLs were detected associated with SPS located on chromosomes 2B, 3B, 6A, 6B, and 7A, of which five were reported earlier (Giunta et al., 2018; Mangini et al., 2018; Mengistu et al., 2016; Roncallo et al., 2018). One of the QTLs on 6B for SPS was reported for the first time. More importantly, four of the six QTLs detected for SPS were detected under FDS and CCDS with a positive effect size. Interestingly, these identified QTLs under drought stresses were also associated with traits such as DGF, PH, TKW, and SPAD, which may indicate the morpho-physiological and genetic relationship between the traits. HI is an important trait directly related to yield. The twelve QTLs for HI were located on chromosomes 1A, 1B, 2A, 2B, 3A, 5A, 6B, and 7A. Recently, a study on association mapping of QTLs for yield and yield-related traits revealed QTLs associated with HI on chromosomes 1B, 2B, 3B, 4B, 5B, 7A, and 7B (Arif et al., 2020). Similarly, in the current study, the two detected QTLs on chromosomes 2A and 6B are located close to the QTL interval reported by Roncallo et al. (2018) and within the reported QTL interval on chromosome 6A (Peleg et al., 2009). In this thesis, the detected QTLs

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for HI located on chromosomes 1A, 3A, and 5A are reported for the first time in durum wheat. The three (one co-located) QTLs for TKW were located on chromosomes 2B, 3B, and 4A. Surprisingly, these QTLs were also identified in multi-location trials in tetraploid wheat in segregating populations and germplasm collections for TKW (Mangini et al., 2018). More importantly, QTLs for TKW on chromosome 2B under CCDS and on 3B under CCNS, as well as on 4A under FNS were found to be in close vicinity and within already detected QTL intervals, respectively (Mangini et al., 2018), showing the stable nature of the QTLs. On the other hand, recent studies also identified QTLs for TKW on chromosomes 1A, 1B, 2A, 3A, 4B, 5A, 5B, and 6B in durum wheat (Giancaspro et al., 2019; Mangini et al., 2021), which were not detected in our study.

Genome-wide association study on drought indices traits is an alternative for QTL detection and provides valuable information for marker-assisted selection in wheat (Ballesta et al., 2018). Hence, in this study out of the 102 QTLs detected for drought indices, the 13 QTLs (six co-located) detected for DSI were on chromosomes 2B, 4A (2 QTLs), 4B, 6B, and 7A (**see publication 2.3, Table S3**). Accordingly, studies reported QTLs for DSI on chromosomes 2B, 4A (2 QTLs), 4B, 6B, and 7A (Dashti et al., 2007; Edae et al., 2014; Sukumaran et al., 2018; Ballesta et al., 2018). Furthermore, QTLs were reported for SPS-DSI on chromosomes 7A and 7B and GY-DSI on chromosome 4A using DArT markers (Edae et al., 2014). However, in this thesis, no QTL was detected for SPS-DSI and GY-DSI on those chromosomes. Regarding the 27 QTLs (10 co-located) for GMP on chromosomes 1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, and 7B these QTLs may play an important role to identify stable and high yielding genotypes under drought stress. Similarly, a QTL was reported on chromosome 3B using an SSR marker in a doubled haploid bread wheat population for GMP (Dashti et al. 2007). In the present study, three out of the 13 QTLs for RDI were detected on chromosomes 4A, 4B, and 5B. Similarly, studies reported QTLs for RDI on chromosomes 4A (Arif et al., 2020) and 4B (Ballesta et al., 2018) and chromosome 5B (Arif et al., 2020).

In our study, 12 of the 28 detected QTLs (9 co-located) for STI were located on chromosomes 1A, 2B (2 QTLs), 2A, 2B, 4A, 5A, 5B, 6B, and 7A (2 QTLs). In agreement with this, in studies on wheat QTLs were reported for STI on these chromosomes (Dashti et al., 2007; Sukumaran et al., 2018; Ballesta et al., 2018; Qaseem et al., 2019; Arif et al., 2020), suggesting the potential of STI for identifying QTL regions across the wheat genome (**see publication 2.3, Table S3**). Moreover, six out of the 11 QTLs (2 co-located) identified for TOL were detected on chromosomes 2B, 3A, 5A, 5B (2 QTLs), and 7B. Consistent with this result, studies revealed QTLs for TOL on these chromosomes (Dashti et al., 2007; Sukumaran et al., 2018; Ballesta et al., 2018; Arif et al., 2020). Out of the detected 10 QTLs (5 co-located) for YSI, two were located on chromosomes 4B and 6B. Similarly, Ballesta et al. (2018) reported QTLs for YSI on chromosomes 4B and 6B. In general, 30 out of the 102 detected QTLs for drought indices were



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previously reported (Dashti et al., 2007; Sukumaran et al., 2018; Ballesta et al., 2018; Qaseem et al., 2019; Arif et al., 2020) while 72 QTLs reported in this study are likely novel QTLs (see **publication 2.3, Table S3**). In this thesis, 55 out of 70 detected QTLs for the morpho-physiological traits were previously reported and only 15 QTLs were reported as putatively novel (see **publication 2.2, Table S5**). In the current study, the putatively novel QTLs identified may be used for MAS in wheat breeding programs for drought tolerance.

Despite the detection of significant positive correlations between climate chamber and field results for several traits, we did not observe common QTLs for any trait under the two environments. However, only one stable MTA was detected for SPS (RAC875\_c60169\_200) under FDS and FNS, which is located on chromosome 3B at 25269809 bp (see **publication 2.2, Table S4**). Hence, this is showing the limitation in the current study, which may be due to the lack of the contribution of the rare alleles, since alleles with <5% minor allele frequency were removed in the GWAS analysis and/or may be explained by the effect of the environment leading to varying regulatory scenarios for the various traits under the two watering conditions. As a result, selection for drought stress has to be conducted in the target environment and ideally may include the design of ideotypes for certain growth scenarios (Senapati and Semenov, 2019). Additionally, in this thesis, only two major MTAs were detected for traits HI under CCDS and SL under FNS with 10.6% and 11.83% PVE, respectively (see **publication 2.2, Table S4**). This demonstrates the polygenic control of the quantitative traits measured in this study as it was reported in other studies in durum wheat (Wang et al., 2019) and bread wheat (Liu et al., 2018). Hence, such a phenomenon also explains that a quantitative trait is controlled by numerous genes with each gene having a relatively small effect and is in addition affected by the environment (Zhang et al., 2020). In the future, PCR-based markers may be developed and validated for the detected QTLs which are associated with yield stability and yield improvement under drought stress conditions. Therefore, QTLs with favorable SNP alleles identified in this study may be used to develop Polymerase Chain Reaction (PCR) based markers like Competitive Allele-Specific polymerase chain reaction (KASP) markers to facilitate future marker-assisted breeding in wheat.

### 3.5 Identification of putative candidate genes

In this study, MTAs that were previously reported for drought tolerance and/or their annotation linked with drought tolerance are considered candidate genes. Accordingly, the MTA for GY-GMP on chromosome 4A is annotated as a U-box domain-containing protein. This protein is also known to be involved in drought stress in barley (Ryu et al., 2019) and in drought and salinity stresses in Arabidopsis

## GENERAL DISCUSSION

(Cho et al., 2006) (see **publication 2.3, Table S2**). Likewise, the MTA detected for GY-GMP on chromosome 3B (RFL\_Contig2569\_2187) at 752,249,328 bp is annotated as a potassium transporter. Following this, Ouyang et al. (2010) and Cheng et al. (2018) reported that overexpression of this gene in rice enhanced drought tolerance. The other MTA on chromosome 5A (Kukri\_rep\_c116526\_98) for GY-GMP at 112,213,041 bp is annotated as a Protein MODIFIER OF SNC1 1 G. In line with this, the role of MOS14 (protein modifier of snc1-1, 14) in drought tolerance was reported in *Arabidopsis* (Xu et al., 2016). An MTA for GY-RDI on chromosome 7A (Excalibur\_c24593\_1217) at 7,721,495 bp is annotated as a Cytochrome P450 family protein. Similarly, it has been reported that this protein family is involved in drought and salinity stress tolerance (Narusaka et al. 2004; Ehltting et al. 2008; Jun et al. 2015). Particularly, Melloul et al. (2014) showed the up-regulation of Cytochrome P450 family protein in durum wheat leaves under drought stress. Regarding the MTA identified for DGF-TOL on chromosome 4A (IAAV1775) at 590,188,609 bp, a methyltransferase was annotated. Respectively, this protein is reported to enhance drought resistance in poplar (Lu et al., 2020). An MTA for TKW-TOL on chromosome 2B (Kukri\_c36879\_83) at 96,408,120 bp is annotated as an acyl-CoA dehydrogenase-related family protein. Similarly, it was revealed that this protein is one of the drought-responsive protein species in leaves and its expression is altered under dehydration (Wang et al., 2016). The other MTA for GY-GMP on chromosome 6B (wsnp\_Ex\_c3940\_7144946) at 508,076,861 bp is annotated as a DNA topoisomerase 2. Likewise, studies reported that this protein is upregulated under abiotic stresses such as cold and salinity in tobacco and pea (Tammara et al., 2016; John et al., 2016).

On the other hand, in the current study, many MTAs were detected annotated for drought tolerance linked with more than one drought index, suggesting the existence of linear relationships between respective traits, which may allow the simultaneous improvement of multiple traits (Bhoite et al., 2018; Shariatipour et al., 2021) (see **publication 2.3, Figure 2**). Hence, the MTA for GY-GMP and GY-STI on chromosome 2A (Tdurum\_contig10785\_2433) at 12,102,513 bp is annotated as an NBS-LRR-like resistance protein. It is known that NBS-LRR-like resistance proteins are particularly involved in resistance to various diseases (Dubey and Singh, 2018; Shao et al., 2022), as well as in drought stress resistance (Chini et al., 2004; Rampino et al., 2017). Regarding the MTA for GY-STI, HI-GMP, HI-STI, SPAD-GMP, and SPS-GMP on chromosome 5A (Tdurum\_contig76578\_537) at 110,830,599 bp, these are annotated as UNC93-like protein. Likewise, a study indicated that UNC93 functions as a positive regulator of drought stress resistance via ABA-dependent signal transduction pathways in *Arabidopsis thaliana* (Xiang et al., 2018). An MTA for DGF-RDI, DGF-TOL, and DGF-YSI on chromosome 6B (Tdurum\_contig61383\_627) at 36,557,072 bp is annotated as a leucine-rich repeat receptor-like protein kinase family protein. Likewise, these proteins increase drought resistance by promoting root growth while reducing plant height in rice (Kang et al., 2017). Another MTA was detected associated with HI-RDI, HI-TOL, and HI-YSI, on

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chromosome 4B (tplb0050b23\_546) at 4,927,519 bp annotated as a Ribosomal protein. In agreement, it is indicated that ribosomal proteins are up-regulated under drought stress in the root of drought-tolerant bread wheat cultivars (Ma et al., 2016). Most importantly, in the current study, the newly detected MTAs under drought stress conditions may be novel and add to the existing knowledge to contribute to drought resistance improvement in wheat.

## SUMMARY

### 4 Summary

In this thesis, the differences in drought stress responses have been investigated in a genetically diverse set of durum wheat (*Triticum turgidum* ssp. *durum*). Drought stress is caused by the limited availability of water that affects growth and development, which results in a severe reduction in yield. From the three-seasons field and one-season climate chamber experiments, descriptive statistics, ANOVA, AMOVA, diversity indices, and population structure showed a large genetic diversity in the study panel. The study panel was clustered into two populations, which were used as covariate during the GWAS analysis. Genetic diversity within a population was higher than variation among populations. Diversity indices were higher for the Ethiopian durum wheat landraces than for the advanced lines, which could be exploited for drought tolerance. Drought stress results in a significant reduction of the traits investigated compared to non-stress conditions. Genotypes DW084, DW082, DZ004, C037, and DW092 were identified as the most drought-tolerant ones taking into account GY-DSI, GY-RDI, GY-TOL, and GY-YSI. Similarly, C010, DW033, DW080, DW124-2, and C011 were selected as the most stable accessions both under FDS and FNS conditions based on the combined rank of GY-GMP and GY-STI. The identified drought tolerant and stable genotypes may be used as potential parents for breeding. By GWAS based on the 90K iSelect Wheat chip 191/70 and 184/102 MTAs/QTLs significantly ( $p < 0.0001$ ) associated with grain biomass and related traits, and for drought indices traits, respectively were detected mainly with a small effect and some of its novel. Detected QTLs on chromosomes 1A, 3B (2), and 5A may contribute to higher grain biomass and on chromosomes 1B and 6B to a higher harvest index under FDS. Similarly, QTLs detected on chromosomes 1B and 2B contributed to higher SPAD and a QTL on chromosome 7A to the number of seeds per spike. Chromosomes 6B, 1A, 2B, and 7A are QTL hotspots for morphophysiological traits embracing 10, 8, 7, and 7 QTLs, respectively. Chromosomes 1A, 2B, and 7A are QTL hotspots for drought indices; each with 11 QTLs identified and may play a pivotal role in drought tolerance in wheat. QTLs associated with drought index GY-GMP on chromosomes 4A, 7B, 6B, 5B, and 3B revealed a positive effect size with 26.61%, 22.21%, 21.91%, 21.16%, and 10.07% of PVE, respectively. Linked genes may increase grain yield in wheat via MAS. Major MTAs with favorable SNP alleles identified in this study could be used to develop KASP markers for marker-assisted breeding for drought stress tolerance in wheat.

## SUMMARY

### 5 Zusammenfassung

In dieser Arbeit wurden Unterschiede in der Reaktion auf Trockenstress in einem genetischen Diversitätsset von Hartweizen (*Triticum turgidum* ssp. *durum*) untersucht. Trockenstress wird durch eine begrenzte Wasserverfügbarkeit verursacht, die das Wachstum und die Entwicklung beeinträchtigt, was zu einer starken Ertragsminderung führt. Deskriptive Statistiken, ANOVA, AMOVA, Diversitätsindizes und die Populationsstruktur der dreijährigen Feldversuche und der einjährigen Klimakammerversuche zeigten eine große genetische Vielfalt im Diversitätsset. Das Diversitätsset wurde zwei Populationen zugeordnet, die bei der GWAS-Analyse als Kovariate verwendet wurden. Die genetische Vielfalt innerhalb der Akzessionen einer Population war größer als die Variation zwischen den Populationen. Die Diversitätsindizes waren größer für die äthiopischen Landrassen als für etablierte Linien, was für die Züchtung auf Trockentoleranz genutzt werden könnten. Trockenstress führt zu einer signifikanten Verringerung aller untersuchten Merkmale. Die Genotypen DW084, DW082, DZ004, C037 und DW092 zeigten unter Berücksichtigung von GY-DSI, GY-RDI, GY-TOL und GY-YSI die größte Trockenstresstoleranz. Die stabilsten Akzessionen sowohl unter FDS- als auch unter FNS-Bedingungen waren C010, DW033, DW080, DW124-2 und C011, basierend auf der kombinierten Bewertung von GY-GMP und GY-STI. Die identifizierten trockenstresstoleranten und stabilen Genotypen können als potenzielle Eltern für die Züchtung verwendet werden. Mittels GWAS wurden bereits bekannte und neue MTAs/QTLs für Trockenstresstoleranz bei Hartweizen identifiziert. Auf der Grundlage des 90K iSelect Wheat Chips wurden 191/70 und 184/102 MTAs/QTLs entdeckt, die signifikant ( $p < 0,0001$ ) mit der Kornbiomasse und verwandten Merkmalen bzw. mit Trockenheitsindizes assoziiert sind, wobei die Effekte meist gering sind. Die auf den Chromosomen 1A, 3B (2) und 5A entdeckten QTLs könnten zu einer höheren Kornbiomasse und auf den Chromosomen 1B und 6B zu einem höheren Ernteindex unter FDS beitragen. In ähnlicher Weise trugen die auf den Chromosomen 1B und 2B entdeckten QTLs zu einem höheren SPAD bei, und ein QTL auf Chromosom 7A zu der Anzahl der Samen pro Ähre. Die Chromosomen 6B, 1A, 2B und 7A sind QTL-Hotspots für morpho-physiologische Merkmale, die 10, 8, 7 bzw. 7 QTLs umfassen. Bei den Chromosomen 1A, 2B und 7A handelt es sich um QTL-Hotspots für Trockenheitsindizes mit jeweils 11 identifizierten QTLs, die möglicherweise eine zentrale Rolle bei der Trockenstresstoleranz von Weizen spielen. QTLs, die mit dem Trockenheitsindex GY-GMP auf den Chromosomen 4A, 7B, 6B, 5B und 3B assoziiert sind, zeigten eine positive Effektgröße mit 26,61%, 22,21%, 21,91%, 21,16% bzw. 10,07% der PVE. Verknüpfte Gene können den Kornertrag bei Weizen über MAS erhöhen. Wichtige MTAs mit günstigen SNP-Allelen, die in dieser Studie identifiziert wurden, könnten zur Entwicklung von KASP-Markern für die Marker gestützte Züchtung auf Trockenstresstoleranz bei Weizen verwendet werden.

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## SUPPLEMENTARY FILES

### 7 Supplementary files.

**Publication 2.1).** Negisho, K., Shibu, S., Pillen, K., Ordon, F., & Wehner, G. (2021). Genetic diversity of Ethiopian durum wheat landraces. *PLoS ONE*,16(2). <https://doi.org/10.1371/journal.pone.0247016>.

**Table S1.** Population STRUCTURE analysis results for SP, n = 285 with Delta K at k = 2, and ETDWL, n = 215 with Delta K at k = 4. SP: Study panel, ETDWL: Ethiopian durum wheat landrace. Column under population shows structure analyses based colors designated for the identified population in SP and in ETDWL by number after hyphen.

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
231584	DW208	Amhara	NORTH WELLO	Landrace	2920	Pop1-1
8333-1	DW003-1	Amhara	EAST GOJAM	Landrace	2580	Pop1-1
204560-2	DW029-2	Oromia	NORTH SHEWA	Landrace	2501	Pop1-1
208261	DW094	Oromia	ARSI	Landrace	2420	Pop1-1
208931	DW035	Oromia	WEST SHEWA	Landrace	2400	Pop1-1
204560-1	DW029-1	Oromia	NORTH SHEWA	Landrace	2500	Pop1-1
222299	DW069	Oromia	BALE	Landrace	2545	Pop1-1
222372	DW080	Oromia	ARSI	Landrace	2040	Pop1-1
214307	DW038	Oromia	EAST SHEWA	Landrace	2680	Pop1-1
222462-2	DW097-2	Oromia	WEST SHEWA	Landrace	2601	Pop1-1
214587	DW059	Oromia	MISRAK WELLEGA	Landrace	2340	Pop1-1
231524	DW199	Oromia	WEST SHEWA	Landrace	2830	Pop1-1
8333-2	DW003-2	Amhara	EAST GOJAM	Landrace	2581	Pop1-1
231613	DW225	Oromia	EAST HARERGE	Landrace	2510	Pop1-1
204564	DW032	Oromia	NORTH SHEWA	Landrace	2500	Pop1-1
231588	DW212	Amhara	NORTH WELLO	Landrace	2820	Pop1-1
231597	DW219	Amhara	SOUTH WELLO	Landrace	2600	Pop1-1
231589-1	DW213-1	Amhara	NORTH WELLO	Landrace	2890	Pop1-1
238134	DW256	Tigray	EAST AWI	Landrace	2600	Pop1-1
222684-2	DW124-2	Amhara	NORTH WELLO	Landrace	2841	Pop1-1
231599	DW220	Amhara	SOUTH WELLO	Landrace	2600	Pop1-1
238135	DW257	Tigray	EAST AWI	Landrace	2470	Pop1-1
203996	DW011	Amhara	NORTH SHEWA	Landrace	3060	Pop1-1
226207	DW131	Amhara	NORTH GONDAR	Landrace	2100	Pop1-1
226963	DW184	Oromia	EAST SHEWA	Landrace	2200	Pop1-1
222352	DW072	Amhara	WEST GOJAM	Landrace	2560	Pop1-1
212564	DW037	Amhara	NORTH SHEWA	Landrace	2640	Pop1-1
226922	DW176	SNNP	NORTH OMO	Landrace	2350	Pop1-1
216072	DW064	Oromia	ARSI	Landrace	2800	Pop1-1
222732	DW126	Amhara	NORTH SHEWA	Landrace	2740	Pop1-1
231589-2	DW213-2	Amhara	NORTH WELLO	Landrace	2891	Pop1-1
226903	DW174	Oromia	NORTH SHEWA	Landrace	2510	Pop1-1
8175	DW141	SNNP	KEMBATA ALABANA TEMB	Landrace	2780	Pop1-1

## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
204483	DW019	Oromia	NORTH SHEWA	Landrace	2880	Pop1-1
204562	DW030	Oromia	NORTH SHEWA	Landrace	2500	Pop1-1
212561-1	DW036	Amhara	NORTH SHEWA	Landrace	2680	Pop1-1
212561-2	DW036-2	Amhara	NORTH SHEWA	Landrace	2681	Pop1-1
215276	DW063	Amhara	NORTH SHEWA	Landrace	2920	Pop1-1
222619	DW114	Amhara	SOUTH GONDAR	Landrace	3040	Pop1-1
226245	DW133	Tigray	SOUTH AWI	Landrace	2687	Pop1-1
226830	DW159	Amhara	EAST GOJAM	Landrace	2480	Pop1-1
231536-1	DW200-1	Amhara	NORTH SHEWA	Landrace	3010	Pop1-1
231585	DW209	Amhara	NORTH WELLO	Landrace	2920	Pop1-1
231594	DW217	Amhara	NORTH WELLO	Landrace	2780	Pop1-1
238127	DW251	Tigray	EAST AWI	Landrace	2930	Pop1-1
226834-1	DW160-1	Amhara	EAST GOJAM	Landrace	2460	Pop1-2
204555	DW028	Oromia	NORTH SHEWA	Landrace	2500	Pop1-2
204544	DW027	Oromia	NORTH SHEWA	Landrace	2600	Pop1-2
222708	DW125	Oromia	EAST HARERGE	Landrace	2380	Pop1-2
222431	DW091	Oromia	ARSI	Landrace	2460	Pop1-2
236984	DW232	Oromia	ARSI	Landrace	1995	Pop1-2
214315	DW216	Amhara	NORTH WELLO	Landrace	2780	Pop1-2
214518	DW052	Amhara	EAST GOJAM	Landrace	2660	Pop1-2
222358	DW073	Amhara	EAST GOJAM	Landrace	2560	Pop1-2
226837	DW161	Amhara	EAST GOJAM	Landrace	2510	Pop1-2
226352	DW144	Oromia	ARSI	Landrace	2400	Pop1-2
222462-1	DW097-1	Oromia	WEST SHEWA	Landrace	2600	Pop1-2
222426	DW090	Oromia	ARSI	Landrace	2460	Pop1-2
214352	DW041	Oromia	WEST SHEWA	Landrace	2810	Pop1-2
226819	DW158	Oromia	BALE	Landrace	2600	Pop1-2
226327	DW138	SNNP	HADIYA	Landrace	2590	Pop1-2
222568	DW108	Oromia	WEST HARERGE	Landrace	2030	Pop1-2
231536-2	DW200-2	Amhara	NORTH SHEWA	Landrace	3011	Pop1-2
214366	DW044	Amhara	NORTH SHEWA	Landrace	3000	Pop1-2
222632	DW117	Amhara	SOUTH GONDAR	Landrace	2850	Pop1-2
204563	DW031	Oromia	NORTH SHEWA	Landrace	2500	Pop1-2
222360	DW075	Amhara	EAST GOJAM	Landrace	2550	Pop1-2
208293-1	DW142-2	Oromia	DZARC	Landrace	NA	Pop1-2
222413	DW086	Oromia	ARSI	Landrace	2430	Pop1-2
226838-2	DW162-2	Amhara	EAST GOJAM	Landrace	2510	Pop1-2
231586	DW210	Amhara	NORTH WELLO	Landrace	2820	Pop1-2
236986	DW234	Amhara	NORTH SHEWA	Landrace	2010	Pop1-2
204488-1	DW022-1	Oromia	NORTH SHEWA	Landrace	2850	Pop1-3
222382	DW081	Oromia	ARSI	Landrace	2930	Pop1-3
222404	DW084	Oromia	ARSI	Landrace	2650	Pop1-3

## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
222191	DW065	Oromia	EAST SHEWA	Landrace	2300	Pop1-3
231540	DW202	Amhara	NORTH SHEWA	Landrace	3190	Pop1-3
236981	DW230	Oromia	ARSI	Landrace	2150	Pop1-3
223257	DW128	Tigray	SOUTH AWI	Landrace	2600	Pop1-3
231541	DW203	Amhara	NORTH SHEWA	Landrace	3190	Pop1-3
226838-1	DW162-1	Amhara	EAST GOJAM	Landrace	2510	Pop1-3
222684-1	DW124-1	Amhara	NORTH WELLO	Landrace	2840	Pop1-3
214557	DW054	Amhara	SOUTH WELLO	Landrace	2450	Pop1-3
226881	DW167	Oromia	WEST SHEWA	Landrace	2850	Pop1-3
204488-2	DW023-2	Oromia	NORTH SHEWA	Landrace	2851	Pop1-3
222415	DW087	Oromia	ARSI	Landrace	2400	Pop1-3
222198	DW066	Oromia	ARSI	Landrace	2520	Pop1-3
222387	DW082	Oromia	ARSI	Landrace	2490	Pop1-3
236985	DW233	Oromia	ARSI	Landrace	2000	Pop1-3
222408	DW085	Oromia	ARSI	Landrace	2490	Pop1-3
222418	DW088	Oromia	ARSI	Landrace	2400	Pop1-3
226357	DW147	Oromia	ARSI	Landrace	2440	Pop1-3
222465	DW098	Oromia	WEST SHEWA	Landrace	2600	Pop1-3
222469	DW099	Oromia	WEST SHEWA	Landrace	2490	Pop1-3
15359	DW009	Oromia	EAST SHEWA	Landrace	2372	Pop1-3
208152	DW026	Oromia	NORTH SHEWA	Landrace	2710	Pop1-3
222421	DW089	Oromia	ARSI	Landrace	2415	Pop1-3
231569	DW205	SNNP	KEMBATA ALABANA TEMB	Landrace	2540	Pop1-3
226886	DW171	Oromia	WEST SHEWA	Landrace	2850	Pop1-3
222346	DW071	Amhara	AGEW AWI	Landrace	2540	Pop1-3
231547	DW204	Oromia	ARSI	Landrace	2400	Pop1-3
226209	DW132	Amhara	SOUTH GONDAR	Landrace	2700	Pop1-3
222533	DW105	Amhara	NORTH GONDAR	Landrace	2004	Pop1-3
226301	DW135	Oromia	WEST SHEWA	Landrace	2590	Pop1-3
204470	DW017	Oromia	ARSI	Landrace	2520	Pop1-3
226840	DW163	Amhara	EAST GOJAM	Landrace	2550	Pop1-3
222608-2	DW112-2	Amhara	SOUTH GONDAR	Landrace	3051	Pop1-3
204417	DW016	Oromia	ARSI	Landrace	2730	Pop1-3
204392	DW013	Oromia	ARSI	Landrace	2440	Pop1-3
222508	DW101	Amhara	NORTH GONDAR	Landrace	2550	Pop1-3
226356	DW146	Oromia	ARSI	Landrace	2440	Pop1-3
226888	DW173	Amhara	NORTH SHEWA	Landrace	2720	Pop1-3
226958	DW180	Amhara	NORTH GONDAR	Landrace	2927	Pop1-3
226978	DW189	Oromia	ARSI	Landrace	2420	Pop1-3
203724	DW194	Oromia	ARSI	Landrace	2520	Pop1-3
231573	DW207	Amhara	EAST GOJAM	Landrace	2510	Pop1-3
236974-1	DW227-1	Oromia	ARSI	Landrace	2850	Pop1-3

## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
5739-1	DW258	Tigray	MEHAKELEGNAW	Landrace	NA	Pop1-3
238138	DW259	Tigray	MEHAKELEGNAW	Landrace	2180	Pop1-3
222362	DW076	Amhara	EAST GOJAM	Landrace	2510	Pop1-4
226876	DW166	Oromia	WEST SHEWA	Landrace	2880	Pop1-4
238123	DW247	Tigray	MEHAKELEGNAW	Landrace	2000	Pop1-4
238120	DW244	Tigray	MEHAKELEGNAW	Landrace	2030	Pop1-4
238121	DW245	Tigray	MEHAKELEGNAW	Landrace	1850	Pop1-4
238139	DW260	Amhara	EAST GOJAM	Landrace	2440	Pop1-4
204493-1	DW023-1	Oromia	NORTH SHEWA	Landrace	2850	Pop1-4
222433	DW093	Oromia	ARSI	Landrace	2420	Pop1-4
8436	DW005	SNNP	BENCH MAJI	Landrace	1820	Pop1-4
214333	DW040	Oromia	NORTH SHEWA	Landrace	2510	Pop1-4
222432	DW092	Oromia	ARSI	Landrace	2460	Pop1-4
204485	DW021	Oromia	NORTH SHEWA	Landrace	2880	Pop1-4
222298	DW068	Oromia	BALE	Landrace	2545	Pop1-4
226971-2	DW186-2	Oromia	ARSI	Landrace	2441	Pop1-4
238119	DW243	Tigray	MEHAKELEGNAW	Landrace	2000	Pop1-4
238128	DW252	Tigray	EAST AWI	Landrace	2990	Pop1-4
204566	DW033	Oromia	EAST SHEWA	Landrace	2350	Pop1-4
204573-1	DW034-1	Oromia	EAST SHEWA	Landrace	2490	Pop1-4
238132	DW254	Tigray	EAST AWI	Landrace	2600	Pop1-4
226381	DW148	Oromia	NORTH SHEWA	Landrace	2598	Pop1-4
236987	DW235	Amhara	NORTH SHEWA	Landrace	2019	Pop1-4
222574	DW109	Oromia	EAST HARERGE	Landrace	2260	Pop1-4
214356	DW043	Oromia	NORTH SHEWA	Landrace	2650	Pop1-4
222644	DW121	Amhara	SOUTH GONDAR (BG)	Landrace	2980	Pop1-4
226393	DW153	Oromia	EAST SHEWA	Landrace	2160	Pop1-4
238124	DW248	Tigray	MEHAKELEGNAW	Landrace	2000	Pop1-4
208271	DW074	Amhara	EAST GOJAM	Landrace	2550	Pop1-4
226882	DW168	Oromia	WEST SHEWA	Landrace	2850	Pop1-4
231538	DW201	Oromia	ARSI	Landrace	2750	Pop1-4
231610	DW224	Oromia	EAST HARERGE	Landrace	2630	Pop1-4
7961	DW002	Amhara	NORTH SHEWA	Landrace	2600	Pop1-4
222639	DW119	Amhara	SOUTH GONDAR	Landrace	2680	Pop1-4
231597-1	DW219-1	Amhara	SOUTH WELLO	Landrace	2601	Pop1-4
226331	DW139	Amhara	NORTH SHEWA	Landrace	2835	Pop1-4
226914	DW175	Amhara	AGEW AWI	Landrace	2510	Pop1-4
231592-1	DW215-1	Amhara	NORTH WELLO	Landrace	2260	Pop1-4
7960	DW001	Amhara	NORTH SHEWA	Landrace	2600	Pop1-4
8356	DW004	Amhara	EAST GOJAM	Landrace	2150	Pop1-4
222435	DW095	Oromia	ARSI	Landrace	2420	Pop1-4
222554	DW106	Oromia	ARSI	Landrace	2465	Pop1-4



## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
214353	DW042	Oromia	WEST SHEWA	Landrace	2810	Pop1-4
222530	DW104	Amhara	NORTH GONDAR	Landrace	2510	Pop1-4
236988	DW236	Oromia	EAST SHEWA	Landrace	2200	Pop1-4
214517	DW051	Amhara	EAST GOJAM	Landrace	2580	Pop1-4
7148	DW127	Oromia	BALE	Landrace	1760	Pop1-4
203776	DW010	Amhara	NORTH GONDAR	Landrace	2100	Pop1-4
214591	DW061	Amhara	SOUTH WELLO	Landrace	2600	Pop1-4
222608-1	DW112-1	Amhara	SOUTH GONDAR	Landrace	3050	Pop1-4
226809	DW157	Amhara	NORTH GONDAR	Landrace	2840	Pop1-4
227007	DW190	Amhara	EAST GOJAM	Landrace	2502	Pop1-4
222600	DW111	Amhara	SOUTH GONDAR	Landrace	3000	Pop1-4
238117	DW241	Tigray	MEHAKELEGNAW	Landrace	1920	Pop1-4
231499	DW198	Oromia	NORTH SHEWA	Landrace	2853	Pop1-4
222370	DW206	Amhara	EAST GOJAM	Landrace	2390	Pop1-4
226312-1	DW137-1	Amhara	NORTH SHEWA	Landrace	2860	Pop1-4
227008	DW191	Amhara	EAST GOJAM	Landrace	2502	Pop1-4
227009	DW192	Oromia	ARSI	Landrace	2995	Pop1-4
7217	DW197	Oromia	ARSI	Landrace	1540	Pop1-4
214377	DW046	Oromia	WEST SHEWA	Landrace	2210	Pop1-4
227016	DW195	Oromia	WEST SHEWA	Landrace	2635	Pop1-4
222613	DW113	Amhara	SOUTH GONDAR	Landrace	3130	Pop1-4
20666-1	DW014	Oromia	DZARC	Landrace	NA	Pop1-4
222629	DW116	Amhara	SOUTH GONDAR	Landrace	2850	Pop1-4
226808	DW156	Amhara	NORTH GONDAR	Landrace	2840	Pop1-4
214497	DW048	Oromia	ARSI	Landrace	2720	Pop1-4
208332-2	DW045	Amhara	NORTH SHEWA	Landrace	2841	Pop1-4
204349	DW012	Oromia	BALE	Landrace	2560	Pop1-4
222578	DW110	Oromia	EAST HARERGE	Landrace	2410	Pop1-4
226971-1	DW186-1	Oromia	ARSI	Landrace	2440	Pop1-4
204411	DW015	Oromia	ARSI	Landrace	2275	Pop1-4
204482	DW018	Oromia	NORTH SHEWA	Landrace	2890	Pop1-4
214490	DW047	Amhara	NORTH GONDAR	Landrace	2720	Pop1-4
214515	DW049	Amhara	EAST GOJAM	Landrace	2560	Pop1-4
7208	DW055	Amhara	EAST GOJAM	Landrace	2200	Pop1-4
214571	DW056	Amhara	EAST GOJAM	Landrace	2200	Pop1-4
222503	DW100	Amhara	NORTH GONDAR	Landrace	2400	Pop1-4
222514	DW102	Amhara	NORTH GONDAR	Landrace	2660	Pop1-4
222627	DW115	Amhara	SOUTH GONDAR	Landrace	2850	Pop1-4
226093	DW129	Amhara	SOUTH WELLO	Landrace	2570	Pop1-4
226342	DW140	Oromia	EAST SHEWA	Landrace	2755	Pop1-4
226354-1	DW145-1	Oromia	ARSI	Landrace	2400	Pop1-4
226807	DW155	Amhara	NORTH GONDAR	Landrace	2840	Pop1-4

## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
226834	DW160	Amhara	EAST GOJAM	Landrace	2460	Pop1-4
226844	DW164	Amhara	EAST GOJAM	Landrace	2580	Pop1-4
216648	DW177	Oromia	ARSI	Landrace	2570	Pop1-4
214537-1	DW214-1	Amhara	NORTH WELLO	Landrace	2260	Pop1-4
238122	DW246	Tigray	MEHAKELEGNAW	Landrace	1750	Pop1-4
214308	DW039	Oromia	EAST SHEWA	Landrace	2680	Pop2-4
15356	DW006	Oromia	EAST SHEWA	Landrace	2300	Pop2-4
15357	DW007	Oromia	EAST SHEWA	Landrace	2326	Pop2-4
204484	DW020	Oromia	NORTH SHEWA	Landrace	2880	Pop2-4
222735	DW050	Amhara	EAST GOJAM	Landrace	2560	Pop2-4
208180	DW188	Oromia	ARSI	Landrace	2420	Pop2-4
15358	DW008	Oromia	EAST SHEWA	Landrace	2310	Pop2-4
226351	DW143	Oromia	ARSI	Landrace	2800	Pop2-4
208746-2-2	DW185	Oromia	ARSI	Landrace	2780	Pop2-4
DZ005	DZ005	DZARC	DZARC	Advanced	NA	Pop2
Salam	Selam	DZARC	DZARC	Released	NA	Pop2
DZ008	DZ008	DZARC	DZARC	Advanced	NA	Pop2
DZ009	DZ009	DZARC	DZARC	Advanced	NA	Pop2
Top-66	Top-66	DZARC	DZARC	Released	NA	Pop2
DZ006	DZ006	DZARC	DZARC	Advanced	NA	Pop2
Metaya	Metaya	DZARC	DZARC	Released	NA	Pop2
Megnagna	Megnagna	DZARC	DZARC	Released	NA	Pop2
Werer	Werer	DZARC	DZARC	Released	NA	Pop2
DZ004	DZ004	DZARC	DZARC	Advanced	NA	Pop2
DZ010	DZ010	DZARC	DZARC	Released	NA	Pop2
Quami	Quamy	DZARC	DZARC	Released	NA	Pop2
Yerer	Yerer	DZARC	DZARC	Released	NA	Pop2
DZ003	DZ003	DZARC	DZARC	Advanced	NA	Pop2
Ude	Ude	DZARC	DZARC	Released	NA	Pop2
DZ001	DZ001	DZARC	DZARC	Advanced	NA	Pop2
Mosobo	Mosobo	DZARC	DZARC	Released	NA	Pop2
Asasa	Asasa	DZARC	DZARC	Released	NA	Pop2
DZ002	DZ002	DZARC	DZARC	Advanced	NA	Pop2
DZ007	DZ007	DZARC	DZARC	Advanced	NA	Pop2
521610	C001	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
521637	C002	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
537861	C003	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547732	C004	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547734	C005	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547919	C006	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547944	C007	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547944	C008	CIMMYT	CIMMYT	CIMMYT	NA	Pop2

## SUPPLEMENTARY FILES

Acc. No	Geno code	Seed origin	Seed collection zone	Type	Altitude meter above sea level	population
547949	C009	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547973	C010	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548022	C011	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548091	C012	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548465	C013	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548474	C014	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548636	C015	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548642	C016	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548644	C017	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
527306	C018	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
521278	C019	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
537883	C020	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
537883	C021	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
537893	C022	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
538013	C023	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
538044	C024	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
538123	C025	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
531727	C026	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
531800	C027	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
531517	C028	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547914	C029	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547919	C030	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547963	C031	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547973	C032	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547988	C033	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547989	C034	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
547989	C035	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548017	C036	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548030	C037	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548030	C038	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548097	C039	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548462	C040	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548465	C041	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548605	C042	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548605	C043	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548633	C044	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548642	C045	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548667	C046	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548690	C047	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548699	C048	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
548152	C049	CIMMYT	CIMMYT	CIMMYT	NA	Pop2
541942	C050	CIMMYT	CIMMYT	CIMMYT	NA	Pop2

## SUPPLEMENTARY FILES

Acc. No: Accession number, Geno-code: Genome code, DW: Durum wheat, C: CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo), DZARC: Debre Zeit Agricultural Research Center, DZ: Debre Zeit, SNNP: South Nation Nationalities and Peoples. Names under Acc.No are released durum varieties in Ethiopia.

**Table S2.** Passport data of the Ethiopian durum wheat landraces.

SN	Source region	Latitude	Longitude	SN	Source region	Latitude	Longitude
1	Amara	10.4167	38.2000	41	Tigray	14.5000	39.8333
2	Oromia	9.4500	39.2500	42	Oromia	8.9500	39.1500
3	Oromia	9.4000	39.2667	43	Oromia	8.9500	39.1833
4	Oromia	8.1500	39.9000	44	Oromia	9.0167	38.1333
5	Tigray	13.0667	39.5833	45	Oromia	8.9667	38.0500
6	Tigray	13.0667	39.5833	46	Oromia	8.7333	36.4833
7	Amara	11.5667	39.1500	47	Amara	10.4167	38.2000
8	Oromia	8.0667	39.7167	48	Oromia	9.2667	38.0667
9	Tigray	13.0667	39.5833	49	Amara	11.5167	39.0833
10	Amara	10.3500	38.2167	50	Tigray	13.1500	39.1333
11	Amara	10.8167	38.0833	51	Amara	10.8167	38.0833
12	Oromia	8.9667	38.9833	52	Amara	10.7333	38.0667
13	Oromia	8.9333	38.9833	53	Amara	10.4833	38.1833
14	Oromia	7.5000	40.0833	54	Amara	11.5333	39.0833
15	Amara	14.0333	37.1500	55	Oromia	9.9500	38.3000
16	Oromia	9.4500	39.2500	56	Oromia	9.2833	41.7667
17	Oromia	9.0500	37.9333	57	Amara	9.5000	39.3333
18	Oromia	8.9333	38.9833	58	Oromia	8.9333	38.9833
19	Oromia	8.8333	39.0167	59	Amara	11.2000	39.6000
20	Oromia	7.2667	39.8833	60	Oromia	9.3667	41.4667
21	Oromia	9.3667	38.0500	61	Oromia	9.4000	39.2667
22	Oromia	8.7833	39.2500	62	Oromia	9.1833	39.0667
23	Oromia	8.5667	39.8667	63	Amara	11.7333	38.4167
24	Oromia	7.5000	40.0833	64	Oromia	8.8667	38.8500
25	Oromia	9.3000	41.2333	65	Oromia	9.4500	39.2500
26	SNNP	5.3000	37.3000	66	Amara	11.5667	39.1500
27	Oromia	8.8333	39.0167	67	Amara	10.8500	39.0000
28	Oromia	9.0500	39.0667	68	Tigray	14.0333	38.0667
29	Oromia	7.5167	40.0500	69	Oromia	9.4500	39.2500
30	Oromia	7.5167	40.0500	70	Amara	10.6500	38.1667
31	Oromia	9.3667	38.0500	71	Oromia	7.7500	39.6667
32	Amara	10.2667	39.7167	72	Oromia	9.4500	39.2500
33	Oromia	8.1500	39.3500	73	Oromia	7.6000	39.4667
34	Oromia	9.4000	39.2667	74	Oromia	9.3000	41.7500
35	Oromia	7.2667	39.8833	75	Amara	9.6500	39.3333

## SUPPLEMENTARY FILES

SN	Source region	Latitude	Longitude	SN	Source region	Latitude	Longitude
36	Tigray	17.6833	39.4667	76	Oromia	7.9167	39.6000
37	Oromia	7.8333	39.5833	77	Oromia	7.6667	39.9333
38	Amara	10.2667	39.7167	78	Amara	11.6000	38.5667
39	Oromia	7.6667	40.2000	79	Amara	10.4167	38.2000
40	Tigray	14.0667	38.0667	80	Amara	11.5667	39.1500
81	Amara	10.8000	38.0500	124	Amara	12.7500	37.5333
82	Oromia	7.6667	40.2000	125	Amara	10.4500	38.3167
83	Tigray	13.1500	39.1333	126	Oromia	7.6000	39.4667
84	Amara	11.5333	39.0833	127	Amara	10.9833	36.9167
85	Amara	10.8500	39.0000	128	Amara	11.7167	38.4500
86	Oromia	7.9000	39.7833	129	Amara	9.8500	39.7500
87	Oromia	7.7000	39.7333	130	Oromia	7.1667	39.2333
88	Amara	9.9667	39.6167	131	Oromia	7.8333	39.5667
89	Oromia	7.8333	39.5667	132	Tigray	14.0333	38.0667
90	Amara	10.9667	36.9167	133	Oromia	8.2500	39.2167
91	Amara	11.5833	39.0667	134	SNNP	7.2833	37.8833
92	Amara	10.8500	39.0000	135	Oromia	9.2667	38.6667
93	Tigray	13.8667	39.7167	136	Amara	10.5667	38.2333
94	Amara	9.6500	36.4333	137	Amara	11.9833	37.6167
95	Oromia	9.3667	38.0500	138	Amara	9.6333	39.5833
96	Oromia	7.8333	39.5833	139	Amara	11.5667	39.1500
97	Amara	10.3333	38.1333	140	Oromia	8.3667	39.9500
98	Amara	10.3000	39.5833	141	Amara	12.5500	37.4000
99	Oromia	7.5000	40.0833	142	Oromia	9.2167	41.1167
100	Oromia	9.3667	38.0500	143	Oromia	9.0167	38.9333
101	Oromia	8.9667	38.0000	144	Amara	10.4500	38.3167
102	Oromia	7.6333	39.5000	145	Oromia	8.3167	39.9167
103	Oromia	8.9667	39.1167	146	Oromia	8.5833	39.9333
104	Oromia	9.3167	39.2833	147	Amara	10.3333	39.6333
105	Oromia	7.5333	39.9833	148	Amara	9.8167	39.7000
106	Amara	12.5500	37.4000	149	Oromia	9.0167	38.3333
107	Amara	12.6333	37.4667	150	Oromia	9.3667	38.0500
108	Oromia	8.9167	39.1667	151	SNNP	9.5667	39.4833
109	Oromia	9.3167	39.2833	152	Oromia	8.9000	37.9333
110	Oromia	8.8667	38.9000	153	Amara	11.6500	38.4500
111	Oromia	9.6000	38.8167	154	Oromia	7.8833	39.7333
112	Amara	10.8000	38.0500	155	Amara	11.6333	38.4667
113	Benishangul Gumuz	10.9333	35.3333	156	Amara	12.7500	37.5333
114	Oromia	7.7000	39.7333	157	Oromia	8.0667	39.6167
115	Oromia	6.9667	40.5333	158	Amara	10.5000	38.4000

## SUPPLEMENTARY FILES

SN	Source region	Latitude	Longitude	SN	Source region	Latitude	Longitude
116	Oromia	6.9833	40.0167	159	Amara	11.6000	38.5500
117	SNNP	7.2833	37.8667	160	Amara	9.9667	39.6167
118	Amara	12.6333	37.4667	161	Amara	11.6500	38.4500
119	Amara	10.4167	39.2167	162	Oromia	8.3833	39.9333
120	Amara	10.7833	38.6667	163	Oromia	7.2000	39.9333
121	Amara	11.6500	38.4500	164	Oromia	9.4667	41.8000
122	Oromia	9.4500	39.2500	165	Oromia	7.8333	39.5833
123	SNNP	6.5167	37.7500	166	Oromia	8.5000	39.7833

**Table S3.** Highly informative selected 420 SNP markers for genetic diversity analysis and stratification.

SNP	Chr	Alleles	Str.pos. in bp	PIC
BobWhite_c1027_1127	1A	A/G	578720187	0.37
BobWhite_c11946_277	1A	T/G	508253611	0.37
BobWhite_c12568_900	1A	C/T	483577474	0.37
BobWhite_c1265_247	1A	C/T	11906386	0.37
BobWhite_c22134_398	1A	G/A	535547470	0.37
BobWhite_c23632_322	1A	T/C	531035019	0.37
BobWhite_c46007_582	1A	G/A	504760784	0.37
BobWhite_c46501_92	1A	C/T	17213410	0.37
BobWhite_c5356_1272	1A	G/A	477616168	0.37
BobWhite_c721_74	1A	G/A	531435634	0.37
BS00002216_51	1A	C/T	474655218	0.37
BS00011521_51	1A	A/G	572302344	0.37
BS00012210_51	1A	T/G	39715924	0.37
BS00021889_51	1A	T/C	474024718	0.37
BS00022239_51	1A	T/C	526410713	0.37
RAC875_rep_c112044_340	1A	T/C	491265980	0.35
RAC875_rep_c71093_1070	1A	A/G	541014873	0.35
TA003955-1138	1A	G/A	492068742	0.35
Tdurum_contig47006_1641	1A	C/A	585260046	0.35
Tdurum_contig56158_60	1A	T/C	532933342	0.35
Tdurum_contig60323_605	1A	G/A	1161699	0.35
tplb0021i12_383	1A	A/G	541027860	0.35
tplb0025b13_150	1A	A/G	4123810	0.35
wsnp_Ex_c1255_2411550	1A	G/T	581428153	0.35
wsnp_Ex_c13724_21535046	1A	A/C	173777869	0.35
wsnp_Ex_c572_1138770	1A	C/T	454314732	0.35
wsnp_Ex_rep_c102067_87314043	1A	A/C	532795199	0.35
wsnp_JD_rep_c49006_33254974	1A	T/C	541014833	0.35
wsnp_Ku_c1818_3557408	1A	T/C	4122180	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
wsnp_Ra_c2895_5488879	1A	C/T	454313706	0.35
BobWhite_c44460_821	1B	C/T	649750680	0.38
IAAV2324	1B	A/G	92357396	0.38
BobWhite_c16280_521	1B	G/A	529566738	0.37
BobWhite_c17257_454	1B	A/G	485193291	0.37
BobWhite_c17644_112	1B	C/T	583138970	0.37
BobWhite_c19733_149	1B	C/T	636309715	0.37
BobWhite_c20015_225	1B	G/A	505495844	0.37
BobWhite_c20015_300	1B	A/G	505495919	0.37
BobWhite_c20621_683	1B	A/G	625532899	0.37
BobWhite_c3771_441	1B	G/A	187239287	0.37
BobWhite_c39656_106	1B	C/A	584136290	0.37
BobWhite_c39901_338	1B	T/C	649749173	0.37
BobWhite_c6803_387	1B	C/T	505497887	0.37
BobWhite_c8218_162	1B	C/T	187239270	0.37
BobWhite_rep_c62985_546	1B	A/G	159630261	0.37
Tdurum_contig43346_108	1B	C/T	302037983	0.35
Tdurum_contig48396_341	1B	T/C	303478652	0.35
Tdurum_contig50473_889	1B	G/A	513848364	0.35
Tdurum_contig52086_524	1B	A/G	668928613	0.35
Tdurum_contig9874_547	1B	T/C	29332080	0.35
tplb0024i16_1177	1B	C/T	299978233	0.35
tplb0043k02_463	1B	T/C	626565205	0.35
tplb0049h18_765	1B	G/A	668932387	0.35
wsnp_BE494527B_Ta_2_1	1B	A/G	617298701	0.35
wsnp_BE495786B_Ta_2_2	1B	C/T	503651635	0.35
wsnp_CAP11_c543_375403	1B	A/G	534692879	0.35
wsnp_CAP8_rep_c4452_2170021	1B	T/C	534692880	0.35
wsnp_Ex_c1058_2020681	1B	A/G	668991372	0.35
wsnp_Ku_c18881_28259811	1B	G/T	637360298	0.35
wsnp_Ku_c2797_5284087	1B	C/T	668990224	0.35
BS00023214_51	2A	C/T	689739909	0.38
BS00000479_51	2A	A/G	759510498	0.37
BS00007689_51	2A	T/C	762397596	0.37
BS00022393_51	2A	T/C	6557997	0.37
BS00029224_51	2A	T/C	556826479	0.37
BS00064905_51	2A	C/T	43876302	0.37
BS00067159_51	2A	C/T	22153129	0.37
BS00070797_51	2A	C/T	32051040	0.37
BS00073382_51	2A	A/G	32050887	0.37

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
BS00077597_51	2A	G/A	693878966	0.37
BS00080752_51	2A	G/A	715768389	0.37
BS00081507_51	2A	G/A	716162075	0.37
BS00090128_51	2A	G/A	555657628	0.37
BS00108775_51	2A	G/A	716154304	0.37
BS00111069_51	2A	G/A	21254785	0.37
IACX794	2A	C/A	617294164	0.35
Kukri_c17269_1349	2A	G/A	41827536	0.35
Kukri_c42972_148	2A	T/C	743504679	0.35
TA004785-1734	2A	C/T	745751728	0.35
Tdurum_contig10785_2433	2A	T/C	12102513	0.35
Tdurum_contig12952_114	2A	T/C	41504404	0.35
Tdurum_contig12952_263	2A	G/A	41504255	0.35
Tdurum_contig26621_200	2A	T/C	36293622	0.35
Tdurum_contig26621_264	2A	T/C	36293686	0.35
Tdurum_contig55610_742	2A	C/T	41832438	0.35
Tdurum_contig55610_784	2A	G/T	41832480	0.35
Tdurum_contig70306_425	2A	A/C	73236640	0.35
Tdurum_contig9731_62	2A	C/T	73284543	0.35
wsnp_Ex_c19556_28530231	2A	C/T	35711654	0.35
wsnp_Ex_rep_c67542_66164609	2A	T/G	29525472	0.35
RAC875_c14316_584	2B	A/G	601518044	0.38
Tdurum_contig31911_195	2B	T/G	634933373	0.38
BobWhite_c12144_216	2B	T/C	970296	0.37
BobWhite_c2521_117	2B	C/T	686204384	0.37
BobWhite_c47357_535	2B	G/A	686063287	0.37
BobWhite_c4831_490	2B	G/A	686207867	0.37
BobWhite_c54696_56	2B	C/T	523276250	0.37
BobWhite_c54909_261	2B	G/A	523276609	0.37
BobWhite_c7326_70	2B	G/A	448264837	0.37
BobWhite_c9351_274	2B	G/A	514694140	0.37
BobWhite_c9690_94	2B	C/T	730212313	0.37
BobWhite_rep_c50285_700	2B	A/C	749155662	0.37
BS00004224_51	2B	T/C	717551361	0.37
BS00022374_51	2B	C/T	731174771	0.37
BS00022486_51	2B	T/G	120783180	0.37
Tdurum_contig1653_190	2B	T/C	100535943	0.35
Tdurum_contig68806_537	2B	G/A	104658949	0.35
Tdurum_contig81323_291	2B	G/A	104336022	0.35
Tdurum_contig81917_141	2B	A/G	105710592	0.35



## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
wsnp_BG608232B_Ta_2_1	2B	A/G	445599810	0.35
wsnp_BG608232B_Ta_2_2	2B	A/G	445599715	0.35
wsnp_BQ172173B_Ta_2_2	2B	C/T	712473571	0.35
wsnp_CAP11_c5255_2442548	2B	G/A	445442060	0.35
wsnp_Ex_c114_229879	2B	A/G	570335910	0.35
wsnp_Ex_c21092_30220702	2B	T/C	60521695	0.35
wsnp_Ex_c2445_4573233	2B	A/C	635828443	0.35
wsnp_Ex_c4218_7618252	2B	G/A	370091207	0.35
wsnp_Ex_c45468_51254978	2B	A/G	719777934	0.35
wsnp_Ex_c55735_58127324	2B	A/C	594972739	0.35
wsnp_JD_c4699_5834958	2B	G/A	174656631	0.35
Excalibur_c12875_1573	3A	C/T	2913871	0.38
BobWhite_c17852_511	3A	T/C	50530572	0.37
BobWhite_c17879_519	3A	C/T	650235115	0.37
BobWhite_c20157_293	3A	A/G	730207415	0.37
BobWhite_c2453_460	3A	T/C	3698080	0.37
BobWhite_c36118_246	3A	C/T	3453657	0.37
BobWhite_c4057_365	3A	G/A	727965	0.37
BobWhite_c5461_338	3A	A/G	1572560	0.37
BobWhite_c9704_273	3A	G/A	50736062	0.37
BobWhite_c9992_811	3A	G/A	3621326	0.37
BobWhite_c9992_862	3A	C/T	3621275	0.37
BobWhite_rep_c51301_1261	3A	A/G	478259292	0.37
BS00007502_51	3A	G/A	51971974	0.37
BS00022586_51	3A	G/A	38206785	0.37
BS00022746_51	3A	C/A	21260083	0.37
Kukri_s117068_130	3A	C/T	344482	0.35
Ra_c7114_619	3A	T/G	723859434	0.35
RAC875_c61934_186	3A	A/G	729517491	0.35
Tdurum_contig12008_1001	3A	C/T	4433644	0.35
Tdurum_contig12557_1382	3A	A/G	606316327	0.35
Tdurum_contig47186_1897	3A	A/G	630286778	0.35
Tdurum_contig48522_635	3A	A/G	638061474	0.35
Tdurum_contig56748_632	3A	C/T	460603081	0.35
tplb0053a24_2232	3A	A/G	4431667	0.35
wsnp_CAP11_rep_c8581_3702222	3A	G/A	725686368	0.35
wsnp_Ex_c2573_4788116	3A	G/A	2173807	0.35
wsnp_Ex_c55096_57733841	3A	G/A	730053460	0.35
wsnp_Ex_rep_c104141_88935451	3A	C/A	729514798	0.35
wsnp_JD_c9434_10274598	3A	C/A	460959678	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
wsnp_Ku_c10468_17301216	3A	G/T	691460574	0.35
BobWhite_c23887_134	3B	G/A	37185596	0.37
BobWhite_c23887_53	3B	C/A	37185900	0.37
BobWhite_c24194_255	3B	C/T	45342772	0.37
BobWhite_c2937_1426	3B	T/C	736293620	0.37
BobWhite_c4514_298	3B	G/A	45337767	0.37
BobWhite_c5611_281	3B	C/T	2768888	0.37
BobWhite_rep_c64247_261	3B	A/C	44966830	0.37
BS00015891_51	3B	G/A	797224445	0.37
BS00025792_51	3B	C/T	35307657	0.37
BS00042029_51	3B	C/T	597391516	0.37
BS00043730_51	3B	C/T	485967931	0.37
BS00044942_51	3B	A/G	818527985	0.37
BS00044944_51	3B	C/T	818528036	0.37
BS00044955_51	3B	A/C	818531586	0.37
BS00045330_51	3B	T/G	478917217	0.37
Kukri_c50837_251	3B	A/G	818379203	0.35
Kukri_c66923_217	3B	G/A	75221912	0.35
Kukri_rep_c93484_422	3B	T/G	754481350	0.35
RAC875_c35310_770	3B	T/C	75220130	0.35
RAC875_rep_c109105_57	3B	G/A	572415185	0.35
RAC875_rep_c72275_185	3B	C/T	812865028	0.35
Tdurum_contig49804_392	3B	T/C	3415514	0.35
Tdurum_contig51355_601	3B	T/G	821929833	0.35
Tdurum_contig67690_183	3B	G/A	58780133	0.35
wsnp_CAP7_c5097_2266314	3B	C/T	778469145	0.35
wsnp_Ex_c29631_38640100	3B	A/C	559307368	0.35
wsnp_Ex_c7756_13218814	3B	A/G	575656184	0.35
wsnp_Ex_c8695_14561512	3B	T/G	74708095	0.35
wsnp_JD_rep_c50820_34666611	3B	A/G	812865953	0.35
wsnp_Ra_rep_c72670_70836439	3B	C/T	812865930	0.35
BobWhite_c12128_187	4A	G/A	604365729	0.37
BobWhite_c28137_293	4A	C/T	714174165	0.37
BobWhite_c31621_148	4A	G/A	81389367	0.37
BobWhite_c3351_329	4A	T/C	727217219	0.37
BobWhite_c33898_150	4A	T/C	624347345	0.37
BobWhite_c39599_82	4A	G/A	112184714	0.37
BobWhite_c4089_73	4A	A/G	577090263	0.37
BobWhite_c5633_59	4A	A/G	37674472	0.37
BobWhite_rep_c66057_98	4A	A/C	37674735	0.37

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
BS00010202_51	4A	G/A	720860017	0.37
BS00010339_51	4A	G/T	576555858	0.37
BS00011224_51	4A	A/G	585378511	0.37
BS00021716_51	4A	C/T	700600	0.37
BS00021752_51	4A	C/A	24056269	0.37
BS00032622_51	4A	G/T	697005718	0.37
Tdurum_contig46583_2203	4A	A/G	730463264	0.35
Tdurum_contig8061_56	4A	T/C	24061051	0.35
Tdurum_contig93100_149	4A	T/G	703802646	0.35
Tdurum_contig93100_640	4A	G/A	703802155	0.35
Tdurum_contig93100_712	4A	A/C	703802083	0.35
Tdurum_contig93100_77	4A	T/C	703802718	0.35
Tdurum_contig9906_89	4A	A/G	44605698	0.35
tplb0062c24_1758	4A	G/A	646468406	0.35
wsnp_CAP7_c32_19340	4A	A/G	100363448	0.35
wsnp_Ex_c2352_4405961	4A	G/A	635388157	0.35
wsnp_Ex_c33778_42210283	4A	T/C	720085690	0.35
wsnp_Ex_c3988_7221220	4A	T/C	655228466	0.35
wsnp_Ex_c64593_63334637	4A	C/T	576144191	0.35
wsnp_Ex_rep_c67779_66463916	4A	A/G	516982227	0.35
wsnp_Ra_c33762_42584098	4A	G/A	516670368	0.35
BobWhite_c22580_115	4B	T/C	607755186	0.37
BobWhite_c30050_125	4B	T/C	17280529	0.37
BobWhite_rep_c49034_589	4B	A/G	36327129	0.37
BS00009439_51	4B	C/T	65410547	0.37
BS00018707_51	4B	C/T	93599096	0.37
BS00030571_51	4B	G/A	606290375	0.37
BS00033614_51	4B	G/A	37707432	0.37
BS00060041_51	4B	C/T	6122844	0.37
BS00063035_51	4B	G/A	41570672	0.37
BS00064041_51	4B	G/A	606999906	0.37
BS00066024_51	4B	A/G	561871714	0.37
BS00095286_51	4B	A/G	35049334	0.37
BS00095416_51	4B	C/T	38637958	0.37
BS00105791_51	4B	T/C	104510182	0.37
Excalibur_c32467_676	4B	C/T	538382521	0.37
Tdurum_contig66820_466	4B	G/A	98482981	0.35
Tdurum_contig82364_132	4B	G/A	36154504	0.35
Tdurum_contig83679_281	4B	G/A	81671370	0.35
Tdurum_contig92931_787	4B	T/C	37187854	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
Tdurum_contig92931_882	4B	T/C	37187186	0.35
Tdurum_contig93168_52	4B	G/A	95133294	0.35
Tdurum_contig98399_114	4B	T/C	86419163	0.35
wsnp_CAP12_c1101_569783	4B	T/C	613234341	0.35
wsnp_Ex_c22648_31848819	4B	T/C	562464583	0.35
wsnp_Ex_c26285_35531324	4B	A/G	642343933	0.35
wsnp_Ex_c26285_35531618	4B	A/G	642344227	0.35
wsnp_Ex_c26285_35532440	4B	T/C	642346860	0.35
wsnp_Ex_c4148_7494801	4B	C/T	661642454	0.35
wsnp_Ku_c10515_17368422	4B	G/A	657297532	0.35
wsnp_Ku_rep_c104382_90867406	4B	G/A	536092361	0.35
CAP8_c2014_192	5A	A/G	435710212	0.38
tplb0057m23_1318	5A	C/T	437909883	0.38
BobWhite_c13900_53	5A	G/T	437909628	0.37
BobWhite_c38929_56	5A	T/C	427405578	0.37
BobWhite_c41847_333	5A	C/T	437027138	0.37
BobWhite_c5457_1440	5A	T/C	468101559	0.37
BobWhite_rep_c48815_538	5A	A/G	436213158	0.37
BobWhite_rep_c64197_143	5A	G/A	437634436	0.37
BobWhite_rep_c64318_615	5A	G/A	468003948	0.37
BobWhite_rep_c64579_593	5A	G/A	437088469	0.37
BS00010698_51	5A	G/A	499809769	0.37
BS00022500_51	5A	G/A	399255732	0.37
BS00022815_51	5A	A/G	437784182	0.37
BS00035256_51	5A	C/T	527515679	0.37
BS00065386_51	5A	A/G	436143495	0.37
wsnp_Ex_c31017_39858962	5A	A/G	445189347	0.35
wsnp_Ex_c3838_6980909	5A	C/T	443254522	0.35
wsnp_Ex_c6117_10704945	5A	A/G	107465483	0.35
wsnp_Ex_rep_c101994_87256479	5A	C/T	554958716	0.35
wsnp_JD_c8448_9444839	5A	C/T	94495449	0.35
wsnp_Ku_c16812_25759885	5A	G/A	101007703	0.35
wsnp_Ku_c328_679106	5A	T/C	105920335	0.35
wsnp_Ku_c5445_9668131	5A	A/G	633372138	0.35
wsnp_Ra_c10053_16636851	5A	T/C	101006699	0.35
wsnp_Ra_c14112_22155312	5A	G/A	110803770	0.35
wsnp_Ra_c14112_22155451	5A	C/A	110803875	0.35
wsnp_Ra_c18459_27525981	5A	T/C	110803987	0.35
wsnp_Ra_c21347_30731133	5A	C/T	442780286	0.35
wsnp_Ra_c6788_11804894	5A	G/A	96071832	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
wsnp_Ra_rep_c69221_66574148	5A	A/C	43344228	0.35
Tdurum_contig94033_487	5B	C/T	619617213	0.38
wsnp_Ex_c43518_49814933	5B	A/G	106176590	0.38
BobWhite_c11038_605	5B	C/T	646590215	0.37
BobWhite_c15241_604	5B	G/A	673097295	0.37
BobWhite_c17133_107	5B	C/T	63501707	0.37
BobWhite_c31_3667	5B	G/A	696841474	0.37
BobWhite_c34676_81	5B	G/A	666780370	0.37
BobWhite_c43731_313	5B	A/G	673538661	0.37
BobWhite_c47620_226	5B	G/A	472969291	0.37
BobWhite_c6017_1096	5B	A/G	619642998	0.37
BobWhite_c6017_1147	5B	A/G	619642947	0.37
BobWhite_c7818_278	5B	T/C	683776109	0.37
BS00021868_51	5B	A/G	648246336	0.37
BS00022231_51	5B	A/G	645528123	0.37
BS00022662_51	5B	G/A	356154768	0.37
Tdurum_contig48658_802	5B	T/C	413838175	0.35
Tdurum_contig63161_121	5B	A/G	475596886	0.35
Tdurum_contig77918_477	5B	A/G	660537862	0.35
Tdurum_contig97407_196	5B	C/T	641527170	0.35
wsnp_BE517711B_Ta_2_1	5B	C/T	487492354	0.35
wsnp_BE517711B_Ta_2_2	5B	A/C	487492642	0.35
wsnp_Ex_c10842_17637744	5B	T/C	60993432	0.35
wsnp_Ex_c12119_19382820	5B	A/G	409176715	0.35
wsnp_Ex_c19724_28720939	5B	A/G	480058158	0.35
wsnp_Ex_c46217_51790399	5B	C/T	486724593	0.35
wsnp_Ex_c8962_14947544	5B	A/G	31759036	0.35
wsnp_Ex_rep_c102070_87317290	5B	C/T	478323641	0.35
wsnp_Ex_rep_c68023_66768770	5B	A/G	456422703	0.35
wsnp_JD_c11594_12033647	5B	A/G	379318093	0.35
wsnp_JD_c4372_5494161	5B	A/G	641527297	0.35
BobWhite_c10740_179	6A	C/T	31622279	0.37
BobWhite_c13839_111	6A	A/C	20124417	0.37
BobWhite_c13839_135	6A	A/G	20124393	0.37
BobWhite_c2568_115	6A	G/A	529670734	0.37
BobWhite_c5092_422	6A	A/G	11214049	0.37
BobWhite_c62620_150	6A	A/G	37190258	0.37
BobWhite_rep_c52979_181	6A	C/T	2773209	0.37
BobWhite_rep_c63152_444	6A	T/C	549384075	0.37
BS00009331_51	6A	T/G	19062489	0.37

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
BS00011436_51	6A	T/C	19063038	0.37
BS00022951_51	6A	G/A	16753143	0.37
BS00023140_51	6A	C/T	31762856	0.37
BS00023192_51	6A	C/A	11959829	0.37
BS00036635_51	6A	G/T	10268926	0.37
BS00063096_51	6A	A/G	546014258	0.37
wsnp_Ex_c16491_24996576	6A	G/A	16754294	0.35
wsnp_Ex_c2192_4108709	6A	T/C	445183707	0.35
wsnp_Ex_c36801_44683992	6A	G/A	563920498	0.35
wsnp_Ex_c7002_12063325	6A	C/T	597277839	0.35
wsnp_Ex_c7002_12063380	6A	G/A	597277894	0.35
wsnp_Ex_rep_c70951_69806211	6A	C/T	563918329	0.35
wsnp_JD_c19278_17450072	6A	G/A	445318216	0.35
wsnp_JD_c19278_17450210	6A	T/G	445318078	0.35
wsnp_JD_c22766_19622512	6A	A/G	558221423	0.35
wsnp_Ku_c1075_2160065	6A	T/G	561478432	0.35
wsnp_Ku_c14219_22455933	6A	C/A	563915637	0.35
wsnp_Ku_c44079_51438574	6A	C/T	560271021	0.35
wsnp_Ra_c11651_18855691	6A	T/C	598708421	0.35
wsnp_Ra_c12086_19452422	6A	T/C	559099941	0.35
wsnp_RFL_Contig2523_2130662	6A	G/A	445318266	0.35
BobWhite_c1633_643	6B	C/T	645616232	0.37
BobWhite_c1905_98	6B	G/A	140189688	0.37
BobWhite_c22767_189	6B	T/C	163124390	0.37
BobWhite_c26504_163	6B	C/A	149534201	0.37
BobWhite_c27364_124	6B	C/A	689149063	0.37
BobWhite_c27364_296	6B	G/A	689149235	0.37
BobWhite_c41574_185	6B	C/A	43829234	0.37
BobWhite_c47659_100	6B	G/T	158232853	0.37
BobWhite_c6546_423	6B	G/T	682454889	0.37
BobWhite_c9563_377	6B	G/A	227566262	0.37
BobWhite_s63779_147	6B	A/G	151143114	0.37
BS00003214_51	6B	C/T	139472770	0.37
BS00010676_51	6B	C/T	430198438	0.37
BS00011795_51	6B	T/G	692561322	0.37
BS00022832_51	6B	T/G	657185956	0.37
IAAV8886	6B	T/C	115775616	0.35
Kukri_c21409_283	6B	G/A	436692510	0.35
Kukri_c22391_192	6B	A/C	682329684	0.35
RAC875_c19250_188	6B	A/G	17167162	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
RAC875_c47035_70	6B	G/A	442960966	0.35
RAC875_rep_c112646_106	6B	C/A	682339579	0.35
Tdurum_contig10729_986	6B	G/A	690593422	0.35
Tdurum_contig10729_989	6B	C/T	690593419	0.35
Tdurum_contig42655_1256	6B	A/G	10814769	0.35
Tdurum_contig44173_792	6B	A/G	552725128	0.35
wsnp_CAP12_c475_258416	6B	T/C	638627998	0.35
wsnp_Ex_c4728_8444212	6B	C/T	18303554	0.35
wsnp_Ra_c22075_31509915	6B	A/G	115751757	0.35
wsnp_Ra_c57648_59682822	6B	A/G	174846977	0.35
wsnp_Ra_rep_c108218_91556581	6B	G/A	119626602	0.35
RAC875_c101928_381	7A	A/C	97775951	0.38
BobWhite_c1635_691	7A	G/A	715980616	0.37
BobWhite_c34887_239	7A	C/T	99397775	0.37
BobWhite_c40583_146	7A	G/A	121281425	0.37
BobWhite_c47709_141	7A	T/C	65599406	0.37
BS00003455_51	7A	A/C	715979988	0.37
BS00010796_51	7A	C/T	17293924	0.37
BS00021692_51	7A	G/T	63099065	0.37
BS00022145_51	7A	G/T	80604261	0.37
BS00022442_51	7A	A/G	27549945	0.37
BS00023027_51	7A	T/C	671339044	0.37
BS00023225_51	7A	C/A	73206737	0.37
BS00026056_51	7A	A/C	535969373	0.37
BS00040600_51	7A	T/G	99370164	0.37
BS00040601_51	7A	C/A	99370171	0.37
wsnp_BF482529A_Ta_2_5	7A	C/T	511715573	0.35
wsnp_Ex_c4996_8885500	7A	C/T	535281348	0.35
wsnp_Ex_c558_1105911	7A	A/G	509600605	0.35
wsnp_Ex_c9971_16412270	7A	T/C	693393261	0.35
wsnp_Ex_c9971_16412758	7A	G/A	693392773	0.35
wsnp_JD_c1219_1766041	7A	C/T	724280142	0.35
wsnp_JD_c15333_14824351	7A	T/C	508401166	0.35
wsnp_JD_c8919_9843202	7A	T/C	508866196	0.35
wsnp_Ku_c26118_36079171	7A	C/T	693396172	0.35
wsnp_Ku_c28104_38042857	7A	T/C	715981220	0.35
wsnp_Ku_c2958_5561339	7A	T/C	535193439	0.35
wsnp_Ku_c6065_10682531	7A	C/T	107276540	0.35
wsnp_Ku_rep_c103889_90513365	7A	T/C	673054032	0.35
wsnp_Ku_rep_c110993_94857161	7A	G/A	537457522	0.35

## SUPPLEMENTARY FILES

SNP	Chr	Alleles	Str.pos. in bp	PIC
w SNP_Ra_c1303_2598907	7A	G/A	535281206	0.35
Tdurum_contig48824_476	7B	A/G	48060131	0.38
BobWhite_c10448_80	7B	A/C	67157055	0.37
BobWhite_c15796_315	7B	T/C	205081531	0.37
BobWhite_c16787_205	7B	C/T	207911881	0.37
BobWhite_c36693_210	7B	T/C	33661749	0.37
BobWhite_c39364_231	7B	A/G	55073589	0.37
BobWhite_c4253_568	7B	G/A	13162796	0.37
BobWhite_c7907_657	7B	A/C	190466059	0.37
BobWhite_rep_c48793_750	7B	C/T	155739487	0.37
BobWhite_rep_c63008_468	7B	C/A	490592914	0.37
BobWhite_rep_c66957_84	7B	T/C	181389780	0.37
BS00022106_51	7B	A/G	612153072	0.37
BS00022175_51	7B	G/A	717658031	0.37
BS00031141_51	7B	G/T	207908556	0.37
BS00031611_51	7B	T/C	172250085	0.37
RAC875_c96195_73	7B	T/C	374053419	0.35
RAC875_rep_c78007_394	7B	T/C	682153189	0.35
Tdurum_contig20921_424	7B	T/C	566226246	0.35
Tdurum_contig4658_346	7B	C/T	663797774	0.35
Tdurum_contig48934_425	7B	A/G	700013080	0.35
Tdurum_contig53901_177	7B	G/A	500327966	0.35
Tdurum_contig59440_1621	7B	G/A	497591028	0.35
Tdurum_contig63792_639	7B	C/T	496617953	0.35
Tdurum_contig66398_976	7B	T/C	23862240	0.35
w SNP_be591305B_Ta_1_1	7B	C/T	255141044	0.35
w SNP_BQ169669B_Ta_2_2	7B	C/T	247272507	0.35
w SNP_Ex_c11106_18003332	7B	T/C	41729218	0.35
w SNP_Ex_c14979_23133600	7B	G/A	547067781	0.35
w SNP_Ex_c9813_16193536	7B	C/T	41719425	0.35
w SNP_RFL_Contig4753_5709032	7B	G/A	547066917	0.35



## SUPPLEMENTARY FILES

**Publication 2.2)** Negisho, K., Shibru, S., Matros, A., Pillen, K., Ordon, F., & Wehner, G. (2022a). Genomic dissection reveals QTLs for grain biomass and correlated traits under drought stress in Ethiopian durum wheat (*Triticum turgidum* ssp. *durum*). *Plant Breeding*, 141(3), 338–354. <https://doi.org/10.1111/pbr.13010>.

**Table S1.** List of accessions included in the study panel (SP). Accession number, accession code, taxon, seed origin, seed collection zone, latitude, longitude and altitude of the durum wheat study panel for GWAS. All accessions were assessed for drought stress tolerance under field conditions in Ethiopia. Accession from serial numbers 1-185 were additionally tested in climate chamber experiments at 20% soil water capacity (SWC) = climate chamber drought stress (CCDS) and at 70% SWC = climate chamber non-stress (CCNS). NA = not available

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
222362	DW076	<i>T.durum</i>	Amhara	EAST GOJAM	2510	10-25-00-N	38-12-00-E
204488-1	DW022-1	<i>T.durum</i>	Oromia	NORTH SHEWA	2850	09-27-00-N	39-15-00-E
Salam	Selam	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
226876	DW166	<i>T.durum</i>	Oromia	WEST SHEWA	2880	09-24-00-N	39-16-00-E
DZARC	DZ008	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
DZARC	DZ009	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
222382	DW081	<i>T.durum</i>	Oromia	ARSI	2930	08-09-00-N	39-54-00-E
238123	DW247	<i>T.durum</i>	Tigray	MEHAKELEGNAW	2000	13-04-00-N	39-35-00-E
Top-66	Top-66	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
DZARC	DZ006	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
238120	DW244	<i>T.durum</i>	Tigray	MEHAKELEGNAW	2030	13-04-00-N	39-35-00-E
231584	DW208	<i>T.durum</i>	Amhara	NORTH WELLO	2920	11-34-00-N	39-09-00-E
Metaya	Metaya	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
222404	DW084	<i>T.durum</i>	Oromia	ARSI	2650	08-04-00-N	39-43-00-E
238121	DW245	<i>T.durum</i>	Tigray	MEHAKELEGNAW	1850	13-04-00-N	39-35-00-E
Megnagna	Megnagna	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
Werer	Werer	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
226834-1	DW160-1	<i>T.durum</i>	Amhara	EAST GOJAM	2460	10-21-00-N	38-13-00-E
DZARC	DZ004	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
DZARC	DZ005	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
8333-1	DW003-1	<i>T.durum</i>	Amhara	EAST GOJAM	2580	10-49-00-N	38-05-00-E
204555	DW028	<i>T.durum</i>	Oromia	NORTH SHEWA	2500	08-58-00-N	38-59-00-E
204560-2	DW029-2	<i>T.durum</i>	Oromia	NORTH SHEWA	2501	08-56-00-N	38-59-00-E
208261	DW094	<i>T.durum</i>	Oromia	ARSI	2420	07-30-00-N	40-05-00-E
238139	DW260	<i>T.durum</i>	Amhara	EAST GOJAM	2440	14-02-00-N	37-09-00-E
DZARC	DZ010	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
Quami	Quamy	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
204493-1	DW023-1	<i>T.durum</i>	Oromia	NORTH SHEWA	2850	09-27-00-N	39-15-00-E
208931	DW035	<i>T.durum</i>	Oromia	WEST SHEWA	2400	09-03-00-N	37-56-00-E
Yerer	Yerer	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
DZARC	DZ003	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
204560-1	DW029-1	<i>T.durum</i>	Oromia	NORTH SHEWA	2500	08-56-00-N	38-59-00-E
214308	DW039	<i>T.durum</i>	Oromia	EAST SHEWA	2680	08-50-00-N	39-01-00-E
222299	DW069	<i>T.durum</i>	Oromia	BALE	2545	07-16-00-N	39-53-00-E
Ude	Ude	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
204544	DW027	<i>T.durum</i>	Oromia	NORTH SHEWA	2600	09-22-00-N	38-03-00-E
222191	DW065	<i>T.durum</i>	Oromia	EAST SHEWA	2300	08-47-00-N	39-15-00-E
222372	DW080	<i>T.durum</i>	Oromia	ARSI	2040	08-34-00-N	39-52-00-E
222433	DW093	<i>T.durum</i>	Oromia	ARSI	2420	07-30-00-N	40-05-00-E
222708	DW125	<i>T.durum</i>	Oromia	EAST HARERGE	2380	09-18-00-N	41-14-00-E
8436	DW005	<i>T.durum</i>	SNNP	BENCH MAJI	1820	05-18-00-N	37-18-00-E
214307	DW038	<i>T.durum</i>	Oromia	EAST SHEWA	2680	08-50-00-N	39-01-00-E
214333	DW040	<i>T.durum</i>	Oromia	NORTH SHEWA	2510	09-03-00-N	39-04-00-E
222431	DW091	<i>T.durum</i>	Oromia	ARSI	2460	07-31-00-N	40-03-00-E
222432	DW092	<i>T.durum</i>	Oromia	ARSI	2460	07-31-00-N	40-03-00-E
222462-2	DW097-2	<i>T.durum</i>	Oromia	WEST SHEWA	2601	09-22-00-N	38-03-00-E
231540	DW202	<i>T.durum</i>	Amhara	NORTH SHEWA	3190	10-16-00-N	39-43-00-E
236981	DW230	<i>T.durum</i>	Oromia	ARSI	2150	08-09-00-N	39-21-00-E
204485	DW021	<i>T.durum</i>	Oromia	NORTH SHEWA	2880	09-24-00-N	39-16-00-E
222298	DW068	<i>T.durum</i>	Oromia	BALE	2545	07-16-00-N	39-53-00-E
223257	DW128	<i>T.durum</i>	Tigray	SOUTH AWI	2600	17-41-00-S	39-28-00-E
226971-2	DW186-2	<i>T.durum</i>	Oromia	ARSI	2441	07-50-00-N	39-35-00-E
231541	DW203	<i>T.durum</i>	Amhara	NORTH SHEWA	3190	10-16-00-N	39-43-00-E
236984	DW232	<i>T.durum</i>	Oromia	ARSI	1995	07-40-00-N	40-12-00-E
238119	DW243	<i>T.durum</i>	Tigray	MEHAKELEGNAW	2000	14-04-00-N	38-04-00-E
238128	DW252	<i>T.durum</i>	Tigray	EAST AWI	2990	14-30-00-N	39-50-00-E
Mukiye	DZ001	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
15356	DW006	<i>T.durum</i>	Oromia	EAST SHEWA	2300	08-57-57-N	39-09-06-E
15357	DW007	<i>T.durum</i>	Oromia	EAST SHEWA	2326	08-57-11-N	39-11-18-E

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
204566	DW033	<i>T.durum</i>	Oromia	EAST SHEWA	2350	09-01-00-N	38-08-00-E
204573-1	DW034-1	<i>T.durum</i>	Oromia	EAST SHEWA	2490	08-58-00-N	38-03-00-E
214587	DW059	<i>T.durum</i>	Oromia	MISRAK WELLEGA	2340	08-44-00-N	36-29-00-E
226838-1	DW162-1	<i>T.durum</i>	Amhara	EAST GOJAM	2510	10-25-00-N	38-12-00-E
231524	DW199	<i>T.durum</i>	Oromia	WEST SHEWA	2830	09-16-00-N	38-04-00-E
214315	DW216	<i>T.durum</i>	Amhara	NORTH WELLO	2780	11-31-00-N	39-05-00-E
238132	DW254	<i>T.durum</i>	Tigray	EAST AWI	2600	13-09-00-N	39-08-00-E
8333-2	DW003-2	<i>T.durum</i>	Amhara	EAST GOJAM	2581	10-49-00-N	38-05-00-E
214518	DW052	<i>T.durum</i>	Amhara	EAST GOJAM	2660	10-44-00-N	38-04-00-E
222358	DW073	<i>T.durum</i>	Amhara	EAST GOJAM	2560	10-29-00-N	38-11-00-E
222684-1	DW124-1	<i>T.durum</i>	Amhara	NORTH WELLO	2840	11-32-00-N	39-05-00-E
226381	DW148	<i>T.durum</i>	Oromia	NORTH SHEWA	2598	09-57-00-N	38-18-00-E
231613	DW225	<i>T.durum</i>	Oromia	EAST HARERGE	2510	09-17-00-N	41-46-00-E
236987	DW235	<i>T.durum</i>	Amhara	NORTH SHEWA	2019	09-30-00-N	39-20-00-E
204564	DW032	<i>T.durum</i>	Oromia	NORTH SHEWA	2500	08-56-00-N	38-59-00-E
214557	DW054	<i>T.durum</i>	Amhara	SOUTH WELLO	2450	11-12-00-N	39-36-00-E
222574	DW109	<i>T.durum</i>	Oromia	EAST HARERGE	2260	09-22-00-N	41-28-20-E
204484	DW020	<i>T.durum</i>	Oromia	NORTH SHEWA	2880	09-24-00-N	39-16-00-E
214356	DW043	<i>T.durum</i>	Oromia	NORTH SHEWA	2650	09-11-00-N	39-04-00-E
222644	DW121	<i>T.durum</i>	Amhara	SOUTH GONDAR (BG)	2980	11-44-00-N	38-25-00-E
226393	DW153	<i>T.durum</i>	Oromia	EAST SHEWA	2160	08-52-00-N	38-51-00-E
226881	DW167	<i>T.durum</i>	Oromia	WEST SHEWA	2850	09-27-00-N	39-15-00-E
231588	DW212	<i>T.durum</i>	Amhara	NORTH WELLO	2820	11-34-00-N	39-09-00-E
231597	DW219	<i>T.durum</i>	Amhara	SOUTH WELLO	2600	10-51-00-N	39-00-00-E
238124	DW248	<i>T.durum</i>	Tigray	MEHAKELEGNAW	2000	14-02-00-N	38-04-00-E
Mesobe	Mosobo	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
204488-2	DW023-2	<i>T.durum</i>	Oromia	NORTH SHEWA	2851	09-27-00-N	39-15-00-E
208271	DW074	<i>T.durum</i>	Amhara	EAST GOJAM	2550	10-39-00-N	38-10-00-E
222415	DW087	<i>T.durum</i>	Oromia	ARSI	2400	07-45-00-N	39-40-00-E
226882	DW168	<i>T.durum</i>	Oromia	WEST SHEWA	2850	09-27-00-N	39-15-00-E
231538	DW201	<i>T.durum</i>	Oromia	ARSI	2750	07-36-00-N	39-28-00-E
231610	DW224	<i>T.durum</i>	Oromia	EAST HARERGE	2630	09-18-00-N	41-45-00-E
7961	DW002	<i>T.durum</i>	Amhara	NORTH SHEWA	2600	09-39-00-N	39-20-00-E

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
222198	DW066	<i>T.durum</i>	Oromia	ARSI	2520	07-55-00-N	39-36-00-E
222387	DW082	<i>T.durum</i>	Oromia	ARSI	2490	07-40-00-N	39-56-00-E
222639	DW119	<i>T.durum</i>	Amhara	SOUTH GONDAR	2680	11-36-00-N	38-34-00-E
226837	DW161	<i>T.durum</i>	Amhara	EAST GOJAM	2510	10-25-00-N	38-12-00-E
231589-1	DW213-1	<i>T.durum</i>	Amhara	NORTH WELLO	2890	11-34-00-N	39-09-00-E
Asasa	Asasa	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
222735	DW050	<i>T.durum</i>	Amhara	EAST GOJAM	2560	10-48-00-N	38-03-00-E
236985	DW233	<i>T.durum</i>	Oromia	ARSI	2000	07-40-00-N	40-12-00-E
238134	DW256	<i>T.durum</i>	Tigray	EAST AWI	2600	13-09-00-N	39-08-00-E
222684-2	DW124-2	<i>T.durum</i>	Amhara	NORTH WELLO	2841	11-32-00-N	39-05-00-E
231597-1	DW219-1	<i>T.durum</i>	Amhara	SOUTH WELLO	2601	10-51-00-N	39-00-00-E
222408	DW085	<i>T.durum</i>	Oromia	ARSI	2490	07-54-00-N	39-47-00-E
222418	DW088	<i>T.durum</i>	Oromia	ARSI	2400	07-42-00-N	39-44-00-E
226331	DW139	<i>T.durum</i>	Amhara	NORTH SHEWA	2835	09-58-00-N	39-37-00-E
226352	DW144	<i>T.durum</i>	Oromia	ARSI	2400	07-50-00-N	39-34-00-E
226914	DW175	<i>T.durum</i>	Amhara	AGEW AWI	2510	10-58-00-N	36-55-00-E
231592-1	DW215-1	<i>T.durum</i>	Amhara	NORTH WELLO	2260	11-35-00-N	39-04-00-E
231599	DW220	<i>T.durum</i>	Amhara	SOUTH WELLO	2600	10-51-00-N	39-00-00-E
238135	DW257	<i>T.durum</i>	Tigray	EAST AWI	2470	13-52-00-N	39-43-00-E
7960	DW001	<i>T.durum</i>	Amhara	NORTH SHEWA	2600	09-39-00-N	36-26-00-E
222462-1	DW097-1	<i>T.durum</i>	Oromia	WEST SHEWA	2600	09-22-00-N	38-03-00-E
226357	DW147	<i>T.durum</i>	Oromia	ARSI	2440	07-50-00-N	39-35-00-E
8356	DW004	<i>T.durum</i>	Amhara	EAST GOJAM	2150	10-20-00-N	38-08-00-E
203996	DW011	<i>T.durum</i>	Amhara	NORTH SHEWA	3060	10-18-00-N	39-35-00-E
222435	DW095	<i>T.durum</i>	Oromia	ARSI	2420	07-30-00-N	40-05-00-E
222465	DW098	<i>T.durum</i>	Oromia	WEST SHEWA	2600	09-22-00-N	38-03-00-E
222469	DW099	<i>T.durum</i>	Oromia	WEST SHEWA	2490	08-58-00-N	38-00-00-E
222554	DW106	<i>T.durum</i>	Oromia	ARSI	2465	07-38-00-N	39-30-00-E
15359	DW009	<i>T.durum</i>	Oromia	EAST SHEWA	2372	08-58-35-N	39-07-20-E
214353	DW042	<i>T.durum</i>	Oromia	WEST SHEWA	2810	09-19-00-N	39-17-00-E
222426	DW090	<i>T.durum</i>	Oromia	ARSI	2460	07-32-00-N	39-59-00-E
222530	DW104	<i>T.durum</i>	Amhara	NORTH GONDAR	2510	12-33-00-N	37-24-00-E
226207	DW131	<i>T.durum</i>	Amhara	NORTH GONDAR	2100	12-38-00-N	37-28-00-E

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
236988	DW236	<i>T.durum</i>	Oromia	EAST SHEWA	2200	08-55-00-N	39-10-00-E
214352	DW041	<i>T.durum</i>	Oromia	WEST SHEWA	2810	09-19-00-N	39-17-00-E
226963	DW184	<i>T.durum</i>	Oromia	EAST SHEWA	2200	08-52-00-N	38-54-00-E
208152	DW026	<i>T.durum</i>	Oromia	NORTH SHEWA	2710	09-36-00-N	38-49-00-E
214517	DW051	<i>T.durum</i>	Amhara	EAST GOJAM	2580	10-48-00-N	38-03-00-E
222352	DW072	<i>T.durum</i>	Amhara	WEST GOJAM	2560	10-56-00-N	35-20-00-E
222421	DW089	<i>T.durum</i>	Oromia	ARSI	2415	07-42-00-N	39-44-00-E
7148	DW127	<i>T.durum</i>	Oromia	BALE	1760	06-58-00-N	40-32-00-E
226819	DW158	<i>T.durum</i>	Oromia	BALE	2600	06-59-00-N	40-01-00-E
231569	DW205	<i>T.durum</i>	SNNP	KEMBATA ALABANA TEMB	2540	07-17-00-N	37-52-00-E
203776	DW010	<i>T.durum</i>	Amhara	NORTH GONDAR	2100	12-38-00-N	37-28-00-E
212564	DW037	<i>T.durum</i>	Amhara	NORTH SHEWA	2640	10-25-00-N	39-13-0 -E
214591	DW061	<i>T.durum</i>	Amhara	SOUTH WELLO	2600	10-47-00-N	38-40-00-E
222608-1	DW112-1	<i>T.durum</i>	Amhara	SOUTH GONDAR	3050	11-39-00-N	38-27-00-E
226886	DW171	<i>T.durum</i>	Oromia	WEST SHEWA	2850	09-27-00-N	39-15-00-E
226922	DW176	<i>T.durum</i>	SNNP	NORTH OMO	2350	06-31-00-N	37-45-00-E
226809	DW157	<i>T.durum</i>	Amhara	NORTH GONDAR	2840	12-45-00-N	37-32-00-E
227007	DW190	<i>T.durum</i>	Amhara	EAST GOJAM	2502	10-27-00-N	38-19-00-E
216072	DW064	<i>T.durum</i>	Oromia	ARSI	2800	07-36-00-N	39-28-00-E
222346	DW071	<i>T.durum</i>	Amhara	AGEW AWI	2540	10-59-00-N	36-55-00-E
222600	DW111	<i>T.durum</i>	Amhara	SOUTH GONDAR	3000	11-43-00-N	38-27-00-E
222732	DW126	<i>T.durum</i>	Amhara	NORTH SHEWA	2740	09-51-00-N	39-45-00-E
208180	DW188	<i>T.durum</i>	Oromia	ARSI	2420	07-10-00-N	39-14-00-E
231547	DW204	<i>T.durum</i>	Oromia	ARSI	2400	07-50-00-N	39-34-00-E
238117	DW241	<i>T.durum</i>	Tigray	MEHAKELEGNAW	1920	14-02-00-N	38-04-00-E
15358	DW008	<i>T.durum</i>	Oromia	EAST SHEWA	2310	08-15-46-N	39-13-21-E
226327	DW138	<i>T.durum</i>	SNNP	HADIYA	2590	07-17-00-N	37-53-00-E
231499	DW198	<i>T.durum</i>	Oromia	NORTH SHEWA	2853	09-16-00-N	38-40-00-E
222370	DW206	<i>T.durum</i>	Amhara	EAST GOJAM	2390	10-34-00-N	38-14-00-E
226209	DW132	<i>T.durum</i>	Amhara	SOUTH GONDAR	2700	11-59-00-N	37-37-00-E
226312-1	DW137-1	<i>T.durum</i>	Amhara	NORTH SHEWA	2860	09-38-00-N	39-35-00-E
231589-2	DW213-2	<i>T.durum</i>	Amhara	NORTH WELLO	2891	11-34-00-N	39-09-00-E
226351	DW143	<i>T.durum</i>	Oromia	ARSI	2800	08-22-00-N	39-57-00-E

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
222533	DW105	<i>T.durum</i>	Amhara	NORTH GONDAR	2004	12-33-00-N	37-24-00-E
222568	DW108	<i>T.durum</i>	Oromia	WEST HARERGE	2030	09-13-00-N	41-07-00-E
226903	DW174	<i>T.durum</i>	Oromia	NORTH SHEWA	2510	09-01-00-N	38-56-00-E
227008	DW191	<i>T.durum</i>	Amhara	EAST GOJAM	2502	10-27-00-N	38-19-00-E
227009	DW192	<i>T.durum</i>	Oromia	ARSI	2995	08-19-00-N	39-55-00-E
7217	DW197	<i>T.durum</i>	Oromia	ARSI	1540	08-35-00-N	39-56-00-E
231536-2	DW200-2	<i>T.durum</i>	Amhara	NORTH SHEWA	3011	10-20-00-N	39-38-00-E
214366	DW044	<i>T.durum</i>	Amhara	NORTH SHEWA	3000	09-49-00-N	39-42-00-E
214377	DW046	<i>T.durum</i>	Oromia	WEST SHEWA	2210	09-01-00-N	38-20-00-E
226301	DW135	<i>T.durum</i>	Oromia	WEST SHEWA	2590	09-22-00-N	38-03-00-E
8175	DW141	<i>T.durum</i>	SNNP	KEMBATA ALABANA TEMB	2780	09-34-00-N	39-29-00-E
227016	DW195	<i>T.durum</i>	Oromia	WEST SHEWA	2635	08-54-00-N	37-56-00-E
222613	DW113	<i>T.durum</i>	Amhara	SOUTH GONDAR	3130	11-39-00-N	38-27-00-E
20666-1	DW014	<i>T.durum</i>	Oromia	DZARC	NA	NA	NA
204470	DW017	<i>T.durum</i>	Oromia	ARSI	2520	07-53-00-N	39-44-00-E
222629	DW116	<i>T.durum</i>	Amhara	SOUTH GONDAR	2850	11-38-00-N	38-28-00-E
226808	DW156	<i>T.durum</i>	Amhara	NORTH GONDAR	2840	12-45-00-N	37-32-00-E
214497	DW048	<i>T.durum</i>	Oromia	ARSI	2720	08-04-00-N	39-37-00-E
226840	DW163	<i>T.durum</i>	Amhara	EAST GOJAM	2550	10-30-00-N	38-24-00-E
222632	DW117	<i>T.durum</i>	Amhara	SOUTH GONDAR	2850	11-36-00-N	38-33-00-E
208332-2	DW045	<i>T.durum</i>	Amhara	NORTH SHEWA	2841	09-58-00-N	39-37-00-E
222608-2	DW112-2	<i>T.durum</i>	Amhara	SOUTH GONDAR	3051	11-39-00-N	38-27-00-E
204417	DW016	<i>T.durum</i>	Oromia	ARSI	2730	08-23-00-N	39-56-00-E
204349	DW012	<i>T.durum</i>	Oromia	BALE	2560	07-12-00-N	39-56-00-E
222578	DW110	<i>T.durum</i>	Oromia	EAST HARERGE	2410	09-28-00-N	41-48-00-E
226971-1	DW186-1	<i>T.durum</i>	Oromia	ARSI	2440	07-50-00-N	39-35-00-E
204411	DW015	<i>T.durum</i>	Oromia	ARSI	2275	08-30-00-N	39-47-00-E
204392	DW013	<i>T.durum</i>	Oromia	ARSI	2440	07-46-00-N	39-47-00-E
204482	DW018	<i>T.durum</i>	Oromia	NORTH SHEWA	2890	09-19-00-N	39-16-00-E
204483	DW019	<i>T.durum</i>	Oromia	NORTH SHEWA	2880	09-24-00-N	39-16-00-E
204562	DW030	<i>T.durum</i>	Oromia	NORTH SHEWA	2500	08-56-00-N	38-59-00-E
204563	DW031	<i>T.durum</i>	Oromia	NORTH SHEWA	2500	08-56-00-N	38-59-00-E
212561-1	DW036	<i>T.durum</i>	Amhara	NORTH SHEWA	2680	10-25-00-N	39-16-00-E

## SUPPLEMENTARY FILES

Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
212561-2	DW036-2	<i>T.durum</i>	Amhara	NORTH SHEWA	2681	10-25-00-N	39-16-00-E
214490	DW047	<i>T.durum</i>	Amhara	NORTH GONDAR	2720	13-10-00-N	37-52-00-E
214515	DW049	<i>T.durum</i>	Amhara	EAST GOJAM	2560	10-48-00-N	38-03-00-E
7208	DW055	<i>T.durum</i>	Amhara	EAST GOJAM	2200	10-28-00-N	38-14-00-E
214571	DW056	<i>T.durum</i>	Amhara	EAST GOJAM	2200	10-13-00-N	38-02-00-E
DZARC	DZ002	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
215276	DW063	<i>T.durum</i>	Amhara	NORTH SHEWA	2920	09-57-00-N	39-44-00-E
222360	DW075	<i>T.durum</i>	Amhara	EAST GOJAM	2550	10-39-00-N	38-10-00-E
DZARC	DZ007	<i>T.durum</i>	DZARC	DZARC	NA	NA	NA
222503	DW100	<i>T.durum</i>	Amhara	NORTH GONDAR	2400	13-04-00-N	37-48-00-E
222508	DW101	<i>T.durum</i>	Amhara	NORTH GONDAR	2550	12-58-00-N	37-45-00-E
222514	DW102	<i>T.durum</i>	Amhara	NORTH GONDAR	2660	12-52-00-N	37-44-00-E
222619	DW114	<i>T.durum</i>	Amhara	SOUTH GONDAR	3040	11-38-00-N	38-32-00-E
222627	DW115	<i>T.durum</i>	Amhara	SOUTH GONDAR	2850	11-38-00-N	38-28-00-E
226093	DW129	<i>T.durum</i>	Amhara	SOUTH WELLO	2570	10-45-00-N	38-45-00-E
226245	DW133	<i>T.durum</i>	Tigray	SOUTH AWI	2687	13-30-00-N	39-33-00-E
226342	DW140	<i>T.durum</i>	Oromia	EAST SHEWA	2755	08-32-00-N	38-52-00-E
208293-1	DW142-2	<i>T.durum</i>	Oromia	DZARC	NA	NA	NA
226354-1	DW145-1	<i>T.durum</i>	Oromia	ARSI	2400	07-50-00-N	39-34-00-E
226356	DW146	<i>T.durum</i>	Oromia	ARSI	2440	07-50-00-N	39-35-00-E
226807	DW155	<i>T.durum</i>	Amhara	NORTH GONDAR	2840	12-45-00-N	37-32-00-E
226830	DW159	<i>T.durum</i>	Amhara	EAST GOJAM	2480	10-14-00-N	38-03-00-E
226834	DW160	<i>T.durum</i>	Amhara	EAST GOJAM	2460	10-21-00-N	38-13-00-E
222413	DW086	<i>T.durum</i>	Oromia	ARSI	2430	07-44-00-N	39-53-00-E
226838-2	DW162-2	<i>T.durum</i>	Amhara	EAST GOJAM	2510	10-25-00-N	38-12-00-E
226844	DW164	<i>T.durum</i>	Amhara	EAST GOJAM	2580	10-37-00-N	38-11-00-E
226888	DW173	<i>T.durum</i>	Amhara	NORTH SHEWA	2720	09-46-00-N	39-10-00-E
216648	DW177	<i>T.durum</i>	Oromia	ARSI	2570	07-01-00-N	38-56-00-E
226958	DW180	<i>T.durum</i>	Amhara	NORTH GONDAR	2927	12-55-00-N	37-47-00-E
208746-2-2	DW185	<i>T.durum</i>	Oromia	ARSI	2780	08-22-00-N	39-57-00-E
226978	DW189	<i>T.durum</i>	Oromia	ARSI	2420	07-10-00-N	39-14-00-E
203724	DW194	<i>T.durum</i>	Oromia	ARSI	2520	07-53-00-N	39-44-00-E
231536-1	DW200-1	<i>T.durum</i>	Amhara	NORTH SHEWA	3010	10-20-00-N	39-38-00-E

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Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
231573	DW207	<i>T.durum</i>	Amhara	EAST GOJAM	2510	10-38-00-N	38-10-00-E
231585	DW209	<i>T.durum</i>	Amhara	NORTH WELLO	2920	11-34-00-N	39-09-00-E
231586	DW210	<i>T.durum</i>	Amhara	NORTH WELLO	2820	11-34-00-N	39-09-00-E
214537-1	DW214-1	<i>T.durum</i>	Amhara	NORTH WELLO	2260	11-35-00-N	39-04-00-E
231594	DW217	<i>T.durum</i>	Amhara	NORTH WELLO	2780	11-31-00-N	39-05-00-E
236974-1	DW227-1	<i>T.durum</i>	Oromia	ARSI	2850	07-19-00-N	39-16-00-E
236986	DW234	<i>T.durum</i>	Amhara	NORTH SHEWA	2010	09-30-00-N	39-20-00-E
238122	DW246	<i>T.durum</i>	Tigray	MEHAKELEGNAW	1750	13-04-00-N	39-35-00-E
238127	DW251	<i>T.durum</i>	Tigray	EAST AWI	2930	14-30-00-N	39-50-00-E
5739-1	DW258	<i>T.durum</i>	Tigray	MEHAKELEGNAW	NA	NA	NA
238138	DW259	<i>T.durum</i>	Tigray	MEHAKELEGNAW	2180	12-09-00-N	38-08-00-E
521610	C001	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
521637	C002	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
537861	C003	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547732	C004	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547734	C005	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547919	C006	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547944	C007	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547944	C008	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547949	C009	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547973	C010	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548022	C011	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548091	C012	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548465	C013	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548474	C014	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548636	C015	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548642	C016	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548644	C017	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
527306	C018	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
521278	C019	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
537883	C020	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
537883	C021	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
537893	C022	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA



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Accession number	Accession code	Taxon	Seed origin	Seed collection zone	Altitude in meter above sea level	Latitude	Longitude
538013	C023	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
538044	C024	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
538123	C025	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
531727	C026	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
531800	C027	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
531517	C028	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547914	C029	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547919	C030	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547963	C031	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547973	C032	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547988	C033	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547989	C034	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
547989	C035	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548017	C036	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548030	C037	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548030	C038	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548097	C039	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548462	C040	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548465	C041	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548605	C042	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548605	C043	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548633	C044	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548642	C045	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548667	C046	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548690	C047	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548699	C048	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
548152	C049	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA
541942	C050	<i>T.durum</i>	CIMMYT	CIMMYT	NA	NA	NA

## SUPPLEMENTARY FILES

**Table S2.** Summary of ANOVA of the effects of accessions (A), treatments (T), and accession by treatment interaction (AxT).

Trait	Treatment	Effect	F value	P-value	Trait	Treatment	Effect	F value	P-value	
GB	FNS versus FDS	A	5.31	<.0001	PH	FNS versus FDS	A	11.53	<.0001	
		T	151.93	<.0001			T	216.9	<.0001	
		AxT	3.66	<.0001			AxT	6.51	<.0001	
	CCNS versus CCDS	A	2.93	<.0001		CCNS versus CCDS	A	6.53	<.0001	
		T	732.67	<.0001			T	25.37	<.0001	
		AxT	1.25	0.034			AxT	0.96	0.62	
DH	FNS versus FDS	A	10.33	<.0001	SL	FNS versus FDS	A	7.87	<.0001	
		T	22.62	<.0001			T	85.99	<.0001	
		AxT	2.78	<.0001			AxT	6.04	<.0001	
	CCNS versus CCDS	A	3.43	<0.0001		HI	FNS versus FDS	A	1.33	0.0001
		T	5.35	0.02				T	0.93	0.336
		AxT	1.02	0.42				AxT	1.14	0.053
DGF	FNS versus FDS	A	4.39	<.0001	SPS	CCNS versus CCDS	A	2.23	<.0001	
		T	1222.3	<.0001			T	222.04	<.0001	
		AxT	1.68	<.0001			AxT	1.18	0.091	
	CCNS versus CCDS	A	1.6	<0.0001		FNS versus FDS	A	4.63	<.0001	
		T	2628.65	<0.0001			T	96.97	<.0001	
		AxT	1.13	0.15			AxT	2.77	<.0001	
DM	FNS versus FDS	A	2.04	<.0001	TKW	CCNS versus CCDS	A	3.42	<.0001	
		T	156.28	<.0001			T	37.49	<.0001	
		AxT	1.36	<.0001			AxT	0.79	0.967	
	CCNS versus CCDS	A	2.53	<0.0001		FNS versus FDS	A	6.28	<.0001	
		T	3501.45	<0.0001			T	56.98	<.0001	
		AxT	1.25	0.04			AxT	2.17	<.0001	
SPAD	FNS versus FDS	A	4.07	<.0001	CCNS versus CCDS	A	4	<0.0001		
		T	0.02	<.0001			T	279.07	<0.0001	
		AxT	0.89	<.0001			AxT	1.31	0.01	
	CCNS versus CCDS	A	2.79	<.0001						
		T	193.84	<.0001						
		AxT	0.85	0.895						

FNS: Field non-stress; FDS: Field drought stress; CCNS: Climate chamber non-stress; CCDS: Climate chamber drought stress. GB: Grain biomass, DH: Days to heading, DM: Days to maturity, DGF: Days to grain filling, SPAD, PH: Plant height, SL: Spike length HI: Harvest index, SPS: Seed per spike, TKW: Thousand kernel weight.

**Table S3.** Linkage disequilibrium decay (LD) for the study panel (SP) of 285 accessions based on 11,919 SNPs.

Chromosome	LD decay in Mb
1A	3.13
1B	3.81
2A	6.13
2B	7.62
3A	7.38
3B	7.13
4A	1.47
4B	5.86
5A	6.18
5B	4.44

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<b>Chromosome</b>	<b>LD decay in Mb</b>
6A	3.41
6B	2.37
7A	3.6
7B	4.22
<b>Overall LD value at (r2 ≥ 0.15)</b>	<b>5.01</b>
<b>Critical (r2 &gt; 0.2) LD value</b>	<b>4.78</b>

**Table S4.** Identified significant (-log10p ≥ 4) marker trait association (MTA) for grain yield and related traits under drought stress and non-stress conditions in the durum wheat study panel. Gray shade showed significant MTAs at FDR 5%.

<b>SN</b>	<b>Trait</b>	<b>Trt</b>	<b>SNP</b>	<b>Chr</b>	<b>Alleles</b>	<b>Position st</b>	<b>LCI</b>	<b>HCI</b>	<b>LOD</b>	<b>Effect size</b>	<b>% PVE</b>
1	GB	FDS	Kukri_c43410_348	1A	A/G	498819507	495694477	501944537	7.00	2.97	2.08
2	GB	FDS	Tdurum_contig10785_2433	2A	T/C	12102513	5969113	18235913	4.41	-2.03	1.89
3	GB	FDS	RFL_Contig5015_668	3B	T/C	423382012	416256124	430507900	5.14	4.10	3.76
4	GB	FDS	Excalibur_c8208_993	3B	A/G	752483046	745357158	759608934	4.82	2.35	2.85
5	GB	FDS	Tdurum_contig76578_537	5A	A/G	110830599	104655367	117005831	8.20	5.57	5.54
6	GB	FDS	BS00015136_51	5B	C/T	17863912	13427657	22300167	6.67	-3.07	4.17
7	GB	FNS	BS00037020_51	4B	G/T	599279630	593416763	605142497	4.10	3.84	2.99
8	GB	FNS	Kukri_c9520_288	5B	T/G	458315917	453879662	462752172	6.26	5.43	2.45
9	GB	FNS	wsnp_Ex_c3940_7144946	6B	A/G	508076861	505703728	510449994	4.38	5.86	4.13
10	GB	FNS	BS00077891_51	7A	T/G	641532101	637937043	645127159	4.31	-3.43	1.92
11	GB	CCDS	BS00021995_51	1B	T/C	110067743	106256279	113879207	4.91	-0.14	6.62
12	GB	CCDS	wsnp_CAP8_rep_c4452_2170021	1B	T/C	534692880	530881416	538504344	5.92	0.17	5.38
13	GB	CCDS	IACX1369	2A	T/C	578301307	572167907	584434707	4.16	0.23	2.73
14	GB	CCDS	IAAV2576	2A	A/G	747379314	741245914	753512714	5.53	-0.14	1.50
15	GB	CCDS	Ku_c39003_290	4B	G/T	566937979	561075112	572800846	4.94	0.17	3.60
16	GB	CCDS	tp1b0056o05_409	4B	A/C	664648757	658785890	670511624	4.11	0.14	4.24
17	GB	CCDS	BobWhite_rep_c48815_538	5A	A/G	436213158	430037926	442388390	4.11	-0.10	4.61
18	GB	CCDS	Kukri_c22967_1272	5B	A/G	422232900	417796645	426669155	4.87	-0.13	4.61
19	GB	CCNS	wsnp_CAP11_c543_375403	1B	A/G	534692879	530881415	538504343	6.11	-0.38	8.95
20	GB	CCNS	IAAV4191	4B	G/A	562470112	556607245	568332979	6.44	0.50	6.12
21	GB	CCNS	Tdurum_contig52015_1568	7A	C/T	3077629	3595058	6672687	4.97	-0.45	4.60
22	DH	FDS	BS00094681_51	1A	T/C	368023048	364898018	371148078	20.17	-9.85	1.12
23	DH	FDS	RAC875_c63624_753	1B	C/T	10778560	6967096	14590024	4.91	-0.71	3.97
24	DH	FDS	tp1b0052d08_1158	2A	C/T	716955222	710821822	723088622	5.66	1.24	2.04
25	DH	FDS	RAC875_c16752_283	2B	T/C	731958769	724139202	739778336	6.44	-0.76	1.63
26	DH	FDS	BS00010659_51	4B	T/C	541269142	535406275	547132009	5.54	-0.87	1.62
27	DH	FNS	Ex_c6028_1602	1B	C/T	311945021	308133557	315756485	4.54	1.02	2.73
28	DH	FNS	TA001195-0515	4A	A/C	47760186	46286166	49234206	5.00	-0.91	1.15
29	DH	FNS	wsnp_Ex_c58286_59646499	4A	T/C	514104964	512630944	515578984	7.70	-5.44	3.18
30	DH	FNS	IAAV2346	5B	G/A	17863862	13427607	22300117	5.18	-0.86	3.76
31	DH	CCDS	Excalibur_c12819_216	1A	C/T	580841266	577716236	583966296	4.05	-1.96	2.64
32	DH	CCDS	Ex_c16090_1439	6B	C/T	4048852	1675719	6421985	4.14	-2.35	3.96
33	DH	CCDS	RAC875_rep_c74471_125	6B	C/A	5570509	3197376	7943642	4.12	-2.34	3.71
34	DH	CCDS	Tdurum_contig54525_2045	6B	C/T	527683877	525310744	530057010	4.49	-4.15	5.39
35	DH	CCDS	Excalibur_c3336_1007	6B	T/C	527687474	525314341	530060607	4.48	-3.39	5.48
36	DH	CCDS	BobWhite_c520_181	6B	C/T	527845738	525472605	530218871	4.48	-3.39	5.48
37	DH	CCDS	Tdurum_contig17582_178	6B	T/C	528550943	526177810	530924076	4.11	-3.47	4.48
38	DH	CCDS	Tdurum_contig76473_357	6B	T/C	529134631	526761498	531507764	4.27	-3.71	5.54
39	DH	CCDS	Tdurum_contig42629_2594	6B	G/A	531531212	529158079	533904345	4.49	-4.15	5.39
40	DH	CCDS	wsnp_RFL_Contig4236_4881643	7B	A/G	616616464	612394582	620838346	4.16	2.53	4.55
41	DH	CCNS	Ra_c18323_183	1B	G/A	381876470	378065006	385687934	6.69	-1.78	3.26
42	DH	CCNS	wsnp_CAP11_c543_375403	1B	A/G	534692879	530881415	538504343	4.43	1.25	8.95
43	DH	CCNS	CAP11_c3226_221	2B	C/T	768263080	760443513	776082647	5.88	1.48	6.01
44	DH	CCNS	BS00093063_51	6B	T/C	4650326	2277193	7023459	6.41	-2.93	4.90
45	DH	CCNS	BS00040415_51	7B	G/A	161692387	157470505	165914269	5.14	1.00	3.67
46	DGF	FDS	Excalibur_c22768_811	1A	T/C	531344066	528219036	534469096	4.64	0.61	

**SUPPLEMENTARY FILES**

SN	Trait	Trt	SNP	Chr	Alleles	Position st	LCI	HCI	LOD	Effect size	% PVE
47	DGF	FDS	Ex_c16691_96	1B	G/A	379469519	375658055	383280983	4.23	0.74	3.36
48	DGF	FDS	Ra_c18323_183	1B	G/A	381876470	378065006	385687934	4.24	0.74	3.26
49	DGF	FDS	RAC875_c26469_480	2B	C/T	66718832	58899265	74538399	4.96	1.48	4.02
50	DGF	FDS	Tdurum_contig92997_676	4B	G/A	492236533	486373666	498099400	6.57	-1.14	4.44
51	DGF	FDS	Tdurum_contig48179_1051	6A	G/A	20001658	16594482	23408834	6.77	-0.66	4.60
52	DGF	FNS	BS00108242_51	1A	G/A	6060158	2935128	9185188	4.71	0.48	3.32
53	DGF	FNS	BS00065324_51	1A	T/C	495875504	492750474	499000534	5.48	-0.54	1.85
54	DGF	FNS	w SNP_Ku_c17322_26392311	1A	T/C	520098848	516973818	523223878	4.29	0.50	1.48
55	DGF	FNS	Kukri_rep_c69810_502	1B	C/T	462815112	459003648	466626576	5.56	-0.99	1.62
56	DGF	FNS	BS00021710_51	1B	A/G	555772857	551961393	559584321	8.80	-1.35	2.58
57	DGF	FNS	w SNP_Ex_c64005_62987067	3B	T/C	740008335	732882447	747134223	4.80	0.45	0.59
58	DGF	FNS	w SNP_Ex_c19207_28125072	4A	C/T	605552785	604078765	607026805	6.19	0.61	1.76
59	DGF	FNS	Kukri_rep_c116526_98	5A	C/T	112213041	106037809	118388273	7.08	-0.69	3.29
60	DGF	FNS	IAAV7384	6A	G/T	451613919	448206743	455021095	7.17	-0.69	3.32
61	DGF	FNS	BS00003760_51	7B	A/G	547800081	543578199	552021963	6.03	1.00	3.31
62	DM	FDS	w SNP_RFL_Contig3881_4265086	1A	G/A	579774985	576649955	582900015	6.21	-0.72	2.82
63	DM	FDS	RAC875_c63624_753	1B	C/T	10778560	6967096	14590024	9.65	-0.74	5.52
64	DM	FDS	tp1b0028k07_1268	2B	C/T	477041458	469221891	484861025	7.54	0.94	4.38
65	DM	FDS	RAC875_rep_c69241_454	4A	A/G	100948177	99474157	102422197	4.33	-0.50	1.28
66	DM	FDS	RAC875_c96675_51	6B	G/A	582709596	580336463	585082729	5.63	0.74	2.00
67	DM	FDS	Excalibur_c9083_981	7A	A/G	697027966	697027966	700623024	9.80	1.66	2.48
68	DM	FNS	w SNP_BE445121A_Ta_1_8	1A	T/G	52277305	49152275	55402335	6.11	1.27	1.59
69	DM	FNS	Tdurum_contig50555_944	1B	G/A	13558276	9746812	17369740	5.05	0.56	3.92
70	DM	FNS	Tdurum_contig28305_106	1B	A/G	419925976	416114512	423737440	4.91	-0.73	4.76
71	DM	FNS	Excalibur_c7964_1290	4B	G/A	485705797	479842930	491568664	4.74	-0.67	4.88
72	DM	FNS	Ex_c6870_1704	7A	T/C	263513525	259918467	267108583	5.82	1.00	3.15
73	DM	FNS	CAP7_c12333_392	7A	C/T	558401058	554806000	561996116	4.52	-0.60	2.40
74	DM	FNS	JD_c149_3175	7A	C/T	663974573	660379515	667569631	5.05	0.76	2.47
75	DM	CCNS	IAAV9048	5B	G/A	356154255	351718000	360590510	4.41	-1.74	2.80
76	PH	FDS	w SNP_Ex_c25730_34991010	1A	A/G	570723895	567598865	573848925	4.41	-0.88	1.47
77	PH	FDS	RAC875_c61801_262	2B	C/T	66725082	58905515	74544649	5.21	2.19	2.45
78	PH	FDS	w SNP_Ex_c5123_9087869	2B	C/T	683879232	676059665	691698799	4.63	1.15	3.51
79	PH	FDS	Tdurum_contig50596_825	3A	A/C	6451139	100000	13831545	4.82	-2.70	2.84
80	PH	FDS	Excalibur_c15848_960	3A	G/A	457068370	449687964	464448776	8.72	-1.36	2.75
81	PH	FDS	Tdurum_contig11967_234	6B	C/T	460348769	457975636	462721902	4.94	1.03	2.40
82	PH	FNS	Tdurum_contig15440_616	2B	T/C	21617081	13797514	29436648	4.04	1.17	2.71
83	PH	FNS	RFL_Contig2277_1527	4B	C/T	12573269	6710402	18436136	8.77	-5.11	3.93
84	PH	FNS	Tdurum_contig53125_1716	6B	T/C	606965578	604592445	609338711	4.79	1.35	2.47
85	PH	FNS	Excalibur_c33259_1379	7A	A/G	80864397	80864397	84459455	9.46	3.20	4.78
86	PH	FNS	Ku_c25443_1454	7B	G/A	693074448	688852566	697296330	7.93	4.06	4.53
87	SPAD	FDS	Excalibur_c5592_178	2B	C/T	28481500	20661933	36301067	4.42	-2.38	2.27
88	SPAD	FDS	RAC875_c18928_529	2B	C/T	769794873	761975306	777614440	4.21	-0.83	0.15
89	SPAD	FDS	Kukri_rep_c115927_102	4B	T/C	546670085	540807218	552532952	4.58	-1.15	1.17
90	SPAD	FDS	RFL_Contig2597_451	6B	C/T	689680372	687307239	692053505	4.04	0.82	0.11
91	SPAD	FNS	CAP11_rep_c7878_143	1A	G/A	1197117	800000	4322147	4.96	0.89	0.36
92	SPAD	FNS	BS00066336_51	1A	G/T	338991825	335866795	342116855	6.36	1.30	4.10
93	SPAD	FNS	BS00033469_51	1A	G/T	464926602	461801572	468051632	4.69	0.97	2.47
94	SPAD	FNS	BS00040968_51	1A	C/A	472637059	469512029	475762089	4.62	0.88	1.33
95	SPAD	FNS	CAP12_c1979_117	1A	A/G	507881110	504756080	511006140	7.25	1.09	4.09
96	SPAD	FNS	Kukri_c47131_569	1A	T/G	559929847	556804817	563054877	4.07	-0.77	1.51
97	SPAD	FNS	CAP11_c5573_163	1A	G/A	582981061	579856031	586106091	4.12	0.80	1.91
98	SPAD	FNS	Tdurum_contig46647_623	1B	G/A	664162432	660350968	667973896	6.47	-1.02	2.38
99	SPAD	FNS	BS00062869_51	2A	G/A	759800700	753667300	765934100	5.25	0.78	1.85
100	SPAD	FNS	Tdurum_contig55335_316	3A	C/T	165087117	157706711	172467523	4.00	-0.64	2.16
101	SPAD	FNS	Kukri_c36207_91	4B	G/A	605263129	599400262	611125996	5.05	0.96	1.78
102	SPAD	FNS	Kukri_c25454_496	6B	G/A	684809294	682436161	687182427	5.47	-0.91	1.98
103	SPAD	CCDS	w SNP_BG274294B_Ta_2_3	1B	T/C	535359528	531548064	539170992	5.16	-3.78	4.33
104	SPAD	CCDS	BS00022775_51	1B	A/G	606172193	602360729	609983657	4.23	8.80	3.64
105	SPAD	CCDS	BS00022486_51	2B	T/G	120783180	112963613	128602747	6.00	4.24	2.26
106	SPAD	CCDS	w SNP_Ex_c46217_51790399	5B	C/T	486724593	482288338	491160848	5.87	-10.15	1.55
107	SPAD	CCDS	Ku_c19745_892	7A	G/A	704957655	704957655	708552713	5.08	-3.60	4.01

**SUPPLEMENTARY FILES**

SN	Trait	Trt	SNP	Chr	Alleles	Position st	LCI	HCI	LOD	Effect size	% PVE
108	SPAD	CCNS	wsnp_CAP7_rep_c12606_5316797	2B	A/G	130854626	123035059	138674193	5.13	4.43	3.32
109	SPAD	CCNS	Tdurum_contig29027_92	6A	G/A	46731194	43324018	50138370	4.88	-3.17	4.05
110	SPAD	CCNS	Excalibur_c28771_400	6B	C/T	222325710	219952577	224698843	4.83	4.17	6.33
111	SPAD	CCNS	Kukri_c25082_328	6B	T/C	611585740	609212607	613958873	4.11	4.64	2.20
112	SPAD	CCNS	BS00071558_51	7A	T/C	621795323	621795323	625390381	4.04	-2.78	2.76
113	SPAD	CCNS	RAC875_c21489_908	7B	C/T	618427783	614205901	622649665	5.11	4.55	4.47
114	SL	FDS	Tdurum_contig10208_452	2B	T/G	1343174	7819567	9162741	4.64	-0.13	1.76
115	SL	FDS	Excalibur_c9206_671	3B	T/C	17838629	10712741	24964517	4.25	-0.09	1.30
116	SL	FDS	BobWhite_rep_c64247_261	3B	A/C	44966830	37840942	52092718	4.32	-0.09	5.69
117	SL	FDS	Excalibur_c15838_535	5A	A/G	52717033	46541801	58892265	4.53	-0.12	3.03
118	SL	FDS	Kukri_rep_c116526_98	5A	C/T	112213041	106037809	118388273	5.50	0.14	3.14
119	SL	FNS	BS00022133_51	1B	C/A	437062132	433250668	440873596	4.55	-0.45	3.66
120	SL	FNS	Kukri_rep_c117487_334	2B	G/A	70922954	63103387	78742521	6.68	0.39	0.27
121	SL	FNS	Ex_c30319_438	4A	G/A	176911148	175437128	178385168	7.66	-0.49	11.83
122	SL	FNS	wsnp_Ex_c5839_10246915	7A	C/T	709145347	709145347	712740405	4.46	0.16	1.89
123	SL	FNS	Excalibur_rep_c67533_78	7B	C/A	144904755	140682873	149126637	4.87	0.18	3.47
124	SL	FNS	BS00059062_51	7B	T/C	530193276	525971394	534415158	5.49	-0.37	0.11
125	SL	FNS	Kukri_rep_c70697_875	7B	A/G	599182331	594960449	603404213	4.04	0.12	2.49
126	SL	CCDS	BS00040739_51	3B	G/A	751656033	744530145	758781921	4.06	0.28	2.58
127	SL	CCDS	wsnp_Ex_rep_c103148_88169427	5B	G/A	121692572	117256317	126128827	6.56	-0.40	3.87
128	SL	CCDS	wsnp_BF473658B_Ta_2_1	5B	A/G	124910471	120474216	129346726	4.15	3.32	2.80
129	SL	CCDS	wsnp_RFL_Contig4236_4881643	7B	A/G	616616464	612394582	620838346	4.60	0.39	4.55
130	SL	CCNS	wsnp_Ra_c48924_54032104	3B	T/C	739991587	732865699	747117475	5.07	-0.36	3.46
131	SL	CCNS	wsnp_Ex_c9928_16346945	4A	T/G	6689936	5215916	8163956	4.12	0.36	2.87
132	SL	CCNS	wsnp_CAP8_c954_618139	4A	G/A	563579589	562105569	565053609	5.55	0.52	3.74
133	SL	CCNS	wsnp_Ex_c53170_56501500	5B	C/T	636914479	632478224	641350734	5.15	0.84	1.08
134	SL	CCNS	BS00065680_51	6B	C/A	76313985	73940852	78687118	4.30	0.40	1.75
135	SPS	FDS	Tdurum_contig27880_75	2B	G/A	521954141	514134574	529773708	4.70	0.82	0.86
136	SPS	FDS	RAC875_c60169_200	3B	G/A	25269809	18143921	32395697	4.31	0.88	0.03
137	SPS	FDS	Excalibur_c33274_498	3B	C/T	748882411	741756523	756008299	4.21	0.53	0.97
138	SPS	FDS	wsnp_JD_c4413_5541607	3B	G/T	752482037	745356149	759607925	5.91	0.72	1.94
139	SPS	FDS	Tdurum_contig48766_257	5A	C/T	405258364	399083132	411433596	4.84	0.66	0.72
140	SPS	FNS	Tdurum_contig51167_534	1A	A/G	545579418	542454388	548704448	4.15	1.02	3.71
141	SPS	FNS	BS00043055_51	2B	C/T	15805908	7986341	23625475	5.32	0.76	2.16
142	SPS	FNS	RAC875_c60169_200	3B	G/A	25269809	18143921	32395697	4.94	1.19	0.03
143	SPS	FNS	Tdurum_contig55751_315	3B	T/C	752251753	745125865	759377641	6.56	0.82	3.00
144	SPS	FNS	Tdurum_contig65805_1015	5A	A/G	263157191	256981959	269332423	4.97	1.41	3.56
145	SPS	FNS	BS00062617_51	5B	T/C	21615066	17178811	26051321	4.06	-0.91	0.61
146	SPS	FNS	Ra_c4568_960	6A	A/C	608840780	605433604	612247956	4.08	-1.31	2.19
147	SPS	CCDS	Excalibur_c14911_976	1B	T/C	558560978	554749514	562372442	5.31	-3.20	3.31
148	SPS	CCDS	RAC875_c34231_812	4A	T/G	610380471	608906451	611854491	4.36	-1.74	6.68
149	SPS	CCDS	BS00067983_51	6B	A/C	659033636	656660503	661406769	4.17	1.03	8.02
150	SPS	CCDS	RAC875_c55351_223	7A	T/C	13039779	9444721	16634837	4.42	2.34	4.59
151	SPS	CCDS	GENE-4703_160	7A	A/G	212424376	208829318	216019434	4.25	1.34	5.61
152	HI	FDS	Ra_c2895_591	1A	G/T	454315618	451190588	457440648	6.61	-1.34	4.64
153	HI	FDS	Tdurum_contig33207_282	1B	A/G	348260183	344448719	352071647	5.51	2.31	5.05
154	HI	FDS	TA004947-0758	1B	A/C	348593655	344782191	352405119	5.92	2.53	5.16
155	HI	FDS	BobWhite_c2022_245	2A	G/A	29222931	23089531	35356331	4.29	1.07	1.13
156	HI	FDS	Tdurum_contig42013_538	2A	T/C	771226463	765093063	777359863	4.50	-1.58	2.16
157	HI	FDS	Excalibur_c7964_1290	4B	G/A	485705797	479842930	491568664	5.77	1.12	4.37
158	HI	FDS	RAC875_c13394_924	6A	A/G	3084526	700000	6491702	4.69	-0.91	2.78
159	HI	FDS	Excalibur_rep_c70364_129	6B	T/C	539467780	537094647	541840913	5.25	1.77	5.82
160	HI	FDS	JD_c1201_631	7A	T/G	663956092	663956092	667551150	4.81	-1.82	2.26
161	HI	FNS	Excalibur_c9149_1789	1B	G/T	559835637	556024173	563647101	4.62	-1.26	3.52
162	HI	FNS	Kukri_c36879_83	2B	A/G	96408120	88588553	104227687	6.01	2.70	2.50
163	HI	FNS	Kukri_c33640_640	3A	C/T	630286793	622906387	637667199	5.53	-1.26	2.67
164	HI	FNS	BobWhite_c4089_73	4A	A/G	577090263	575616243	578564283	7.78	1.80	4.38
165	HI	FNS	Tdurum_contig76578_537	5A	A/G	110830599	104655367	117005831	6.64	2.45	6.90
166	HI	FNS	Kukri_c14679_1082	6A	G/A	12639100	9231924	16046276	4.60	1.56	0.62
167	HI	FNS	wsnp_Ex_c7907_13427724	6B	A/G	115175100	112801967	117548233	8.35	2.47	0.77
168	HI	FNS	wsnp_BF293311B_Ta_2_3	6B	C/A	439365045	436991912	441738178	5.43	1.17	2.78

## SUPPLEMENTARY FILES

SN	Trait	Trt	SNP	Chr	Alleles	Position st	LCI	HCI	LOD	Effect size	% PVE
169	HI	FNS	Tdurum_contig14075_328	7A	T/C	59620092	59620092	63215150	4.05	1.35	1.78
170	HI	CCDS	Tdurum_contig57927_171	1B	G/A	624061642	620250178	627873106	4.27	0.06	6.39
171	HI	CCDS	Tdurum_contig57927_460	1B	G/A	624061931	620250467	627873395	4.27	0.06	6.39
172	HI	CCDS	Tdurum_contig18326_142	3A	C/T	733922818	726542412	741303224	4.55	-0.08	10.61
173	HI	CCNS	RAC875_c8045_231	2B	T/C	197538224	189718657	205357791	5.93	0.03	4.59
174	HI	CCNS	BS00052057_51	3B	G/A	748670433	741544545	755796321	4.83	-0.02	3.90
175	HI	CCNS	Tdurum_contig10759_260	5A	G/A	535739588	529564356	541914820	4.28	0.03	0.94
176	HI	CCNS	Kukri_c34173_518	5B	C/T	528635625	524199370	533071880	4.24	-0.02	3.96
177	HI	CCNS	w SNP_Ex_c3858_7011837	6B	T/C	407630784	405257651	410003917	6.01	-0.02	2.61
178	HI	CCNS	Tdurum_contig52015_1090	7A	A/G	3076769	3076769	6671827	6.01	-0.04	4.78
179	TKW	FDS	Excalibur_c16851_835	1B	G/A	14884193	11072729	18695657	5.99	0.83	4.03
180	TKW	FDS	BobWhite_c29596_649	2B	A/C	703333584	695514017	711153151	5.94	1.26	2.63
181	TKW	FDS	IAAV5564	4B	A/G	655250234	649387367	661113101	4.16	0.72	0.67
182	TKW	FDS	Tdurum_contig47033_367	5B	C/T	657289470	652853215	661725725	4.06	-0.72	1.59
183	TKW	FDS	w SNP_Ku_c22358_32187765	6A	G/A	526408675	523001499	529815851	8.52	-1.10	4.17
184	TKW	FDS	w SNP_CAP11_c639_424059	7A	C/T	715946364	715946364	719541422	7.55	-2.35	3.98
185	TKW	FNS	RAC875_rep_c107984_187	4A	T/C	735878452	734404432	737352472	5.19	-1.36	4.92
186	TKW	FNS	Excalibur_rep_c101314_252	5B	C/T	438003877	433567622	442440132	4.10	-0.70	3.79
187	TKW	FNS	Tdurum_contig28010_191	6A	C/T	546197082	542789906	549604258	4.39	-0.99	2.75
188	TKW	CCDS	Tdurum_contig56331_545	2B	C/A	91076191	83256624	98895758	11.27	-9.96	8.24
189	TKW	CCNS	Kukri_c12534_559	1A	T/G	26057000	22931970	29182030	4.12	-1.30	6.57
190	TKW	CCNS	Tdurum_contig82242_224	3B	C/T	27343778	20217890	34469666	6.56	2.75	0.06
191	TKW	CCNS	w SNP_Ex_c2639_4899517	3B	A/G	675141992	668016104	682267880	4.45	2.73	2.89

\* Favorable alleles are in bold. MTA significant at FDR 5% was shown by gray color. Trt: Treatment, FDS: Field drought stress, FNS: Field non-stress, CCDS: Climate chamber drought stress, CCNS: Climate chamber non-stress. Chr: durum wheat chromosome representing A and B genome. Pos. (Mb<sup>a</sup>): physical position of SNP markers based on the recently released annotated sequences of durum wheat (cv. Svevo) RefSeq Release 1.0 and according to the International Durum Wheat Genome Sequencing Consortium (IDWGSC) of durum wheat (cv. Svevo) genome reference sequence (Maccaferri et al. 2019). LOD: logarithm of odds, LOD values with gray shade is significant at FDR 5%, %PVE: percentage of phenotypic variance explained. Lower class interval (LCI) and higher class interval (HCI).

**SUPPLEMENTARY FILES**

**Table S5. Summary of significant ( $-\log_{10}p \geq 4$ ) QTLs for grain biomass and related traits under drought stress and non-stress conditions in the durum wheat study panel. QTLs, Trait associated with, co-localized trait(s), Treatment, SNP marker, and QTL intervals for identified and the reported QTLs in bp.**

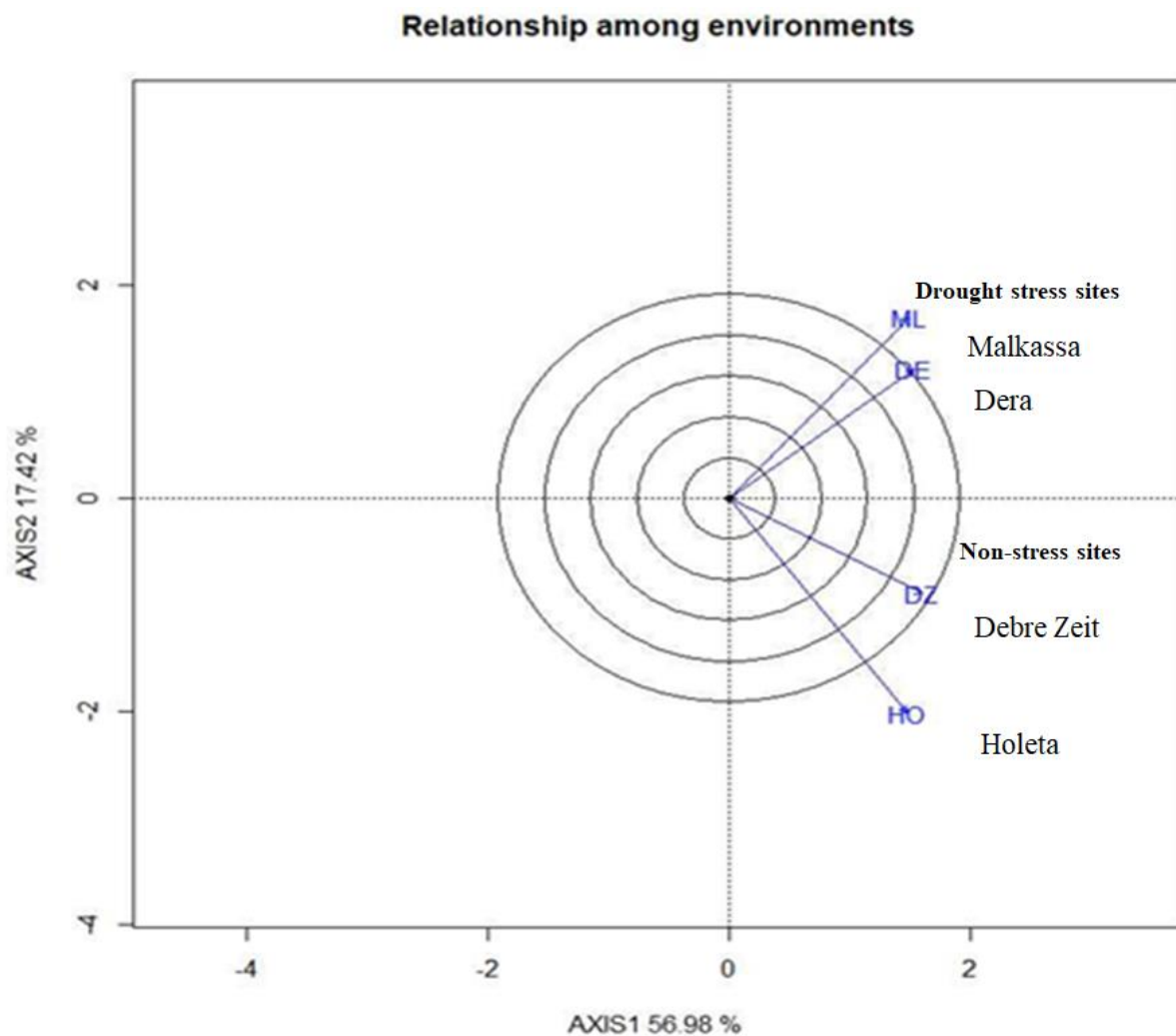
QTL	Trait associated	Co-localized trait(s)	Trt	SNP marker	Chromosome	Alleles	Position (bp)	QTL interval(s) (bp)		LOD	Effect size	% PVE	Reported QTL	QTL interval(s) (bp)	
								start	End						
1	GB	DGF	FDS	Kukri_c43410_348	1A	A/G	4.99E+08	4.96E+08	5.02E+08	7.00	2.97	2.08	-	-	
2	GB	DM	FDS	Excalibur_c8208_993	3B	A/G	4.23E+08	4.16E+08	4.31E+08	4.82	2.35	2.85	QTL0893_GY-Soriano et al 2017	419638287..563008547	
3	GB	SL,SPS	FDS	RFL_Contig5015_668	3B	T/C	7.52E+08	7.45E+08	7.6E+08	5.14	4.10	3.76	QTL0777_GY-Mengistu et al_2016	734725082..748314497,	
4	GB	SL	FNS	BS00037020_51	4B	G/T	5.67E+08	5.61E+08	5.73E+08	4.10	3.84	2.99	QTL499_3B-Maccafferi et al_2008b,	781655762..789335527	
5	GB	SL	CCDS	Ku_c39003_290	4B	G/T	5.99E+08	5.93E+08	6.05E+08	4.94	0.17	3.60	QTL1638_4B-Milner et al_2016_	533539066..587851058	
6	GB	HLDM,SPAD	CCDS	tp1b0056605_409	4B	A/C	6.65E+08	6.59E+08	6.71E+08	4.11	0.14	4.24	QTL677_4B-Patil et al_2013	599963582..613362327	
7	GB	SPAD	FNS	wsnp_Ex_c3940_7144946	6B	A/G	5.08E+08	5.06E+08	5.1E+08	4.38	5.86	4.13	QTL1606_6B-Marcotuli et al_2017	455758746..530320764	
8	GB	SL	FNS	BS00077891_51	7A	T/G	6.42E+08	6.38E+08	6.45E+08	4.31	-3.43	1.92	QTL0741_GY-Mengistu et al_2016	637203569..651255097	
9	DH		FDS	BS00094681_51	1A	T/C	3.68E+08	3.65E+08	3.71E+08	20.17	-9.85	1.12	QTL1619_1A-Milner et al_2016_	8114055..461341317	
10	DH		FNS	Ex_c6028_1602	1B	C/T	3.12E+08	3.08E+08	3.16E+08	4.54	1.02	2.73	QTL1620_1B-Milner et al_2016_	88740151..398680744,	
11	DH	TKW	FDS	tp1b0052408_1158	2A	C/T	7.17E+08	7.11E+08	7.23E+08	5.66	1.24	2.04	QTL1192_2A-Giunta et al_2018,	731958793..751045514	
12	DH	SL,SPAD	FNS	TA001195-0515	4A	A/C	47760186	46286166	49234206	5.00	-0.91	1.15	Zaim et al.2020	QTL0576_HD-Maccafferi et al_2011	25942682..56387718,
13	DH		FNS	wsnp_Ex_c58286_59646499	4A	T/C	5.14E+08	5.13E+08	5.16E+08	7.70	-5.44	3.18	QTL1633_4A-Milner et al_2016	40374238..442770858	
14	DH	HI	FDS	BS00010659_51	4B	T/C	5.41E+08	5.35E+08	5.47E+08	5.54	-0.87	1.62	QTL0576_HD-Maccafferi et al_2011	25942682..56387718	
15	DH	GB,SPAD,SL,HI	CCDS	RAC875_rep_c74471_125	6B	C/A	5570509	3197376	7943642	4.12	-2.34	3.71	QTL0590_HD-Maccafferi et al_2011	80052042..533539162	
16	DGF	DGF	FDS	Ra_e18323_183	1B	G/A	3.82E+08	3.78E+08	3.86E+08	4.24	0.74	3.26	QTL062_6B-Roncallo et al_2018,	91110891491,	
17	DGF	SL	FNS	wsnp_Ex_c64005_62987067	3B	T/C	7.4E+08	7.33E+08	7.47E+08	4.80	0.45	0.59	QTL0612_HD-Maccafferi et al_2011	6048149..22240725	
18	DGF	SPS,TKW,SPAD	FNS	BS00003760_51	7B	A/G	5.48E+08	5.44E+08	5.52E+08	6.03	1.00	3.31	QTL0868_GFD-Soriano et al_2017	542..14703065	
19	DM	DH,DGF,PH,SL	FDS	RAC875_c63624_753	1B	C/T	10778560	6967096	14590024	9.65	-0.74	5.52	-	-	
20	DM	SPAD	FDS	tp1b0028807_1268	2B	C/T	4.77E+08	4.69E+08	4.85E+08	7.54	0.94	4.38	-	-	
21	DM	HI	FDS	RAC875_rep_c69241_454	4A	A/G	101E+08	99474157	102E+08	4.33	-0.50	1.28	QTL0188_DM-Kidane et al_2017	70018656..442770858	
22	DM		CCNS	IAAV9048	5B	G/A	3.56E+08	3.52E+08	3.61E+08	4.41	-1.74	2.80	-	-	
23	DM	SPS	FDS	Excalibur_c9083_981	7A	A/G	2.64E+08	2.6E+08	2.67E+08	9.80	1.66	2.48	-	-	
24	DM		FNS	Ex_c6870_1704	7A	T/C	6.97E+08	6.93E+08	7.01E+08	5.82	1.00	3.15	QTL0829_DM-Mengistu et al_2016	718407476..728024500	
25	PH		FDS	wsnp_Ex_c25730_34991010	1A	A/G	5.71E+08	5.68E+08	5.74E+08	4.41	-0.88	1.47	(Mangani et al.2021)	-	

**SUPPLEMENTARY FILES**

26	PH	SL,DH,GB,DGF,SPS	FNS	Tdurum_contig15440_616	2B	T/C	21617081	13797514	29436648	4.04	1.17	2.71	(Arif et al. 2020, Chai et al. 2021)
27	PH	GB	FDS	Tdurum_contig11967_234	6B	C/T	4.6E+08	4.58E+08	4.63E+08	4.94	1.03	2.40	QTL0818_PH-Mengistu_et_al_2016, 55574028.60108612, (Hu et al. 2015, Mangani et al. 2021)
28	PH	SL	FNS	Excalibur_c33259_1379	7A	A/G	80864397	80864397	84459455	9.46	3.20	4.78	(Hu et al. 2015; Chai et al. 2021)
29	PH	SPAD	FNS	Ku_c25443_1454	7B	G/A	6.93E+08	6.89E+08	6.97E+08	7.93	4.06	4.53	(QTL0625_PH-Maccacferri_et_al_2011, 69311524..703941212 Chai et al. 2021)
42	SPAD		FNS	BS00066336_51	1A	G/T	3.39E+08	3.36E+08	3.42E+08	6.36	1.30	4.10	Huang et al. 2018
43	SPAD	DGF	FNS	BS00033469_51	1A	G/T	4.65E+08	4.62E+08	4.68E+08	4.69	0.97	2.47	Huang et al. 2018
44	SPAD	DGF,DM,SPS,HI	FNS	Kukri_c47131_569	1A	T/G	5.6E+08	5.57E+08	5.63E+08	4.07	-0.77	1.51	Huang et al. 2018
45	SPAD	HL,GB,DM,DH	FNS	CAP_1L_c5573_163	1A	G/A	5.83E+08	5.8E+08	5.86E+08	4.12	0.80	1.91	Huang et al. 2018
46	SPAD	HI	FNS	BS00062869_51	1B	G/A	6.24E+08	6.2E+08	6.28E+08	5.25	0.78	1.85	Huang et al. 2018
47	SPAD		CCNS	wspn_CAP7_rep_c12606_53167972A	2A	A/G	7.6E+08	7.54E+08	7.66E+08	5.13	4.43	3.32	Huang et al. 2018
48	SPAD		FNS	Tdurum_contig55335_316	2B	C/T	131E+08	123E+08	139E+08	4.00	-0.64	2.16	Hu et al. 2015
49	SPAD	DH	CCDS	wspn_Ex_c46217_51790399	3A	C/T	165E+08	158E+08	172E+08	5.87	-10.15	1.55	Huang et al. 2018
50	SPAD	DM,HI	FNS	Kukri_c25454_496	5B	G/A	4.87E+08	4.82E+08	4.91E+08	5.47	-0.91	1.98	Huang et al. 2018
51	SPAD		CCNS	Excalibur_c28771_400	6B	C/T	2.22E+08	2.2E+08	2.25E+08	4.83	4.17	6.33	Huang et al. 2018
52	SPAD	PH	CCNS	Kukri_c25082_328	6B	T/C	6.85E+08	6.82E+08	6.87E+08	4.11	4.64	2.20	Huang et al. 2018
53	SPAD	DH,SL	CCNS	RAC875_c21489_908	7B	C/T	6.18E+08	6.14E+08	6.23E+08	5.11	4.55	4.47	Huang et al. 2018
54	SL	DGF,PH	FNS	Kukri_rep_c117487_334	2B	G/A	70922954	63103387	78742521	6.68	0.39	0.27	Hu et al. 2015
55	SL		FNS	Ex_c30319_438	4A	G/A	177E+08	175E+08	178E+08	7.66	-0.49	11.83	Hu et al. 2015
56	SL	DM	FDS	Excalibur_c15838_535	5A	A/G	52717033	46541801	58892265	4.53	-0.12	3.03	QTL068_PH-Giraklo_et_al_2016, 613838400..630533637, QTL0628_PH-Maccacferri_et_al_2011, 69311524..703941212, QTL0940_PH-Soriano_et_al_2017, 691900103..702547875, QTL0625_PH-Maccacferri_et_al_2011, 69311524..703941212
57	SL	GB,HL,DGF	FDS	Kukri_rep_c116526_98	5A	C/T	112E+08	106E+08	118E+08	5.50	0.14	3.14	Hu et al. 2015
58	SL	SPAD	CCDS	wspn_BF473658B_Ta_2_1	5B	A/G	125E+08	12E+08	129E+08	4.15	3.32	2.80	-
59	SL	TKW,SPAD	FNS	wspn_Ex_c5839_10246915	7A	C/T	7.09E+08	7.1E+08	7.1E+08	4.46	0.16	1.89	QTL2046_7B-Thanh_et_al_2013, 459321833..538036086 Hu et al. 2015
60	SL		FNS	Excalibur_rep_c67533_78	7B	C/A	145E+08	141E+08	149E+08	4.87	0.18	3.47	Hu et al. 2015
61	SL	TKW,DH,HI	FNS	BS00059062_51	7B	T/C	5.3E+08	5.26E+08	5.34E+08	5.49	-0.37	0.11	Hu et al. 2015
62	SPS	DGF	FDS	Tdurum_contig27880_75	2B	G/A	5.22E+08	5.14E+08	5.3E+08	4.70	0.82	0.86	QTL0766_KNS-Mengistu_et_al_2016, 12382976..24935557, QTL1846_2B-Roncallo_et_al_2018, 41975105..70601229
63	SPS	GB,HI	FNS	BS00043055_51	3B	C/T	7.49E+08	7.42E+08	7.56E+08	5.32	0.76	2.16	QTL1899_3B-Roncallo_et_al_2018, 776512971.789335527
64	SPS	SPAD,DGF,SPAD,PH	FDS	Excalibur_c33274_498	6A	C/T	6.09E+08	6.05E+08	6.12E+08	4.21	0.53	0.97	QTL1961_6A-Roncallo_et_al_2018, 604310428..615641791, QTL1297_6A-Giunta_et_al_2018, 601615123..615641791
65	SPS	SPAD	FNS	Ra_c4568_960	6B	A/C	6.12E+08	6.09E+08	6.14E+08	4.08	-1.31	2.19	QTL0723_KNS-Mangini_et_al_2018, 601135266..645996827
66	SPS	TKW	CCDS	BS00067983_51	6B	A/C	6.59E+08	6.57E+08	6.61E+08	4.17	1.03	8.02	-
67	SPS		CCDS	GENE-4703_160	7A	A/G	2.12E+08	2.09E+08	2.16E+08	4.25	1.34	5.61	QTL1979_7A-Roncallo_et_al_2018, 159412663..534866316
30	HI	DGF	FDS	Ra_c2895_591	1A	G/T	4.54E+08	4.51E+08	4.57E+08	6.61	-1.34	4.64	-
31	HI		FDS	TA004947-0758	1B	A/C	6.24E+08	6.2E+08	6.28E+08	5.92	2.53	5.16	Arif et al. 2020
32	HI	HI	CCDS	Tdurum_contig57927_460	1B	G/A	3.49E+08	3.45E+08	3.52E+08	4.27	0.06	6.39	-
33	HI	SPS,TKW,SPAD	FDS	BobWhite_c2022_245	2A	G/A	29222931	23089531	35356331	4.29	1.07	1.13	QTL1837_2A-Roncallo_et_al_2018, 58512829..73236728
34	HI	SPAD,DH	FDS	Tdurum_contig42013_538	2A	T/C	7.71E+08	7.65E+08	7.77E+08	4.50	-1.58	2.16	QTL1695_2A-Peleg_et_al_2009b, 80154046..591261191
35	HI		CCNS	RAC875_c8045_231	2B	T/C	198E+08	19E+08	2.05E+08	5.93	0.03	4.59	-
36	HI		FNS	Kukri_c33640_640	3A	C/T	6.3E+08	6.23E+08	6.38E+08	5.53	-1.26	2.67	-
37	HI	DGF,DH,GB,SPAD	CCNS	Tdurum_contig10759_260	5A	G/A	5.36E+08	5.3E+08	5.42E+08	4.28	0.03	0.94	QTL1712_6B-Peleg_et_al_2009b, 42019483..139081270
38	HI		FNS	wspn_Ex_c7907_13427724	6B	A/G	115E+08	113E+08	118E+08	8.35	2.47	0.77	Arif et al. 2020
39	HI	DH,SPS	FNS	wspn_BF29311B_Ta_2_3	6B	C/A	4.08E+08	4.05E+08	4.1E+08	5.43	1.17	2.78	Arif et al. 2020
40	HI	GB,SL,TKW	CCNS	wspn_Ex_c3858_7011837	6B	T/C	4.39E+08	4.37E+08	4.42E+08	6.01	-0.02	2.61	-
41	HI		FNS	Tdurum_contig14075_328	7A	T/C	59620092	59620092	63215150	4.05	1.35	1.78	Arif et al. 2020
68	TKW		CCDS	Tdurum_contig56331_545	2B	C/A	91076191	83256624	98895758	11.27	-9.96	8.24	QTL0683_TKW-Mangini_et_al_2018, 99222798..172750090
69	TKW		CCNS	wspn_Ex_c2639_4899517	3B	A/G	6.75E+08	6.68E+08	6.82E+08	4.45	2.73	2.89	QTL0686_TKW-Mangini_et_al_2018, 742628705..774081325
70	TKW	DH,HI	FNS	RAC875_rep_c107984_187	4A	T/C	7.36E+08	7.34E+08	7.37E+08	5.19	-1.36	4.92	QTL0695_TKW-Mangini_et_al_2018, 720935666..736870383

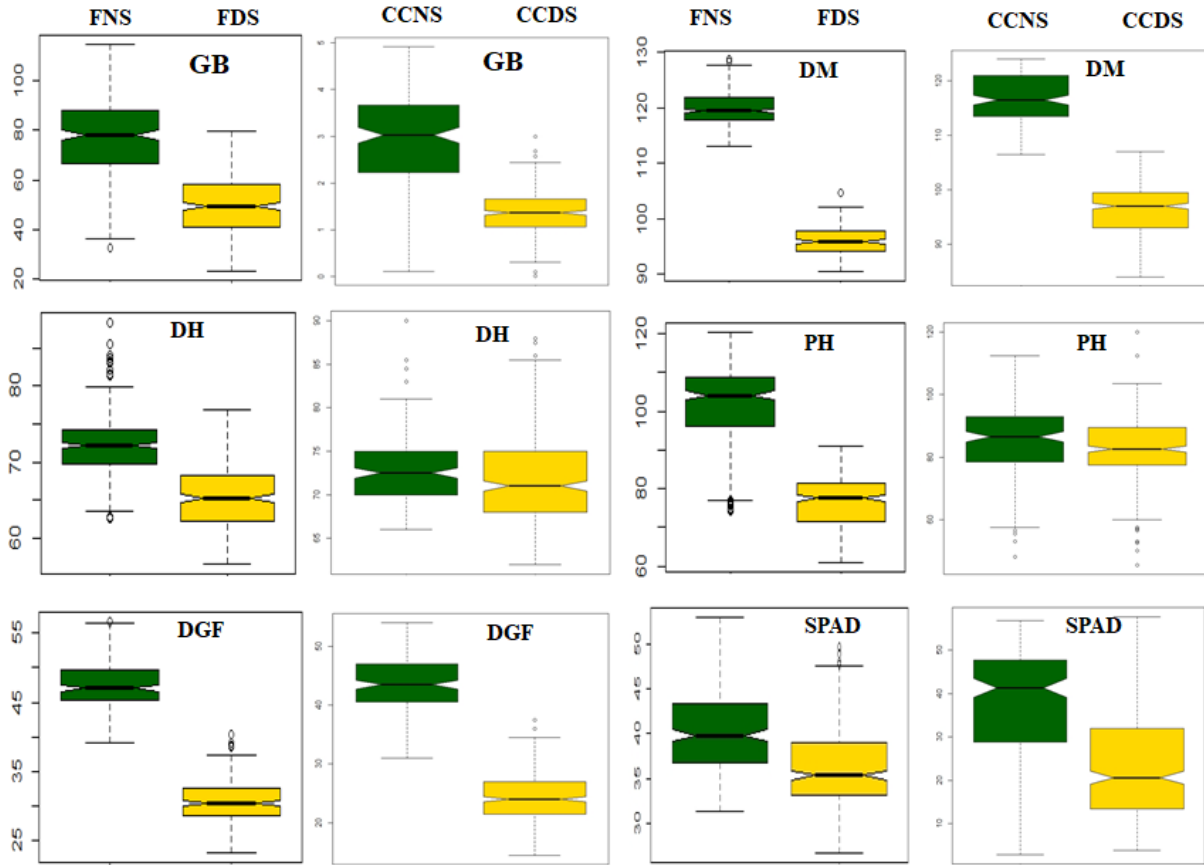


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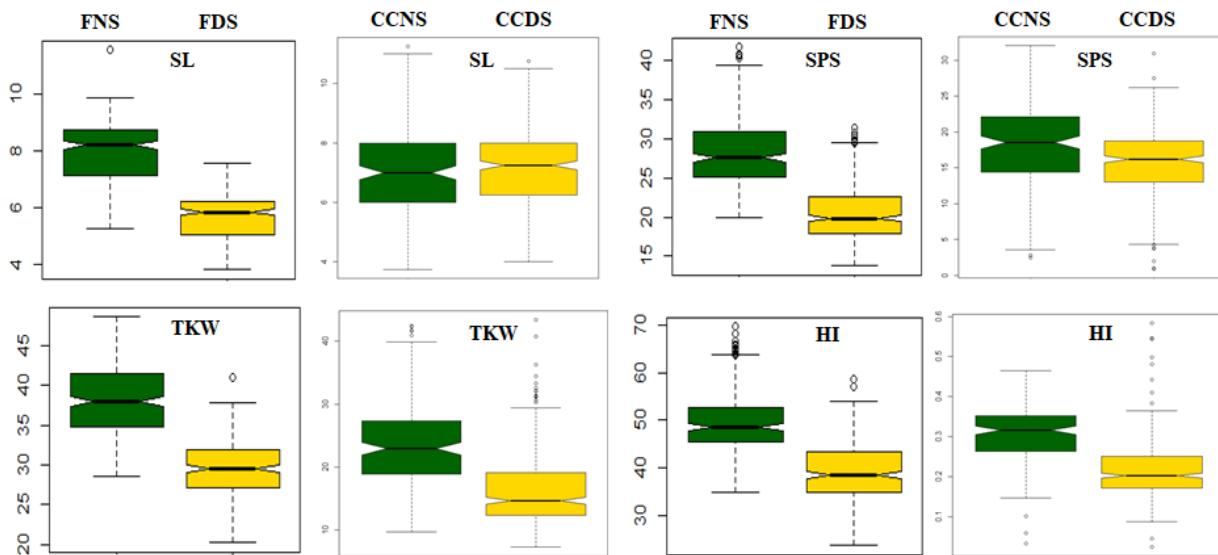


**Figure S1** Biplot analysis for the relationship among environments explained 74.40% variation by PCA1 and PCA2, where drought stress sites closely clustered and high yield potential sites were grouped.

SUPPLEMENTARY FILES



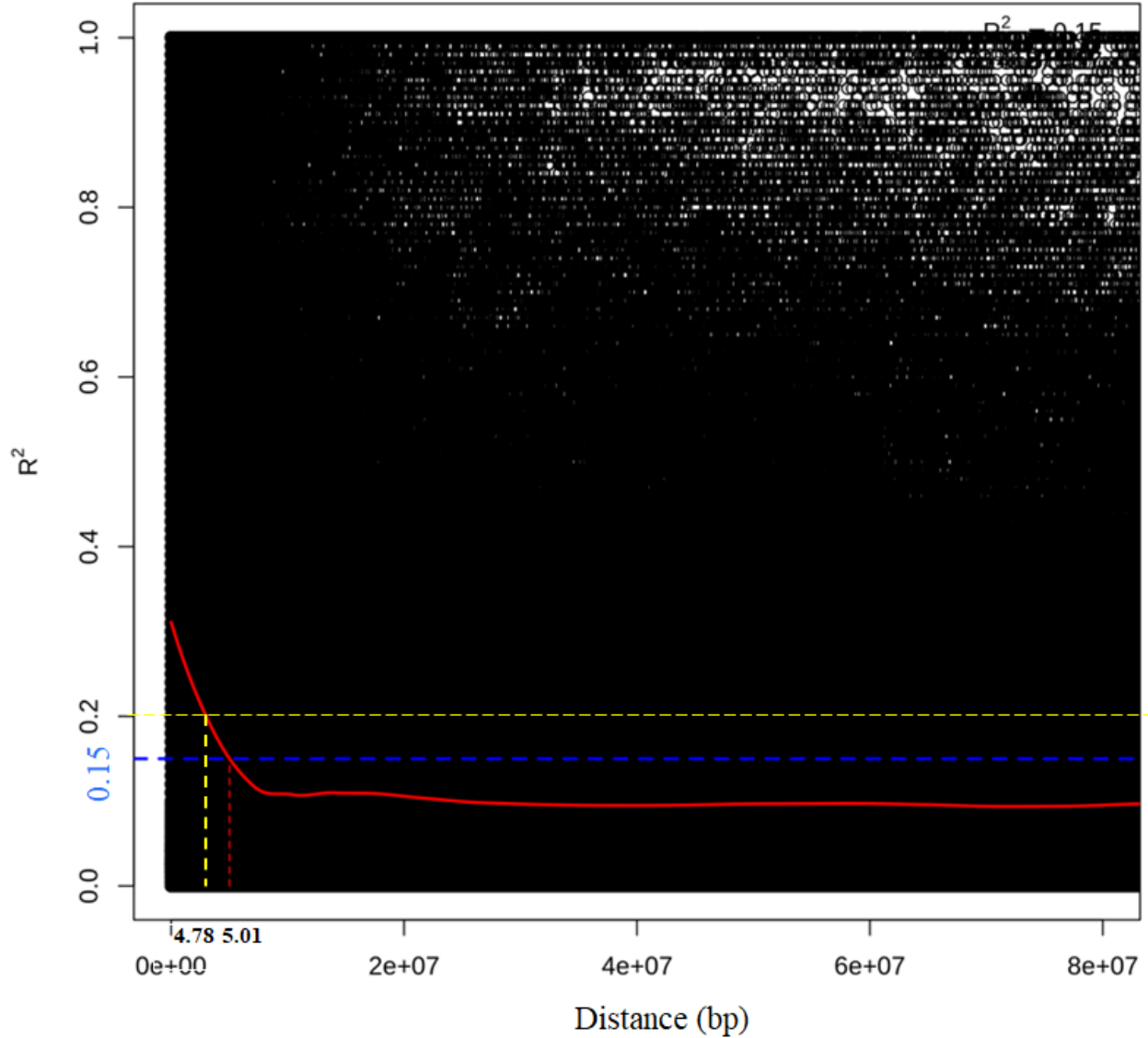
**Figure S2** Box plots of the means of yield and related traits of durum wheat accessions under non-stress and drought stress conditions. FNS: Field non-stress, FDS: Field drought stress, CCNS: Climate chamber non-stress = 70% soil water capacity (SWC), CCDS: Climate chamber drought stress = 20% SWC. GB: Grain biomass, DH: Days to heading, DGF: days to grain filling, DM, Days to maturity, PH: Plant height, SPAD. The middle line indicates the median, the box indicates the range of the 25th and 75th percentiles of the total data, the whiskers indicate the interquartile range, and the outer dots are outliers.



**Figure S3.** Boxplots of the means of yield-related traits of durum wheat accessions under non-stress and drought stress conditions. FNS: Field non-stress, FDS: Field drought stress, CCNS: Climate chamber non-stress = 70% soil water capacity (SWC), CCDS: Climate chamber drought stress = 20% SWC. SL: Spike length, SPS: Seed per spike, TKW: Thousand kernel

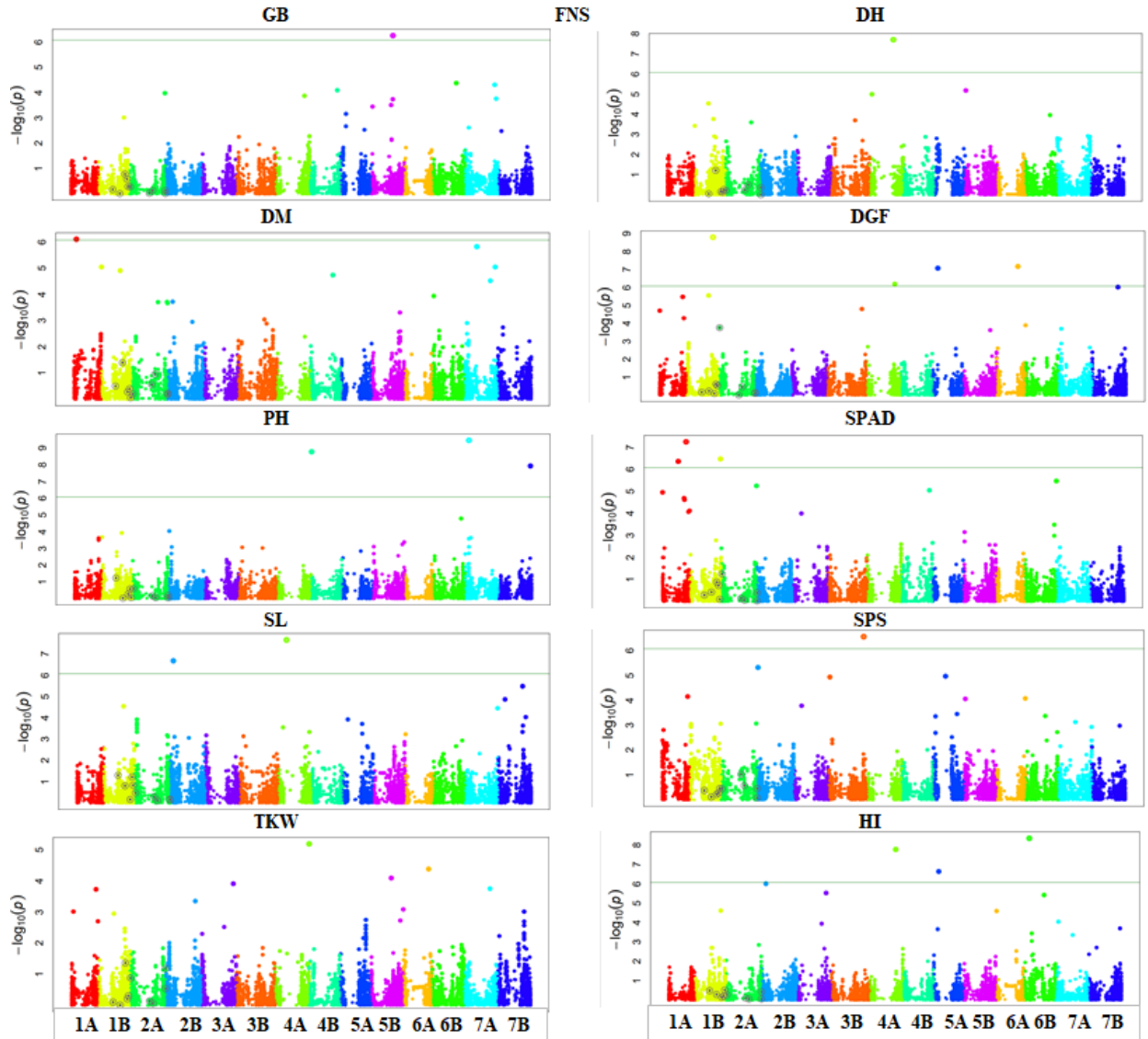
## SUPPLEMENTARY FILES

weight, HI: Harvest index. The middle line indicates the median, the box indicates the range of the 25th and 75th percentiles of the total data, the whiskers indicate the interquartile range, and the outer dots are outliers.



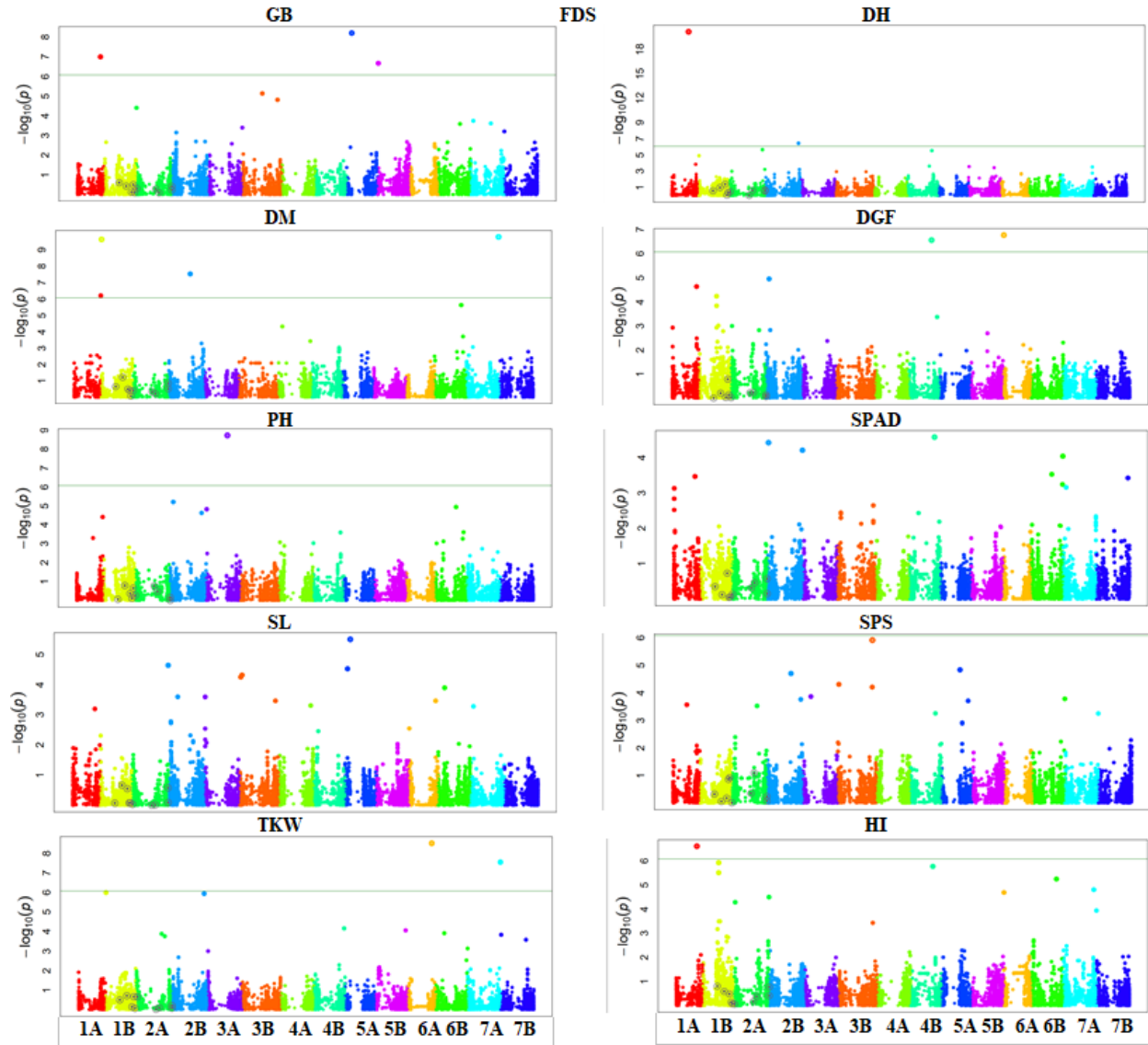
**Figure S4.** Biplot of pairwise SNPs for genome-wide linkage disequilibrium (LD) decay. Genetic distance in bp is plotted against the LD estimate ( $r^2$ ) for pairs of markers. The red solid curve represents the smoothing spline regression model fitted to LD decay. The horizontal blue dashed line represents the  $r^2$  value of the genome ( $r^2 = 0.15$ ), and the vertical red dashed line represents the physical distance at (5.0 Mb) at which the  $r^2$  intersects with the LD decay curve. The horizontal yellow line represents the standard critical  $r^2$  value of the genome ( $r^2 = 0.20$ ), the vertical yellow dashed line represents the genetic distance (4.78 Mb) at which the standard critical  $r^2$  intersects with the LD decay curve.

SUPPLEMENTARY FILES



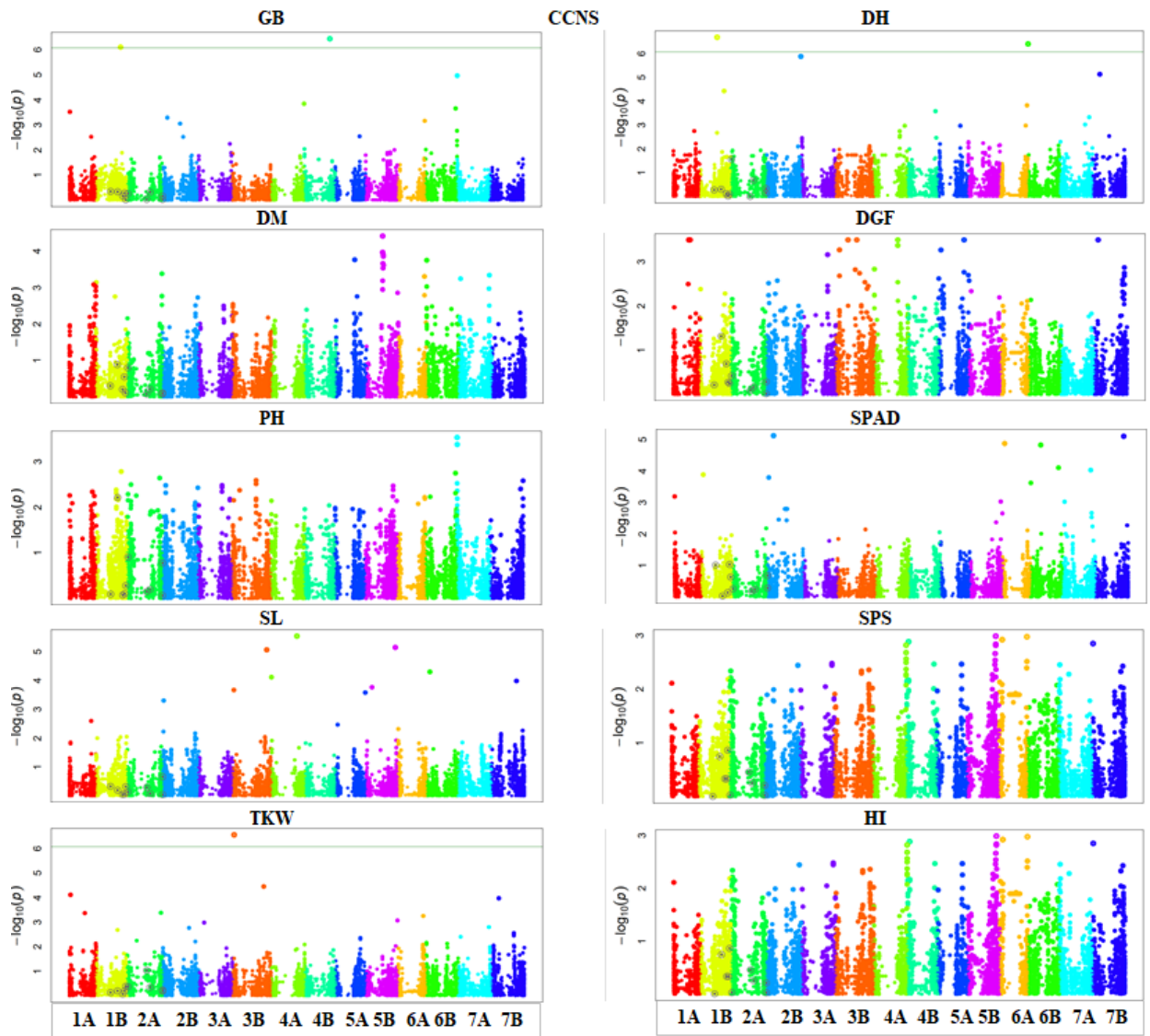
**Figure S5.** Manhattan plots for yield-related traits under FNS condition using GAPIT in R (Lipka et al. 2012). The X-axis represents the physical position of the SNPs on the chromosomes, and the Y-axis shows the  $-\log_{10}p$ . MTA significant at  $-\log_{10}p \geq 6$  (solid green line).

SUPPLEMENTARY FILES



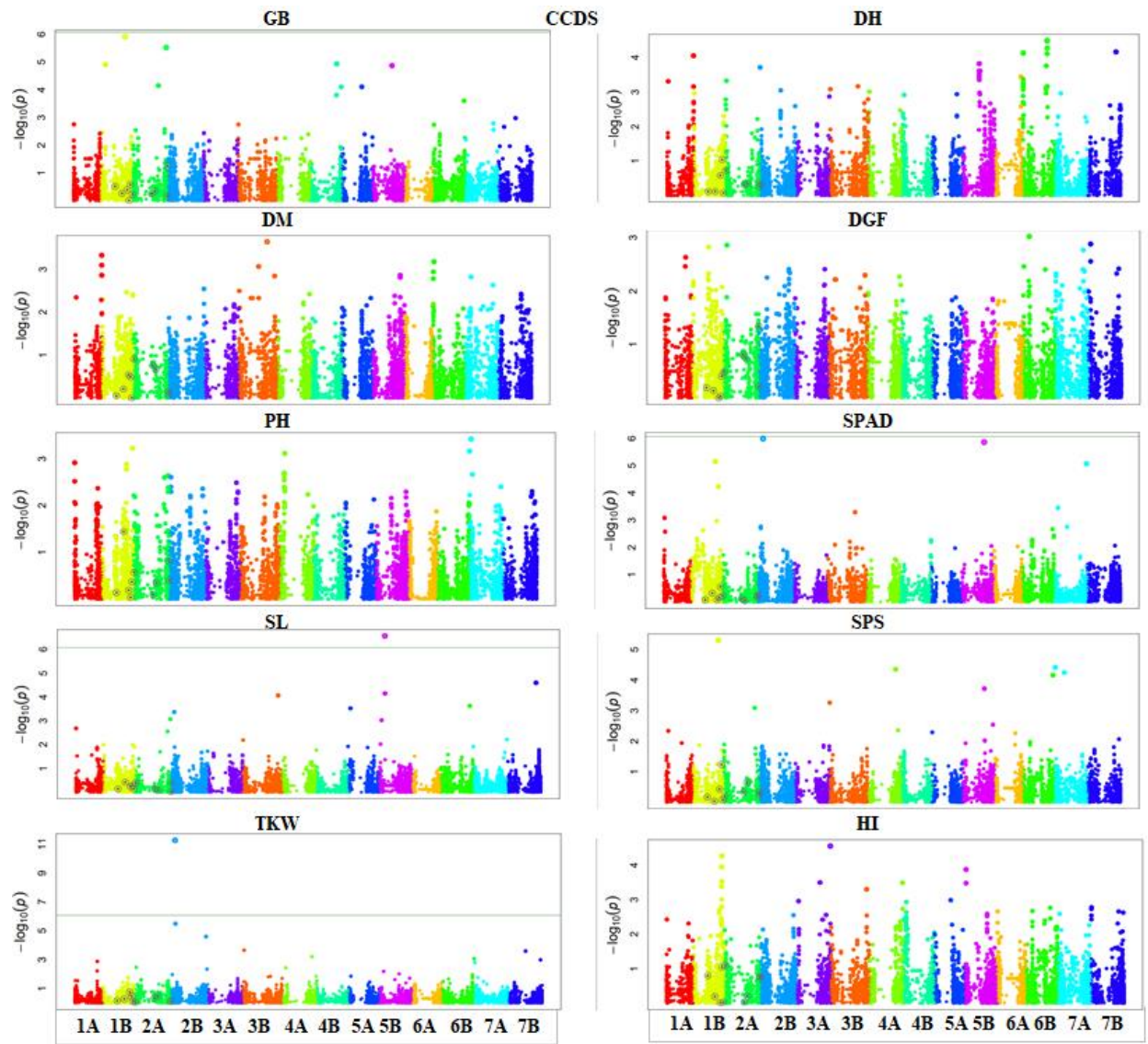
**Figure S6.** Manhattan plots for yield-related traits under FDS condition using GAPIT in R (Lipka et al., 2012). The X-axis represents the physical position of the SNPs on the chromosomes, and the Y-axis shows the  $-\log_{10}p$ . MTA significant at  $-\log_{10}p \geq 6$  (solid green line).

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**Figure S7.** Manhattan plots for yield-related traits under CCNS condition using GAPIT in R (Lipka et al., 2012). The X-axis represents the physical position of the SNPs on the chromosomes, and the Y-axis shows the  $-\log_{10}p$ . MTA significant at  $-\log_{10}p \geq 6$  (solid green line).

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**Figure S8.** Manhattan plots for yield-related traits under CCDS condition using GAPIT in R (Lipka et al., 2012). The X-axis represents the physical position of the SNPs on the chromosomes, and the Y-axis shows the  $-\log_{10}p$ . MTA significant at  $-\log_{10}p \geq 6$  (solid green line).

SUPPLEMENTARY FILES

**Publication 2.3)** Negisho K, Shibu S, Matros A, Pillen K, Ordon F, & Wehner G. (2022b). Association Mapping of Drought Tolerance Indices in Ethiopian Durum Wheat (*Triticum turgidum ssp. durum*). *Frontiers in Plant Sciences* 13:838088. <https://doi.org/10.3389/fpls.2022.838088>.

**Table S1.** Least Squares Means (lsmeans) comparison of drought tolerance indices based on grain yield of durum wheat study pan el under FDS and FNS conditions combined from three seasons (2016-2018). Yellow formatting indicates top five selected accessions based on combined ranks of DSI, RDI, TOL and YSI (A), as well as based on combined ranks of STI and GMP (B).

A														B													
Pedigree	Taxa	Region	Geno	AccNO	GY_FNS	GY_FDS	DSI	Rank	RDI	Rank	TOL	Rank	YSI	Rank	Pedigree	Taxa	Region	Geno	AccNO	GY_FNS	GY_FDS	STI	Rank	GMP	Rank		
Landrace	G04	Oromia	DV004	222484	44.64	47.32	-0.07	1	1.05	1	2.80	3	1.06	1	CCSS091002705-099Y-028M-8Y-0M-04Y-0B	G270	CM	C00	547973	101.96	79.92	137	1	50.27	1		
Landrace	G094	Oromia	DV082	222387	56.05	54.38	0.08	2	1.51	2	1.67	2	0.97	2	Landrace	G060	Oromia	DV033	204566	114.63	66.89	123	2	87.56	2		
Advanced	G018	DZAPC	DZ004	DZAPC	32.75	31.51	0.11	3	1.5	3	1.24	1	0.96	3	Landrace	G608	Oromia	DV090	222272	106.19	71.08	127	3	88.88	3		
CCSS091002705-099Y-048M-7Y-0M-04Y-0B	G297	CM	C07	548030	74.65	79.92	0.14	4	1.44	4	3.83	4	0.96	4	Landrace	G003	Amhara	DV024.2	222894.2	99.13	74.62	124	4	86.01	4		
Landrace	G045	Oromia	DV082	222432	53.74	49.49	0.22	5	1.43	5	4.25	5	0.92	5	CCSS091002705-099Y-028M-8Y-0M-04Y-0B	G271	CM	C00	548002	101.9	64.41	12	5	84.52	5		
Landrace	G023	Oromia	DV029.2	204560.2	70.3	63.29	0.29	8	1.4	7	7.02	11	0.9	6	CCSS091002705-099Y-028M-8Y-0M-04Y-0B	G201	CM	C041	548465	99.21	71.99	12	6	84.51	6		
Landrace	G004	Tigray	DV248	239124	76.91	69.3	0.28	7	1.8	9	7.61	2	0.9	7	CCSS091002803-099Y-028M-8Y-0M-04Y-0B	G294	CM	C034	547989	108.31	62.34	114	7	82.17	7		
Landrace	G092	Amhara	DV002	7961	60.35	54.47	0.27	6	1.41	6	5.98	7	0.9	8	CCSS091002803-099Y-028M-8Y-0M-04Y-0B	G207	CM	C047	548690	89.64	74.44	112	8	81.69	8		
Mamouli1	G017	DZAPC	View	View	55.41	48.13	0.37	9	1.35	9	7.20	14	0.87	9	CCSS091002925-099Y-028M-8Y-0M-04Y-0B	G204	CM	C004	547732	91.19	71.07	105	9	80.5	9		
Landrace	G015	Tigray	DV245	239121	66.35	74.09	0.40	13	1.34	12	12.26	31	0.86	10	CCSS091002925-099Y-027M-25Y-0M-04Y-0B	G293	CM	C033	547988	88.26	73.41	109	10	80.49	10		
Advanced	G020	DZAPC	DZ005	DZAPC	44.8	38.73	0.38	10	1.35	10	6.07	8	0.86	11	CCSS091002415-099Y-022M-17Y-0M-04Y-0B	G268	CM	C008	547944	92.17	69.75	108	11	80.18	11		
Landrace	G025	Amhara	DV260	239139	36.72	31.73	0.38	11	1.35	11	4.99	6	0.86	12	CCSS091002415-099Y-022M-17Y-0M-04Y-0B	G267	CM	C007	547944	95.54	67.38	108	12	80.11	12		
Landrace	G077	Oromia	DV020	204484	51.22	44.06	0.39	12	1.34	13	7.16	13	0.86	13	Landrace	G015	Tigray	DV245	239121	66.35	74.09	108	13	79.99	13		
Landrace	G021	Amhara	DV003.1	6333-1	70.4	59.76	0.42	16	1.32	16	10.64	21	0.85	14	Landrace	G039	Oromia	DV059	226819	89.26	70.74	106	14	79.46	14		
Landrace	G006	Oromia	DV023.2	204489.2	69.22	59.3	0.41	14	1.33	14	9.32	20	0.85	15	Landrace	G056	Tigray	DV252	239120	95.39	69.12	106	15	79.42	15		
CCSS091002705-099Y-022M-25Y-0M-04Y-0B	G300	CM	C040	548462	84.99	71.83	0.43	17	1.32	17	10.36	26	0.85	16	Landrace	G202	Oromia	DV030	204563	102.44	59.95	104	16	78.75	16		
CCSS091002947-099Y-023M-24Y-0M-04Y-0B	G308	CM	C049	548639	75.66	64.73	0.41	15	1.33	15	11.33	25	0.85	17	Landrace	G033	Oromia	DV039	243438	94.29	69.71	104	17	79.71	17		
Landrace	G008	Tigray	DV247	239123	76.72	64.6	0.44	19	1.31	18	12.12	28	0.84	18	Landrace	G096	Amhara	DV061	226817	100.42	56.31	103	18	78.14	18		
CCSS091002415-099Y-028M-8Y-0M-04Y-0B	G286	CM	C036	548017	78.23	66.03	0.44	18	1.31	19	12.2	29	0.84	19	CCSS091002925-099Y-027M-25Y-0M-04Y-0B	G300	CM	C040	548462	84.99	71.83	103	19	78.13	19		
Landrace	G105	Amhara	DV219.1	219371.1	51.21	42.44	0.49	24	1.29	23	6.77	17	0.83	20	CCSS091002705-099Y-028M-8Y-0M-04Y-0B	G288	CM	C028	539157	87.82	69.09	102	20	77.89	20		
Landrace	G254	Tigray	DV246	239122	57.03	47.54	0.46	20	1.3	20	9.49	18	0.83	21	Landrace	G201	Oromia	DV030	204562	102.02	65.18	102	21	77.62	21		
CCSS091002415-099Y-028M-8Y-0M-04Y-0B	G289	CM	C039	547949	71	59.85	0.47	21	1.3	21	10.95	26	0.83	22	CCSS091004493-099Y-008M-2Y-0M-04Y-0B	G309	CM	C049	548952	89.76	66.67	101	22	77.36	22		
Landrace	G282	CM	C022	537893	76.39	63.26	0.48	25	1.29	24	13.13	35	0.83	23	Landrace	G028	Amhara	DV031	226207	93.51	63.72	1	23	77.19	23		
CCSS091002925-099Y-027M-25Y-0M-04Y-0B	G293	CM	C033	547988	89.26	75.41	0.47	22	1.3	22	14.95	45	0.83	24	CCSS091002925-099Y-028M-8Y-0M-04Y-0B	G305	CM	C045	548462	85.3	69.83	1	24	77.89	24		
CCSS091002927-099Y-028M-8Y-0M-04Y-0B	G297	CM	C047	548639	89.64	74.44	0.47	23	1.29	25	15.2	47	0.83	25	Landrace	G078	Oromia	DV043	243556	95.4	62.39	1	25	77.03	25		
Landrace	G059	Oromia	DV007	6557	39.21	31.3	0.51	27	1.28	26	6.91	9	0.82	26	Landrace	G024	Oromia	DV094	208261	98.2	60.1	0.99	26	76.82	26		
Landrace	G091	Amhara	DV012.2	220080.2	65.13	53.63	0.49	28	1.28	27	11.5	24	0.82	27	Landrace	G115	Oromia	DV097.1	222462.1	106.3	55.45	0.99	27	76.77	27		
CCSS091003037-099Y-028M-8Y-0M-04Y-0B	G305	CM	C045	548462	85.3	69.83	0.51	28	1.27	30	15.47	49	0.82	28	Landrace	G220	Amhara	DV055	226807	99.24	59.32	0.99	28	76.73	28		
Advanced	G005	DZAPC	DZ008	DZAPC	36.31	29.3	0.54	35	1.28	31	7.01	9	0.81	29	CCSS091002925-099Y-028M-8Y-0M-04Y-0B	G290	CM	C030	547919	96.74	59.43	0.99	29	76.8	29		
Advanced	G006	DZAPC	DZ009	DZAPC	37.87	30.8	0.52	29	1.27	28	7.07	12	0.81	30	Landrace	G250	Oromia	DV227.1	238794.1	90.07	65.09	0.99	30	76.57	30		
Landrace	G147	Oromia	DV071	226806	81.73	66.36	0.53	33	1.26	32	15.57	51	0.81	31	CCSS091003037-099Y-028M-27Y-0M-04Y-0B	G303	CM	C043	548605	90.66	64.36	0.98	31	76.39	31		
Landrace	G177	Oromia	DV046	243377	65.24	52.83	0.53	32	1.26	33	12.41	32	0.81	32	Landrace	G034	Oromia	DV069	222289	101.18	57.57	0.98	32	76.32	32		
CCSS091002705-099Y-028M-8Y-0M-04Y-0B	G273	CM	C00	548465	74.35	60.02	0.54	34	1.26	34	14.33	42	0.81	33	Landrace	G065	Amhara	DV216	21435	100.22	57.55	0.97	33	75.95	33		
CCSS091002947-099Y-023M-24Y-0M-04Y-0B	G287	CM	C027	539800	62.81	67.29	0.52	30	1.27	29	15.52	50	0.81	34	CCSS091003037-099Y-028M-12Y-0M-04Y-0B	G304	CM	C044	548823	89.05	64.89	0.97	34	75.9	34		
CCSS091002945-099Y-053M-12Y-0M-04Y-0B	G299	CM	C029	548097	76.18	61.82	0.53	31	1.26	35	14.36	43	0.81	35	Landrace	G095	Tigray	DV243	239119	95.17	60.2	0.96	35	75.69	35		
Landrace	G149	Oromia	DV021	204495	74.42	59.82	0.56	36	1.25	36	14.6	44	0.8	36	Landrace	G181	SNMP	DV108	226237	101.99	56.23	0.96	36	75.58	36		
Landrace	G183	Amhara	DV071	222346	69.07	54.6	0.55	37	1.25	37	13.47	39	0.8	37	Landrace	G081	Oromia	DV067	226891	100.98	56.52	0.96	37	75.55	37		
Landrace	G187	Oromia	DV193	226351	61.8	49.56	0.55	38	1.25	38	12.24	30	0.8	38	CCSS091002925-099Y-028M-8Y-0M-04Y-0B	G282	CM	C002	526237	86.35	64.42	0.96	38	75.44	38		
Advanced	G209	DZAPC	DZ002	DZAPC	38.11	30.39	0.57	39	1.24	40	7.72	16	0.8	39	CCSS091002925-099Y-028M-8Y-0M-04Y-0B	G291	CM	C031	547963	99.03	57.36	0.96	39	75.37	39		
Landrace	G053	Amhara	DV023	219541	62.77	49.34	0.60	43	1.22	44	13.43	38	0.79	40	Landrace	G122	Oromia	DV099	222469	89.95	62.96	0.95	40	75.25	40		
Landrace	G089	Oromia	DV080	226802	66.47	52.82	0.57	40	1.24	39	13.05	40	0.79	41	Landrace	G195	Amhara	DV026	222732	96.34	58.73	0.95	41	75.22	41		
CCSS091003037-099Y-028M-8Y-0M-04Y-0B	G288	CM	C028	539157	87.82	69.09	0.60	42	1.23	42	16.73	72	0.79	43	Landrace	G287	CM	C027	539800	62.81	67.29	0.94	42	74.85	42		
Landrace	G102	Amhara	DV268	239584	72.31	56.3	0.62	50	1.21	50	16.01	54	0.78	44	Landrace	G113	Tigray	DV257	239155	92.25	60.82	0.93	44	74.5			





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Landrace	G229	Amhara	DV059	226820	64.78	42.36	0.97	133	102	102	22.42	102	0.65	142	Landrace	G432	Amhara	DV010	203776	72.36	53.63	0.65	142	62.28	142
Landrace	G243	Amhara	DV207	239573	66.45	42.96	0.99	144	101	144	23.49	111	0.65	143	CDSS091004235-099Y-020M-01V-0M-04Y-0E	G260	CM	C020	537803	81.87	47.96	0.65	143	62.02	143
CDSS09100932T-099Y-020M-01V-0M-04Y-0E	G275	CM	C015	548526	69.24	57.7	0.99	143	101	145	31.54	100	0.65	144	Landrace	G216	Amhara	DV075	222627	67.01	43.68	0.65	144	61.93	144
CDSS091002865-099Y-030M-12V-0M-04Y-0E	G295	CM	C035	547989	91.11	59.6	0.97	132	102	105	31.51	106	0.65	145	DZ-2212	G003	DZARC	Metajo	Metajo	79.46	47.66	0.64	145	61.84	145
Advanced	G006	DZARC	DZ209	DZARC	49.07	31.26	1.01	95	0.99	92	17.81	63	0.64	147	Landrace	G048	Oromia	DV220	236981	76.46	49.69	0.64	146	61.51	146
Landrace	G032	Oromia	DV023-1	204568-1	67.6	56	1.01	95	1	147	31.6	103	0.64	149	Landrace	G018	Amhara	DV159	226331	77.33	48.44	0.63	147	61.2	147
Landrace	G041	SNMP	DV005	8436	60.31	51.11	1.02	95	0.92	93	28.2	109	0.64	149	Landrace	G067	Amhara	DV003-2	6332-2	74.02	50.37	0.63	149	61.06	149
DZ-2385	G089	DZARC	Asasa	Asasa	74.74	46.05	1.00	148	1	148	28.63	137	0.64	150	Landrace	G063	Amhara	DV962-1	226838-1	79.89	46.73	0.63	149	61.02	149
Landrace	G089	Amhara	DV017	222632	59.35	37.74	1.02	93	0.99	95	21.61	93	0.64	151	Landrace	G053	Amhara	DV071	222346	68.07	54.6	0.63	150	60.96	150
CDSS091000375-099Y-030M-01V-0M-04Y-0E	G265	CM	C005	547724	71.9	45.92	1.01	149	1	149	25.89	134	0.64	152	Landrace	G018	Amhara	DV966-1	226834-1	81.82	45.45	0.62	151	60.87	151
CDSS091005525-099Y-030M-12V-0M-04Y-0E	G283	CM	C023	538033	66.30	55.61	0.99	147	1	150	30.72	101	0.64	153	Landrace	G064	Oromia	DV079	229524	73.56	50.08	0.62	152	60.7	152
Landrace	G004	Oromia	DV066	226876	82.54	52.29	1.02	94	0.99	92	30.85	171	0.63	154	Landrace	G075	Amhara	DV200-2	23936-2	74.29	49.36	0.62	153	60.6	153
Landrace	G007	Oromia	DV081	222592	79.67	49.99	1.04	92	0.98	98	23.69	164	0.63	155	Landrace	G223	Amhara	DV064	226944	77.52	47.36	0.62	154	60.59	154
Landrace	G039	Oromia	DV093	222433	75.47	47.2	1.05	95	0.97	95	26.27	149	0.63	156	Landrace	G078	Oromia	DV155	226301	76.92	47.72	0.62	155	60.55	155
Landrace	G043	Oromia	DV040	243033	65.4	53.30	1.05	96	0.97	96	32.02	193	0.63	157	Landrace	G068	Amhara	DV052	24958	70.33	46.79	0.62	156	60.54	156
Landrace	G051	Tigray	DV128	223257	81.92	51.6	1.03	95	0.98	99	30.32	176	0.63	158	Landrace	G244	Amhara	DV209	23935	72.04	50.4	0.61	157	60.28	157
Landrace	G055	Tigray	DV243	239819	85.17	60.2	1.03	95	0.97	94	34.97	213	0.63	159	Landrace	G093	Oromia	DV066	222398	98.08	36.97	0.61	158	60.22	158
Landrace	G087	Amhara	DV074	208271	59.9	37.3	1.03	95	0.98	90	21.68	97	0.63	160	Landrace	G16	Oromia	DV047	226367	78.19	47.45	0.61	159	60.13	159
Landrace	G089	Amhara	DV159	226331	77.30	48.44	1.04	94	0.98	91	28.89	157	0.63	161	Landrace	G121	Oromia	DV099	222485	69	41	0.61	160	60.07	160
Landrace	G129	Oromia	DV236	236988	74.29	46.81	1.04	90	0.98	92	27.58	145	0.63	162	DZ-2005	G133	Oromia	DV026	208952	88.92	49.55	0.61	161	60.03	161
Landrace	G170	Oromia	DV098	222568	88	55.34	1.04	94	0.91	98	32.66	198	0.63	163	Landrace	G099	DZARC	Asasa	Asasa	74.74	48.05	0.62	161	59.83	162
Landrace	G207	Amhara	DV055	7209	44.25	40.77	1.02	95	0.99	96	22.48	110	0.63	164	Landrace	G050	Oromia	DV068	222298	83.86	42.61	0.6	163	59.78	163
CDSS091003895-099Y-041M-0M-04Y-0E	G272	CM	C012	548091	91.95	57.41	1.04	93	0.98	94	34.4	208	0.63	165	Landrace	G029	Oromia	DV035	209931	79.81	44.74	0.6	164	59.76	164
CDSS09100602T-099Y-030M-22V-0M-04Y-0E	G302	CM	C042	548605	74.67	47.49	1.02	96	0.99	97	27.38	144	0.63	166	CDSS09100602T-099Y-030M-22V-0M-04Y-0E	G032	CM	C042	548605	74.67	47.49	0.6	166	59.63	166
Landrace	G047	Amhara	DV202	239540	65.98	53.30	1.06	171	0.97	97	32.58	197	0.62	167	Landrace	G032	Oromia	DV250	5739-1	62.48	43.9	0.6	167	59.57	167
Landrace	G071	Oromia	DV040	226301	69.11	42.97	1.06	173	0.97	80	26.24	135	0.62	168	Landrace	G065	Amhara	DV079	222639	66.25	41.06	0.6	168	59.51	168
Landrace	G176	Oromia	DV047	220557	76.19	47.45	1.05	96	0.97	99	28.74	154	0.62	169	Landrace	G085	Amhara	DV056	226908	77.5	45.4	0.59	169	59.32	169
Landrace	G190	Oromia	DV105	226301	76.82	47.72	1.06	170	0.97	170	29.1	150	0.62	170	Landrace	G089	Oromia	DV068	226892	66.47	52.82	0.59	170	59.25	170
Landrace	G196	Amhara	DV045	208332-2	62.41	38.98	1.05	167	0.97	171	23.43	109	0.62	171	Landrace	G136	Oromia	DV069	222421	67.1	52.13	0.59	171	59.14	171
Landrace	G198	Oromia	DV098	204492	66.76	41.4	1.06	175	0.97	172	25.36	131	0.62	172	Landrace	G174	Oromia	DV197	7217	88.07	49.62	0.59	172	59.13	172
Landrace	G203	Amhara	DV036	225941	80.93	55.24	1.06	169	0.97	173	33.59	204	0.62	173	Landrace	G191	Amhara	DV02-2	222809-2	65.10	53.63	0.59	173	59.1	173
Landrace	G225	Amhara	DV045-1	225941-2	80.25	49.62	1.06	172	0.97	174	30.43	178	0.62	174	Landrace	G029	Oromia	DV236	236988	74.29	46.81	0.59	174	59.01	174
CDSS0908046T-099Y-099M-01V-0M-04Y-0E	G261	CM	C001	52670	91.69	56.87	1.06	174	0.97	175	34.82	212	0.62	175	Landrace	G040	Oromia	DV025	222708	92.35	37.72	0.58	175	58.96	175
Landrace	G124	Oromia	DV094	208291	80.2	60.1	1.06	177	0.95	176	30.1	220	0.61	176	Landrace	G184	Amhara	DV08	226229	83.63	41.25	0.58	176	58.73	176
Landrace	G059	Oromia	DV006	8556	60.11	36.42	1.10	182	0.94	102	22.69	115	0.61	177	Landrace	G177	Oromia	DV046	243377	65.24	52.93	0.58	177	58.71	177
Landrace	G055	Amhara	DV105	222732	66.34	59.79	1.09	180	0.95	177	37.61	223	0.61	178	Landrace	G093	Amhara	DV219	219597	67.22	38.73	0.57	178	58.7	178
Landrace	G121	Amhara	DV063	252376	40.98	25.06	1.08	179	0.95	179	35.92	253	0.61	179	Landrace	G098	Oromia	DV067	222485	78.14	44.95	0.56	179	58.76	179
Landrace	G233	Amhara	DV064	226844	77.52	47.36	1.09	179	0.95	179	30.16	173	0.61	180	Landrace	G062	Oromia	DV059	249587	66.66	47.4	0.56	180	58.74	180
CDSS091004235-099Y-020M-01V-0M-04Y-0E	G291	CM	C021	537803	94.95	58.8	1.08	176	0.95	180	26.79	220	0.61	181	CDSS091004235-099Y-020M-01V-0M-04Y-0E	G295	CM	C005	547724	71.9	45.92	0.55	181	57.42	181
Landrace	G319	CM	C050	54942	89.9	54.1	1.09	181	0.95	181	34.8	211	0.61	182	Landrace	G092	Amhara	DV002	7961	60.35	54.47	0.55	182	57.33	182
DZ-2212	G013	DZARC	Metajo	Metajo	79.46	47.66	1.12	189	0.93	187	31.18	192	0.6	183	Landrace	G206	Amhara	DV049	24955	70.73	46.8	0.55	183	56.92	183
Landrace	G068	Amhara	DV052	24958	78.33	45.79	1.13	190	0.93	188	31.54	187	0.6	184	Landrace	G214	Amhara	DV000	222503	73.98	43.8	0.55	184	56.92	184
Landrace	G079	Amhara	DV021	222544	95.27	67.49	1.11	183	0.94	183	37.78	224	0.6	185	Landrace	G216	Amhara	DV010	203776	81.36	39.8	0.55	185	56.81	185
Landrace	G126	Oromia	DV099	222426	82.13	49.29	1.12	197	0.93	189	32.84	199	0.6	186	DZ-2178	G085	DZARC	Mecobe	Mecobe	67.81	47.22	0.54	186	56.99	186
Landrace	G167	Oromia	DV204	23847	84.2	50.22	1.13	191	0.93	190	33.98	207	0.6	187	CDSS091006635-099Y-08M-20V-0M-0Y-0E	G295	CM	C025	539123	79.26	43.36	0.54	187	56.96	187
Landrace	G195	Amhara	DV127-1	226320-1	67.23	52.02	1.13	192	0.93	191	35.21	236	0.6	188	Landrace	G217	Amhara	DV014	222839	70.07	46.23	0.53	188	56.83	188
Landrace	G173	Oromia	DV192	227009	59.71	36.03	1.11	184	0.94	184	23.69	114	0.6	189	Landrace	G184	Amhara	DV011	222600	73.44	43.85	0.53	189	56.29	189
Landrace	G204	Amhara	DV036-2	225941-2	95.8	67.33	1.11	195	0.94	185	37.85	225	0.6	190	Landrace	G006	Oromia	DV085	222488	64.73	36.83	0.53	190	55.86	190
Landrace	G220	Amhara	DV055	226807	69.24	59.32	1.12	193	0.93	192	39.92	239	0.6	191	Landrace	G130	Oromia	DV041	24352	67.32	35.41	0.52	191	55.8	191
CDSS091002865-099Y-030M-12V-0M-04Y-0E	G266	CM	C006	547989	94.07	56.07	1.13	193	0.93	193	38	227	0.6	192	Top-66	G099	DZARC	Top-66	Top-66	67.35	46.14	0.52	192	55.75	192
Landrace	G270	CM	C008	527306	83.34	49.62	1.13	194	0.93	194	33.72	205	0.6	193	Landrace	G062	Amhara	DV012	219598	73.81	42.03	0.52	193	55.7	193
CDSS091002865-099Y-030M-20V-0M-04Y-0E	G290	CM	C030	547989	96.74	59.43	1.11	186	0.94	186	39.31	237	0.6	194	Landrace	G053									

**SUPPLEMENTARY FILES**

Landrace	G161	SNMF	DIV138	226127	70159	56.23	1.25	229	0.86	229	45.36	262	0.55	229	Landrace	G179	SNMF	DIV141	8175	60.94	42.52	0.44	229	50.9	229
Landrace	G180	Oromia	DIV195	227096	72.08	39.85	1.25	230	0.86	230	32.23	196	0.55	230	Landrace	G180	Amhara	DIV150	222735	61.67	41.55	0.43	230	50.58	230
Landrace	G216	Amhara	DIV102	222594	87.39	47.81	1.27	232	0.85	231	39.58	239	0.55	231	Landrace	G208	Amhara	DIV155	214571	66.17	38.56	0.43	231	50.51	231
Landrace	G224	Oromia	DIV142-2	206293-1	71.04	38.92	1.26	231	0.85	232	32.12	195	0.55	232	Landrace	G182	Oromia	DIV104	20666-1	61.77	41.21	0.43	232	50.45	232
Landrace	G245	Amhara	DIV210	219586	95.05	51.93	1.27	233	0.85	233	43.12	249	0.55	233	Landrace	G231	Oromia	DIV108	222413	60.86	41.43	0.42	233	50.21	233
Landrace	G189	Amhara	DIV193	226849	64.65	34.86	1.29	238	0.84	236	29.79	187	0.54	234	Landrace	G197	Oromia	DIV103	204332	73.29	34.17	0.42	234	50.04	234
Landrace	G194	Oromia	DIV110	222579	72.42	39.27	1.28	237	0.84	237	33.15	201	0.54	235	Landrace	G182	Tigray	DIV255	238104	58.24	42.52	0.42	235	49.76	235
Landrace	G246	Amhara	DIV214-1	214537-1	64.57	35.12	1.28	234	0.85	234	29.47	182	0.54	236	Advanced	G213	DZAPC	DZ007	DZAPC	59.5	40.95	0.41	236	49.36	236
Landrace	G247	Amhara	DIV217	219584	85.74	46.52	1.28	236	0.84	238	39.22	235	0.54	237	Landrace	G180	Amhara	DIV145	208332-2	62.41	38.98	0.41	237	49.32	237
Landrace	G260	Tigray	DIV259	218138	95.45	51.88	1.28	235	0.85	235	43.57	252	0.54	238	Landrace	G192	Oromia	DIV106	204417	64.36	28.31	0.4	238	49.87	238
Landrace	G110	Amhara	DIV175	226394	64.21	34.15	1.31	240	0.83	239	30.06	170	0.53	239	CD 165214-24	G205	DZAPC	Use	Use	58.37	42.64	0.4	239	48.59	239
Landrace	G112	Amhara	DIV220	219599	93.69	49.3	1.32	241	0.82	241	44.39	257	0.53	240	Landrace	G195	Oromia	DIV106-1	226971-1	73.12	32.1	0.39	240	49.45	240
Landrace	G241	Oromia	DIV194	200724	71.48	38.12	1.30	239	0.83	240	33.26	203	0.53	241	Landrace	G199	Oromia	DIV119	204483	70.61	32.68	0.39	241	49.04	241
Landrace	G259	Tigray	DIV258	21578-1	82.36	43.19	1.33	242	0.82	242	39.97	233	0.53	242	Landrace	G246	Amhara	DIV214-1	214537-1	64.57	35.1	0.39	242	47.61	242
Landrace	G096	Amhara	DIV161	226837	108.43	56.31	1.34	244	0.81	243	52.12	275	0.52	243	Landrace	G177	Oromia	DIV120	204494	51.22	44.06	0.39	243	47.51	243
Landrace	G115	Oromia	DIV197-1	222482-1	106.3	55.45	1.34	243	0.81	244	50.85	274	0.52	244	Landrace	G188	Amhara	DIV163	228840	64.65	34.86	0.39	244	47.47	244
Landrace	G123	Oromia	DIV106	222954	59.31	30.88	1.35	245	0.8	246	28.73	193	0.52	245	Landrace	G189	Amhara	DIV117	222832	93.35	37.74	0.39	245	47.33	245
Landrace	G090	Oromia	DIV108	222289	83.86	42.61	1.37	248	0.79	247	41.25	241	0.51	246	Landrace	G220	Amhara	DIV129	228993	61.42	36.3	0.39	246	47.22	246
Landrace	G119	Amhara	DIV101	203996	61	31.22	1.36	246	0.8	245	29.78	185	0.51	247	Landrace	G124	Oromia	DIV109	18399	73.89	30.1	0.37	247	47.36	247
CD550817006635-0991-09M-2017-AM-017	G205	CIM	C125	539123	79.26	40.36	1.37	247	0.79	248	38.9	232	0.51	248	Landrace	G167	Amhara	DIV174	206271	59.18	37.3	0.37	248	46.98	248
Landrace	G218	Amhara	DIV115	222627	87.81	43.68	1.40	250	0.77	253	44.13	255	0.5	249	Landrace	G110	Amhara	DIV175	226914	64.21	34.15	0.37	249	46.93	249
Landrace	G221	Tigray	DIV133	228245	88.38	44.07	1.40	249	0.78	249	44.31	256	0.5	250	Landrace	G058	Oromia	DIV106	18356	60.11	36.42	0.37	250	46.79	250
Landrace	G069	Amhara	DIV173	222358	92.6	45.28	1.43	256	0.76	254	47.32	268	0.49	251	Landrace	G125	Oromia	DIV142	214363	56.35	38.58	0.37	251	46.73	251
Landrace	G182	Oromia	DIV164	216072	66.33	32.46	1.43	254	0.76	255	33.87	208	0.49	252	Landrace	G105	Amhara	DIV218-1	23597-1	51.21	42.44	0.37	252	46.82	252
Landrace	G186	Amhara	DIV213-2	219589-2	77.77	38.49	1.41	251	0.77	250	39.28	238	0.49	253	Landrace	G182	Oromia	DIV164	216072	66.33	32.46	0.36	253	46.4	253
Landrace	G172	Amhara	DIV191	227089	76.4	37.69	1.42	252	0.77	251	38.71	230	0.49	254	Landrace	G173	Oromia	DIV192	227089	59.73	36.03	0.36	254	46.38	254
Landrace	G184	Amhara	DIV116	222629	83.63	41.25	1.42	253	0.77	252	42.38	246	0.49	255	Landrace	G146	Oromia	DIV197-2	222482-2	56.41	37.92	0.36	255	46.25	255
Landrace	G215	Amhara	DIV101	222580	81.36	39.81	1.43	255	0.76	256	41.55	242	0.49	256	Landrace	G161	Oromia	DIV104-1	204573-1	60.61	35.08	0.36	256	46.11	256
Landrace	G095	Amhara	DIV119	222639	86.25	41.06	1.46	258	0.74	258	45.19	261	0.48	257	Landrace	G114	Oromia	DIV104	222404	64.64	47.32	0.36	257	45.96	257
Landrace	G235	Amhara	DIV173	228880	103.67	50.12	1.44	257	0.75	257	53.95	277	0.48	258	Landrace	G176	Oromia	DIV109	222574	55.95	37.25	0.35	258	45.59	258
Landrace	G121	Oromia	DIV108	222485	88	41	1.49	262	0.73	260	47	267	0.47	259	Landrace	G138	Oromia	DIV127	7149	71.62	28.84	0.32	259	43.84	259
Landrace	G182	Oromia	DIV198	219499	58.86	27.79	1.47	259	0.74	259	31.07	183	0.47	260	Landrace	G119	Amhara	DIV101	203996	61	31.22	0.32	260	43.64	260
Landrace	G174	Oromia	DIV197	7217	98.07	48.62	1.48	260	0.73	261	45.45	264	0.47	261	Landrace	G193	Oromia	DIV107	214470	49.86	37.9	0.32	261	43.47	261
Landrace	G197	Oromia	DIV193	204392	73.28	34.17	1.49	261	0.73	262	39.11	234	0.47	262	Advanced	G100	DZAPC	DZ006	DZAPC	49.22	38.11	0.32	262	43.31	262
CD 14628-44	G130	DZAPC	Yeer	Yeer	58.14	25.24	1.52	265	0.75	265	29.9	188	0.46	263	Landrace	G097	Amhara	DIV213-1	219589-1	56.68	32.21	0.31	263	42.73	263
Landrace	G133	Oromia	DIV108	208182	88.92	40.53	1.52	266	0.71	266	49.39	272	0.46	264	Landrace	G123	Oromia	DIV106	222554	59.31	30.58	0.31	264	42.93	264
Landrace	G199	Oromia	DIV119	204483	70.61	32.68	1.50	263	0.72	263	37.93	226	0.46	265	Landrace	G140	SNMF	DIV205	219569	51.04	34.62	0.3	265	42.84	265
Landrace	G205	Amhara	DIV147	244480	57.88	26.79	1.50	264	0.72	264	31.19	184	0.46	266	Landrace	G242	Amhara	DIV200-1	219536-1	64.62	27.24	0.3	266	41.96	266
Landrace	G107	Oromia	DIV105	222191	106.99	49.36	1.53	267	0.7	267	58.83	282	0.45	267	Advanced	G200	DZAPC	DZ005	DZAPC	44.8	38.73	0.29	267	41.65	267
Landrace	G152	Oromia	DIV196-2	226971-2	79.74	34.76	1.58	270	0.69	269	44.90	260	0.44	268	Landrace	G186	Oromia	DIV148	214497	54.87	30.91	0.29	268	41.81	268
Landrace	G193	Amhara	DIV219	219587	87.22	38.73	1.55	268	0.69	268	48.49	273	0.44	269	Landrace	G189	Amhara	DIV185	222533	47.29	34.76	0.29	269	40.54	269
Landrace	G195	Oromia	DIV188-1	226971-1	73.12	32.1	1.57	269	0.68	271	41.02	240	0.44	270	Landrace	G162	Oromia	DIV198	219499	58.86	27.79	0.29	270	40.44	270
Landrace	G106	Oromia	DIV195	222498	84.73	36.83	1.58	271	0.68	270	47.9	271	0.43	271	Advanced	G131	DZAPC	DZ003	DZAPC	45.42	35.96	0.27	271	40.89	271
Landrace	G240	Oromia	DIV189	226978	101.54	43.32	1.60	272	0.68	274	58.22	281	0.43	272	Landrace	G181	Amhara	DIV113	222813	66.87	23.5	0.26	272	39.64	272
Landrace	G142	Oromia	DIV103	214537	78.83	33.46	1.61	274	0.68	272	45.37	263	0.42	273	Landrace	G170	Amhara	DIV124-1	222844-1	52.32	29.98	0.26	273	39.53	273
Landrace	G176	Amhara	DIV144	214286	98.19	41.72	1.61	273	0.68	273	56.47	280	0.42	274	STJ310BCPLKSL45MTER-3	G157	DZAPC	DZ001	Makge	45.66	34.11	0.26	274	39.46	274
Landrace	G242	Amhara	DIV200-1	219536-1	64.62	27.24	1.62	275	0.68	275	37.38	222	0.42	275	Landrace	G205	Amhara	DIV147	214499	57.88					

## SUPPLEMENTARY FILES

**Table S2.** Marker trait associations (MTAs) were detected at ( $-\log_{10}p \geq 4.0$ ) for drought indices calculated from grain yield and traits that were significantly ( $p < 0.001$ ) positively correlated with grain yield under FDS and FNS.

SN	SNP Marker*	Trait	Chr	Allele <sup>b</sup>	St. Pos.	LCI (bp)	HCI (bp)	LOD = -log <sub>10</sub> p ≥ 4.0 <sup>c</sup>	Effect size	% PVE	Annotation <sup>d</sup>
1	Ku_c8810_903	DGF-GMP	1A	A/G	7130729	2,116,602	12144856	4.03	0.02	0.00	
2	Ku_c8810_903	DGF-DSI	1A	A/G	7130729	2,116,602	12144856	4.03	0.02	0.00	
3	Ku_c8810_903	DGF-RDI	1A	A/G	7130729	2,116,602	12144856	4.21	-0.01	0.00	
4	Tdurum_contig8382_300	SPS-STI	1A	T/C	26390023	21,375,896	31404150	4.52	-0.03	0.00	
5	w SNP_CAP12_c2438_1180601	SPAD-RDI	1A	T/C	37655344	32,641,217	42669471	4.26	0.02	0.00	
6	w SNP_Ku_rep_c107796_931182	HI-GMP	1A	G/A	71040273	66,026,146	76054400	4.64	3.20	1.95	
7	w SNP_RFL_Contig2185_1520256	HI-GMP	1A	C/T	74203355	69,195,228	79223482	4.64	3.20	1.95	
8	Ra_c2895_591	GY-RDI	1A	G/T	454315618	449,301,491	459329745	4.31	-0.04	0.01	RNA-binding protein
9	Ra_c2895_591	HI-DSI	1A	G/T	454315618	449,301,491	459329745	6.61	-1.34	2.24	RNA-binding protein
10	BS00033469_51	SPAD-GMP	1A	G/T	464926602	459,912,475	469940729	5.61	0.81	1.31	
11	BS00033469_51	SPAD-STI	1A	G/T	464926602	459,912,475	469940729	9.85	0.06	0.01	
12	BobWhite_c12568_900	GY-STI	1A	C/T	483577474	478,563,347	488591601	4.03	0.04	0.01	
13	IAAV6234	SPAD-DSI	1A	T/C	505968264	500,954,137	510982391	4.49	0.27	0.17	
14	IAAV6234	SPAD-YSI	1A	T/C	505968264	500,954,137	510982391	4.84	-0.03	0.00	
15	BS00022788_51	SPAD-YSI	1A	C/A	508253590	503,239,463	513267717	4.78	-0.02	0.00	
16	Tdurum_contig51167_534	GY-RDI	1A	A/G	545579418	540,585,291	550593545	5.17	-0.06	0.01	
17	Tdurum_contig51167_534	SPS-STI	1A	A/G	545579418	540,585,291	550593545	7.01	0.07	0.01	
18	Kukri_c310_1953	TKW-GMP	1A	T/C	572871043	567,856,916	577885170	4.23	0.60	0.86	
19	BS00035273_51	SPS-GMP	1A	C/T	579085882	574,071,755	584100009	6.06	0.71	1.33	
20	CAP11_c5573_163	SPAD-GMP	1A	G/A	582981061	577,966,934	587995188	8.59	1.05	2.14	
21	RAC875_c63624_753	SPS-RDI	1B	C/T	10778560	5,764,433	15792687	4.15	0.04	0.01	
22	RAC875_c63624_753	SPS-YSI	1B	C/T	10778560	5,764,433	15792687	4.16	0.03	0.00	
23	RAC875_c63624_753	SPS-DSI	1B	C/T	10778560	5,764,433	15792687	4.20	-0.09	0.04	
24	Tdurum_contig33207_282	HI-DSI	1B	A/G	348260183	343,246,056	353274310	5.51	2.31	2.40	
25	Tdurum_contig33207_282	HI-STI	1B	A/G	348260183	343,246,056	353274310	5.51	2.31	2.40	
26	Tdurum_contig33207_282	HI-GMP	1B	A/G	348260183	343,246,056	353274310	5.32	1.55	1.09	
27	Tdurum_contig25337_77	GY-RDI	1B	A/G	381117637	376,103,510	386131764	4.57	0.05	0.01	

## SUPPLEMENTARY FILES

28	BobWhite_c26850_78	DGF-RDI	1B	C/A	522063544	517,049,417	527077671	5.55	-0.03	0.01	
29	IAAV2619	DGF-STI	1B	G/A	632532296	627,518,169	637546423	7.61	-0.01	0.00	
30	wsnp_Ek_c1058_2020681	SPAD-STI	1B	A/G	668991372	663,977,245	674005499	4.56	-0.04	0.01	
31	Tdurum_contig10785_1669	DGF-STI	2A	A/G	12101749	7,087,622	17115876	4.54	0.01	0.00	
32	Tdurum_contig10785_2433	GY-STI	2A	T/C	12102513	7,088,386	17116640	7.53	-0.06	0.01	NBS-LRR-like resistance protein
33	Tdurum_contig10785_2433	GY-GMP	2A	T/C	12102513	7,088,386	17116640	4.36	-1.99	14.59	NBS-LRR-like resistance protein
34	BobWhite_c2022_245	HI-DSI	2A	G/A	29222931	24,208,804	34237058	4.29	1.07	1.24	
35	IAAV5656	HI-RDI	2A	A/G	498802328	493,788,201	503816455	5.19	-0.04	0.00	
36	IAAV5656	HI-YSI	2A	A/G	498802328	493,788,201	503816455	7.34	-0.04	0.00	
37	IAAV5656	HI-TOL	2A	A/G	498802328	493,788,201	503816455	5.39	-1.94	2.78	
38	RAC875_c5742_1357	SPS-GMP	2A	T/C	523878879	518,864,752	528893006	4.03	0.86	1.01	
39	BS00066607_51	SPS-GMP	2A	A/G	525499400	520,485,273	530513527	4.03	-0.86	1.01	
40	IACX319	SPS-GMP	2A	A/G	533814335	528,800,208	538828462	4.03	-0.86	1.01	
41	IAAV2718	HI-TOL	2A	T/C	675832863	670,818,736	680846990	4.30	-2.27	2.83	
42	Excalibur_c6660_746	HI-YSI	2A	T/C	685865821	680,851,694	690879948	6.94	0.07	0.00	
43	Excalibur_c6660_746	HI-RDI	2A	T/C	685865821	680,851,694	690879948	4.45	0.07	0.00	
44	Excalibur_C20335_198	SPS-STI	2A	A/G	757621502	752,607,375	762635629	4.26	-0.03	0.00	
45	Tdurum_contig42013_538	HI-DSI	2A	T/C	771226463	766,212,336	776240590	4.50	-1.58	1.95	
46	Excalibur_c1787_1037	SPS-GMP	2B	G/T	15643691	10,629,564	20657818	4.19	0.45	0.80	
47	RAC875_c4314_993	TKW-RDI	2B	T/C	49648750	44,634,623	54662877	4.35	-0.02	0.00	
48	RAC875_c4314_993	TKW-DSI	2B	T/C	49648750	44,634,623	54662877	4.57	-0.06	0.01	
49	wsnp_Ek_C2349_7841003	SPAD-YSI	2B	T/C	57179677	52,165,550	62193804	4.58	0.02	0.00	
50	wsnp_Ek_C2349_7841003	SPAD-DSI	2B	T/C	57179677	52,165,550	62193804	4.53	-0.26	0.17	
51	Kukri_c36879_83	TKW-TOL	2B	A/G	96408120	91,393,993	101422247	7.48	-1.85	2.71	Acyl-CoA dehydrogenase-related family protein
52	RAC875_c8045_231	DGF-YSI	2B	T/C	197538224	192,524,097	202552351	5.94	0.02	0.00	
53	RFL_Contig1987_3440	DGF-STI	2B	G/A	546427607	541,413,480	551441734	4.11	0.00	0.00	
54	BS00104667_51	SPAD-STI	2B	G/A	677950622	672,936,495	682964749	5.27	0.06	0.00	
55	wsnp_Ek_c5123_9087869	HI-GMP	2B	C/T	683879232	678,865,105	688893359	5.48	1.05	1.10	

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56	wsnp_Ku_c9901_16493072	GY-GMP	2B	C/I/T	683881666	678,867,539	688895793	4.37	2.68	14.72	
57	wsnp_Ex_c24135_33382521	SPS-RDI	2B	G/A	702731805	697,717,678	707745932	4.44	0.04	0.00	
58	wsnp_Ex_c24135_33382521	SPS-YSI	2B	G/A	702731805	697,717,678	707745932	4.40	0.03	0.00	
59	wsnp_Ex_c24135_33382521	SPS-DSI	2B	G/A	702731805	697,717,678	707745932	4.46	-0.11	0.02	
60	BobWhite_c29596_649	TKW-GMP	2B	A/C	703333584	698,319,457	708347711	8.14	1.36	2.53	
61	BobWhite_c29596_649	TKW-STI	2B	A/C	703333584	698,319,457	708347711	4.85	0.05	0.00	
62	Ra_c5004_2032	SPAD-STI	2B	G/T	720400852	715,386,725	725414979	7.52	0.04	0.01	
63	wsnp_Ex_c10441_17078853	TKW-GMP	2B	C/A	750924664	745,910,537	755938791	4.06	-0.77	1.48	
64	RAC875_c7735_338	TKW-DSI	2B	C/T	770419160	765,405,033	775433287	6.97	0.17	0.02	
65	RAC875_c7735_338	TKW-RDI	2B	C/T	770419160	765,405,033	775433287	6.62	0.06	0.00	
66	RAC875_c7735_338	TKW-YSI	2B	C/T	770419160	765,405,033	775433287	7.77	0.05	0.00	
67	Tdurum_contig55335_316	SPS-STI	3A	C/T	165087117	160,072,990	170101244	6.14	-0.03	0.00	
68	Tdurum_contig55335_316	SPS-GMP	3A	C/T	165087117	160,072,990	170101244	5.96	-0.54	0.71	
69	wsnp_Ku_rep_c70479_700796	SPAD-GMP	3A	G/A	520111517	515,097,390	525125644	4.11	0.80	1.23	
70	wsnp_Ku_rep_c70479_700796	SPAD-YSI	3A	G/A	520111517	515,097,390	525125644	4.44	0.04	0.00	
71	BS00039925_51	TKW-TOL	3A	G/T	534691493	529,677,366	539705620	6.34	1.45	2.08	
72	wsnp_Ex_c32404_41067821	DGF-TOL	3B	C/T	76154115	71,139,988	81168242	4.42	-2.17	4.96	
73	BS00108055_51	SPAD-GMP	3B	T/G	517360060	512,345,933	522374187	4.45	0.74	1.42	
74	wsnp_Ex_c5418_9575513	DGF-YSI	3B	T/C	588723822	583,709,695	593737949	4.29	-0.01	0.00	
75	Ex_c4757_635	DGF-RDI	3B	A/G	659747529	654,733,402	664761656	4.19	0.03	0.00	
76	Ex_c4757_635	DGF-DSI	3B	A/G	659747529	654,733,402	664761656	5.31	-0.06	0.00	
77	RFL_Contig2569_2187	GY-GMP	3B	G/A	752249328	747,235,201	757263455	4.35	1.86	10.07	Potassium transporter
78	wsnp_JD_c4413_5541607	GY-STI	3B	G/T	752482037	747,467,910	757496164	4.35	0.04	0.01	
79	wsnp_JD_c4413_5541607	SPS-STI	3B	G/T	752482037	747,467,910	757496164	6.25	0.03	0.00	
80	BS00041837_51	DGF-STI	3B	G/A	758987014	753,972,887	764001141	5.22	0.01	0.00	
81	IAAV1775	DGF-TOL	4A	A/T	590188609	585,174,482	595202736	6.72	1.99	5.28	Methyltransferase
82	Excalibur_c25699_113	TKW-YSI	4A	T/C	617089540	612,075,413	622103667	4.61	-0.04	0.00	
83	Excalibur_c25699_113	TKW-RDI	4A	T/C	617089540	612,075,413	622103667	5.70	-0.05	0.00	
84	Excalibur_c25699_113	TKW-DSI	4A	T/C	617089540	612,075,413	622103667	4.77	-0.12	0.01	
85	RAC875_c6911_391	HI-STI	4A	A/G	626040049	621,025,922	631054176	5.86	0.05	0.00	
86	BS00084042_51	GY-RDI	4A	C/T	709491543	704,477,416	714505670	5.83	-0.05	0.01	
87	RFL_Contig6086_1186	SPAD-GMP	4A	C/T	716843776	711,829,649	721857903	5.05	-0.71	2.01	
88	Kukri_c37227_579	TKW-YSI	4A	G/A	727957603	722,943,476	732971730	4.74	-0.02	0.00	
89	Kukri_c37227_579	TKW-RDI	4A	G/A	727957603	722,943,476	732971730	4.54	-0.02	0.00	
90	Kukri_c37227_579	TKW-DSI	4A	G/A	727957603	722,943,476	732971730	4.95	-0.06	0.01	
91	Kukri_c22602_704	GY-GMP	4A	A/G	733371835	728,357,708	738385962	5.78	5.22	26.61	U-box domain-containing protein
92	Tdurum_contig31218_279	HI-GMP	4A	A/G	733401590	728,367,463	738415717	5.76	-0.88	0.84	
93	RAC875_rep_c107984_187	TKW-STI	4A	T/C	735878452	730,864,325	740892579	4.87	-0.05	0.00	
94	RAC875_rep_c107984_187	TKW-GMP	4A	T/C	735878452	730,864,325	740892579	4.67	-1.00	1.67	
95	tplb0050b23_546	HI-TOL	4B	T/C	4927519	(86,608)	9941646	9.12	4.52	8.20	Ribosomal protein
96	tplb0050b23_546	HI-RDI	4B	T/C	4927519	(86,608)	9941646	7.47	0.10	0.00	Ribosomal protein
97	tplb0050b23_546	HI-YSI	4B	T/C	4927519	(86,608)	9941646	6.84	0.07	0.00	Ribosomal protein
98	Tdurum_contig62310_490	TKW-GMP	4B	A/G	106799903	101,785,776	111814030	4.90	0.98	1.21	
99	RAC875_c35152_372	SPAD-GMP	4B	A/G	162680923	157,666,796	167695050	5.45	1.64	1.45	
100	Excalibur_c7964_1290	GY-STI	4B	G/A	485705797	480,691,670	490719924	5.87	0.05	0.01	
101	Excalibur_c7964_1290	HI-DSI	4B	G/A	485705797	480,691,670	490719924	5.77	1.12	2.27	
102	Excalibur_c7964_1290	HI-GMP	4B	G/A	485705797	480,691,670	490719924	5.63	0.83	1.26	
103	Excalibur_c7964_1290	HI-STI	4B	G/A	485705797	480,691,670	490719924	5.87	0.05	0.01	
104	Tdurum_contig54564_1507	DGF-TOL	4B	A/G	492173352	487,159,225	497187479	6.84	1.26	5.16	
105	Tdurum_contig54564_1507	DGF-YSI	4B	A/G	492173352	487,159,225	497187479	9.05	0.03	0.00	
106	Tdurum_contig54564_1507	DGF-GMP	4B	A/G	492173352	487,159,225	497187479	6.04	-0.07	0.00	
107	Tdurum_contig54564_1507	DGF-DSI	4B	A/G	492173352	487,159,225	497187479	6.04	-0.07	0.00	
108	Tdurum_contig92937_676	DGF-RDI	4B	G/A	492236533	487,222,406	497250660	5.43	-0.03	0.00	
109	Ex_c25467_851	TKW-DSI	4B	C/T	592406255	587,392,128	597420382	4.01	-0.05	0.01	
110	BS00037020_51	SPAD-GMP	4B	G/T	599279630	594,265,503	604293757	4.50	0.59	0.90	

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111	Excalibur_c39876_403	TKW-DSI	4B	C/T	654818945	649,804,818	659833072	7.88	0.16	0.01	
112	Excalibur_c39876_403	TKW-RDI	4B	C/T	654818945	649,804,818	659833072	7.41	0.07	0.00	
113	Excalibur_c39876_403	TKW-YSI	4B	C/T	654818945	649,804,818	659833072	9.68	0.06	0.00	
114	IAAV7394	SPAD-STI	4B	G/A	662483089	657,468,962	667497216	5.17	-0.04	0.01	
115	Ku_c2885_1189	SPS-STI	4B	A/G	674166079	669,151,952	679180206	4.03	-0.06	0.01	
116	GENE-3606_315	GY-STI	5A	C/A	81504827	76,490,700	86518954	4.20	-0.05	0.01	
117	Ku_C2397_2156	HI-GMP	5A	A/G	101409750	96,395,623	106423877	4.82	-0.97	0.81	
118	Tdurum_contig76578_537	GY-STI	5A	A/G	10830599	105,816,472	115844726	7.28	0.11	0.01	UNC93-like protein
119	Tdurum_contig76578_537	SPAD-GMP	5A	A/G	10830599	105,816,472	115844726	4.56	1.14	2.04	UNC93-like protein
120	Tdurum_contig76578_537	SPS-GMP	5A	A/G	10830599	105,816,472	115844726	8.00	1.26	6.87	UNC93-like protein
121	Tdurum_contig76578_537	HI-GMP	5A	A/G	10830599	105,816,472	115844726	6.89	2.12	2.74	UNC93-like protein
122	Tdurum_contig76578_537	HI-STI	5A	A/G	10830599	105,816,472	115844726	8.21	0.08	0.00	UNC93-like protein
123	Kukri_rep_c116526_98	GY-GMP	5A	C/T	112213041	107,198,914	117227168	6.13	-3.33	17.00	Protein MODIFIER OF SNCT11G
124	BobWhite_rep_c63943_76	SPS-STI	5A	G/T	510385096	505,370,969	515399223	4.35	-0.09	0.02	
125	BS00065292_51	TKW-TOL	5A	A/G	518584476	513,570,349	523598603	6.18	1.81	1.84	
126	RFL_Contig3629_1465	SPAD-RDI	5A	T/C	639311345	634,297,218	644325472	4.42	0.04	0.00	
127	IAAV2346	GY-GMP	5B	G/A	17863862	12,849,735	22877989	4.91	2.70	21.16	
128	IAAV2346	GY-STI	5B	G/A	17863862	12,849,735	22877989	5.39	0.06	0.01	
129	Excalibur_c58520_78	SPS-GMP	5B	A/G	26805948	21,791,821	31820075	4.45	-0.50	0.82	
130	BS00064578_51	TKW-TOL	5B	T/C	438028156	433,014,029	443042283	5.30	0.72	2.07	
131	RAC875_C22281_475	DGF-YSI	5B	T/C	545984975	540,970,848	550999102	4.08	-0.01	0.00	
132	RAC875_C22281_475	DGF-TOL	5B	T/C	545984975	540,970,848	550999102	4.39	-0.75	2.14	
133	Tdurum_contig68296_670	DGF-RDI	5B	G/A	635337156	630,323,029	640351283	4.38	-0.03	0.00	
134	RAC875_c13394_924	HI-DSI	6A	A/G	3084526	(1,929,601)	8098653	4.69	-0.91	1.43	
135	GENE-4052_338	TKW-STI	6A	G/A	525722832	520,708,705	530736959	5.45	-0.04	0.00	
136	GENE-4052_338	TKW-GMP	6A	G/A	525722832	520,708,705	530736959	5.30	-0.97	1.88	
137	RAC875_rep_c113731_95	SPS-GMP	6A	T/C	567911737	562,897,610	572925864	4.11	0.56	1.19	
138	Tdurum_contig61383_627	DGF-YSI	6B	C/T	36557072	31,542,945	41571199	4.29	-0.01	0.00	ike protein kinase family protein
139	Tdurum_contig61383_627	DGF-RDI	6B	C/T	36557072	31,542,945	41571199	5.04	-0.02	0.00	ike protein kinase family protein
140	Tdurum_contig61383_627	DGF-TOL	6B	C/T	36557072	31,542,945	41571199	6.22	-0.85	4.57	ike protein kinase family protein
141	RFL_Contig5844_291	SPAD-STI	6B	G/T	141032169	136,018,042	146046296	4.23	-0.03	0.00	
142	RFL_Contig6050_941	DGF-YSI	6B	C/A	490377946	485,363,819	495392073	7.79	-0.10	0.00	
143	RFL_Contig6050_941	DGF-RDI	6B	C/A	490377946	485,363,819	495392073	4.38	-0.11	0.00	
144	wsnp_Ex_c3940_7144946	GY-GMP	6B	A/G	508076861	503,062,734	513090988	5.65	5.20	21.91	DNA topoisomerase 2
145	Excalibur_rep_c70364_129	HI-DSI	6B	T/C	539467780	534,453,653	544481907	5.25	1.77	2.20	
146	wsnp_BE496986B-Ta_2_2	TKW-DSI	6B	G/A	568038975	563,024,848	573053102	5.05	0.08	0.01	
147	wsnp_BE496986B-Ta_2_2	TKW-RDI	6B	G/A	568038975	563,024,848	573053102	4.29	0.03	0.00	
148	wsnp_BE496986B-Ta_2_2	TKW-YSI	6B	G/A	568038975	563,024,848	573053102	5.44	0.03	0.00	
149	BS00064885_51	HI-TOL	6B	A/G	623193581	618,179,454	628207708	6.69	2.04	4.32	
150	BS00064885_51	HI-RDI	6B	A/G	623193581	618,179,454	628207708	6.35	0.05	0.00	
151	BS00064885_51	HI-YSI	6B	A/G	623193581	618,179,454	628207708	6.86	0.04	0.00	
152	BS00011479_51	SPAD-GMP	6B	C/T	638909369	633,895,242	643923496	4.36	0.74	1.25	
153	Kukri_c338_109	SPAD-STI	6B	G/A	684525167	679,511,040	689539294	6.77	-0.05	0.01	
154	Kukri_c338_109	SPAD-GMP	6B	G/A	684525167	679,511,040	689539294	5.63	-0.68	1.57	
155	BS00064478_51	GY-STI	6B	C/T	688744513	683,730,386	693758640	4.51	-0.06	0.01	
156	Ku_c20100_1746	SPAD-GMP	7A	T/C	172269	(4,841,858)	5186396	4.28	0.88	1.07	
157	RAC875_c25517_1067	HI-RDI	7A	T/C	6148026	1,133,899	11162153	4.52	-0.04	0.00	
158	Excalibur_c24593_1217	GY-RDI	7A	C/T	7721495	2,707,368	12735622	6.41	-0.06	0.01	Cytochrome P450
159	Tdurum_contig99143_205	DGF-TOL	7A	A/G	82560391	77,546,264	87574518	6.26	0.64	3.66	Family protein, expressed
160	BS00046977_51	TKW-DSI	7A	T/C	86330759	81,316,632	91344886	6.25	0.09	0.01	
161	BS00046977_51	TKW-RDI	7A	T/C	86330759	81,316,632	91344886	6.59	0.04	0.00	
162	BS00046977_51	TKW-YSI	7A	T/C	86330759	81,316,632	91344886	5.38	0.03	0.00	
163	Excalibur_c10563_523	HI-YSI	7A	A/G	229915391	224,901,264	234929518	4.26	-0.01	0.00	
164	Ku_c3251_1103	HI-GMP	7A	T/G	345776283	340,762,156	350790410	6.98	1.75	1.67	
165	Ku_c3251_1103	HI-STI	7A	T/G	345776283	340,762,156	350790410	10.37	0.08	0.00	
166	RAC875_rep_c73101_932	SPS-GMP	7A	T/C	373453584	368,439,457	378467711	6.66	1.03	0.94	
167	RAC875_rep_c73101_932	SPS-STI	7A	T/C	373453584	368,439,457	378467711	8.90	0.08	0.01	
168	JD_c1201_631	HI-DSI	7A	T/G	663956092	658,941,965	668970219	4.81	-1.82	2.20	
169	Excalibur_c39817_332	TKW-YSI	7A	A/G	685724800	680,710,673	690738927	4.01	-0.02	0.00	
170	Excalibur_c39817_332	TKW-RDI	7A	A/G	685724800	680,710,673	690738927	4.69	-0.03	0.00	
171	BS00098482_51	HI-GMP	7A	T/C	692749406	687,735,279	697763533	4.31	-1.41	1.49	
172	BobWhite_C21378_234	GY-GMP	7A	C/T	693389984	688,375,857	698404111	5.86	-4.80	13.59	
173	wsnp_Ex_c916_1767286	TKW-STI	7A	T/C	707961406	702,947,279	712975533	4.27	-0.03	0.00	
174	wsnp_Ex_c5839_10246915	GY-GMP	7A	C/T	709145347	704,131,220	714159474	4.92	-2.90	16.01	
175	BobWhite_c25527_313	SPS-STI	7A	A/G	709195412	704,181,285	714209539	4.31	-0.05	0.00	
176	Excalibur_c50044_749	HI-GMP	7B	A/G	5953677	939,550	10967804	5.71	1.51	1.77	
177	Excalibur_c50044_749	HI-STI	7B	A/G	5953677	939,550	10967804	6.05	0.05	0.00	
178	GENE-4862_1104	HI-YSI	7B	C/T	60072237	55,058,110	65086364	4.49	-0.05	0.00	
179	GENE-4862_1104	HI-RDI	7B	C/T	60072237	55,058,110	65086364	4.22	-0.06	0.00	
180	Kukri_c11890_709	GY-RDI	7B	A/G	63743279	58,729,152	68757406	4.81	-0.05	0.01	
181	RAC875_C2108_2179	DGF-STI	7B	G/T	87919170	82,905,043	92933297	5.86	0.02	0.00	
182	wsnp_BF200891B-Ta_2_1	HI-STI	7B	T/C	97175925	92,161,798	102190052	4.15	-0.05	0.00	
183	Tdurum_contig4658_346	GY-GMP	7B	C/T	663797774	658,783,647	668811901	5.95	2.61	22.21	
184	BobWhite_c2892_211	TKW-TOL	7B	C/T	700021350	695,007,223	705035477	5.14	1.17	2.23	

<sup>a</sup>SNP marker: Significant SNP markers associated with two or more drought indices traits are indicated in blue color, Traits (GY: Grain yield, DGF: Days to grain filling, SPAD, SPS: Seed per spike, HI: Harvest index and TKW:Thousand kernel weight,DSI: Drought susceptibility index, RDI: Relative drought index, STI: Stress tolerance index, GMP: Geometric mean productivity,

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TOL: Tolerance index and YSI: Yield stability index). Chr: chromosome, <sup>b</sup>Major alleles are bold and positioned at the start. St. Pos.: Start position, LCI: Lower class interval, and HLI: Higher class interval of the SNP marker in bp. LOD (The likelihood of odds value) = -log<sub>10</sub>p ≥ 4.0<sup>c</sup>: MTAs significant at FDR 5% is highlight in gray color, Effect size, % PVE: Percentage of phenotypic variance explained and Annotation<sup>d</sup>: Annotation of SNP markers associated with drought tolerance and major alleles with positive effect size on trait.

**Table S3.** Significant (-log<sub>10</sub>p ≥ 4.0) MTAs grouped into QTLs for drought indices calculated from grain yield (GY) and traits that were significantly (p < 0.001) and positively correlated with grain yield under FDS and FNS. The chromosomes interval of the hotspots is indicated by a red rectangle.

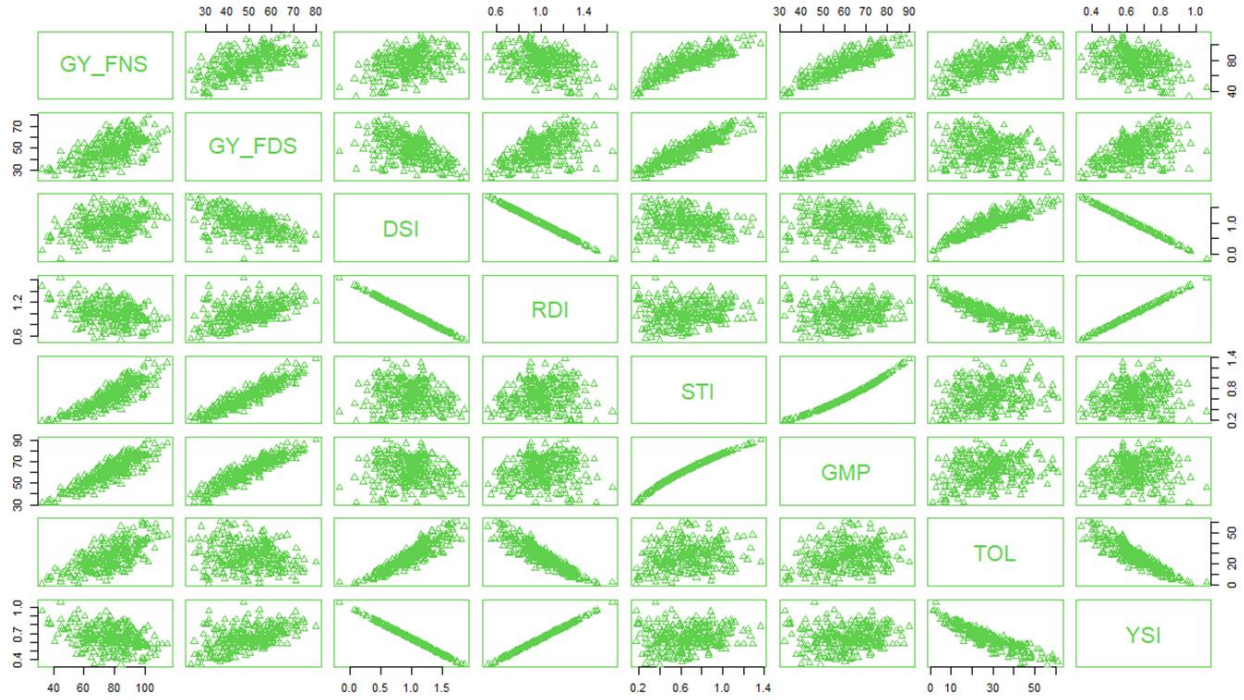
QTL	Trait Associate	Clustered trait(s)	SNP marker	Chr	Position (bp)	LCI (bp)	HLI (bp)	% PVE	Reported QTL	QTL Position
1	DGF-RDI	DGF-GMP, DGF-DSI	Ku_c8810_903	1A	7,130,723	2,116,602	12,144,856	0.00		
2	SPS-STI		Tdurum_contig8382_300	1A	26,390,023	21,375,836	31,404,150	0.00		
3	SPAD-RDI		wznp_CAP12_c2438_1180601	1A	37,655,344	32,641,217	42,663,471	0.00		
4	HI-GMP		wznp_RFL_Contig2185_1520256	1A	71,040,273	66,026,146	76,054,400	1.95		
5	HI-DSI	GY-RDI	Ra_c2835_531	1A	454,315,618	449,301,431	453,323,745	2.24		
6	SPAD-STI	SPAD-GMP	BS00033463_51	1A	464,326,802	459,312,475	469,340,729	1.31		60.25, 80.13, 51.07, 60.25, 61.41, 60.25, 61.89, and 63.53 cM
7	GY-STI		BobvWhite_c12568_900	1A	483,577,474	478,563,347	488,591,601	0.01	Qaseem et al., 2019	
8	SPAD-YSI	SPAD-DSI	BS00022788_51	1A	506,253,590	503,239,463	513,267,717	0.00		
9	SPS-STI	GY-RDI	Tdurum_contig51167_534	1A	545,579,418	540,565,231	550,593,545	0.01		
10	TKW-GMP		KuRFL_c910_1853	1A	572,871,043	567,856,916	577,885,170	0.86		
11	SPAD-GMP	SPS-GMP	CAP1L_c5513_163	1A	582,381,061	577,966,934	587,395,188	2.14		
12	SPS-DSI	SPS-YSI, SPS-RDI	RAC875_c63624_353	1B	10,778,560	5,764,433	15,732,887	1.04		
13	HI-GMP	HI-STI, HI-DSI	Tdurum_contig33207_282	1B	348,260,183	343,246,056	353,274,310	1.09		
14	GY-RDI		Tdurum_contig25337_17	1B	381,117,637	376,103,510	386,131,764	0.01		
15	DGF-RDI		BobvWhite_c26850_78	1B	522,063,544	517,049,417	527,077,671	0.01		
16	DGF-STI		IAAV2619	1B	632,532,296	627,518,169	637,546,423	0.00	Dashri et al., 2007	
17	SPAD-STI		wznp_Ec_c1058_2020681	1B	668,991,372	663,977,245	674,005,499	0.01	Dashri et al., 2007	
18	GY-GMP	GY-STI, DGF-STI	Tdurum_contig10785_2453	2A	12,102,513	7,088,386	17,116,640	14.59		
19	HI-DSI		BobvWhite_c2022_245	2A	29,222,931	24,208,804	34,237,058	1.24		
20	HI-TOL	HI-YSI, HI-RDI	IAAV5656	2A	498,802,328	493,788,201	503,816,455	2.78		
21	SPS-GMP	SPS-GMP	BS00066607_51	2A	525,499,400	520,485,273	530,513,527	1.01		
22	SPS-GMP		IACX319	2A	533,814,335	528,800,208	538,828,462	1.01		
23	HI-TOL		IAAV2718	2A	675,832,863	670,818,736	680,846,990	2.83		
24	HI-RDI	HI-YSI	Excalibur_c6660_746	2A	685,865,821	680,851,694	690,879,948	0.00		
25	SPS-STI		Excalibur_c20335_138	2A	757,621,502	752,607,375	762,635,629	0.00	Ballesta et al., 2018	
26	HI-DSI		Tdurum_contig42013_538	2A	771,226,463	766,212,336	776,240,590	1.95		
27	SPS-GMP		Excalibur_c1181_1037	2B	15,643,691	10,623,564	20,657,818	0.80		
28	TKW-DSI	TKW-RDI	RAC875_c4314_393	2B	49,648,750	44,634,623	54,662,877	0.01	Sukumaran et al. 2018	75, 87 cM
29	SPAD-DSI		wznp_Ec_c2343_7841003	2B	57,179,677	52,165,550	62,193,804	0.17		
30	TKW-TOL		KuRFL_c36873_83	2B	96,408,120	91,393,993	101,422,247	2.71		
31	DGF-YSI		RAC875_c8045_231	2B	197,538,224	192,524,097	202,552,351	0.00		
32	DGF-STI		RFL_Contig1987_3440	2B	546,427,607	541,413,480	551,441,734	0.00		
33	SPAD-STI		BS00104667_51	2B	677,950,622	672,936,495	682,964,749	0.00		
34	GY-GMP	HI-GMP	wznp_Ku_c901_16493072	2B	683,861,666	678,867,539	688,895,793	14.72		
35	TKW-STI	TKW-GMP, SPS-DSI, SPS-YSI, SPS-RDI	BobvWhite_c29396_649	2B	703,333,504	698,319,457	708,347,711	0.00	Ballesta et al., 2018	
36	SPAD-STI		Ra_c5004_2032	2B	720,400,852	715,386,725	725,414,979	0.01		
37	TKW-GMP		wznp_Ec_c1044_L10718053	2B	750,924,664	745,910,537	755,938,791	1.48		
38	SPS-GMP	SPS-STI, TKW-YSI, TKW-RDI, TKW-DSI	Tdurum_contig55335_316	3A	165,087,117	160,072,990	170,101,244	0.71		
39	SPAD-YSI	SPAD-GMP	wznp_Ku_rfp_c10413_70073622	3A	520,111,517	515,097,390	525,125,644	0.00		
40	TKW-TOL		BS00033825_51	3A	534,691,493	529,677,366	539,705,620	2.08	Sukumaran et al. 2018	4, 40, 48, 66 cM
41	SPAD-GMP		BS00108055_51	3B	517,360,060	512,345,933	522,374,187	1.42	Dashri et al., 2007	
42	DGF-YSI		wznp_Ec_c5418_3575513	3B	588,723,822	583,709,695	593,737,949	0.00		
43	DGF-DSI	DGF-RDI	Ec_c4757_695	3B	653,747,529	654,733,402	664,761,656	0.00		
44	SPS-STI	GY-STI, GY-GMP	wznp_ID_c4413_5541607	3B	752,482,037	747,467,910	757,496,164	0.00		
45	DGF-STI		BS00044837_51	3B	758,987,014	753,972,887	764,001,141	0.00		
46	DGF-TOL		IAAV1715	4A	530,188,609	585,174,482	595,202,736	5.28		
47	TKW-DSI	TKW-RDI, TKW-YSI	Excalibur_c25693_113	4A	617,089,540	612,075,413	622,103,667	0.01	Ede et al. 2014,	
48	HI-STI		RAC875_c6911_331	4A	626,040,049	621,025,922	631,054,176	0.00	Sukumaran et al. 2018	96 cM
49	GY-RDI		BS00084042_51	4A	709,491,543	704,477,416	714,505,670	0.01	Anif et al., 2020	44.51, 100.81 cM
50	SPAD-GMP		RFL_Contig6086_1186	4A	716,843,776	711,829,649	721,857,903	2.01	Anif et al., 2020	64.31 cM



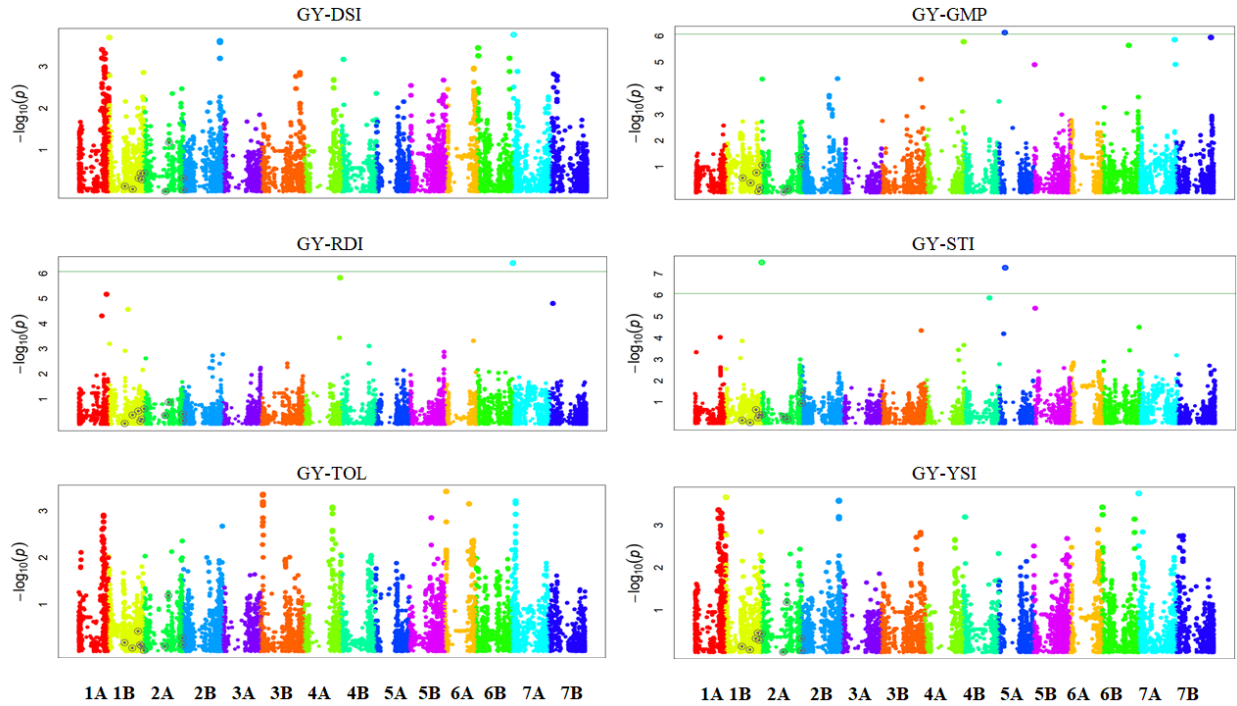
**SUPPLEMENTARY FILES**

51	TKW-DSI	TKW-RDI, TKW-YSI	KukriL_c3722T_579	4A	727,957,603	722,943,476	732,971,730	0.01	Edae et al. 2014,
52	HI-YSI	HI-RDI, HI-TOL, TKW-GMP, TKW-STI, HI-GMP, GY-GM	tpib.0050623_546	4B	4,327,519	4,327,519	3,941,646	0.00	Sukumaran et al. 2018
53	TKW-GMP		Tdurum_ccontig62310_430	4B	106,799,903	101,785,776	111,814,030	1.21	96 cM
54	SPAD-GMP		RAC875_c35152_372	4B	162,680,923	157,666,796	167,695,050	1.45	
55	HI-STI	HI-GMP, HI-DSI, GY-STI	Excilbur_c17864_1290	4B	485,705,737	480,631,670	430,719,324	0.01	
56	DGF-RDI	DGF-DSI, DGF-GMP, DGF-YSI, DGF-TOL	Tdurum_ccontig92997_676	4B	492,236,533	487,222,406	497,250,660	0.00	Ballesta et al., 2018
57	TKW-DSI		Ex_c25467_851	4B	592,406,255	587,392,128	597,420,382	0.01	Dashti et al. 2007,
58	SPAD-GMP		BS00037020_51	4B	599,279,630	594,265,503	604,293,757	0.90	Ballesta et al., 2018
59	TKW-YSI	TKW-RDI, TKW-DSI	Excilbur_c39876_403	4B	654,818,945	649,804,818	659,833,072	0.00	Ballesta et al., 2018
60	SPAD-STI		IAAVT334	4B	662,483,089	657,468,362	667,497,216	0.01	
61	SPS-STI		Ku_c2885_1189	4B	674,166,079	669,151,952	679,180,206	0.01	
62	GY-STI		GENE-3606_315	5A	81,504,827	76,490,700	86,518,954	0.01	Sukumaran et al. 2018,
63	HI-GMP		Ku_c20397_2156	5A	101,409,750	96,395,623	106,423,877	0.81	Qaseem et al., 2019
64	GY-GMP	HI-STI, HI-GMP, SPS-GMP, SPAD-GMP, GY-STI	KukriL_rep_c116526_38	5A	112,213,041	107,198,314	117,227,168	17.00	150 cM,
65	SPS-STI		BobWhite_rep_c63943_76	5A	510,385,096	505,370,969	515,399,223	0.02	87.78 cM
66	TKW-TOL		BS00065292_51	5A	518,584,476	513,570,349	523,598,603	1.84	Ballesta et al., 2018,
67	SPAD-RDI		RFL_Ccontig3629_1465	5A	639,311,345	634,297,218	644,325,472	0.00	Sukumaran et al. 2018,
68	GY-STI	GY-GMP	IAAV2346	5B	17,863,862	12,849,735	22,877,989	0.01	Anif et al., 2020
69	SPS-GMP		Excilbur_c58520_78	5B	26,805,948	21,791,821	31,820,075	0.82	77.81, 143 cM,
70	TKW-TOL		BS00064578_51	5B	438,028,156	433,014,029	443,042,283	2.07	165.81, 179.81 cM
71	DGF-TOL	DGF-YSI	RAC875_C2228L_475	5B	545,964,975	540,970,848	550,999,102	2.14	Ballesta et al., 2018,
72	DGF-RDI		Tdurum_ccontig68296_670	5B	635,337,156	630,323,029	640,351,263	0.00	Anif et al., 2020
73	HI-DSI		RAC875_c13394_324	6A	3,084,526	3,084,526	3,098,653	1.43	32.48 cM
74	TKW-GMP	TKW-STI	GENE-4052_338	6A	525,722,832	520,708,705	530,736,959	1.88	
75	SPS-GMP		RAC875_rep_c113791_95	6A	567,911,737	562,897,510	572,925,864	1.19	
76	DGF-TOL	DGF-RDI, DGF-YSI	Tdurum_ccontig61383_627	6B	36,557,072	31,542,945	41,571,199	4.57	
77	SPAD-STI		RFL_Ccontig5844_291	6B	141,032,169	136,016,042	146,046,296	0.00	
78	DGF-RDI	DGF-YSI	RFL_Ccontig6050_341	6B	490,377,946	485,363,819	495,392,073	0.00	
79	GY-GMP		wznp_E_c3940_7144946	6B	508,076,861	503,062,734	513,090,968	21.91	
80	HI-DSI		Excilbur_rep_c70364_129	6B	539,467,780	534,453,653	544,481,907	2.20	Dashti et al. 2007
81	TKW-YSI	TKW-RDI, TKW-DSI	wznp_BE436986B_Ta_2_2	6B	568,038,975	563,024,848	573,053,102	0.00	Ballesta et al., 2018
82	HI-YSI	HI-RDI	BS00064685_51	6B	623,193,581	618,179,454	628,207,708	0.00	
83	SPAD-GMP		BS00011479_51	6B	638,909,369	633,895,242	643,923,496	1.25	
84	SPAD-GMP	SPAD-STI	KukriL_c338_109	6B	684,525,167	679,511,040	689,539,294	1.57	
85	GY-STI		BS00064478_51	6B	688,744,513	683,730,386	693,758,640	0.01	Sukumaran et al. 2018,
86	SPAD-GMP		Ku_c20100_1746	7A	172,269	172,263	5,186,396	1.07	Qaseem et al., 2019,
87	GY-RDI	HI-RDI	Excilbur_c24599_1217	7A	7,721,495	2,707,368	12,735,622	0.01	Anif et al., 2020
88	DGF-TOL		Tdurum_ccontig99143_205	7A	82,560,391	77,546,264	87,574,518	3.66	31 cM,
89	TKW-YSI	TKW-RDI, TKW-DSI	BS00046977_51	7A	86,330,759	81,316,632	91,344,886	0.00	10.06 and 121.6 cM
90	HI-YSI		Excilbur_c10563_523	7A	229,915,391	224,901,264	234,929,518	0.00	159.91 cM
91	HI-STI	HI-GMP	Ku_c3251_1103	7A	345,776,283	340,762,156	350,790,410	0.00	Ballesta et al., 2018,
92	SPS-STI	SPS-GMP	RAC875_rep_c73101_332	7A	373,453,584	368,439,457	378,467,711	0.01	Anif et al., 2020
93	HI-DSI		JD_c1201_631	7A	663,956,032	658,941,965	668,970,219	2.20	Ballesta et al., 2018,
94	TKW-RDI	TKW-YSI	Excilbur_c39811_332	7A	685,724,800	680,710,673	690,738,927	0.00	Anif et al., 2020
95	GY-GMP	HI-GMP	BobWhite_C21978_234	7A	693,369,984	688,375,857	698,404,111	13.59	0.01 cM
96	SPS-STI	GY-GMP, TKW-STI	BobWhite_c25527_313	7A	709,195,412	704,181,285	714,209,539	1.00	Ballesta et al., 2018,
97	HI-STI	HI-GMP	Excilbur_c50044_749	7B	5,953,677	939,550	10,967,804	0.00	Anif et al., 2020
98	GY-RDI	HI-RDI, HI-YSI	KukriL_c1890_709	7B	63,743,279	58,729,152	68,757,406	0.01	
99	DGF-STI		RAC875_C2108_2179	7B	87,919,170	82,905,043	92,933,297	0.00	
100	HI-STI		wznp_BF200891B_Ta_2_1	7B	97,175,925	92,161,798	102,190,052	0.00	
101	GY-GMP		Tdurum_ccontig4698_346	7B	663,797,774	658,783,647	668,811,901	22.21	
102	TKW-TOL		BobWhite_c2892_211	7B	700,021,350	695,007,223	705,035,477	2.23	36, 39, 40, 47-48,
									92, 128 cM

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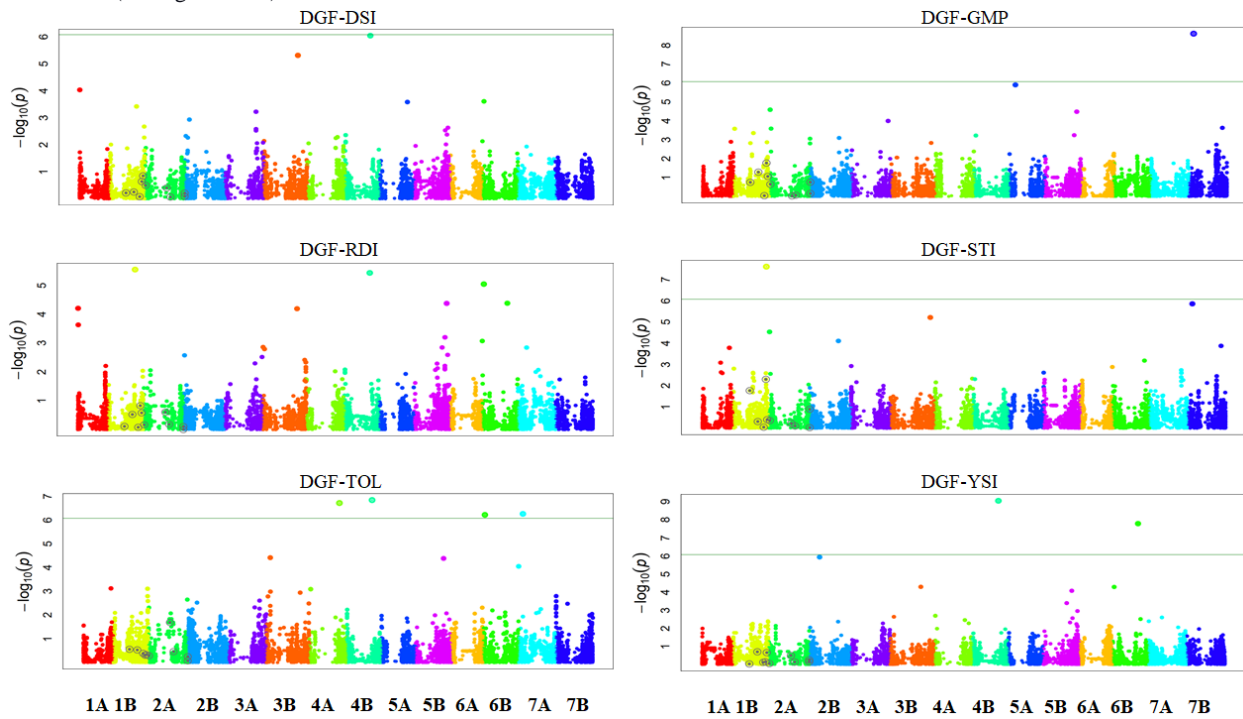
**Figure S1.** Scatter plot matrix showing the relationships among drought indices and grain yield (GY) from which drought indices were calculated. GY\_FNS: Grain yield (means from FNS at (Holeta and Debre Zeit), GY\_FDS: Grain yield (means from FDS at (Dera and Melkassa), DSI: Drought susceptibility index, RDI: Relative drought index, STI: Stress tolerance index, GMP: Geometric mean productivity, TOL: Tolerance index and YSI: Yield stability index.



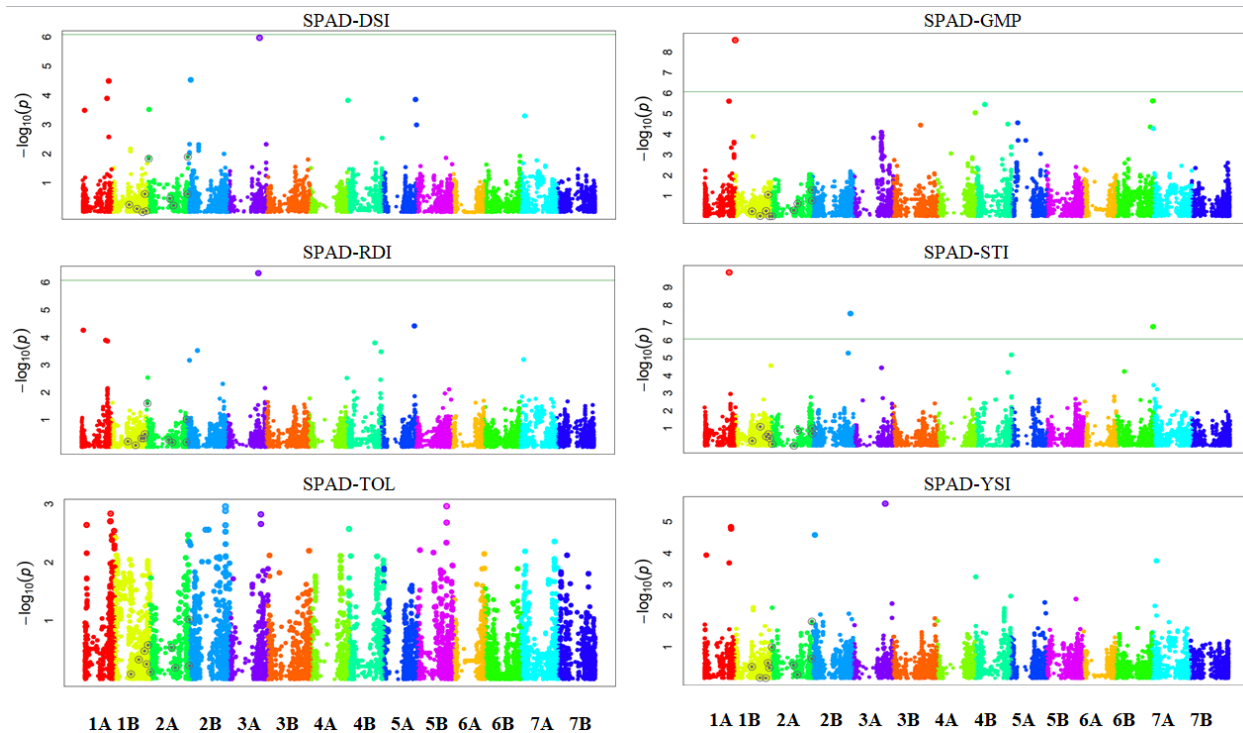
**Figure S2.** Manhattan plots of single nucleotide polymorphism (SNP) markers-trait associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) derived from grain yield (GY). The X-axis indicates 14 chromosomes

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from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).

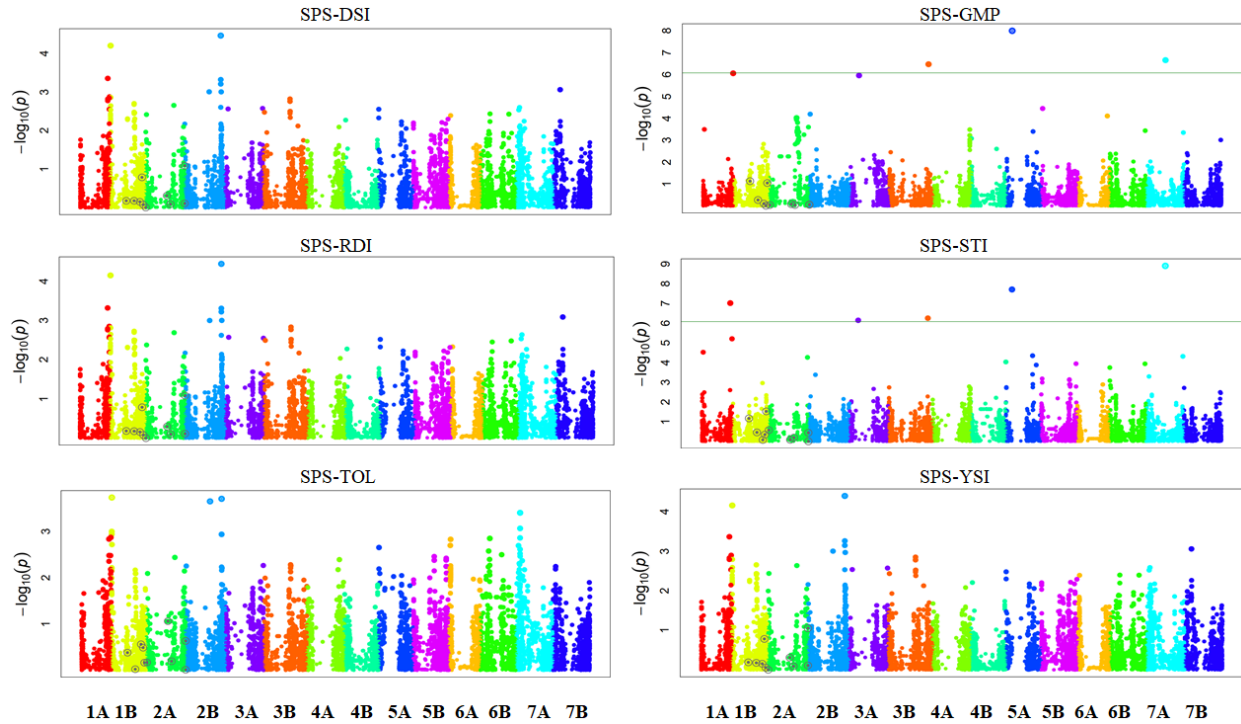


**Figure S3.** Manhattan plots of single nucleotide polymorphism (SNP) markers-traits associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) derived from days to grain filling (DGF). The X-axis indicates 14 chromosomes from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).



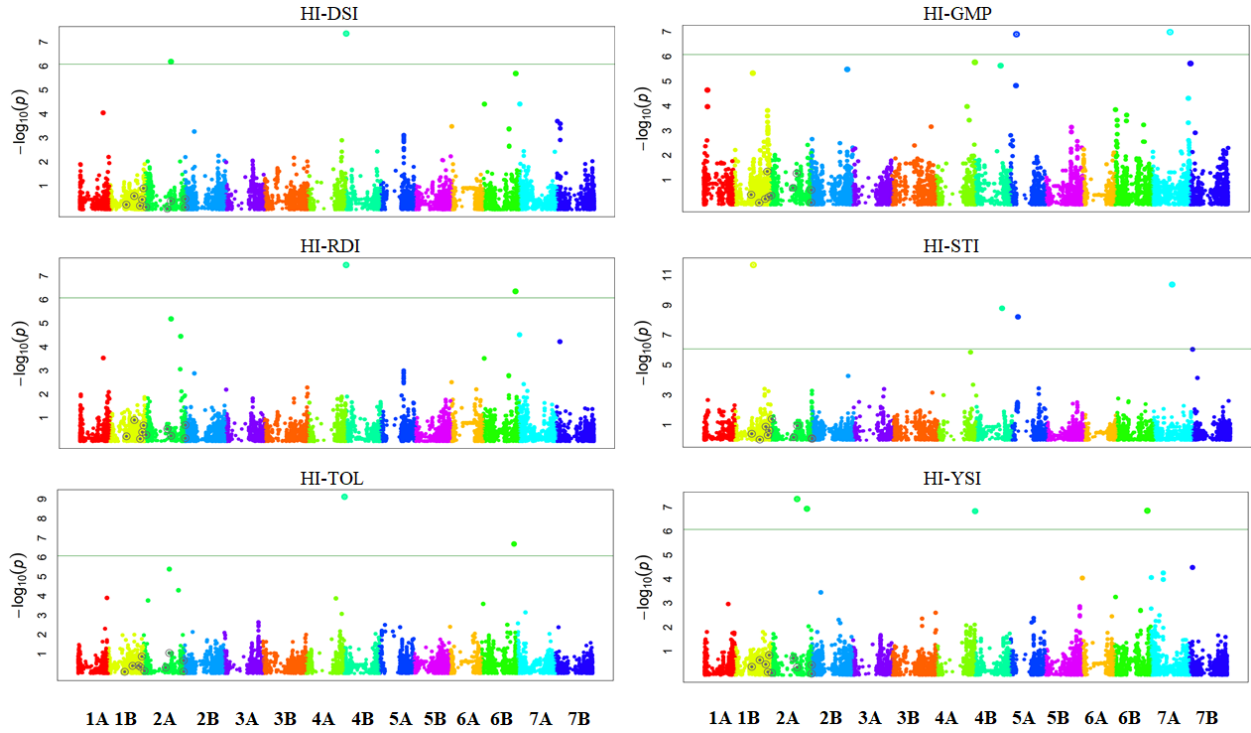
**SUPPLEMENTARY FILES**

**Figure S4.** Manhattan plots of single nucleotide polymorphism (SNP) markers-traits associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) calculated from SPAD. The X-axis indicates 14 chromosomes from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).

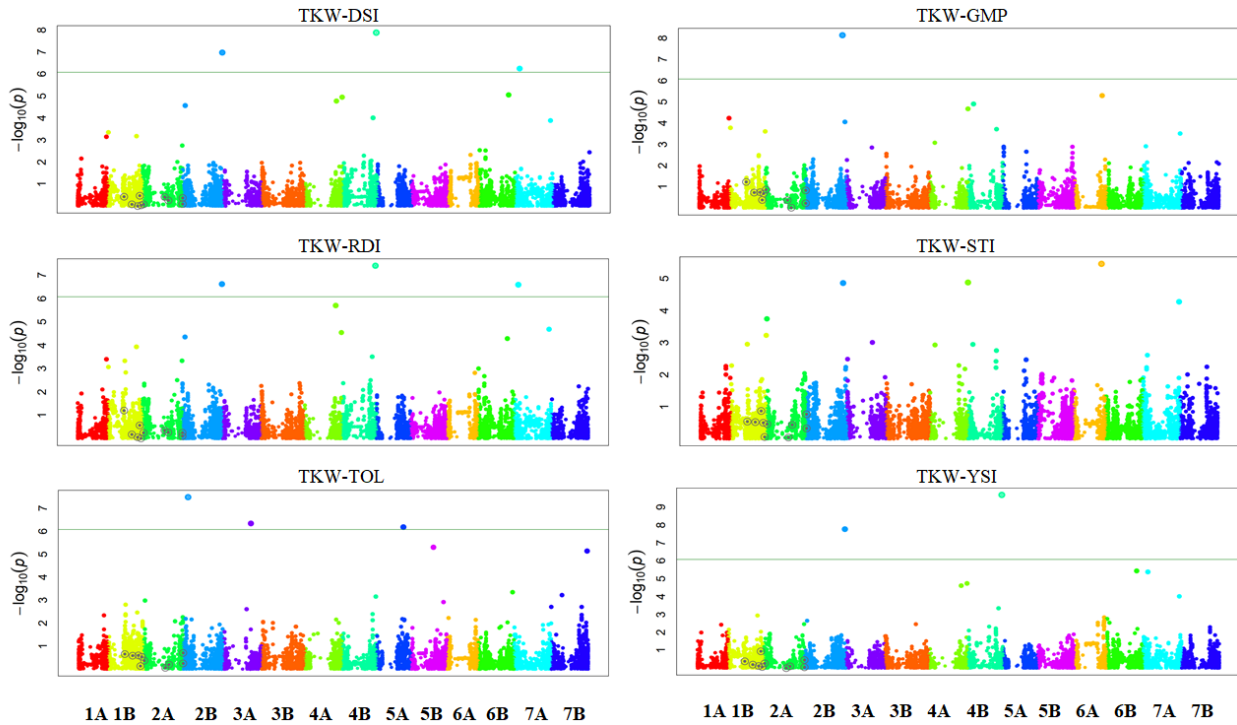


**Figure S5.** Manhattan plots of single nucleotide polymorphism (SNP) markers-traits associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) derived from seed per spike (SPS). The X-axis indicates 14 chromosomes from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).

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**Figure S6.** Manhattan plots of single nucleotide polymorphism (SNP) markers-traits associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) derived from harvesting index (HI). The X-axis indicates 14 chromosomes from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).



**Figure S7.** Manhattan plots of single nucleotide polymorphism (SNP) markers-traits associations for drought susceptible index (DSI), geometric mean productivity (GMP), relative drought index (RDI), stress tolerance index (STI), tolerance index (TOL), and yield stability index (YSI) calculated from thousand kernel weight (TKW). The X-axis indicates

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14 chromosomes from (left to right) and Y-axis represents  $-\log_{10}p$  value. Marker trait associations (MTAs) are significant at  $-\log_{10}p \geq 6$  (solid green line).

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## **DECLARATION**

### **Eidstattliche Erklärung / Declaration under Oath**

Ich erkläre an Eides statt, dass diese Arbeit vollständig von mir selbst und ohne fremde Hilfe verfasst worden ist. Ich habe nur die angegebenen Quellen verwendet und alle Zitate sowohl wörtlich als auch inhaltlich korrekt angegeben.

I declare under penalty of perjury that this thesis is my own work entirely and has been written without any help from other people. I used only the sources mentioned and included all the citations correctly both in word or content.

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# CURRICULUM VITAE

## Curriculum Vitae

### Kefyalew Negisho Bayissa

National Agricultural Biotechnology Research Center

#### Education and career

2020–present: Researcher II, Ethiopian Institute Agricultural Research, National Agricultural Biotechnology Research Center, Plant Molecular Research, Holeta, Ethiopia.

2016–2022 Research associate (PhD student), Federal Research Centre for Cultivated Plants (Julius Kühn-Institut), Institute for Resistance Research and Stress Tolerance, Quedlinburg, Germany.

Genome-wide association study of Ethiopian durum wheat (*Triticum turgidum* ssp. *durum*) accessions under drought stress and non-stress conditions.

2006–2009 Master of Science in International Horticulture, Faculty of Natural Sciences, Major: Plant Nutrition at the University of Hanover, Hanover, Germany.

2000–2002 Bachelor of Science in Plant Science at Haramaya University Ethiopia

1991-1992 Diploma in Plant Science at Jimma College of Agriculture, Jimma, Ethiopia

#### Publications

Alemu, S. K., Hora, O. D., Terfasa, F. K., Teshale, M., Hailu, B., **Negisho, K. B.**, Berhanu, B., Degete, A. G., Bacha, N., Zegeye, H., Tesfaye, T., Tulu, U. T. ; & Gidi, M. (2023). Identification of Stem Rust Resistance Genes in Released Wheat Varieties by Linked SSR Markers and Phenotypic Screening. *International Journal of Genetics and Genomics*. 11(2): 48-59. doi: 10.11648/j.ijgg.20231102.12.

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